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Influence of maternal body size, condition, and age on recruitment of four brown bear populations

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Abstract: Recruitment of brown bear (*Ursus arctos*) offspring into a population is the product of initial cub production and subsequent survival and is a critical component of overall population status and trend. We investigated the relationship between maternal body size, body condition, and age (as a surrogate for gained experience) and recruitment of dependent offspring (≥1 yr old) in 4 Alaska, USA (2014–2017), brown bear populations using logistic regression. Body size alone was our top predictor of the presence of offspring and appeared in all top models. Our data suggest that bear size is the primary driver of productivity across all 4 study populations, with larger bears having a greater chance of being observed with offspring. The effect of body condition was likely confounded by the increased energetic costs of supporting cubs through time and had a negative relationship with recruitment. Age (experience) was positively related to recruitment. Understanding the relative importance of body size, body condition, and age on the recruitment of offspring provides insights into life-history trade-offs female bears must manage as they strive to meet the nutritional costs of cub production and rearing, while minimizing risks to themselves and their offspring. Further assessment of long-term longitudinal studies of brown bears that assess the lifetime reproductive output of individuals would be highly informative to further assess the effect of experience on recruitment and to support the management of brown bear populations for recovery, conservation, sustained yield, and ecosystem function.

Key words: age, Alaska, body condition, body mass index, body size, brown bear, recruitment, *Ursus arctos*

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Recruitment of offspring into a population influences the current status and projected trend of wildlife populations. Recruitment is the product of offspring production and survival rates from birth to independence. Understanding recruitment in brown bears (*Ursus arctos*) is challenging because of the variation across populations and individuals in age of first reproduction, litter size, weaning age, interval between litters (i.e., reproductive pause), partial loss of litters, and unknown fates of weaned individuals. Both maternal body size and condition have been shown to influence initial litter size—females with <19% body fat at den entry do not produce offspring (López-Alfaro et al. 2013), and body mass generally is positively related to the number of cubs produced (Hilderbrand et al. 1999). Gonzalez et al. (2012), however, found that maternal age was the primary determinant for cub litter size. Annual reproductive output for long-lived mammals tends to increase with body mass or condition, before declining as animals approach senescence (e.g., Hayward et al. 2014, Rughetti et al. 2015). Litter size and yearling mass increased with maternal age of reproducing female brown bears in Sweden (Gonzalez et al. 2012).

Cub-of-the-year, yearling, and older cub survival and entry into the breeding population are difficult to assess when offspring are not marked, but mortality is generally greatest in the first year of life. Garshelis et al. (2005)

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reported a cub survival rate of 79% and yearling survival rate of 91% in portions of southwestern Alberta, Canada, and compiled results from 11 other North American brown bear demographic studies where cub-of-the-year survival ranged from 34% to 88%, whereas yearling and subadult survival ranged from 68% to 94% and 77% to 100%, respectively. McLellan (1994) also compiled cub-of-the-year survival rates across 10 North American brown bear studies, with annual rates ranging from 60% to 85%. Estimates of cub-of-the-year survival are likely overestimates because an unknown portion of cubs of the year are lost before being observed, and estimates of yearling survival are likely underestimates because their absence is often interpreted as a mortality, despite some yearlings being successfully weaned. Weaning age can be highly variable even within a given population. For example, Reynolds and Hechtel (1989) reported that some brown bears in the Western Brooks Range of Alaska, USA, weaned 1-year-old offspring, whereas other females retained their offspring up to age 5.

Bears are known to learn based on experience, particularly about foraging (Ditmar et al. 2015) and risk avoidance (Steyaert et al. 2016), so they may have the capacity to become more capable mothers with each additional litter—more effectively balancing the nutritional requirements of supporting offspring with risk avoidance, thereby increasing survival of both the mother and her progeny. Thus, maternal body size, body condition, and age (as a proxy for experience) all appear to have the potential to affect brown bear recruitment. Our objective was to assess the relationship of maternal body size, body condition, and age with recruitment of offspring (defined in this study as ≥1 yr old) in 4 Alaska brown bear populations.

