Litter size and cub age influence weight gain and development in American black bears (*Ursus americanus*)

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We assessed the effects of cub age, litter size, and sex, on body mass (BM), absolute and relative growth rates (AGR, RGR), opening of ears and eyes, and deciduous teeth eruption from 129 cubs of American black bears (*Ursus americanus*) born at Virginia Tech's Black Bear Research Center. Specific ages, related to maternal food consumption, and litter size, best described BM, AGR, RGR, and ear and eye development. Overall, newborns weighed ~0.44 kg at birth and increased ~9-fold by ~14 weeks. Twins were greater in BM than single cubs and triplets. Single and triplet cubs had higher AGR and RGR than twins after mothers resumed food consumption post-hibernation. Newborns displayed RGR > 3.5% that decreased until den emergence (RGR < 3.5% after emergence). RGR differed among litter sizes, particularly after den emergence. Ear and eye opening occurred concurrently at ~44 days of age, while teeth erupted ~10 days later. Single cubs experienced delayed development of these organs compared to other litter sizes. Postnatal developmental differences between black bears and other carnivores likely stem from strategies allowing black bears to minimize energy expenditure during the gestational period when hibernating.

Key words: American black bear, body mass, growth rates, litter size, neonatal development, *Ursus americanus*

Life history plays an important role in determining postnatal offspring development in eutherian mammals (Derrickson 1992). Cubs of American black bears, *Ursus americanus* (hereafter, black bears), are the product of exceptional gestational adaptations. After mating, fertilized embryos of black bears experience obligate delayed implantation for over 100 days (Hamlett 1935). Thereafter, in the late fall, embryos resume their developmental activity to complete a 60-day active gestational phase that times parturition with hibernation (Hellgren et al. 1991). Prior to, or during, this active gestational phase, females seek a den and subsequently reduce their metabolic rates and physical activity, as well as endure anorexia, adipsia (i.e., appetite loss), and anuria (i.e., lack of urination—Nelson et al. 1983; Hellgren et al. 1990; Tøien et al. 2011). Parturition and the onset of lactation occur during winter (mid-January to mid-February), the time of lowest productivity in the Northern Hemisphere (Alt 1983; Spady et al. 2007). At this stage, altricial cubs are born with closed eyelids and ear canals, very short hair, and are smaller in relation to the mother's mass compared to other mammals (Leitch et al. 1959; Case 1978). Physiological constraints related to inability of mammalian fetal tissue to use free fatty acids, and toxicity of ketone bodies produced by energy usage during maternal black bear hibernation, may influence the relatively short active gestational phase, thereby producing relatively immature neonates (Ramsay and Dunbrack 1986). Neonatal cubs weigh between 0.3% and 0.4% of adult body weight (Oftedal et al. 1993). In contrast, young of other mammalian species weigh much greater proportions of maternal body mass (BM) at birth, such as American beavers (*Castor canadensis*) 3.8%, humans (*Homo sapiens*) 4–5%, sea

otters (*Enhidra lutris*) 7%, and American porcupines (*Erethizon dorsatum*) 20% (Case 1978). Moreover, black bear cubs exhibit lower absolute growth rates (AGR; e.g., grams gained per day) than other carnivores, such as canids (Case 1978).

Most altricial species, including eutherian (placental) mammals, are born with minimal sensorial organ development, including: closed eyelids, closed ear canals, and gums lacking teeth (Fox 1964). Timing at which these organs achieve postnatal functional development varies greatly across species (Bekoff and Jamieson 1975; Braastad and Heggelund 1984; Suárez et al. 2017; Van Cruchten et al. 2017). For instance, spotted hyenas (*Crocuta crocuta*) are born with a set of emerged teeth, eyes and ears open, and appear to be sensitive to sound stimuli, whereas raccoons (*Procyon lotor*) open their eyes and show tooth eruption 21 and 30 days after birth, respectively (Pournelle 1965; Ewer 1998). Sexual dimorphism is not evident in denning black bear cubs of the year, and morphological characteristics such as hair length and cranium width are positively associated with cub age (Godfrey 1996; Ryan 1997; Echols 2000; Bridges et al. 2002). There is limited information on the growth rates of black bear cubs, but an analysis that combined both wild (North Carolina and Pennsylvania) and captive-reared cubs (University of Washington) during the maternal hibernating period estimated AGR around 50 g/day (Farley and Robbins 1995).

Developmental biology focuses on estimating and capturing growth processes within and among individuals. Statistical growth modeling is a key tool in understanding development in plants, bacteria, birds, and mammals (McKinnon et al. 2012; Chatterjee et al. 2015; Teleken et al. 2017). Most growth processes in biogical systems are nonlinear in nature, as complex internal or external factors can influence acceleration or deceleration of growth in a living organism during different stages of development (Grimm et al. 2011; Paine et al. 2012; Tjørve and Tjørve 2017). Growth models such as logistic, Gompertz, Richards, and von Bertalanffy, assuming an asymptotic final size, are well established in zoological research (Selvaggi et al. 2017; Teleken et al. 2017). Traditionally, most growth analyses require the estimation of AGR and relative growth rates (RGR) to compare time or biomass-specific functions across factors of interest such as species, treatments, or time-based events (Paine et al. 2012; Selvaggi et al. 2017). Most recently, mixed growth modeling approaches have provided advantages to test hypotheses that include both fixed effects (e.g., sex—Beath 2007), or experimental factors (e.g., exposure to silviculture—Fang and Bailey 2001), associated with individual experimental units. For instance, from genome-wide tests in domestic pigs (*Sus domesticus*), mixed growth modeling techniques identified three specific genes influencing time to achive adult weight and maturity using repeated measures of individuals over time (Fonseca e Silva et al. 2017). In addition, a wide variety of models, such as spline growth, also are available to explore specific developmental stages or suspected bimodal growth trends. Spline growth modeling has the ability to find transition points or knots, where one developmental phase ends and another begins (Grimm et al. 2017). Spline growth models have

