Movement patterns and space use of maternal grizzly bears influence cub survival in Interior Alaska

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Abstract: Foraging decisions and movement strategies by animals often involve a trade-off between meeting nutritional demands and minimizing risk of predation. We evaluated the influence of space use and movement patterns of maternal female grizzly bears (*Ursus arctos*) on cub (defined as first year of life) survival in eastern Interior Alaska, USA, during 2008–2012. We monitored 9 GPS radiocollared females that produced 28 cubs in 12 litters ($\bar{x}$ litter size = 2.3, range = 2–3). The estimated annual cub survival rate was 0.39 (95% CI = 0.20–0.57). In all cases the entire litter survived or died prior to den entrance. All cubs in a litter died either concurrently or within 14 days in 5 of 7 litters lost. Sixty-nine percent of cub mortality occurred between 31 May and 16 June. We did not document cub mortality before 31 May. Females with surviving cubs remained within 1 km of the den for a longer period following emergence than those that lost cubs. Between den emergence and the onset of vegetation green-up, females with surviving cubs used fewer habitat patches and remained in individual habitat patches longer than females that lost their cubs later in the summer. Females with surviving cubs exhibited different activity patterns compared with females that lost their cubs, particularly by moving less between midnight and mid-morning during 15 May–16 June. Once vegetation green-up occurred, movement rates of all maternal females were similar except that females with surviving cubs continued to move less during the morning hours (0000–1200 hr). We did not find evidence that the body size of the mother was a factor explaining cub survival nor was there evidence that cub survival was directly influenced by human causes. The most successful behavioral strategies used by maternal females to maximize cub survival appeared to be a combination of limiting movements to a few habitat patches between den emergence and vegetation green-up and limiting activity between midnight and mid-morning. We suggest that the ability to find and exploit suitable habitat patches during this period of limited resources may have allowed females to alter movements temporally and spatially and provision themselves and their cubs more effectively. This strategy was likely effective for both minimizing exposure to infanticidal adult bears and allowing cubs to maximize energy efficiency.

Key words: Alaska, behavioral strategies, cub mortality, grizzly bear, home range, seasonal movements, survival, *Ursus arctos*

Causes and rates of grizzly bear (*Ursus arctos*) cub (defined as first year of life) mortality exhibit considerable variation between and within geographic areas and are influenced by nutrition, intraspecific predation, and human disturbance (Swenson et al. 2001, Miller et al. 2003, Swenson 2003, Schwartz et al. 2006b). In the absence of human-caused mortality, nearly all cub mortality is due to starvation and predation (Schwartz et al. 2006b). Infanticide is a common cause of mortality for grizzly bear cubs. Bears of either sex may kill cubs (LeCount 1987, Craighead et al. 1995, Hessing and Aumiller 1994), but adult males are the most common killer of cubs, especially during the breeding season (McLellan

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1994, Miller et al. 2003). Sexually selected infanticide, predation, periodic forage limitations, and competition for resources have been suggested as causes of infanticide (McLellan 1994, Swenson et al. 2001, Miller et al. 2003, McLellan 2005, Obbard and Howe 2008, Zedrosser et al. 2009). Density-dependent effects have also been suggested to reduce cub survival in grizzly bear populations close to carrying capacity (Miller et al. 2003, Schwartz et al. 2006a, but see Obbard and Howe 2008).

Grizzly bear females are long-lived and produce multiple litters, allowing for the development of individual behavioral strategies through experience to optimize resource acquisition and reduce predation risk (Ben-David et al. 2004). Grizzly bear home-range size and use are dependent on metabolic requirements and the availability and spatial dispersion of forage (Dahle and Swenson 2003, Edwards et al. 2013). In addition, females with cubs have higher energetic costs due to lactation (Robbins 1993, Farley and Robbins 1995), requiring increased forage intake to meet their nutritional and milk-production needs. Therefore, their foraging decisions and movement strategies must achieve a balance between satisfying nutritional requirements and avoiding predation (Lima and Dill 1990, Creel and Christianson 2008).

Indeed, previous studies have suggested that maternal females often alter their movement patterns relative to other bears. Throughout their active period, maternal females were found to avoid habitats with the highest quality foods (Wielgus and Bunnell 1994, McLellan 1994, Ben-David et al. 2004, Rode et al. 2006). Pregnant female grizzly bears may avoid males by denning at higher elevations and on steeper slopes (Haroldson et al. 2002, Libal et al. 2011). However, Pigeon et al. (2014) found that male and female grizzly bears selected similar habitat at dens and that maternal females chose den sites in relation to slope, spring foods, and distance from roads, rather than to minimize encounters with males. Pregnant females enter dens earlier compared with males and non-parturient females and emerge later than males (Haroldson et al. 2002, Libal et al. 2011). Additionally, females with cubs remained near the den site longer compared with other females and males (Craighead and Craighead 1972, Vroom et al. 1980, Miller 1990, Haroldson et al. 2002). Dahle and Swenson (2003) found that females with cubs used smaller home ranges than did oestrus females

during the breeding seasons in late May and June, and they suggested that this was a strategy to reduce risk of infanticide. Schwartz et al. (2010) showed differences in activity patterns of grizzly bears between sexes, with females and males being more diurnal and nocturnal, respectively. Although these studies have suggested that maternal grizzly bears modify their behavior to reduce dangerous encounters with males, none have explicitly linked the behavioral strategies of females with data on cub survival to demonstrate the adaptive nature of these behavioral modifications.

Grizzly bears are mobile, have an acute sense of smell and can track potential prey for long distances (Schwartz et al. 2003). If infanticide influences female grizzly bear behavior, it is likely that females with cubs have adopted movement strategies relative to the movement patterns of dominant males (e.g., Dahle and Swenson 2003, Libal et al. 2011). Once confronted, female bears will often defend their offspring against conspecifics, but such encounters are dangerous (McLellan 1994, Obbard and Howe 2008). It seems reasonable that a female with cubs would gain a greater survival advantage by altering movements both temporally and spatially and thereby reducing their scent trail, to inhibit the ability of males to actively track them. Reduced movements should also reduce chance encounters with potentially infanticidal bears and maximize the nutritional efficiency for growing cubs. Thus, we hypothesized that females could maximize survival of cubs by reducing movements, which would reduce encounter rates with other bears (and therefore risk of infanticide) and/or increase energy efficiency for growing cubs. This strategy would be dependent on the female's ability to find habitat patches that offered suitable forage and cover and were not frequented by other grizzly bears.

Since 1981 there has been intense management interest in grizzly bears inhabiting the Fortymile River area in eastern Interior Alaska, USA. Earlier studies evaluated the role of grizzly bears as a predator on moose (*Alces alces*) in the Fortymile River area and provided useful information on population density (10–16 bears/1,000 km^2) and distribution (Boertje et al. 1987, Gasaway et al. 1992). More recent work confirmed that grizzly bears remained at the same or lower density during our study compared with the mid-1980s but suggested that grizzly bear distribution may have changed due to extensive wildfires during 2004 (C.

Gardner, unpublished data). The estimated annual harvest of grizzly bears in this area has remained consistent and ranged between 1% and 5% (Boertje et al. 1987, Gardner 2003, Bentzen 2009) and probably has not strongly limited population growth (Miller et al. 1997). Instead, the Fortymile River grizzly bear population may be primarily limited by food availability. The area lacks large meadows of *Equisetum* spp., anadromous fish, and Arctic ground squirrels (*Urocitellus parryii*). Further, moose (190–270/1,000 km^2) and caribou (*Rangifer tarandus*) densities are low in the area during the summer (Gasaway et al. 1992; C. Gardner, unpublished data). Thus, Fortymile River grizzly bears appear to have few reliable sources of protein. The density of grizzly bears, the average estimated May weight of adult females (approx. 115 kg; C. Gardner, unpublished data), and the lack of salmon (*Oncorhynchus* sp.) in the area likely reflect a low intake of dietary meat by Fortymile River grizzly females, similar to other non-salmon eating populations (3%–4% dietary meat) in Interior Alaska and Yukon, Canada (Hilderbrand et al. 1999). Reliable meat resources can positively affect grizzly bear body size, reproductive success, and density (Hilderbrand et al. 1999). For forage-limited bear populations, compensatory mechanisms can act on grizzly bear demography, including cub mortality, to balance population density and resource availability (McLellan 1989, Schwartz et al. 2006a).