Study areas

This study included portions of Gates of the Arctic National Park and Preserve (Gates), Lake Clark National Park and Preserve (Lake Clark), Katmai National Park and Preserve (Katmai), and Kodiak National Wildlife Refuge (Kodiak; Fig. 1). Our Gates study area included a portion of the south side of the Brooks Range, alpine tundra, spruce (*Picea* spp.) forest, and lowland riparian areas (Wilson et al. 2014). The Lake Clark study area included the Chigmit Mountains, subalpine tundra, spruce forest, and riparian areas (Mangipane et al. 2017). The Katmai study area included a portion of the eastern Aleutian Range, coastal, intertidal, and island habitats (Hilderbrand et al. 2018). The Kodiak study area was a portion of the Kodiak Archipelago and included forest, mountain, and riparian habitat (Deacy et al. 2016). These study areas differed in ecosystem drivers, especially the availability of salmon (*Oncorhynchus* spp.); and thus, relative population density and productivity (litter size, age of first reproduction, interval between litters) is generally greatest in Kodiak and Katmai, intermediate in Lake Clark, and lowest in Gates (McLellan 1994; Hilderbrand et al. 1999, 2018; Mowat and Heard 2006). In addition, hunting pressure varies with sport and subsistence hunting authorized on Kodiak, limited hunting in Gates and Lake Clark, and no legal hunting allowed in Katmai. Nevertheless, we assumed all 4 populations were relatively close to ecological carrying capacity, despite differences in management regime.

Methods

We located and anesthetized adult female brown bears (≥8 yr of age) via helicopter darting using Telazol® (Fort Dodge Laboratories, Fort Dodge, Iowa, USA) during spring, according to Hilderbrand et al. (2018). We recorded the presence and number, and visually estimated the age, of accompanying offspring at the time of capture. We were able to reliably classify cubs of the year by their small body size and, often, markings; however, accurately determining the age of offspring >1 year of age is problematic because of variation in ecosystem productivity, maternal condition and investment, sex-specific growth rates, and variation in size within litters. Thus, we did not categorize offspring into more discrete age categories (e.g., yearlings, 2-yr-olds, 3-yr-olds, etc.). We did not capture females with cubs of the year in Katmai or Kodiak (and we therefore excluded such individuals from Gates and Lake Clark from our analyses), nor did we capture offspring of any age in any of the study areas, to reduce risk of abandonment or mortality. We determined preliminary survival rates for cubs of the year (Gates and Lake Clark) and known yearlings (Gates, Katmai, and Lake Clark) by litter size at the time of initial spring capture or observation and observed litter size during subsequent radiotelemetry flights.

At the time of capture, we weighed each female using an electronic load cell and measured the skull width (straight line distance between the widest portion of zygomatic arches), and skull length (straight-line distance from the upper incisors and occipital condoyle) using calipers, and measured body length (following dorsal body contour from the tip of the nose to the base of the tail with the bear in a sternal recumbent position) using a nylon tape measure (Hilderbrand et al. 2018). We used the sum of skull width and skull length as an