advantages such as simplicity and ability to estimate parameters precisely, as previously shown in a hybrid duck in France (Vitezica et al. 2010), and they can identify transition points that are often abrupt, potentially pinpointing milestones in developmental biology (Grimm et al. 2017).

Most information available for growth and development of black bear cubs remains anecdotal or circumstantial, due to the difficulty in obtaining repeated data from denning females and their newborns in the wild. Patterns of cub growth relative to litter size and timing of postnatal sensory organ development, such as opening of external ear canal, eyelid opening, and teeth eruption, are lacking (Matson 1954; Clarke et al. 1980; Rogers 1986; Gray et al. 2016). Our three objectives therefore were to: 1) assess the effects of cub age, cub sex, and litter size, on cub BM, AGR, and RGR; 2) determine temporal landmarks in sensory (ear and eye) and morphological (teeth) development from birth until 3–4 weeks post-den emergence (~12–14 weeks of age); and 3) determine relationships between maternal food consumption post-hibernation and cub growth parameters.

MATERIALS AND METHODS

We analyzed data from 129 cubs born in 58 different litters (single cubs: $n = 7$, twins: $n = 62$, and triplets: $n = 60$) from adult female black bears temporarily held in captivity (8–10 months) at Virginia Tech's Black Bear Research Center (VT-BBRC) between 1988 and 2016, as previously described in Hellgren et al. (1990). None of the cubs included in this study were fostered individuals. All cubs were born and raised by their biological mothers during the extent of the study. Free-ranging wild bears presumed to have bred were captured by the Virginia Department of Game and Inland Fisheries (VDGIF) in August–September of each year and released back into the wild with their cubs the subsequent spring, when cubs averaged 122 days old.

We provided adult females with dry dog food (two females were supplementary fed with corn) at ~170 kJ/kg/day upon arrival; we then increased food from 1 October until ~2 December (29 November, 5 December, 95% *CI*), to 335–376 kJ/kg/day. Thereafter, we reduced the food available by 50% per week until the first week of January, when food was completely removed if the bear had not already stopped food consumption voluntarily. Food (~170 kJ/kg/day) was slowly reintroduced to bears arousing from hibernation at the end of March or beginning of April, or earlier if bears showed signs of hibernation arousal such as defecation, increased physical activity, and water consumption. We provided water to bears at libitum during the extent of the study.

The active gestational phase was closely monitored via transabdominal ultrasound examinations (Aloka Echo Camera SSD-500V and a 3.5-MHz transducer; Hitachi-Aloka Medical America Inc., Wallingford, Connecticut). Auditory and visual inspections of dens were performed as pregnancies approached term (e.g., ~10 days before expected parturition). Inspections consisted of sessions that lasted between 15 and 30 min twice a day. Cub vocalizations and visual detection of cubs determined time of parturition. We determined birth as the midpoint date

from first positive cub detection and the last negative cub detection. We chemically immobilized adult females and obtained measurements of cubs every 10 days for ~14 weeks. All procedures were previously approved by the Institutional Animal Care and Use Committee at Virginia Tech under protocols 98-069, 09-073, 12-112, and 15-162, and conformed with guidelines of the American Society of Mammalogists for research on wild mammals (Sikes et al. 2016).

Adult females were chemically immobilized with intramuscular injections containing ketamine (4–8 mg/kg) and xylazine (0.8–2 mg/kg), and occasionally we added Telazol (1.5 mg/kg) to the mixture (Ryan et al. 2009; McGee-Lawrence et al. 2015). We transported cubs to a climate-controlled room for observations and morphological measurements, including cub BM (kg), age when ear canal and eyelids opened, and age when deciduous teeth erupted, as previously described in Bridges et al. (2002). We marked all cubs by painting their nails with color-coded nail polish to identify individuals within the same litter in subsequent sampling sessions. We obtained cub BM measurements using spring scales (1988–2012; Pesola Medio-Line, ± 3% precision) or a pediatric digital scale (2013–2016; Brecknell USA, Fairmont, Minnesota, MS-20 ± 10 g sensitivity). We estimated AGR of cubs as grams gained per day (g/day) and RGR as the AGR/BM × 100. In addition we collected information related to individual cubs and litters, such as date of birth, sex (male or female), litter size (single, twin, triplet), date of maternal resumption of food consumption (i.e., hibernation arousal), and date of den emergence. Direct visualization methods (1988–2015) and architectural design of the facilities limited our ability to document exact dates of den emergence in 52 litters. Therefore, we report litter den emergence dates for only six of 58 litters (including two litters observed via remote video monitoring, season 2016).