We studied female grizzly bears and their offspring during 2008–2012 in the Fortymile River area using Global Positioning System (GPS) and Very High Frequency (VHF) telemetry, aerial monitoring, and DNA analysis, with 3 main objectives and several associated questions and hypotheses. First, we evaluated female space use and movement patterns relative to cub encumbrance and survival by comparing home-range size, seasonal and daily movement rates and distances, time spent in isolated areas (habitat patches), and daily activity patterns. We hypothesized that females with cubs would use smaller home ranges and exhibit reduced movement patterns compared with unencumbered females and females with older offspring, similar to previous findings (H_1; Dahle and Swenson 2003, Edwards et al. 2013). We also hypothesized that females that successfully raised cubs would use smaller home ranges, restrict movements, and exhibit different daily movement patterns then females that lost cubs (H_2). Support for H_2 would help clarify the mechanistic link between maternal behavior and cub survival speculated on by previous researchers (e.g., Wielgus and Bunnell 1994, Dahle and Swenson 2003, Ben-David et al. 2004) by demonstrating the adaptive nature of modifying space use for females with cubs.

Our second objective was to evaluate the possibility that GPS movement data from maternal females can be used to determine the timing of cub mortality. We hypothesized that (1) females would display a measurable, abrupt movement response following loss of a litter due to predation (H_3), and (2) after entire litters were lost, females would increase daily movement rates to those similar to unencumbered females (H_4). Finally, we determined the genetic relatedness of females occupying adjacent home ranges to investigate longer term effects of cub survival on social structure of females. Philopatry by females is common for grizzly bears, which often results in considerable overlap of home ranges among related females (Mace and Waller 1998, Schwartz et al. 2003). Although the exact mechanisms that regulate dispersal patterns in mammals remain unclear, philopatry in grizzly bears may be influenced by food availability because inclusive fitness benefits of tolerating female offspring could be outweighed by increased competition in areas with insufficient resources (Waser 1998, Støen et al. 2005). Thus, we were interested in documenting the degree of relatedness among adjacent females in the Fortymile River area where grizzly bears appear to be food-limited.

Study area

The Fortymile River study area (FRSA) encompassed the upper Mosquito, Middle, and West Forks of the Fortymile River drainage in eastern Interior Alaska (area size = 5,154 km^2; Fig. 1). One community (Chicken, Alaska; summer population 17; Fig. 1), one road (Taylor Highway; summer average daily traffic of approx. 175 vehicles), and few trails were within or bordered the area. There was substantially less human use away from the Taylor Highway during May–July. Human use increased throughout the area during 10 August–18 September, coinciding with caribou, moose, and grizzly and black bear (*U. americanus*) hunting seasons.

Habitat and topography in FRSA consists of rolling hills covered with mature black spruce (*Picea mariana*) with limited subalpine and alpine areas, poorly drained lowlands, and drainages lined with willow (*Salix* spp.), shrub birch (*Betula* spp.), alder
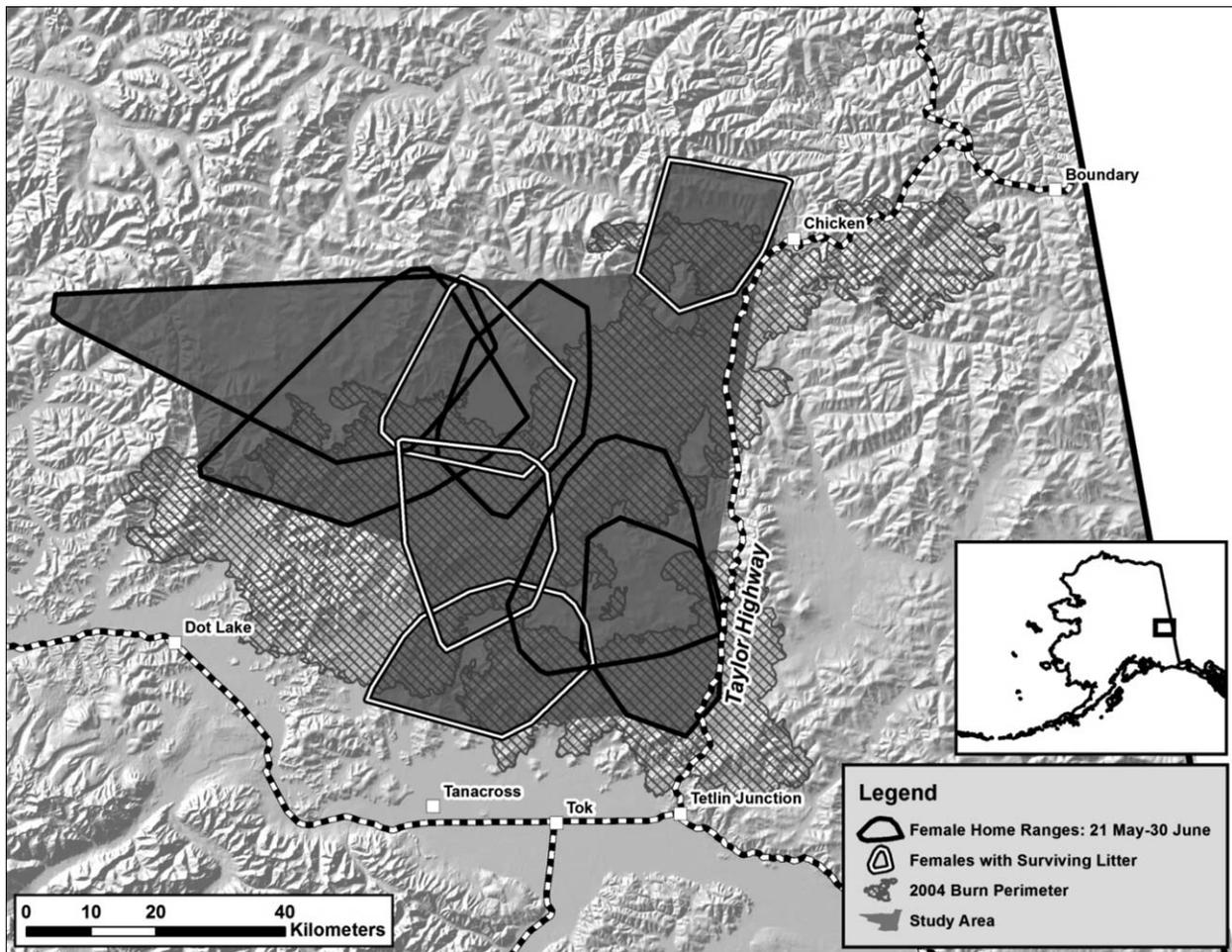
Fig. 1. Study area boundary and home ranges of the 9 female grizzly bears (radiocollared using Global Positioning System) in the Fortymile River study area in eastern Interior Alaska, USA, used to evaluate grizzly bear cub litter size and survival during May 2008–July 2012. Home ranges of bears with surviving cubs outlined in white.

(*Alnus* spp.), and white spruce (*P. glauca*). During summer 2004, wildfires mildly to severely burned 2,853 km² (55.4%) of the study area (Alaska Interagency Coordination Center, http://fire.ak.blm.gov/predsvcs/maps.php). The most common plant species within the burned area 2 years post-fire were shrub willow and birch, fireweed (*Chamerion angustifolium* ssp.), and reedgrasses (*Calamagrostis* spp.). Blueberry (*Vaccinium uliginosum*) is an important mid- to late-summer food source for grizzly bears in Interior Alaska (Miller 1990) and availability varied substantially before and after the 2004 wildfires. In general, blueberries were common prior to the 2004 wildfire, essentially nonexistent during 2004–2008, and abundant during 2009–2013

based on berry abundance trends monitored annually within and adjacent to the FRSA study area (T. Bentzen, Alaska Department of Fish and Game, unpublished data). In addition to conspecifics, other potential large predators on grizzly bear cubs are black bears and wolves (*Canis lupus*). The climate is sub-Arctic and continental. The mean annual low and high temperatures during May–September are about −4°C and 10°C. Leaves emerge on most shrubs during 1–7 June and leaf senescence occurs during late August (Gasaway et al. 1992). The average den emergence date for females with cubs in FRSA is 15 May (Boertje et al. 1987). Gasaway et al. (1992) presents a more thorough description of habitat, topography, and climate.