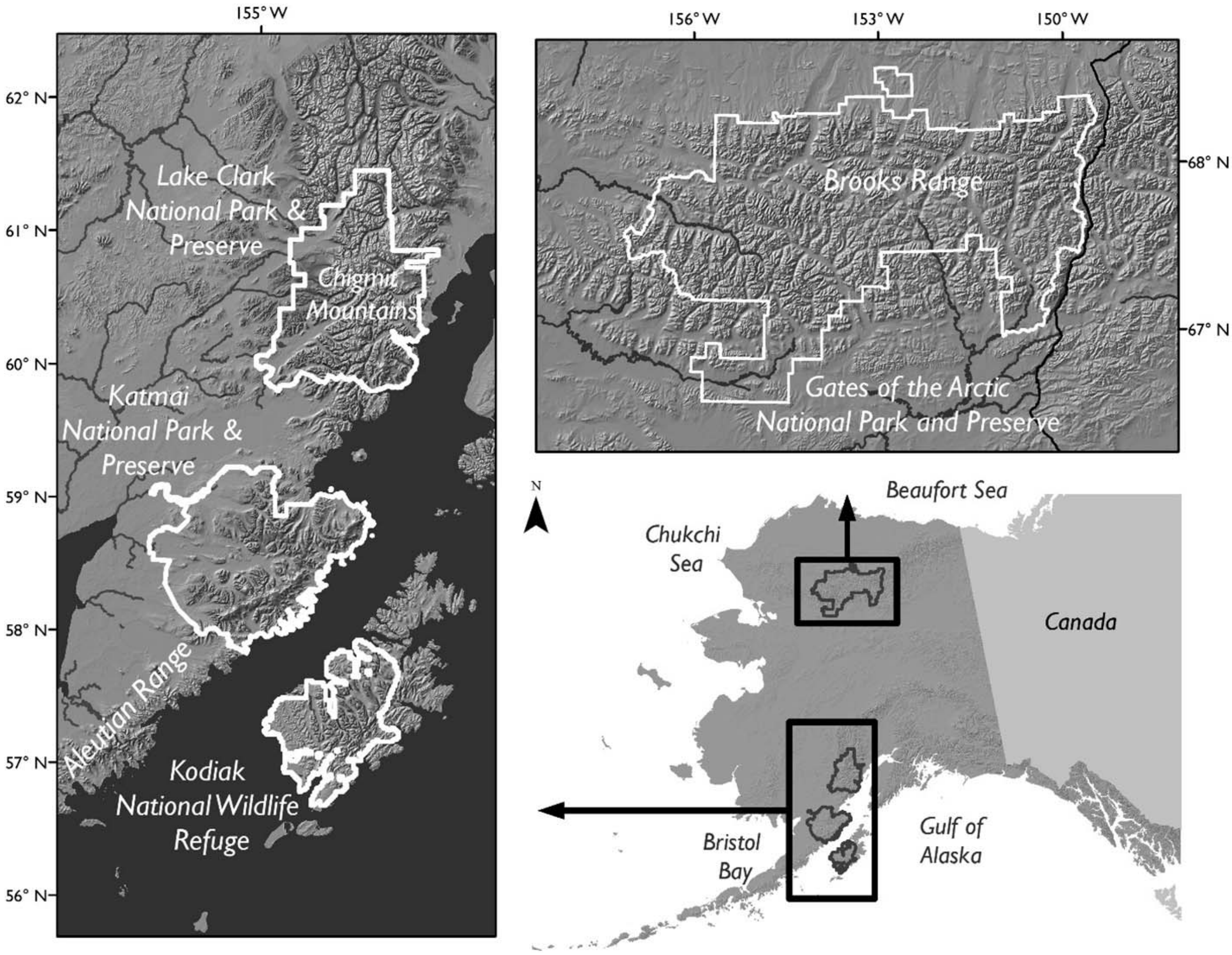

Fig. 1. Four Alaska brown bear (*Ursus arctos*) study areas, Alaska, USA, where we investigated the relationship between maternal body size, body condition, and age (as a surrogate for gained experience) and recruitment of dependent offspring (≥1 yr old) from 2014 to 2017.

index of body size (hereafter referred to as skull size). We used body mass index (BMI; body mass divided by body length^2) as an index of body condition. We determined the age of each individual by analysis of the cementum annuli of a vestigial premolar (Matson's Laboratory, Milltown, Montana, USA) to the maximum extent allowed under the conditions of our various permits. When we were not authorized to extract a tooth, experienced observers (>1,000 captured bears and approx. 500 harvested bears) estimated age based on tooth wear, especially wear of the molars. We used only our first observation of an individual during the study period for which we had measurements, because we caught some animals multiple times. All capture and handling procedures followed project-specific Animal Care and Use Committee approved methods (National Park Service: AKR_KATM_Hilderbrand_BrownBear_2014, AKR_LACL_Mangipane_BrownBear_2014, AKR_GAAR_Gustine_GrizzlyBear_2014); U.S. Geological Survey Alaska Science Center 2014-01, 2015-04, 2015-06, and U.S. Fish and Wildlife Service (USFWS) Alaska Department of Fish and Game Animal Care and Use Committee 07–08, USFWS Institutional Animal Care and Use Committee (IACUC) Permit 2012008, USFWS IACUC Permit 2012008 Renewal, USFWS IACUC Permit 2015-001).

To determine the accuracy of our age estimates based on tooth wear, we assessed the relationship between the absolute difference in estimates (age by cementum annuli minus age estimated from tooth wear) and actual age (by cementum annuli) by linear regression. To assess bias, we also used linear regression, but evaluated the relationship between the difference (rather than the absolute difference) in estimates and age. Whenever an estimate by cementum annuli was available, we used that value in all subsequent analyses.

We used logistic regression to assess the influence of indices of body size, body condition, age, and population on the likelihood that an adult female would have offspring ≥1 year old with her. We considered the presence of offspring of ≥1 year old as a proxy for recruitment because mortality is greatest in the first year of life and the survival of yearlings and subadults approaches that of adult females (Garshelis et al. 2005, Bled et al. 2017). Correlations between predictors were ≤0.7, and we removed individuals with missing values for any measured attribute from the analysis. Our data included relatively few individuals with offspring; therefore, we limited candidate models to 5 parameters (Vittinghoff and McCulloch 2006) and considered all possible combinations of covariates. We performed model selection using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989, Burnham and Anderson 2002) and built models in Program R Version 3.4.3 (R Core Team 2017). We used analysis of variance to test for differences in the means of skull size, BMI, and age in relation to the number of offspring an adult female had with her (range = 0−4) and also in the mean number of offspring among study areas.