We used bilinear spline mixed growth modeling (BSMGM) with a transition point (i.e., knot) estimate to explore whether BM, AGR, or RGR, had any association with explanatory factors such as cub age, sex, and litter size. We generated BSMGMs for each morphological variable using all possible additive combinations of explanatory factors. In addition, we used linear mixed modeling (LMM) techniques to explore whether morphological response variables, such as opening of ear canals and eyelids, and age at eruption of deciduous teeth, had any association with explanatory factors such as cub age, sex, and litter size. We used litter and cubs as random effects to account for repeated measures of individual cubs and within litters (i.e., individual mothers). We generated LMMs for each morphological variable using all possible additive combinations of explanatory factors and two-way interactions, when possible. We performed model selection using the Akaike information criterion (AIC) and considered models as competing if $\Delta AIC \leq 2$. We obtained all estimates using the restricted maximum likelihood (REML) procedure from the top LMM; values are expressed as means ± standard errors, unless otherwise noted. In addition, we used a one-way analysis of variance (ANOVA) to determine differences in timing when mothers resumed food consumption post-hibernation. We implemented BSMGM and LMM techniques in RStudio software ([BLMM, nlme package V 3.1-140; LMM, lme4 package V 1.1-13]; version 1.0.463, RStudio Inc.).

Results

We compared four possible BSMGMs to describe BM of cubs from birth until approximately 14 weeks of age. The additive model including litter size and age best explained patterns of BM in cubs with no competing models (Table 1). Overall, newborns exhibited an average BM of 0.44 ± 0.08 kg that increased on average over 9-fold to 4.08 ± 0.11 kg by 14 weeks of age (Fig. 1A). Cubs born in twin litters tended to display greater

Table 1.—Summary of top three models using bilinear spline mixed growth modeling (BSMGM) and linear mixed modeling (LMM) to describe body mass (BM, kg), absolute growth rates (AGR, g/day), relative growth rates (RGR, %), and postnatal organ development (i.e., ear, eye, deciduous teeth) of American black bear (*Ursus americanus*) cubs from birth until around 14 weeks of age. Model variables include: age, litter size (single, twin, or triplet), sex (male or female), a random effect for repeated measures on cubs (1|cubs), and a random effect for repeated measures within litters (1|litter). Additive models are represented with a plus sign (+) and interaction models with an asterisk (*). ΔAIC: difference in Akaike information criterion between focal and top model; Log(l): maximized log likelihood; K: number of estimable parameters; w_i: Akaike weights.

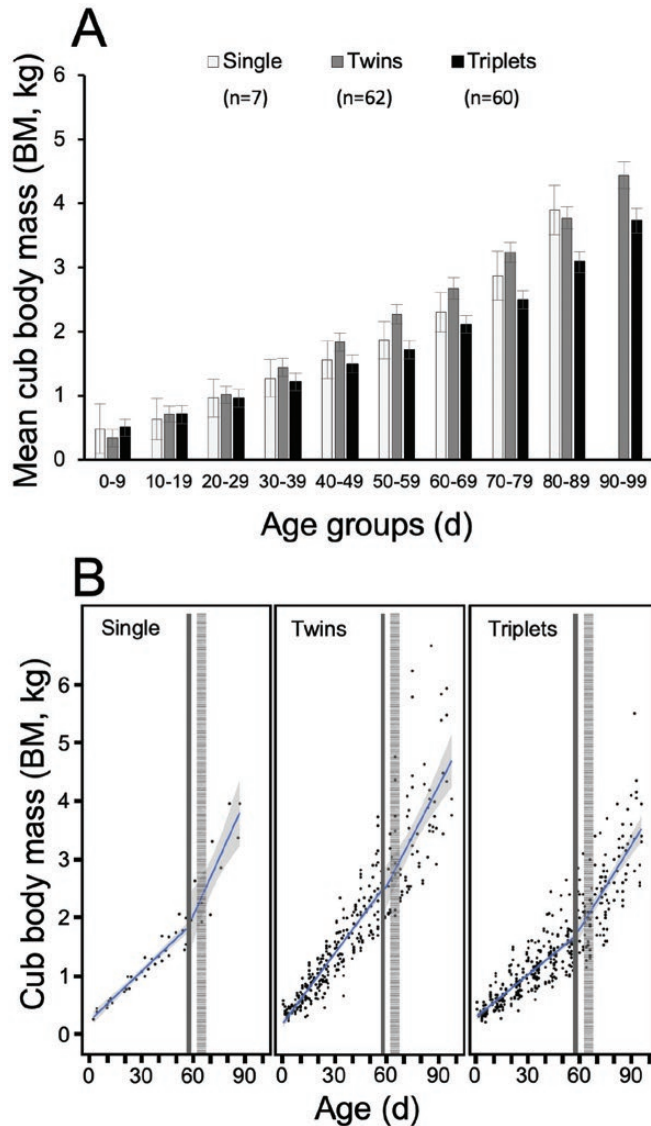| Model definition	ΔAIC	Log(l)	K	w_i
Cub body mass (BM, kg)				
(1|cub) + spline age + litter size	0	−5,355.6	5	0.9730
(1|cub) + spline age + litter size + sex	7.86	−5,353.6	6	0.0191
(1|cub) + spline age + sex	9.71	−5,354.7	5	0.0076
Cub absolute growth rates (AGR, g/day)				
(1|cub) + spline age 57 + litter size	0	109.3	4	0.9734
(1|cub) + spline age 57 + litter size + sex	7.2	111.7	5	0.0266
(1|cub) + spline age 57	21.9	93.4	3	0.0010
Cub relative growth rates (RGR, %)				
(1|cub) + (1|litter) + age * litter size	0	−1,175.9	29	0.9996
(1|cub) + (1|litter) + age + litter size	16.4	−1,999	13	0.0003
(1|cub) + (1|litter) + age + sex + litter size	18.4	−1,199	16	0.0001
Cub postnatal organ development (ear, eye, and teeth)				
(1|litter) + organ type * litter size	0	−486.4	10	0.5660
(1|litter) + organ type + litter size	2.5	−491.6	7	0.1621
(1|litter) + organ type	2.7	−493.8	4	0.1467