Methods

Capture and monitoring protocol

We chemically immobilized all observed grizzly bears thought to be adult females by remote darting from a helicopter during early July 2008 and late May–early June in 2009, 2010, and 2011 using Telazol® (11–12 mg/kg estimated body wt; Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA). Each captured bear was sexed and individually identified with numbered ear tags and lip tattoos. We deployed a collar equipped with both a GPS transmitter (Generation III Spread Spectrum; Telonics, Inc., Mesa, Arizona, USA) and a VHF radio-transmitter on all adult females. The collars were programmed to acquire a location every 1.5 hours between 15 May and 15 October and to release from the bear after 2.75 years. We extracted a premolar tooth for age determination by counting cementum annuli (Matson et al. 1993). We sent ear tissue removed for ear tag placement from captured bears to Wildlife Genetics, Inc. (Nelson, British Columbia, Canada) for microsatellite genotyping to determine relatedness among sampled bears. We did not capture offspring and verified the reunion of all females and offspring within 12 hours of capture by aerial observation. We completed all aspects of capture and radiocollaring in accordance with acceptable methods for field studies adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998; Alaska Department of Fish and Game Protocol 08-08).

We relocated radiocollared bears via VHF telemetry once during April to verify their den location, daily for a 5-day period between 25 May and 4 June (varied by year) to determine presence and number of dependent offspring, and 1–4 times a month during the remainder of the summer to monitor offspring survival. Except during April, our standard monitoring protocol was to maintain a flight altitude of 450–600 m above the collared bear while uploading the stored GPS data, then to descend and assess the number of associated bears. If we did not observe the expected number of offspring during a flight, we extended our search to include an area within 0.8 km of her location. On several occasions we found some to all cubs in trees ≤0.5 km from the female. We assumed any missing cubs had died after 2 consecutive observation surveys without detection. Based on our observations of females with surviving cubs, we found that 2 flights were sufficient to verify cub loss.

Demography

We estimated litter frequency (no. of yr/litter) and reproductive rate (female cubs/female/yr) by calculating a mean of the observed reproductive rates for each radiocollared adult female ≥4 years old for all years, following Schwartz et al. (2006a). We did not handle the cubs to determine sex but assumed the sex ratio was 50:50 (Schwartz et al. 2006a).

We estimated cub, yearling, and litter survival using the Kaplan–Meier product limit estimator generalized for staggered entry (Pollock et al. 2002). Survival history began from the time we first observed the female and her cubs or yearlings during 25–30 May to the last day offspring were seen with the female or until our last monitoring flight, which occurred during 25–30 September. We realize that some cubs could have died between den emergence and our first observation; thus, cub litter size and cub mortality estimates reflect only whether litters with ≥2 cubs were with the female, and are potentially biased low. After each monitoring flight, we recorded offspring as alive, dead (once verified), or censored. We did not know the exact day of death; therefore, we assigned mortality events to the midpoint between the last location a cub was observed alive and the first date we verified a cub missing. In cases where cub survival within a litter is not independent of litter size, a variance inflation factor is required (Schwartz et al. 2006a, Mace et al. 2012a). In our study, an inflation factor was not necessary because we did not observe any partial cub litter survival between den emergence and den entrance. We also evaluated cub mortality using litter as the sampling unit. These litter survival rates were based on the same time period described for individual cubs. We presented 95% confidence intervals (CIs) for both individual and litter survival estimates. None of the females died during the study so we did not have to make the assumption of cub mortality due to the mother's death. Similar to most studies of grizzly bear cub survival, we were unable to determine cause of death for cubs because cubs were not collared (e.g., Schwartz et al. 2003, Miller et al. 2003). The inability to distinguish between mortality events involving infanticide and other causes (e.g., starvation) was a limitation that restricted our inferences as discussed below (see Discussion).

Movement patterns

To test our hypothesis that females could affect survival of cubs by altering movements temporally and spatially, we chronologically plotted all GPS

locations to identify time spent in habitat patches based on location clusters. We defined habitat patches as areas used by bears that moved <400 m between GPS fixes obtained every 1.5 hours. We chose this distance to define a patch after identifying that if a female with cubs moved ≥400 m it was usually in a directional manner away from the cluster of locations, and that the bears did not return to that patch for ≥3 days. We did not assess the habitat characteristics or quality at these patches, but assumed these patches were selected for foraging, resting, or nursing. We calculated the amount of time spent at a habitat patch by adding all sequential 1.5-hour periods when the bear moved <400 m. To evaluate the effects of distance moved between habitat patches on cub survival, we calculated straight-line distances between GPS locations to determine travel length and movement rates using point analyses in GIS Home Range Tools for ArcGIS (Rodgers et al. 2007). We defined travel periods as beginning once bear movements were >400 m during a 1.5-hour GPS acquisition period. We calculated travel length as the total distance moved between habitat patches, not the straight-line distance between the patches. We evaluated movement rates (m/hr) both within the patch and between patches. We expected that movement patterns would change over the course of the study period in response to leaf emergence (green-up; Haroldson et al. 2002) and cub maturation. We also took into account that Miller et al. (2003) found that most cub mortality occurred before 30 June in other portions of Alaska and that Dahle and Swenson (2003) found that females with cubs used smaller home ranges than did oestrus females during the breeding seasons in late May and June. Accordingly, we limited our movement analyses comparing females with surviving cubs to females that lost their litters to the time period between 15 May and 30 June. We further partitioned our study into 3 periods based on the assumption that females with cubs remained in the vicinity of the den after emergence longer than other bears (Haroldson et al. 2002, Miller et al. 2003) and that movement patterns were influenced on the availability of green vegetation as a food source beginning in late May (Haroldson et al. 2002). Our periods were 15–21 May (den influenced), 22–31 May (pre–green-up), and 1–30 June (green vegetation–ungulate calving).

To evaluate the possible effects of snow melt and den-site location on forage availability and timing of movements away from the den, we compared elevation, slope, and aspect and presence of coniferous or deciduous trees for den sites of females emerging with cubs. We did not assess snow melt around the individual dens, but based on 10 years of daily field work during 1993–2002 in the area, the snow pack in the FSRA by mid-May below tree-line is very patchy regardless of slope or aspect (C. Gardner, unpublished data). We were able to begin monitoring movements during the den-influenced period prior to our first radiotelemetry flights during 25–30 May because we verified den locations in April and used the GPS location data to estimate female movements around dens after emergence. We compared home-range size and daily distances moved between females of different maternal status during 15 May–30 June. We estimated home ranges with minimum convex polygons (Mohr 1947). We also compared daily movement rates by periods (Mace et al. 2012b) between females with surviving cubs and females that lost their litters by establishing 8 3-hour diel periods. During the study period, there was no time of the day that was completely dark, but the period 0000–0300 hours included the darkest time of the day. Although potentially informative, we did not obtain corresponding movement data from adult males.

We used a single-factor analysis of variance followed by Tukey's honestly significant different (HSD) test to compare home-range size and den characteristics between females of different maternal status (H_1). We evaluated each year separately to eliminate possible bias due to short-term differences in forage quality or other environmental conditions between years and pooled data if appropriate. We used 2-tailed, 2-sample t-tests assuming unequal variances to compare annual and seasonal home-range sizes, time in habitat patches, distance moved between patches, daily movement rates by period, elevation of den sites, and body size between females who lost litters and females with surviving cub litters (H_2). Because females with cubs used different numbers of habitat patches for different lengths of time during a given period, we weighted the means of females with surviving cubs and females that lost their litters by the variance of the individual bears in each group. We presented standard errors (SE) of the averages. Our null hypotheses were that there would be no difference in the time spent at habitat patches, in the distance moved between habitat patches, and in daily movement rates between

females that lost cubs and females whose cubs survived until 30 June. Statistical tests were considered significant when $P < 0.050$ and marginally significant when $0.05 \leq P < 0.100$.