Table 1. Logistic regression models used to assess the relationship between body size ('Body'; the sum of skull length and skull width), body condition ('BMI'), Age, and Population with the likelihood of an adult female brown bear (*Ursus arctos*) having an offspring (≥1 yr old) with her (response; 'Offspring') across 4 study areas, Alaska, USA, 2014–2017.

Model	*K*	AIC_c	ΔAIC_c	AIC_c weight
Offspring ∼ Body	2	81.01	-	0.31
Offspring ∼ Body + BMI	3	81.31	0.29	0.27
Offspring ∼ Body + Age + BMI	4	82.21	1.19	0.17
Offspring ∼ Body + Age	3	82.41	1.39	0.16
Offspring ∼ Body + Population	5	85.22	4.20	0.04
Offspring ∼ Age + Population	5	86.72	5.71	0.02
Offspring ∼ Population	4	87.61	6.60	0.01
Offspring ∼ BMI + Population	5	88.88	7.86	0.01
Offspring ∼ Age	2	89.75	8.74	0.00
Offspring ∼ 1	1	90.72	9.71	0.00
Offspring ∼ BMI	2	90.80	9.79	0.00
Offspring ∼ Age + BMI	3	90.92	9.91	0.00

Results

We compared paired estimates of female age by cementum annuli and observer estimates based on tooth wear for 38 individual bears with 28.9% and 52.6% of the estimates separated by ≤1 and ≤2 years, respectively. Accuracy decreased with age as the error in our estimates increased (slope = 0.28 yr/yr, intercept = 0.04, $P = 0.02$), resulting in absolute errors of 1.45, 2.86, 4.27, and 5.68 at ages 5, 10, 15, and 20, respectively. Relative to bias, we overestimated age by 0.95 years at age 5 and underestimated age by 0.77, 2.50, and 4.22 years at ages 10, 15, and 20, respectively (slope = 0.35, intercept = −2.68, $P = 0.03$).

We had 68 first-time spring captures of adult (≥8 yr old) female brown bears across our 4 study areas (Gates: $n = 26$; Katmai: $n = 17$; Kodiak: $n = 15$; Lake Clark: $n = 10$) from 2014 to 2017 (Table S1, Supplemental Material). Of the 68 females, 33 (48.5%) were accompanied by ≥1 offspring (Gates: 34.6%; Katmai: 70.6%; Kodiak: 66.7%; Lake Clark: 20%). Some bears were purposefully avoided (e.g., females with cubs of the year in Katmai and Kodiak); therefore, these values are not necessarily reflective of population demographics. Cub-of-the-year survival, determined from aerial tracking flights, was 17% in Gates (2 of 12) and 91% in Lake Clark (20 of 22; Hilderbrand et al., unpublished data). Yearling survival was 67% (4 of 6) in Gates, 90% (9 of 10) in Katmai, and 83% in Lake Clark (5 of 6; Hilderbrand et al., unpublished data).

Maternal body size (as indexed by skull size) occurred in all 4 of the top models ($\Delta AIC_c < 2$) used to predict presence of offspring and was the lone variable in the overall top model (Table 1). In this top univariate model, greater body size was associated with a greater probability of having offspring (Fig. 2; $\beta = 0.19$, SE = 0.06, logit), whereas body size was not strongly collinear with age (Pearson correlation coefficient = 0.29). Body condition and age also entered the other top models, albeit with less pronounced effects. Better body condition (i.e., greater BMI) was associated with a lower probability of having an offspring in these top models, whereas older females were associated with a higher probability of having an offspring with them (Table S2, Supplemental Material). 'Population' did not enter into any of our top models, and we did not find evidence for differences of effects between bear populations for the probability of recruitment. Body size drove the probability of recruitment (Fig. 2). Absolute body size differed among study areas and larger