Fig. 1.—Trends in body mass (BM, kg) of American black bear (*Ursus americanus*) cubs from birth until approximately 14 weeks of age. (A) Mean BM of cubs summarized at 10-day intervals (error bars are 95% *CI*s). (B) Bilinear spline mixed growth models (BSMGMs) of trends in BM separated by litter sizes (single, twins, and triplets). Black dots represent repeated measures of individual cubs, linear trends are shown by lines with 95% *CI*s (gray shaded areas around the line). Vertical bars represent age at growth transition estimate (dark gray bar; bar width = *SE*) from top BSMGM: (1|cub) + spline age + litter size ($w_i = 0.973$), and emergence of cubs from dens (striped bar; bar width = *SE*; only six of 58 litters). We did not have data points from single cubs after 90 days of age.

Fig. 2.—Absolute growth rates (AGR, g/day) of American black bear (*Ursus americanus*) cubs from birth until approximately 14 weeks of age. (A) Mean AGR of cubs summarized at 10-day intervals (error bars are *SE*). (B) Bilinear spline mixed growth models (BSMGMs) of trends in AGR separated by litter sizes (single, twins, and triplets). Black dots represent repeated measures of individual cubs, linear trends are shown by lines with 95% *CI*s (gray shaded areas around the line). Vertical bars represent age at growth transition point (black bar) from top BSMGM: (1|cub) + spline age 57 + litter size ($w_i = 0.973$), and emergence of cubs from dens (striped bar; bar width = *SE*; only six of 58 litters). We did not have data points from single cubs after 90 days of age.

average BM than litters of singles or triplets during the span of this study (Figs. 1A and 1B). The BSMGM estimated a transition point at age 57.2 ± 0.63 days, at which point BM of cubs began to increase faster overall (Fig. 1B). BM differences were the largest at the transition age of 57.2 ± 0.63 days, when cubs from twin litters weighed on average 0.41 and 0.56 kg more than cubs from single and triplet litters, respectively. Thereafter (58–100 days old), cubs from litters of singles reached a similar average BM as twins, whereas triplets continued to experience
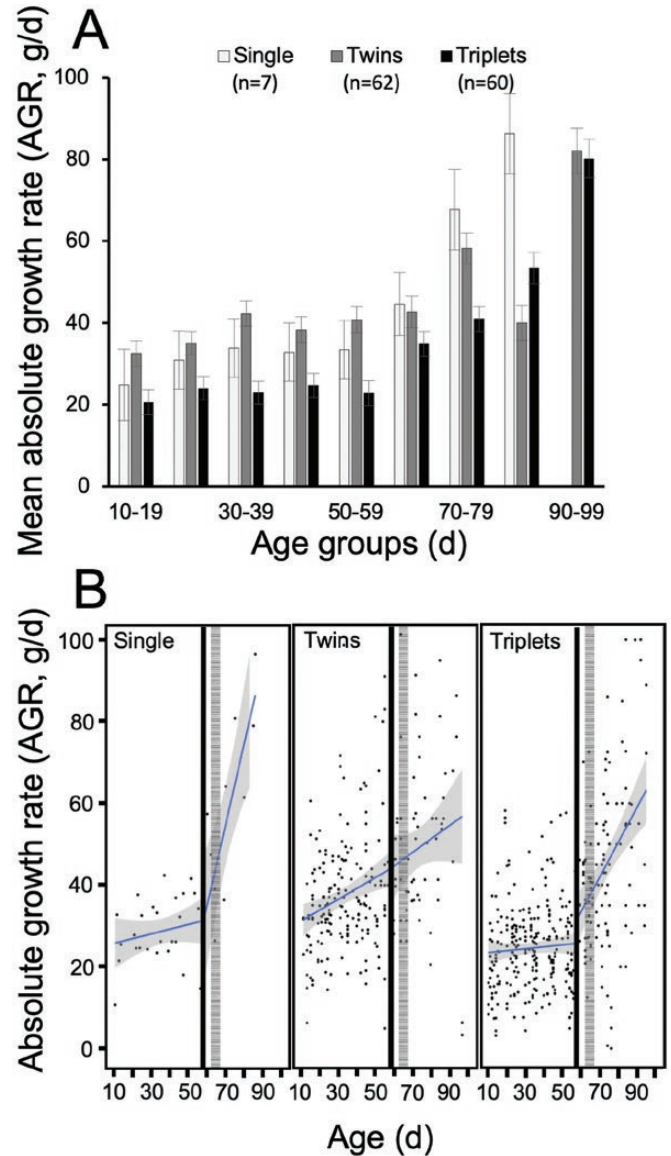
lower average BM than cubs from twin litters (Fig. 1A). Litters of twins displayed greater growth rates than litters of singles and triplets by 17.4 ± 7.1 g/day (Figs. 1A and 2B). Litters of twins had a high positive correlation (0.924) between growth rates and BM from birth until day 57.2. Twins experienced the lowest difference in growth rate slopes before and after the age of 57.2 days, whereas singles and triplets displayed dramatic increases in growth rate slopes (Fig. 1B).