Using movement data to determine timing of cub mortality

We evaluated the possible change in movement patterns by females that lost their litters between 15 May and 30 June by plotting cumulative distance traveled versus cumulative time separately for females that lost and females that kept their litters (Vander Wal and Rodgers 2009). The slope of the curve denotes rate of movement. We hypothesized that any abrupt changes in the slope would indicate behavioral change due to an environmental cue such as an encounter with a predator (H_3). We standardized distances (m) and time (sec) to range from 0 to 1 (Vander Wal and Rodgers 2009). We divided cumulative distance between successive locations by the distance moved by the female between 15 May and 30 June and standardized time by dividing the cumulative time between locations by the total time. We compared the curves to assess whether there were recognizable changes in movements suggested by changes in slope of the curve that occurred during the period the mortality event was verified by aerial observation. If the pattern remained linear, our interpretation was that the female displayed no movement response due to the loss of cubs or to other potentially changing environmental conditions (i.e., vegetation green-up). We further used this analysis to compare movement rates and patterns by females with different maternal status to test our hypothesis that loss of entire litter would result in females exhibiting movement similar to females without cubs (H_4). We standardized movement for these different groups by dividing distances moved by the maximum distance moved that was observed for all individuals (i.e., the same value was used to standardize movement for all bears).

Philopatry

We evaluated the presence of philopatry by identifying genotypes based on 22 microsatellite loci amplified from DNA extracted from tissue to determine family relationships among radiocollared female bears, including one non-parturient female. We used the software PARENTE (Cercueil et al. 2002) to determine the probability that a pair of individuals was related. We also compared these

data with genetic profiles of 56 other bears sampled in a larger but encompassing area during a separate study (C. Gardner, unpublished data) to document past cub production by the radiocollared females.

Results

Overall, we invested approximately 350 hours of aerial search time to catch adult females. During 2008–2012, we radiocollared and monitored 9 adult females over 23 bear-years. Based on the results of a DNA-based capture–recapture study conducted 2 years prior (C. Gardner, unpublished data) and population composition estimates in McLellan (1989), we estimated there were 12 resident females in the FRSA. No females died, and 8 females produced 28 cubs in 12 litters ($\bar{x}$ litter size = 2.3, range = 2–3, SE = 0.16; Table 1). All females of reproductive age produced cubs following a year in which they were not accompanied by dependent offspring after 15 June. The estimated years/litter was 1.9 and the reproductive rate was 0.61 female cubs/female/year. Of the individual females that produced litters, 5 were observed with 1 litter, 2 with 2, and 1 with 3. Ages of parturient females ranged from 6 to 20 years ($\bar{x}$ age = 12.4, SE = 1.76). The only non-parturient female was 4 and 5 years old during the years she was monitored. There was no difference in body length between females with surviving cubs ($n = 4$, $\bar{x}$ body length = 1,782 cm, SE = 42.10) and females that lost their cubs ($n = 4$, $\bar{x}$ body length = 1,844 cm, SE = 123.60; $t = 0.47$, $P = 0.680$). During the study, 4 litters survived, 7 litters were lost, and 1 litter of 2 cubs was censored due to radio failure occurring during early June. Ages of females whose cubs survived to den entrance were 6, 7, 10, and 16. Successful females were distributed across the study area (Fig. 1).

We documented 16 cub mortalities. All mortalities within litters were detected concurrently or within 14 days (observation period) in 5 of 7 lost litters. Mortality occurred over 1–2 months for the other 2 litters (Table 1). In all cases the entire litter survived or died before den entrance in the autumn. The estimated annual cub survival rate was 0.39 (95% CI = 0.21–0.57). Estimated cub survival to 30 June was 0.58 (95% CI = 0.40–0.76). Most (68.8%) of the mortalities occurred between 31 May and 16 June. Estimated litter survival rates were 0.55 (CI = 0.28–0.82) to 30 June and 0.37 (CI = 0.11–0.62) to den entrance. Four of the 5 females that lost their litters

Table 1. Age, litter size, number of cubs lost, estimated timing of cub mortality, and number of cubs surviving for 8 radiocollared maternal female grizzly bears in the Fortymile River study area, eastern Interior Alaska, USA, July 2008–October 2012.

Bear ID	Age	Litter size	No. lost	Estimated mortality date	No. survived
9002	15	3	3	1–16 Jul, 2–28 Aug	0
9002	17	3	3	13 Jun	0
9003	7	3	0	NA	3
9005	18	2	2	14 Jun	0
9005	19	2	2	12 Jun	0
9005	20	2	2	31 May	0
9006	10	2	0	NA	2
9007	6	2	0	NA	2
9008	8	2	2	1–9 Aug, 1–16 Sep	0
9011	6	2	2	16 Jun	0
9011	7	2	Unknown	Censored	Unknown
9014	16	3	0	NA	3

prior to 16 June bred and produced a litter the following year. We could not verify successful breeding for the other female that lost her litter in June because her radio failed after summer but prior to den emergence the following spring. However, she was observed with a large male during June following the loss of her cubs. Of the 8 yearlings, 7 survived to den entrance (0.88, 95% CI = 0.65–1.00).

During 15 May–30 June, females with cubs had smaller home ranges than lone females (ANOVA; $F_{3, 15} = 11.94$, $P < 0.001$, Tukey's HSD, $P < 0.001$), females with yearlings ($P = 0.050$), and females that lost all of their cubs ($P = 0.020$; Table 2). We found no difference in home-range sizes among lone females and females with yearlings ($P = 0.210$). Females that lost their cubs by mid-June increased their home-range size by the end of June to a size comparable to the home ranges of lone females and females with yearlings (Table 2). Between years, mean home-range sizes for individual females decreased between 63–91% when females were accompanied by cubs (Fig. 2). Females with cubs travelled shorter daily distances compared with all other females (Table 2). Further, females with cubs had lower movement rates than did all other females,

but once females lost their litter their movement rates became similar to lone adult females (Fig. 3).

For all 3 study periods, females that raised cubs remained in habitat patches longer than did females that lost their litters; however, only during the pre–green-up period was the difference significant ($n = 9$, $t = 2.84$, $P = 0.030$; Table 3). Females with surviving cubs used significantly fewer habitat patches during the den-influenced period ($n = 5$, $t = 2.44$, $P = 0.030$) and during pre–green-up ($n = 5$, $t = 2.45$, $P = 0.030$) and remained within 1 km of the den following emergence ($n = 5$, $\bar{x} = 119.5$ hr, SE = 20.50), which was significantly longer than females that lost cubs during May and June ($n = 5$, $\bar{x} = 52.9$ hr, SE =19.80; $t = 2.33$, $P = 0.030$). We did not detect differences in distance travelled between habitat patches (Table 3).

Females with surviving cubs exhibited different activity patterns compared with females that lost their cubs, particularly by moving less between midnight and mid-morning during all 3 periods (Fig. 4). All dens were located between 690 m and 1,455 m elevation ($n = 15$, $\bar{x} = 990$ m, SE = 234 m). Den-site elevations for females with cubs ranged between 780 m and 1,265 m ($n = 7$, $\bar{x} = 1,046$ m, SE = 162 m). There was no difference in den-site

Table 2. Mean (±SE) home-range sizes and daily distances traveled by radiocollared adult female grizzly bears with different maternal status in the Fortymile River study area in eastern Interior Alaska, USA, 15 May–30 June, 2009–2012.

