Birth Timing for Mountain Lions (*Puma concolor*); Testing the Prey Availability Hypothesis

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Abstract

We investigated potential advantages in birth timing for mountain lion (*Puma concolor*) cubs. We examined cub body mass, survival, and age of natal dispersal in relation to specific timing of birth. We also investigated the role of maternal age relative to timing of births. We captured mountain lion cubs while in the natal den to determine birth date, which allowed for precise estimates of the population birth pulse and age of natal dispersal. A birth pulse occurred during June–August. Body mass of cubs was related to litter size and timing of birth; heaviest cubs occurred in litters of 2, and those born after 1 July. Cubs born within pulse months exhibited similar survival to those born out of the pulse. We found that cubs born April–June dispersed at younger ages than those born after 1 July. There was less variation in birth timing for 1st litters of females than older females. We hypothesize that cubs born after the peak in births of neonate prey are advantaged by the abundance of vulnerable prey and those cubs and mothers realize an evolutionary advantage.

Introduction

Pattern of births for mountain lions (*Puma concolor*) is better characterized as a pulse over several months [1] than a sudden peak, characteristic of many ungulate populations [2]. Studies of mountain lions over numerous years have documented litters born in every month of the year [3]; however, the majority of births occur from June through October in North America [4]. Logan and Sweanor [1] hypothesized that because the pattern coincided with availability of young ungulates, that cubs born within the pulse had a greater chance of survival. However, Laundre and Hernández [4] tested this prediction and concluded that there were no differences in survival related to timing of birth.

Mountain lion cubs weigh about 400–500 g at birth [3]. Males typically outweigh females throughout their lives [1]. Litter size ranges from 2 to 4 cubs [1]. Despite existing information on reproductive ecology of mountain lions, the extent to which number of cubs in a litter influences birth weights is unknown.

No study has sought to elucidate the age of dispersal in relation to the timing of birth, although geographic patterns of juvenile dispersal in mountain lions are adequately documented [5–8]. Juvenile mountain lions disperse about 1 month after becoming independent of their mothers [7,8], and both sexes become independent at similar ages [1]. Males disperse farther than females [1,8,9].

The birth pulse in mountain lions has been previously investigated by summing all litters born regardless of maternal age or experience [1,4]. Parturitions have been documented an average of 3 months (mean birth interval - mean age of independence [17 - 13.7 = 3.3 months]) following departure of successful litters [1]. Mean gestation length for mountain lions is 3 months [1], thus subsequent litters begin close to departure of previous successful litters. Females that lost litters before cubs reached independence produced litters from 4–10 months later [1], suggesting a breeding lapse of 1–7 months following unsuccessful litters. Introduction of these variables into the birthing schedule suggests that birth timing through the year will become less predictable as females age.

Our objective was to determine if differences occur in body mass at 1 week of age, survival to 1 year, and age of natal dispersal for mountain lions with respect to timing of birth. If timing of births is related to prey availability [1], then we expect a birth pulse (highest frequency of litters born) coincident with availability of neonate ungulates. We expect heavier cubs and higher survival for those cubs born within the pulse. However, natal dispersal is thought to be related to timing of the mother’s estrous cycle [1]; thus, we predict no relation of timing of birth to age of dispersal. We predict that birth timing in younger females or first litters will be more precise than birth timing in older females of subsequent litters, because timing of subsequent litters depends on completion (i.e., mortality, independence) of the previous litter.

Results

Birth pulse

We captured 42 litters from 2005 to 2009. We documented litters born in every month; however, frequency of litters produced was not uniformly distributed through the year (Fig. 1, \[X^2 = 25.43, P<0.01\]). Months with higher than expected births included the period June–August; thus, we defined our birth pulse as occurring from 1 June to 31 August. We further delineated the year as spring (April–May), early pulse (June), middle pulse (July),
late pulse (August), autumn (September–October) and winter (November–March, Table 1).