We compared four models of cub AGR from birth until approximately 14 weeks of age. The additive BSMGM of age and litter size best explained patterns in AGR with no competing models (Table 1). Overall, cubs displayed two different patterns in rate of AGR, where cubs gained 30.11 ± 1 g/day from birth until 57.2 days of age, and thereafter (50–100 days old), cubs almost doubled AGR (55.3 ± 2.3 g/day; Figs. 2A and 2B). Twins experienced higher average AGR (37.8 ± 1.8 g/day) than single (31.1 ± 1.7 g/day) and triplet (22.9 ± 0.7 g/day) cubs from birth until 57.2 days of age (Fig. 2A). However, differences in AGR by litter size decreased after 57.2 days of age, as single cubs (66.2 ± 36.2 g/day) surpassed AGR of twins (55.7 ± 38.6 g/day), whereas triplets (52.3 ± 40.2 g/day) exhibited similar AGR rates as twins (Fig. 2B). Litters of twins experienced a gradual increase in AGR by 1.1 ± 1 g/day from birth until day 57.2. In contrast, singles and triplets maintained somewhat constant AGR during this period (Fig. 2B).

We performed a post hoc analysis to explore differences in AGR among siblings (e.g., within-litter variation of twins and triplets) using a nested (i.e., hierarchical) statistical model that included individual cubs nested within a litter, mother, cub age, litter size, and the interaction between cub age and litter size. This model suggested that siblings within litters did not experience different AGR ($F_{66,644} = 0.954$, $P = 0.579$). However, there were significant differences in AGR of cubs across mothers ($F_{50,644} = 5.12$, $P < 0.001$) and litter sizes, as twins experienced higher AGR than triplets ($F_{1,644} = 14.16$, $P = 0.0002$).

We attempted to fit BSMGMs to RGR, but were unable to achieve model convergence; therefore, we compared 11 possible LMMs to describe the RGR from birth until approximately 14 weeks of age. The interaction of cub age and litter size best explained RGR of cubs with no competing models (Table 1). In general, higher RGR was observed from birth until 39 days of age, when cubs experienced RGR > 3.5% (e.g., Fig. 3A). Triplets exhibited the lowest RGR, at 0.85% lower than cubs from single and twin litters. RGR continued to decline for all litter sizes until maternal food consumption was resumed (Fig. 3B). However, after den emergence (see below), single cubs reached the largest RGR during this latter slow growth phase (3.49 ± 0.82%), followed by triplets and twin cubs, at 2.19 ± 0.23% and 2.04 ± 0.29%, respectively (Figs. 3A and 3B).

We performed a post hoc analysis to explore differences in RGR between siblings (e.g., within-litter variation of twins and triplets) using a nested (i.e., hierarchical) statistical model by nesting individual cubs within a litter, and including fixed effects such as, mother, cub age, litter size, and the interaction between cub age and litter size. This model suggested that siblings within their litters did not experience different RGR ($F_{66,644} = 0.696$, $P = 0.964$). However, there were significant differences in cub RGR across mothers ($F_{50,644} = 3.03$, $P < 0.001$) and litter sizes, where of twins experienced higher RGR than triplets ($F_{1,644} = 9.49$, $P = 0.0022$).

Opening of ear canal and eyelids was evident by direct observation of the ear canal and eyelid separation (Figs. 4A and 4B; Supplementary Data SD1). The iris of cubs retained a
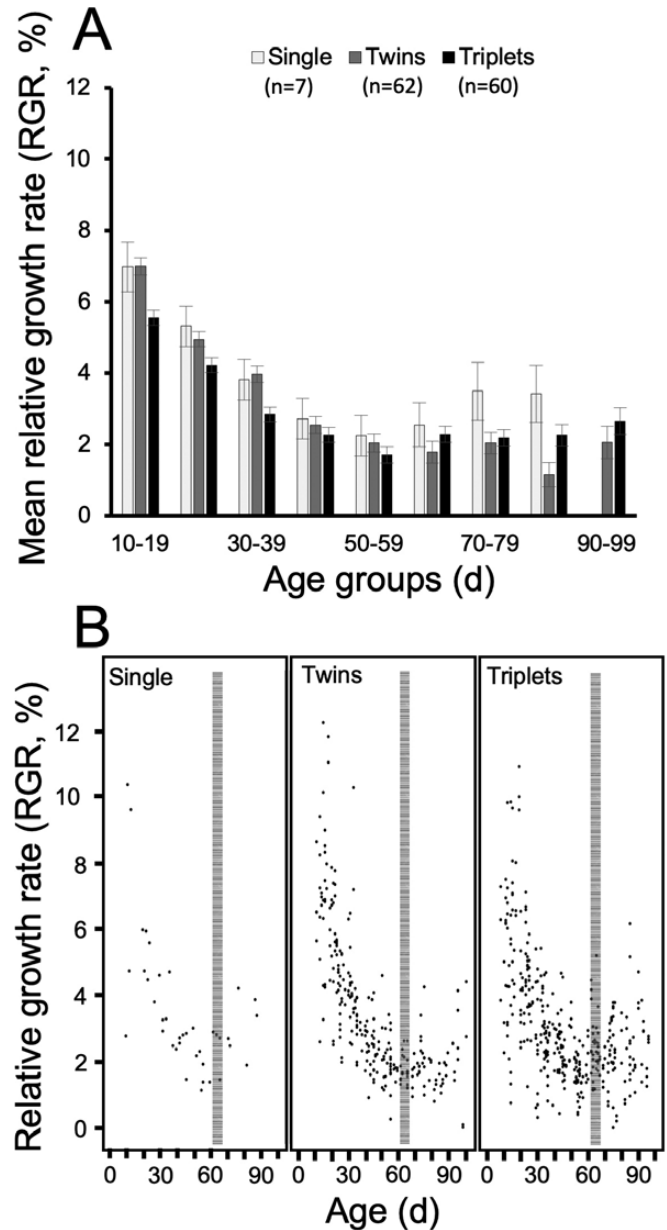