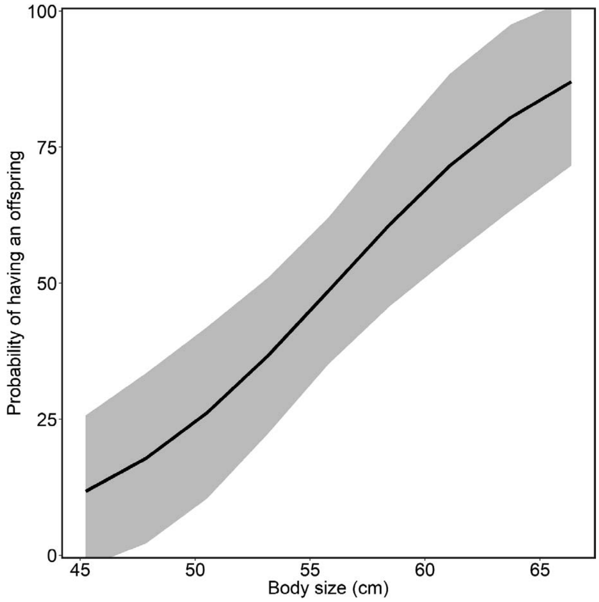

Fig 2. The predicted relationship from the top logistic regression model between body size (skull length plus skull width) and the probability of an adult female brown bear (*Ursus arctos*) having offspring (≥1 yr old) across 4 study areas, Alaska, USA, 2014–2017.

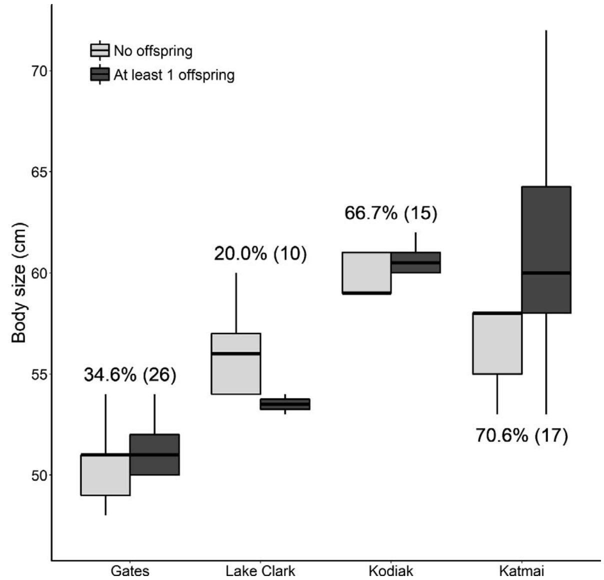

Fig. 3. Relationship between body size (skull length plus skull width) and the presence of offspring (≥1 yr old) with adult female brown bears (*Ursus arctos*) in 4 study areas, Alaska, USA, 2014–2017. The bars indicate the median values, the boxes the 25th and 75th percentiles. Percent of females detected with ≥1 offspring is presented for each population with sample size in parentheses.

females were more likely to be accompanied by offspring (Fig. 3).

The body size of females was positively associated with the number of offspring—larger females had more offspring ($F_{4, 65} = 8.32$, $P < 0.01$; Fig 4). Neither body condition nor age were associated with the number of offspring. Adult females in Katmai (1.59 ± 0.23 [mean ± SE]) and Kodiak (1.40 ± 0.25; $F_{3, 67} = 8.09$, $P < 0.01$) were accompanied by more offspring than were adult females in Gates (0.42 ± 0.19) and Lake Clark (0.20 ± 0.31).

Discussion

Recruitment of offspring into the population by female brown bears is the product of initial litter size and subsequent survival, and is a critical factor influencing population status and trend. Our results from 4 Alaska brown bear populations suggested that body size is a primary driver of recruitment, positively affecting both the presence and number of offspring. Body size was the lone variable in our top model predicting whether an adult female would be accompanied by offspring, and it appeared in all of the top 4 models. Brown bears in our study areas, like other long-lived species, invest early in rapid growth in structural size, which is completed by 8−14 years of age; subsequent growth in lean mass occurs when available resources allow (Hilderbrand et al. 2018). However, there is individual heterogeneity that likely affects life-history tradeoffs between early body growth and reproduction, as seen in other species (see Quesnel et al. 2018). Our data suggest that larger females more successfully reproduce and recruit offspring into the population. We also documented a relationship between body size and the number of offspring with adult female brown bears.