Maternal status	Home-range size (km²)			Daily distance traveled (km²)		
	$\bar{x}$	n	SE	$\bar{x}$	n	SE
Alone	588.7	7	55.3	11.7	6	0.56
Yearlings	388.8	3	78.8	6.2	3	0.36
Cubs lost	414.0	4	97.4	7.6	4	0.56
Cubs survived	99.0	5	26.9	3.2	5	0.17
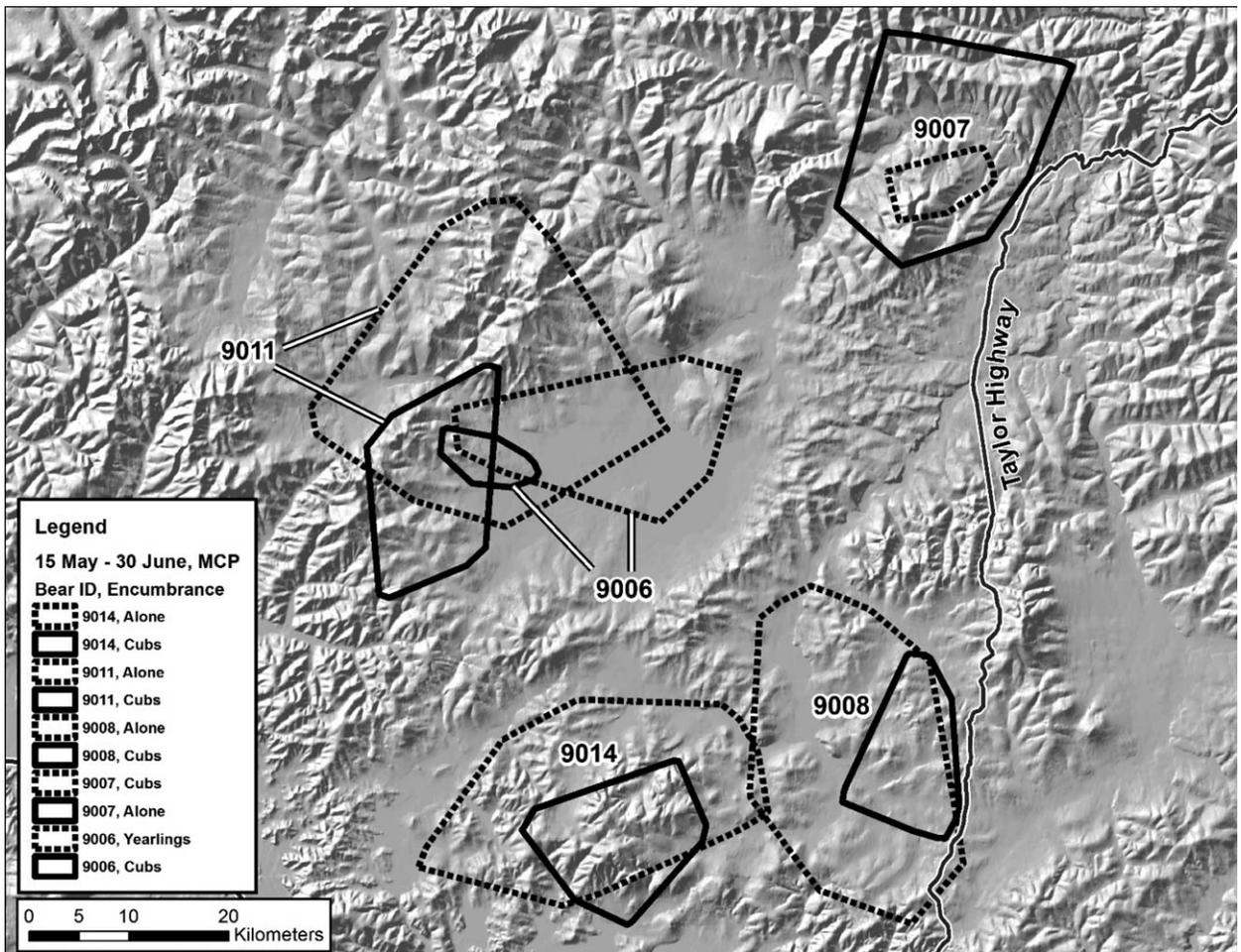
Fig. 2. Home ranges of female grizzly bears during years with and without cubs in the Fortymile River study area in eastern Interior Alaska, USA, during 15 May 2009–30 June 2012. Home ranges are presented as minimum convex polygons (MCP).

elevations between emerging lone females, females with yearlings or 2-year-olds, or females with cubs (ANOVA; $F_{3, 10} = 0.48$, $P = 0.980$). Further, there was no difference between females with surviving cubs and females that lost their litters ($t = 0.08$, $P = 0.950$). Most dens of females with cubs were on south to southwest slopes (71%) and below tree-line (86%).

Movement patterns of all bears that lost their litters displayed abrupt positive changes in slope during the period when cub mortality was known to occur (Figs. 3 and 5). Movement rates (m/hr) increased 1.5–2.4 times compared with the average rates prior to the change. Females that successfully raised cubs did not display these changes in movement patterns or rates for the same time period or during the next 10 days (Fig. 3).

Our analysis of microsatellite data obtained from the 9 radiocollared female bears indicated that none were parent–offspring or sibling relationships. Results from a DNA capture–recapture population estimate study using hair traps, completed in 2006, verified that ≥2 of the collared bears had offspring during or before 2006 (C. Gardner, unpublished data). During 2008–2012, 1 of these females had 2 litters (3 cubs in each) and lost both litters prior to den entrance, whereas the other female had a litter of 3 and all offspring remained alive through 2 summers.

Discussion

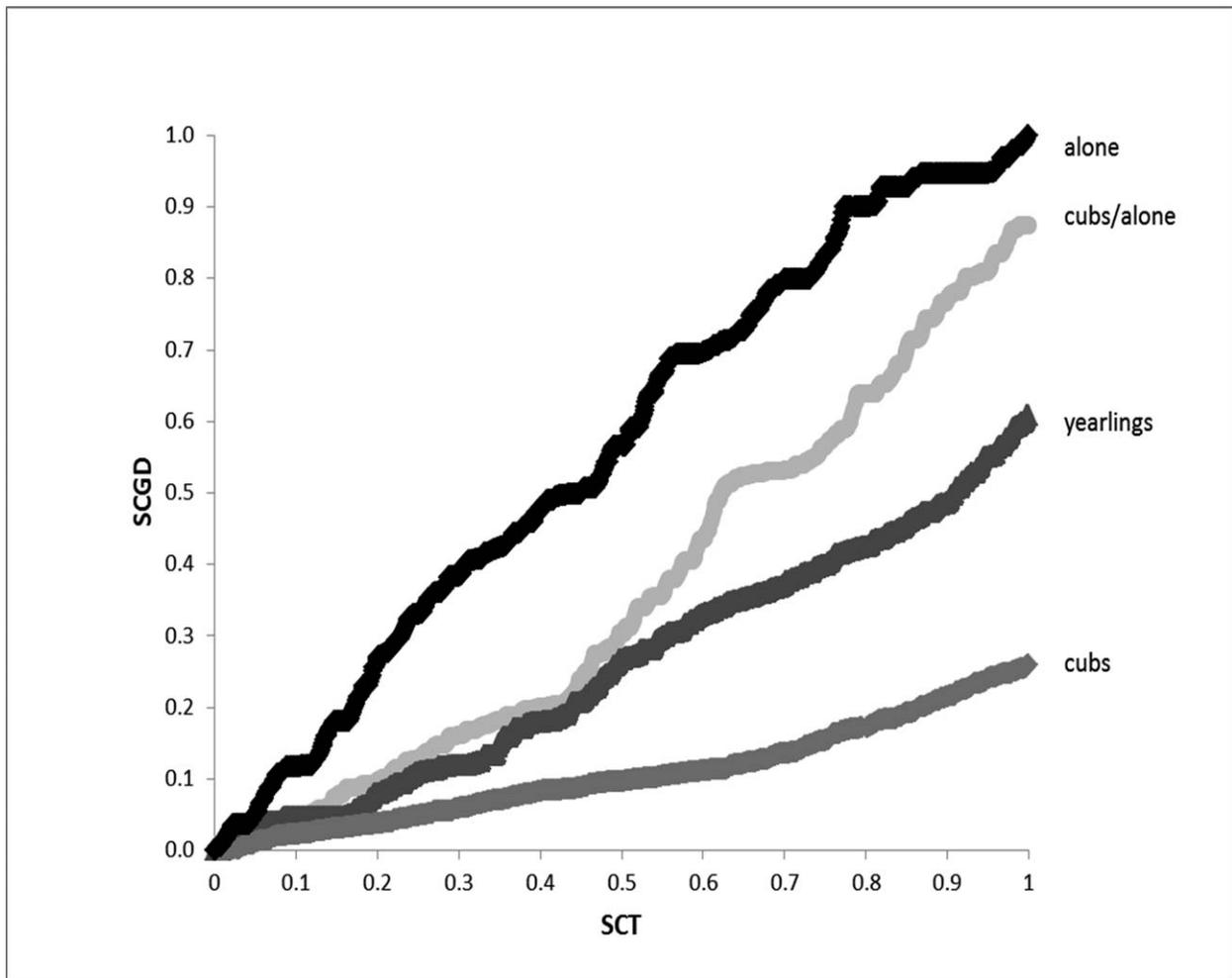Mean litter size in FRSA was 2.3, which was within the range reported for North American

Fig. 3. Cumulative distance standardized to the cumulative greatest distance (SCGD) travelled over standardized cumulative time (SCT) among 4 radiocollared female grizzly bears with different maternal status in the Fortymile River study area in eastern Interior Alaska, USA, during 25 May–15 July 2010. The greatest cumulative distance used for calculations of SCGD was from bear 9008 (status = alone), which appears as the black line at the top of the plot.