Cub body mass

We used data for 74 (34M, 40F) cubs originally captured in natal dens, at ages ranging from 1–4 weeks, to estimate influence of birth timing on weight at 1 week of age. We found few cubs born during winter ($n=4$), so we censored those animals from analyses regarding cub weights. We found that timing of birth ($F_{1,61} = 3.850$, 2-sided $P=0.016$) and litter size ($F_{1,61} = 0.056$) influenced body mass of cubs at 1 week of age, whereas sex ($F_{1,61} = 0.624$, 2-sided $P=0.866$) had no effect. Mean body mass for male ($n=34$) and female ($n=40$) cubs at 1 week of age was 1.162 kg ± 0.112 (SE) and 1.102 kg ± 0.095, respectively.

There was a declining trend in body mass as litter size increased. Mean body mass of cubs in 2-, 3-, and 4-cub litters were 1.114 kg ± 0.135, 1.055 kg ± 0.091, and 0.912 kg ± 0.089, respectively. Cubs born in litters of 2 were 22% larger at 1 week of age than cubs in litters of 4 (Extra sums-of-squares $F_{1,60} = 3.308$, 2-sided $P=0.146$).

After accounting for sex and litter size, mean mass of cubs born within the birth pulse (June–August) was similar to cubs born outside the birth pulse (Extra sums-of-squares $F_{1,61} = 2.40$, 2-sided $P=1.0$); however, a trend existed, with cubs born in spring lightest and body mass of cubs increasing through autumn (Extra-sums-of-squares $F_{1,60} = 3.98$, 2-sided $P=0.102$). Cubs born during spring and early pulse averaged 230 g ± 72 (SE) lighter in mass than cubs born during the middle pulse through autumn (Extra sums-of-squares $F_{1,60} = 12.302$, 2-sided $P=0.002$).

When we reevaluated birth timing relative to ungulate birth periods, we found a strong relationship to timing of birth and weight at 1-week of age ($F_{1,61} = 4.310$, 2-sided $P=0.004$). Cubs born before the ungulate birth peak ($n=10$) weighed 969 g (mean) ± 96 (SE) whereas cubs born coincident with ungulate birth periods and the number of documented mountain lion (Puma concolor) cubs born during each period in the Black Hills, South Dakota, USA.

| Table 1. Environmental characteristics exhibited during annual periods and the number of documented mountain lion (Puma concolor) cubs born during each period in the Black Hills, South Dakota, USA. |

| Period       | Months             | No. cubs | Environmental Characteristics |
|--------------|--------------------|----------|-------------------------------|
| Spring       | April–May          | 12       | Variable snowfall and cold temperatures; adult-sized ungulates with relatively lowest availability |
| Early        | June               | 13       | Warm days, cool nights; neonate ungulates present, but in “hider” phase resulting in low availability |
| Middle       | July               | 15       | Warm days, warm nights; neonate ungulates present and in “flee” phase resulting in highest availability |
| Late         | August             | 16       | Warm days, warm nights; adult and juvenile ungulates present resulting in high availability |
| Autumn       | September–October  | 13       | Cool days; cool nights; adult and larger juvenile ungulates present resulting in high availability |
| Winter       | November–March     | 4        | Snow; cold days, cold nights; adult-sized ungulates available, post-hunting season results in declining availability and harsh environmental conditions. |

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peaks and 30 days following \( n = 20 \) weighed 934\( \pm \)109 g. Those
cubs born 30–60 days after the ungulate birth peak \( n = 31 \)
weighed 1,174\( \pm \)100 g, whereas cubs born >60 days after the
ungulate birth peak \( n = 13 \) weighed 1172\( \pm \)102 g.

**Cub survival**

No difference was documented in sex-specific survival (Male,
\( n = 42 \), \( S_i = 0.55 \), SE = 0.08; Female, \( n = 36 \), \( S_i = 0.58 \), SE = 0.08;
2-sample \( t_{56} = 0.264 \), 2-sided \( P > 0.50 \)); therefore, we pooled sexes
in subsequent analyses. We found no support (evidenced by
overlap in confidence intervals) for our hypothesis that survival
was greater for cubs born within the birth pulse \( n = 47 \), \( S_i = 0.55 \),
95% C.I. = 0.41–0.69) compared to those born outside the pulse
\( n = 31 \), \( S_i = 0.58 \), 95% C.I. = 0.41–0.74). However, we found an
increasing trend in survival relative to prey abundance and
vulnerability (Fig. 2). Cubs born before the ungulate birth period
or <30 days afterward (April–June, \( n = 30 \), \( S_i = 0.50 \), SE = 0.09)
had mean survival rates lower than those born 30–60 days after the
ungulate birth peak, but before winter (Jul–Sep, \( n = 32 \),
\( S_i = 0.53 \), SE = 0.09; Oct–Nov, \( n = 12 \), \( S_i = 0.67 \), SE = 0.14).