The influence of body condition on recruitment is confounded by females with a greater number and/or mass of offspring because these females have greater energy and protein demands that must be met by nutrient intake and/or depletion of body stores, with possible persistent effects over multiple years (Hilderbrand et al. 2000). The number of offspring produced is of obvious importance, but offspring mass is also critical because recruitment may be achieved by producing fewer, but larger, offspring (Gonzales et al. 2012). Our results support the hypothesis that the energetic demands of offspring recruitment can be substantial. When body condition entered our top

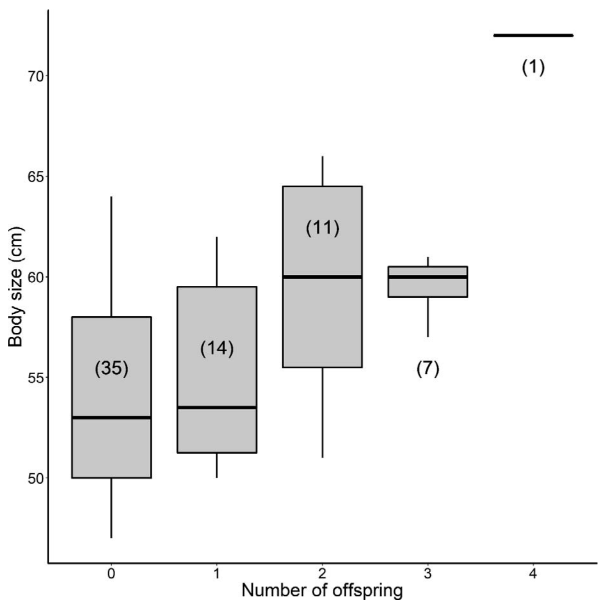

Fig. 4. Relationship between body size (skull length plus skull width) and number of offspring (≥1 yr old) with adult female brown bears (*Ursus arctos*) across 4 study areas, Alaska, USA, 2014–2017. One individual was observed with 4 offspring. The bars indicate the median values, the boxes the 25th and 75th percentiles, and sample sizes are in parentheses.

models, it had a negative relationship with probability of recruitment. In other words, those females that successfully recruited offspring had reduced body condition, likely as a result of investment costs.

Individual females likely gain knowledge and experience with each successive litter, so a positive relationship between age and probability of recruitment would be expected. However, individuals may experience reduced age-specific reproductive success as they approach senescence. We found that when age was in one of the top models, it positively correlated with probability of recruitment. In addition, age may also be the major determinant of initial litter size in some populations (Gonzalez et al. 2012).

Our analyses provide some initial insights into the relative importance of maternal body size, body condition, and age on the recruitment of offspring. Understanding how these factors can influence population status and trajectory is critical to managing ecosystem processes (e.g., salmon escapement; Hilderbrand et al. 2004) and managing for sustained yield because harvest can influence population demography in myriad ways (Zedrosser et al. 2013, Gosselin et al. 2014). When population conservation and/or recovery is the management goal, understanding density-related effects becomes critical, especially as the population approaches carrying capacity (Støen et al. 2006; Zedrosser et al. 2006, 2007; van Manen et al. 2016).

Our data set is unique because it spans populations of varied ecology, nutrient availability, and population density (Hilderbrand et al. 2018), but is limited in sample size, study duration, and by permit conditions that prevented us from determining ages of all bears by cementum annuli. The study of factors influencing offspring recruitment warrants additional analyses, ideally from other bear populations with long-term productivity and recruitment data from individuals where the effect of age and experience on recruitment, as well as senescence, could be more adequately assessed. Increased error and bias associated with age estimates from tooth wear were reported in this study; therefore, we encourage aging by cementum annuli whenever possible. In addition, there is a large range in body size seen across and within brown bear populations, so it would be insightful to conduct a longitudinal study of individuals over a long period of time to compare the lifetime reproductive output of large versus small bears as a surrogate for high-risk energy maximization versus low-risk life-history strategies.

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Supplemental material

Table S1. Data table for adult female brown bears (*Ursus arctos*) with offspring (≥1 yr old) in the spring from 4 study populations in Alaska, USA (2014–2017). 'BearNo' is the number that individual was assigned. 'Offspring' value of 1 means the individual had ≥1 offspring (≥1 yr old) with her at the time. 'Body size' is the combination of skull width and skull length (cm). 'BMI' is a body mass index (kg/m^2). Age is in years. Missing values represent measurements not taken.

Table S2. Estimated coefficients (in logit space) from the 4 top logistic regression models (ΔAIC_c <2) for adult female brown bears (*Ursus arctos*), with presence of offspring (1 yr old) in the spring as the response, from 4 study populations in Alaska, USA (2014–2017). 'Offspring' is the number of offspring (≥1 yr old) with the female at the time, 'Body' is the combination of skull width and skull length, 'BMI' is a body mass index (kg/m^2), and 'Age' is in years.