Table 3. Comparison of time spent in habitat patches in hours and distance between habitat patches between periods by parturient female grizzly bears that kept or lost cubs by 30 June in the Fortymile River study area, eastern Interior Alaska, USA, 2009–2012.

| | Patch use (hr) | | | | Distance moved between patches (km) | | | |
| | Cubs survived | | Cubs lost | | Cubs survived | | Cubs lost | |
Period	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Den influenced	68.4	35.4	13.7	2.8	1.0	0.1	1.2	0.1
Pre–green-up	25.2[a]	6.9	11.6	2.5	1.1	0.2	1.5	0.2
Green vegetation	13.1	3.1	8.9	2.5	1.0	0.2	2.0	0.6

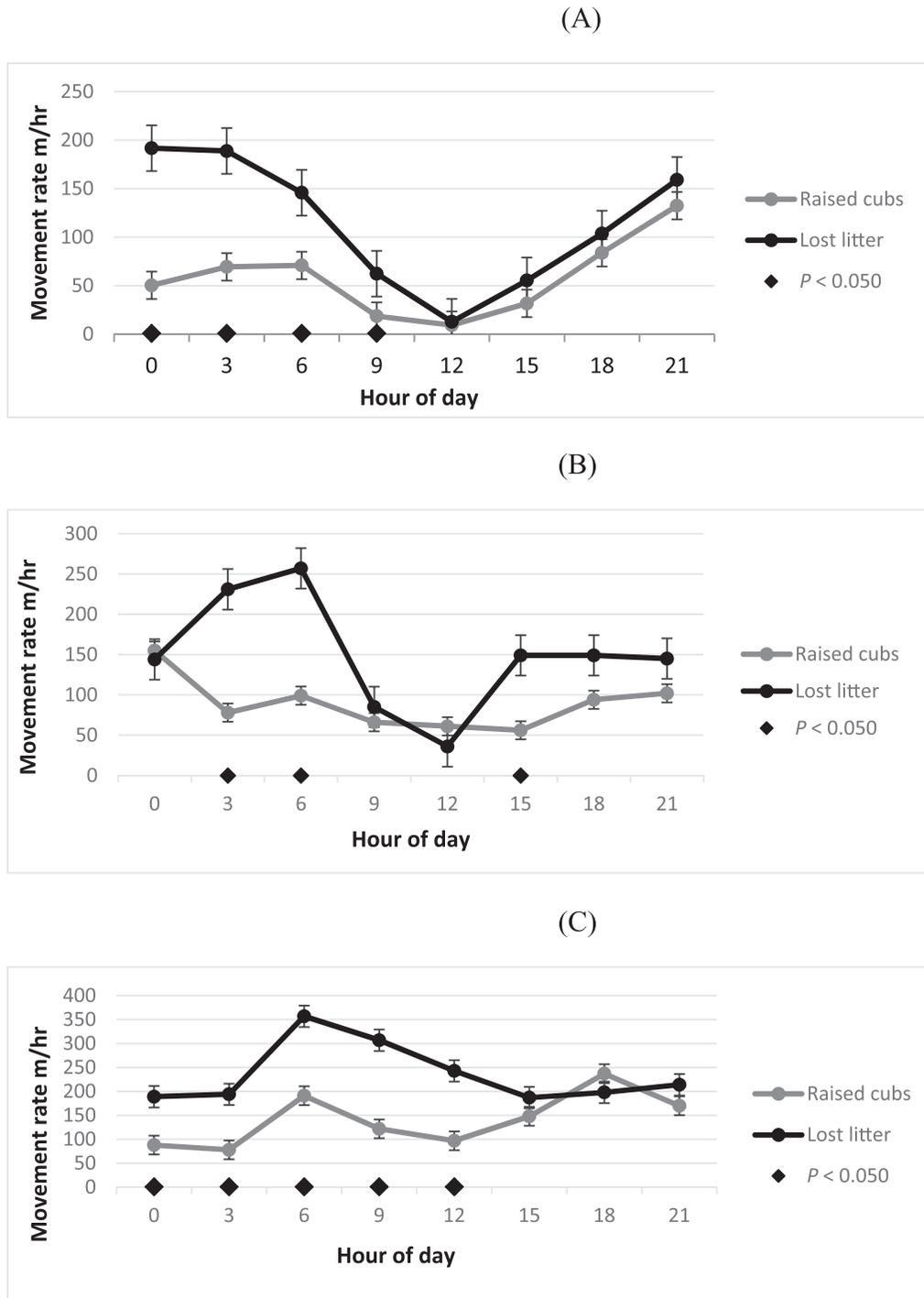[a]Significantly different from females that lost cubs.

(A)

(B)

(C)

Fig. 4. Mean movement rates (m/hr) by 3-hour periods during the day (Alaska Standard Time) by female grizzly bears with cubs in the Fortymile River study area in eastern Interior Alaska, USA, during 15 May 2009–15 June 2012, contrasting females with surviving cubs and females that lost their litters during 15–22 May (A), 23–31 May (B), and 1–15 June (C). Solid diamonds at the bottom of the graphs showed paired 3-hour differences at $P = 0.950$.
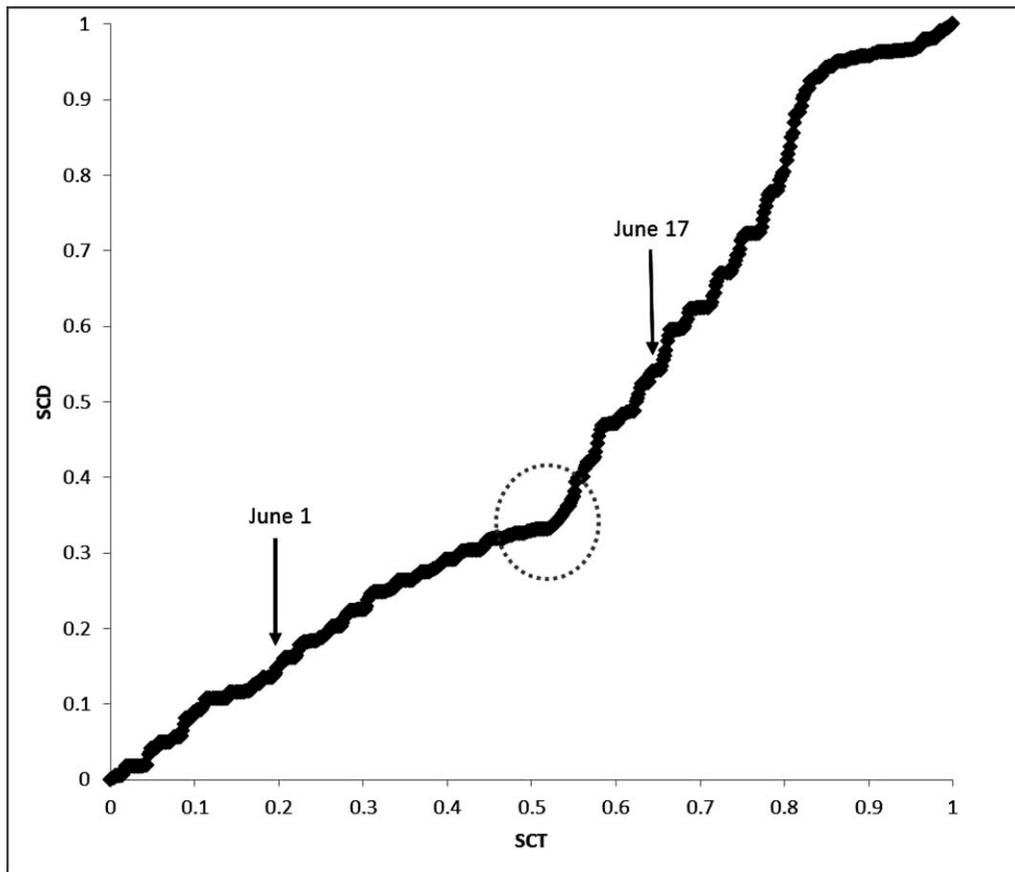
Fig. 5. Example of movement patterns of grizzly bear female 9005 before and after losing her cubs during 1–17 June 2011 in the Fortymile River study area in eastern Interior Alaska, USA. The dotted circle indicates when the female increased her movements. The arrows show the dates of the radiotelemetry flights when the cubs were last observed (1 Jun) and found to be missing (17 Jun). Axes are standardized cumulative time (SCT) versus standardized cumulative distance (SCD).