**Dispersal age**

We obtained dispersal ages for 22 juvenile mountain lions (14M,
8F). Male mountain lions dispersed at a mean age of 14.7
months\( \pm \)0.84 (SE) and females dispersed at 15.3\( \pm \)1.15 months.
While accounting for variation in timing of birth, we found no sex-
related differences in natal dispersal age (\( F_{1,20} = 1.420 \), 2-sided
\( P = 0.50 \)). There was evidence that cubs born during the birth
pulse dispersed when 2.5 months younger (\( \pm \)1.3 SE) than those
born outside the pulse (Extra sums-of-squares \( F_{1,17} = 3.92 \), 2-sided
\( P = 0.120 \). However, there was stronger evidence (Extra sums-of-
squares \( F_{1,15} = 8.971 \), 2-sided \( P = 0.018 \) that cubs born during spring, early-, and mid-pulse (1 April–30 July, \( n = 9 \) dispersed
4\( \pm \)1.3 months younger than cubs born in the last month of the
birth pulse and winter (1 August–31 January, \( n = 13 \). When we
excluded cubs born in July (i.e., middle month of pulse), there was
strong evidence of a mean 4\( \pm \)1.5 month difference in dispersal ages (Extra sums-of-squares \( F_{1,76} = 7.405 \), 2-sided \( P = 0.032 \).

All cubs that were born in early or mid-pulse dispersed during the
summer (June–August) or autumn (September–November)
after attaining an age of 1-year. All cubs born late in the birth
pulse dispersed during winter (December–February) or spring
(March–May) after becoming 1-year of age.

**Mother and first litters**

We documented 31 litters that were born to females that we had
recorded evidence of previous nursing [25]. Birth timing period
was narrower for females that had not previously nursed cubs
\( n = 11 \) and occurred mostly in July \( n = 6 \), and few occurred in
June or August \( n = 3 \), Fig. 3). Birth timing for females that had
previous litters \( n = 20 \) were dispersed throughout the year, while
still exhibiting a pulse in June–August (Fig. 3).

**Discussion**

Logan and Sweanor [1] hypothesized that cub survival might be
higher for cubs born within the birth pulse, than those born
outside the pulse, because the pulse in their central New Mexico
study area generally coincided with ungulate birthing periods.
Laundré and Hernández [4] summarized available data on birth

![Figure 2. Mountain lion (Puma concolor) cub survival in relation to neonate ungulate presence and age in the Black Hills, South Dakota, USA.](doi:10.1371/journal.pone.0044625.g002)
Figure 3. Frequency of births by month for first and non-first litters of adult female mountain lions (Puma concolor) in the Black Hills, South Dakota, USA.

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Birth Timing for Mountain Lions

Our study area

Study area

Materials and Methods

Ethics Statement

Our capture and handling procedures followed guidelines of the American Society of Mammalogists [19] and were approved by the Institutional Animal Care and Use Committee (Approval No. 07-A024) at South Dakota State University.
and bighorn sheep as well as domestic livestock species. No other large carnivores were present in this system. Bobcat (*Lynx rufus*) and coyote (*Canis latrans*) are mesocarnivores that occur sympatrically with mountain lions.