Fig. 3.—Relative growth rates (RGR, %) of American black bear (*Ursus americanus*) cubs from birth until approximately 14 weeks of age. (A) Mean RGR of cubs summarized at 10-day intervals. Estimates are from linear mixed modeling (LMM): (1|cub) + (1|litter) + age * litter size ($w_i = 0.999$, error bars are *SE*). (B) Distribution of RGR of cubs. Bilinear spline models did not converge; thus, we could not generate trend lines. Black dots represent repeated measures of individual cubs. Vertical stripped bars represent emergence of cubs from dens (bar width = *SE*; only six of 58 litters). We did not have data points from single cubs after 90 days of age.

bluish coloration throughout the study (Supplementary Data SD1). The progression of teeth eruption started with deciduous canines, followed by deciduous incisors, and molars (Fig. 4C). We compared six models to describe timing of the opening of ear canals and eyelids, and eruption of teeth. The interaction of organ type (e.g., ear, eye, and teeth) and litter size best explained the timing of postnatal development of assessed organs
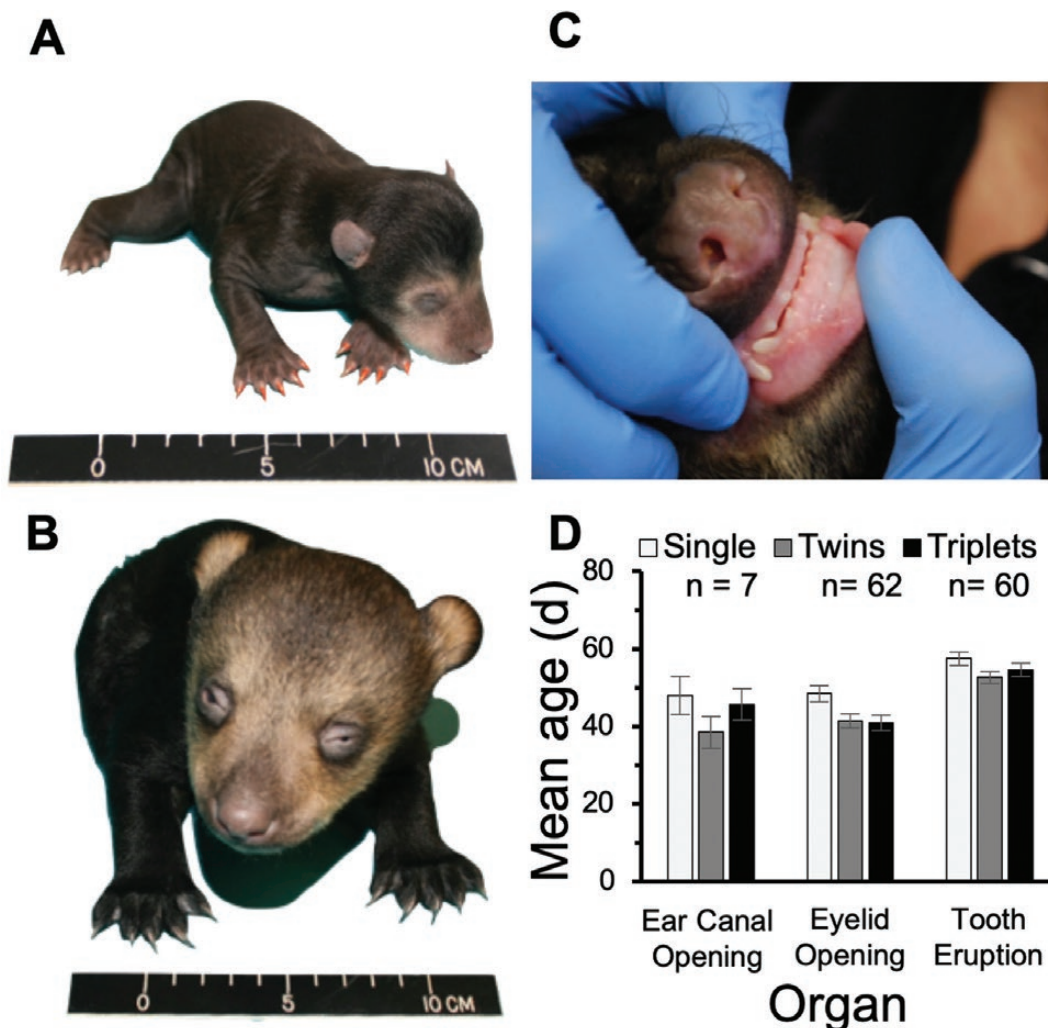
Fig. 4.—Timing of postnatal development of ears, eyes, and deciduous teeth of American black bear (*Ursus americanus*) cubs. (A) 5-day-old cub with ear canal and eye lids closed; (B) 39-day-old cub starting to show separation of eyelids (e.g., eyelid opening); (C) 50-day-old cub experiencing deciduous teeth eruption, canines emerged before incisors; (D) average age when cubs display opening of ear canals and eyelids, and deciduous tooth eruption, estimates are from top statistical model: (1|litter) + organ type * litter size (w_i = 0.566, error bars are *SE*).