grizzly bears (1.7–2.5; summarized in Schwartz et al. 2003) and at the upper range reported for other Interior Alaska grizzly populations (1.9–2.3; Miller and Ballard 1982, Reynolds and Hechtel 1986, Miller et al. 2003). Vital rates for bears may differ stochastically between years (McLellan 1989, Miller et al. 2003, Schwartz et al. 2006a, Obbard and Howe 2008). However, during the 4 years of study all bears that were expected to have cubs had litters of ≥ 2 cubs within 14 days post–den-emergence, indicating that environmental conditions did not cause reduced natality during the study. Our litter-size estimate could be biased if the one 4–5-year-old female not observed with cubs during the study had lost her litter prior to the observation period. Four-year-old to nine-year-old females tend to lose more offspring and produce more single-cub litters compared with

older females (Schwartz et al. 2006b). However, we expect this bear was nulliparous based on an observation of her alone outside the den in late April as a 5-year-old and because the age of first reproduction for grizzly bears in the nearby Alaska Range was 5.9 years (95% CI = 5.5–6.4; Reynolds and Ver Hoef 2000) and in Kluane National Park, Yukon, Canada, it was 7.7 years (Schwartz et al. 2003). Our results do not suggest a density-dependent response in cub production.

In contrast, annual cub survival in FRSA was low (0.39) compared with the range reported for most areas in North America (0.56–0.86; McLellan 1994, Miller et al. 2003, Schwartz et al. 2003). Cub survival rates in FRSA were most comparable to grizzly bear populations documented previously in Denali (0.34; Miller et al. 2003) and Katmai National Park and

Preserves (0.34; Miller et al. 2003), and Yellowstone National Park (0.48; Schwartz et al. 2006b). Grizzly bears in these studies were un-hunted, at higher densities (all ≥37 bears/1,000 km^2), and at or near estimated carrying capacity (Miller et al. 2003, Schwartz et al. 2006a). In most hunted populations in North America, harvest is sufficient to reduce grizzly bear numbers and these populations exhibit better cub survival compared with populations closer to carrying capacity (Miller et al. 2003, McLellan 2005). Based on the low harvest rates, grizzly bear density in FRSA is probably not depressed because of harvest.

We did not find evidence that the body size of the mother was a factor explaining cub survival, nor was there evidence that cub survival was directly influenced by human causes because all dens were far from human influences (>14 km) and cub mortalities occurred in remote areas. Female grizzly bears with cubs have been found to select for habitats within 200 m of roads during spring, thereby increasing their probability of encountering humans and the threat of mortality (Graham et al. 2010). Two of the radiocollared bears with cubs had ranges adjacent to the Taylor Highway, but 0% and 1.0% of their locations were ≤1 km from the road during 15 May–30 June. Instead, our results suggest that bear numbers in FRSA likely exist at or near carrying capacity and are possibly regulated through a density-dependent response in cub survival.

In FRSA, most cub mortality occurred during the breeding season by 30 June (69%), entire litters were lost, and females that lost litters prior to mid-June bred and had cubs the next year. The timing of cub mortality was similar to the Denali, Katmai, and Susitna grizzly populations in Alaska (Miller et al. 2003). If grizzly bears exist at or near carrying capacity in the FRSA, then high offspring mortality would be expected due to food availability to cubs, maternal nutrition constraints, and predation by conspecifics (Swenson et al. 2001, Miller et al. 2003, Schwartz et al. 2006a). Although we did not determine cause of death, based on the timing of mortality and because most litter mates died concurrently or within a short time period, our results were consistent with the hypothesis that most cub mortality was caused by other bears (Swenson et al. 2001, Miller et al. 2003, McLellan 2005). Wolves and black bears are other potential predators in the FRSA and have been noted to kill grizzly cubs (Gunther and Smith 2004), but few predators other than larger conspecifics can overcome the female's willingness and ability to protect her cubs (Miller et al. 2003, McLellan 2005). Therefore, their impact on cub mortality was assumed to be minimal. We recognize that our data were not sufficient to distinguish between nutrition and infanticide as the proximate cause of death. Black bear cub mortality was found to be higher during food-shortage years and could have resulted from either nutritional stress to cubs or increased infanticide (Obbard and Howe 2008). Further, conditions favorable for sexually selected infanticide, including low density and presumably intense breeding competition between resident males, occurred in FRSA; this further complicated a definitive assessment of the interacting influences of nutrition and sexually selected infanticide on cub survival (Miller et al. 2003, McLellan 2005).

Female grizzly bears are hyperphagic during the period between den emergence and mid-June (Nielsen et al. 2010), during which they rely mostly on vegetation (Reynolds 1980, Boertje et al. 1987, Munro et al. 2006, Nielsen et al. 2010). In summer 2004, wildfires mildly to severely burned >50% of the FRSA http://fire.ak.blm.gov/predsvcs/maps.php). If the severity of wildfire was such that the availability and distribution of suitable forage patches were reduced, competition for those patches with other grizzly bears would presumably increase. Blueberries were common in the study area prior to the fire, but were extremely uncommon within the burn area between 2004 and 2009, providing evidence that forage availability was influenced for ≥5 years following the burn (T. Bentzen, unpublished data). The most common plant following the fire was *Calamagrostis canadensis,* which is not known to be a preferred bear food (Murie 1944). Given the observed and expected changes in vegetation associated with the fire, previous foraging experience within their home ranges may not have helped females forage more efficiently during our study. This is consistent with our results because cub survival did not appear to be correlated with maternal age (Table 1), which should reflect experience. Previous studies have found cubs of older, larger, and more experienced females to have higher survival rates (McLellan 2005, Zedrosser et al. 2009), presumably because these females were better at defending and provisioning their cubs.

The efficiency of predators and the quality of the habitat within the home ranges of females with cubs

should determine the anti-predator responses displayed (Creel 2011). Cub survival is subject to chance events but should also be influenced by how often and far a maternal female moves her cubs, her choice of travel routes, and the security and nutritional quality of the chosen habitat patches. Most prey are more conspicuous to predators while moving and foraging (Cassini and Galante 1992) and therefore, should benefit from adapting behaviors to reduce activities during high-risk times of the day and minimizing exposure along common bear travel routes (i.e., rivers, ridge-tops) and forage areas. Munro et al. (2006) found that female grizzly bear activity patterns changed considerably over a 24-hour period, with foraging activities occurring mostly during diurnal and crepuscular periods and bedding at night. Further, Schwartz et al. (2010) found that male grizzly bears were more active at night than at midday, whereas female grizzly bears were more active midday. Mace et al. (2012b) observed no clear timing of inactive periods during the 24-hour period for grizzly bears during May and June in Denali National Park, but they did not directly compare patterns between females with cubs and males. Without knowing the daily movement patterns of males in the FRSA, we could not assess whether females with cubs altered their movement patterns relative to males. We did find strong evidence that females with surviving cubs moved less during the early morning hours compared with females that lost their cubs, whereas they moved similarly during midday to late afternoon during all 3 periods. It may be advantageous for a female with cubs to avoid high-quality habitat patches to minimize encounters with potentially infanticidal males (Wielgus and Bunell 1994), and to utilize patches that are less attractive to other bears but nutritionally adequate. Stenhouse et al. (2005) found that bears with overlapping home ranges were seldom close unless they were associating in some way and suggested that behavioral factors could play a significant role in bear positioning and movements.