displayed by cubs with no competing models (Table 1). Cubs typically opened their ears and eyes simultaneously at 44.07 ± 1.84 and 44.63 ± 1.57 days of age, respectively, whereas deciduous teeth erupted approximately 10 days later (54.9 ± 1.62 days of age; Fig. 4D). On average, twins and triplets experienced ear canal opening 5.8 days earlier than single cubs (Fig. 4D). Twins and triplets also displayed eyelid opening and deciduous teeth eruption 7.2 and 3.9 days earlier, respectively, than single cubs (Fig. 4D).

We determined the onset of maternal food consumption post-hibernation in 51 adult female bears. Seven adult females and their litters were released into the wild before the onset of food consumption. Regardless of litter size, mothers resumed food consumption when cubs were 58.2 ± 1.8 days old. Overall, mothers resumed food consumption regardless of litter size (median, 95% *CI*s; singles: 26 March [15 March, 7 April]; twins: 30 March [27 March, 2 April]; triplets: 1 April [28 March, 2 April]; $F_{2,48}$ = 0.3575, P = 0.701), or irrespective of cub age (single: 53.8 ± 5.7 days, twins: 58.4 ± 2.4 days, triplets:

59.1 ± 2.9 days; $F_{2,48}$ = 0.3535, P = 0.704). Due to limitations of data collection methods from 1988 to 2015, the age of cubs at den emergence could only be determined for six of 58 litters (including two litters observed via remote video monitoring, season 2016). Overall, cubs emerged at 65.3 ± 3.8 days of age and 8.5 ± 5.7 days after their mothers resumed food consumption (Figs. 1B and 2B; Supplementary Data SD1).

DISCUSSION

Postnatal development of cubs aligned with the life history of black bears. First, cubs are born very small relative to mother's BM and underdeveloped (Case 1978; Oftedal et al. 1993). Second, cubs experience higher RGR during their first 40 days of life than at older ages. Third, sensory organs, such as eyes and ears, and eruption of deciduous teeth achieve full development before emergence from dens. Fourth, black bears display maternal trade-offs with litter size, as cubs born in triplet litters gained less absolute and relative mass per day during

the hibernating period, but this trend was partially over-turned after the maternal parent resumed food consumption post-hibernation.

Cub age and litter size, independent of sex, were consistently the best describers of development of black bear cubs in our models. Litter size also influences offspring growth in other eutherian species. Offspring of desert wood rats (*Neotoma lepida*) and European wild rabbits (*Oryctolagus cuniculus*) exhibit lower BM as litter sizes increase (Myers and Poole 1963; Cameron 1973). This effect is likely related to nutritional resources provided by the maternal parent through milk. Milk quality changes very little during hibernation in black bears (Oftedal et al. 1993). However, as litter size increases and more cubs compete for similar milk volumes, AGR and RGR of triplets are negatively affected, as reflected in lower net cub BM. Such effects have been previously suggested for brown (*Ursus arctos*) and polar bears (*Ursus maritimus*—Robbins et al. 2012).

Single cubs also tended to show slightly lower BM and AGR than twins, especially before maternal arousal from hibernation, but that trend was substantially reduced by compensatory growth after the maternal parent resumed food consumption post-hibernation. Indeed, RGR of single cubs increased with age post-hibernation. However, that is not the case in captive Japanese black bear cubs (*Ursus thibetanus japonicus*), where cubs born in litters of singles exhibit greater AGR than cubs born in litters of twins (32.7 versus 19.8 g/day, respectively), reflected in greater BM of single cubs (Iibuchi et al. 2009). It is possible that body condition and age of black bear females producing single cubs are lower than those producing twins (Bridges et al. 2011; Mesa-Cruz 2018). Furthermore, we found significant differences in AGR and RGR of cubs across maternal parents producing twins and triplets. Hence, single and triplet cubs might be exposed to lower milk quality, or lower volumes, than cubs born in litters of twins, thereby limiting single cubs in achieving equal or greater AGR or similar times for organ development than twins. Another alternative is that single cubs exhibit lower AGR than twins or some triplets because they do not stimulate maternal milk production sufficiently, as shown in rats (*Rattus norvegicus*—Russell 1980). Single cubs may lack behavioral sibling "cooperation" to increase milk consumption due to sibling interactions that stimulate teat access (Hudson and Trillmich 2008). The most common litter size in free-ranging black bears is two, with averages ranging from 1.95 to 2.4 cubs (Bridges et al. 2011; Baruch-Mordo et al. 2014; Gray et al. 2016), which coincides with our results supporting better performance of twins in terms of higher BM, AGR, and smoother transitions in BM and AGR between hibernation and resumption of maternal food consumption compared to those of single and triplet litter sizes.

Absolute growth rate of cubs during the hibernating periods in our study was on average ~33% lower than previously reported for long-term captive black bears producing twin litters at the Bear Research Facility at Washington State University (Farley and Robbins 1995). Factors such as nutrient content of milk and maternal body condition are associated with growth rates of brown bear cubs (Robbins et al. 2012). Thus, long-term

captive females in the Farley and Robbins (1995) study may have exhibited higher body conditions resulting in better milk quality for cubs than our temporarily held wild females for which we mimicked conditions normally experienced by free-ranging wild black bears. In addition, our post hoc analyses revealed significant differences across mothers in relation to AGR and RGR of cubs, which could be influenced by differences in maternal body condition and subsequent milk quality.

Maternal energy intake can directly impact AGR of offspring in mammals. For instance, lactating cheetah cubs (*Acinonyx jubatus*) experience increasing AGR as the maternal parent increases food consumption per day (Laurenson 1995). In our study, adult female bears aroused from hibernation and resumed food consumption at similar timing as previously reported in the wild (Johnson and Pelton 1980; Godfrey 1996), when cubs were ~8 weeks old. At this stage, nutrient content of milk increases in black bears (Farley and Robbins 1995). This coincides closely with our statistical models that indicated BM and AGR of cubs experienced a growth rate transition, reflected as increased AGR, at nearly identical timing (57.2 ± 0.63 days old) as that of the maternal parent resuming food consumption post-hibernation (58.2 ± 1.8 days old).

We document that very young cubs experience higher RGR than they do at older ages and that RGR gradually decreases with age until around the time of emergence from dens. At older ages, the RGR trends reversed for singles and triplets, which exhibited an increase in RGR, further suggesting that cubs born in litters of singles, and to a lesser extent triplets, compensate for lower AGR experienced in early ages by displaying higher RGR than litters of twins in later ages. RGR of twins, conversely, continued to decline, but only slightly at older ages.

Altricial species experience postnatal development of sensory organs such as eyes and ears due to immaturity in organ organization and muscular and neural control (Van Cruchten et al. 2017). Black bears experience delayed timing of the opening of ear canals and eyelids, and in tooth eruption, compared to other carnivores at birth. For instance, spotted hyenas are born with a set of emerged teeth, eyes and ears open, and appear to be sensitive to sound stimuli, whereas some canids like coyotes (*Canis latrans*) undergo deciduous teeth eruption at ~10 days old, followed by eyelid opening ~5 days later (Pournelle 1965; Snow 1967; Bekoff and Jamieson 1975). However, fishers (*Martes pennanti*), a species also experiencing delayed implantation, show a relatively delayed postnatal development of deciduous teeth (~40 days old) and simultaneous opening of eyes and ears (~48 days old—Frost and Krohn 2005). Although domestic dogs and wolves (*Canis lupus lupus*) experience opening of eyes and ear canals around the same time (eyes ~13 and ears ~19 days old), both species display a 5- to 10-day delay in responding to visual and auditory stimuli (Bekoff and Jamieson 1975; Lord 2013). Despite the relative delay in postnatal eye and ear development in black bears (e.g., ~44 days of age), cubs have a ~21-day period to achieve complete functionality of these sensorial organs when they emerge from the den (~65 days of age) and they appear fully responsive to auditory and visual cues upon emergence.

Sexual dimorphism is evident in adult black bears (Bartareau et al. 2012; Pope et al. 2017). However, during the extent of our study, sex was not an important variable in postnatal development in black bear cubs, as previously noted (Godfrey 1996; Ryan 1997; Echols 2000; Bridges et al. 2002). Energy allocated to reproduction and access to food at specific life stages may be influencing mammalian sexual dimorphism (Ralls 1977; Johnson et al. 2017; Pope et al. 2017). It is likely that black bear cubs did not display morphological sex differences throughout our study because they were exposed to similar food resources and were sexually immature. Sexual dimorphism in black bears may begin as they reach sexual maturity (e.g., experience the effect of reproductive steroid hormones).

Assessing the impacts of maternal age, body condition, and milk quality on growth of cubs could explain the unaccounted variation in growth rates across litter sizes that we found. Our study was focused on cubs and litters, yet other factors, such as maternal effects and the environment, are likely to play a role in development and fitness (Lindström 1999). Nevertheless, we provide new knowledge on postnatal cub development that also is relevant to fostering orphan cubs to surrogate females (Carney and Vaughan 1987; Benson and Chamberlain 2006), including the importance of taking litter size into account.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Postnatal morphological changes in an American black bear (*Ursus americanus*) born in a litter of triplets. This cub showed eyelid and ear opening at 39 days old and den emergence was observed after 63 days of age.

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