Similar to other studies (Dahle and Swenson 2003, Edwards et al. 2013), we found that FRSA females with cubs had smaller home ranges and moved less compared with lone females and females with yearlings. Additionally, after losing entire litters, females increased movements promptly, further indicating that movement is constrained for females with cubs (Edwards et al. 2013). However, in FRSA, just reducing home-range size was not adequate to

improve cub survival. We found that females with surviving cubs further limited movements to a few habitat patches between den emergence and vegetation green-up (6–11 patches compared with 15–30 habitat patches for females that lost cubs). During this period, cubs are growing rapidly but forage quality is low. The ability to find and exploit suitable forage habitat patches not frequented by other bears during this period of limited resources would allow females to restrict movements. This strategy would be effective for both minimizing exposure to adult bears and allowing cubs to maximize energy efficiency. Energy efficiency would in turn allow cubs to grow larger and become mobile more quickly, thereby improving their ability to escape predators sooner. Offspring survival has been correlated with the nutritional condition of the offspring and the female (Zedrosser et al. 2009). Contrary to our hypothesis, the distance moved between patches did not appear to be as important to cub survival as the ability of the female with cubs to reduce the number of inter–habitat-patch moves and to limit movements during morning hours. Once vegetation green-up occurred and more nutritious foods were available, the amount of time spent at patches and movement patterns became similar between all females; however, the timing of daily movements remained different, with females with surviving cubs moving less during the early morning hours (0000–1200 hr).

The initial habitat patch available to all females with cubs is the area immediately around the den. Several studies suggested that pregnant females selected den sites to maintain sexual segregation to avoid infanticidal males (Haroldson et al. 2002, Libal et al. 2011). However, Pigeon et al. (2014) found that pregnant females selected den sites based on habitat characteristics including dry conifer stands with abundant high-quality spring food. We did not measure the availability of spring forage; but den-characteristic data (elevation, aspect, and slope) indicated that pregnant females in the FRSA did not select for den sites at high elevations as found by Libal et al. (2011), but selected for den sites within tree-line similar to Pigeon et al. (2014). Previous studies have found that adult female grizzly bears remain at den sites longer following emergence than do males and females not encumbered by cubs (Miller 1990, Haroldson et al. 2002) even though body mass loss during lactation in the den was found to be 95% higher relative to non-lactating bears of

the same mass (Farley and Robbins 1995). Our results are unique in that, within females with cubs, those that successfully raised cubs remained at den sites longer than those that lost litters. Females may remain at dens longer to conserve energy until green-up occurs and to wait for adult males to disperse from den areas (Libal et al. 2011). Within the Susitna River Basin, Alaska, females with cubs that moved farther away from their dens in early spring lost their cubs more often (mostly to infanticide) compared with females that remained close to their dens (Miller 1990). We found that females with surviving cubs remained at den locations 2–3 days longer than females that lost their litters. This finding was probably not explained by extensive snowpack covering forage because most den sites for females with cubs were within tree-line and located on southwest slopes, and snowpack in these habitats was patchy by mid-May. It is difficult to know with certainty how important remaining near dens for 2–3 additional days would be in terms of influencing cub survival. However, assuming resources near these dens allowed for efficient foraging, these extra days could have contributed to higher survival probability of cubs, both by reducing encounters with males (Miller 1990) and maximizing energy efficiency. Although 2–3 days might only make a small difference as an isolated factor, this result may be cumulative when considered with the lower move-ment rates and smaller home ranges we documented for females that raised cubs after leaving the den area until green-up.

The abrupt changes in movements we documented were likely a consequence of mortality events and the fact that the change in slope was an indicator of when the litter failure occurred. Assuming these recognizable changes in movements were related to mortality events, a more precise documentation of the timing and rate of litter loss is possible from our data set. Specifically, movement data strongly suggested that the censored litter (Table 1) was also lost around 4 June, but this was not verified by observation prior to transmitter failure. If true, our estimates of cub and litter survival during 15 May–30 June would be 0.54 (CI = 0.36–0.71) and 0.50 (CI = 0.24–0.76) instead of 0.58 (CI = 0.40–0.76) and 0.55 (CI = 0.28–0.82) as reported above. Further, these data indicate that the one radiocollared bear we never observed with cubs did not lose litters between 15 May (average emergence date) and 25 May (the date we initiated aerial observations) and

that our assessment that she was nulliparous was correct. Future studies with more intensive survival monitoring programs would be beneficial to assess adult female movements relative to litter loss.

Philopatry beyond 3 years of age is common for female grizzly bears, resulting in considerable overlap of home ranges among related females (Mace and Waller 1998, Schwartz et al. 2003). In addition to the selective advantages of range familiarity and tolerance of offspring, it was suggested that having close kin as neighbors could also reduce conflicts between unrelated adult fe-males, who sometimes kill conspecifics' cubs (Hes-sing and Aumiller 1994). Killing cubs of unrelated females may benefit a female's fitness by reducing competition with her own cubs or by direct nutritional gains (Miller et al. 2003). We did not find evidence of philopatry in FRSA even after concentrating our capture efforts to collar adjacent adult females in the study area and monitoring an estimated 75% of the adult females. We suggest the lack of philopatry was caused by the combination of poor cub survival and possibly by the disruption of previous matrilineal assemblages due to a shuffling of home ranges as a result of the shortage of food caused by the extensive wildfires in 2004. Reduced black bear cub survival was documented by Cun-ningham and Ballard (2004) for ≥4 years following a catastrophic fire. Grizzly bear distribution can change due to substantial habitat alterations (Apps et al. 2004). If the severity of wildfire was such that large areas no longer offered adequate and predict-able food resources, grizzly bear distribution may have shifted and competition for areas not severely burned may have increased among bears. The radiotelemetry study conducted by Boertje et al. (1987) found that grizzly bear distribution was complete within the study area during the mid-1980s; however, a DNA-based mark–recapture study using hair traps conducted 2 years post-fire found evidence that grizzly bears, particularly females, were not present within the areas severely affected by wildfire (C. Gardner, unpublished data). Another alternative would be that some resident females died in the fires, thereby opening ranges to unrelated bears (Cunningham and Ballard 2004).

Many researchers have suggested that maternal grizzly bears alter their space use, habitat selection, or movement behavior to reduce cub mortality from infanticide (Wielgus and Bunnell 1994, McLellan 1994, Dahle and Swenson 2003, Miller et al. 2003,

Ben-David et al. 2004, Munroe et al. 2006, Rode et al. 2006, Schwartz et al. 2010, Libal et al. 2011, Edwards et al. 2013). However, we believe our study is the first to demonstrate that different maternal behavioral strategies have different fitness costs and benefits by linking female movement data directly with cub survival. We acknowledge that our results were limited because we did not know the causes of death for cubs, because we were unable to characterize the habitat quality and forage availability within habitat patches used by females, and because we did not have movement data for male bears. These limitations made it difficult to know whether the movement strategies adopted by successful females were in response to infanticidal males or the dispersion of resources. Additionally, the relative importance of spatial and temporal alterations to movement patterns would be better understood by relating these strategies to telemetry data from males. Nonetheless, our work provides clear, alternative hypotheses that can be tested to advance our understanding of this phenomenon. Specifically, future studies could relate movement strategies of maternal females to habitat quality and food resources within patches, as well as concurrent GPS telemetry data from males to determine whether females are influencing cub survival primarily by increasing energy efficiency or by avoiding infanticidal males. Linking maternal behavior with resource selection, male movements, and cub survival would help elucidate the mechanisms underlying the behavioral strategies we documented.

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