**Field Methods.**—We used foot-snare [22], trained hounds [23], and cage-traps [24] to capture adult female (>3 yrs) mountain lions throughout the year. We used a mixture of telazol and xylazine and administered them at recommended dosages [25]. We aged mountain lions by tooth wear and pelage characteristics and noted previous reproductive activity [26]. We outfitted each mountain lion with a radiocollar (MOD-500, Telonics, Mesa, Arizona, USA) and relocated radiocollared mountain lions 1-time per week by using homing-telemetry techniques from a fixed-wing aircraft [27]. We used homing techniques while on foot for females where ≥2 aerial telemetry locations were within 500 m of each other over a 3-week period. Closer investigations normally revealed adult female mountain lions located within nursery dens [1,28] with newly-born cubs. We captured all cubs by hand without chemical immobilization, often while the mother was away from the site [1]. We determined sex and age of cubs by tooth eruption and appearance of eyes (e.g., open or closed; [29]). Based on tooth eruption patterns and relatively young age of cubs, birth dates were within a few days to <2 weeks of the true birth date. At the time of capture, we gave each cub a unique tattoo and some were radiocollared with small, expandable collars (MOD-125, Telonics).

When cubs were approximately 9 months old, we recaptured them by using the same techniques as those used for adult mountain lions and refitted cubs with larger radiocollars (MOD-500, Telonics) or global positioning system (GPS) collars (single D-cell, Northstar, Virginia, USA). We used fixed-wing aircraft or satellite-telemetry to relocate subadults and mothers. When a juvenile mountain lion left the natal area, we recorded the mid-date between the last location in the natal area and the first location outside the natal area. In some cases, dispersing mountain lions made exploratory movements and returned to the natal area and subsequently left again or established a home area at least partly overlapping the natal area (e.g., female philopatry). We recorded dispersal age as the mid-date the juvenile made the initial exploratory movement, regardless of subsequent return to the natal area. If an animal was not located outside the natal area until the animal became 3 years old, we censored the animal from analyses. These animals were censored because exploratory movements can be of short duration [30,31] and frequency of exploratory movements might not have detected exploratory movements.

We plotted all birth dates and defined the birth pulse as the period where ≥40% of births occurred and number of births were higher than expected [1,4]. We delineated the birth within or outside birth pulse months and also as early (1st one-third), middle (central one-third), late (final one-third), and outside pulse. In addition, we delineated cub births as before ungulate birth peak (before 1 June), before neonate ungulates switch predator avoidance strategies (hiding vs. fleeing [11,14]; 1 June–23 June), <60 days after strategy switch (23 June–23 August), >60 days after strategy switch (23 August–23 October), and winter (December–February). In our study area, deer and elk dominate the diets of mountain lions (Smith and Jenks, South Dakota State University, *unpublished data*). The birth peak for male deer was 7–14 June [32], for white-tailed deer it was 7–17 June [33], and for elk it was 20 May–4 June (Schmitz 2010, South Dakota Game, Fish, and Parks, *unpublished data*).

**Analysis**

We used JMP 8.0 (SAS Institute, Cary, North Carolina, USA) statistical software to perform statistical analyses. We used chi-squared test for independence to determine if the monthly distribution of litters was uniform through the year [1,4]. We ran MANOVA to examine the influence of birth timing on body mass and age of dispersal of mountain lions, while accounting for other potential influences (i.e., sex, litter size, age at capture). We used extra sums-of-squares F-tests within a MANOVA framework to test for differences in birth timing, while accounting for differences in sex, litter size, and age at capture. We used a known-fates model in Program MARK [34–36] to estimate survival. We used a 2-sample t-test to determine if differences in survival occurred between male and female cubs, despite timing of birth. We ran Program MARK analyses with and without sex as a covariate to determine if sex was related to survival. We analyzed cub survival in 2 ways. First, we placed cubs in categories; within or outside of the birth pulse to replicate the analysis conducted by Laundre and Hernández [4]. Second, we delineated the birth pulse according to our description of the predator-avoidance strategy switch, which provided a more detailed examination.

To investigate the role of mother’s age on birth timing, we calculated the monthly frequency distribution of litters born by mother’s age (i.e., 3–4 yrs, 4–6 yrs, >6 yrs). We also calculated the monthly frequency distribution of litters born by litter sequence (i.e., 1st litter, >1st litter). We visually compared birth month frequencies by mother’s age and litter sequence.

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**Author Contributions**

Conceived and designed the experiments: BDJ JAJ. Performed the experiments: BDJ. Analyzed the data: BDJ. Contributed reagents/materials/analysis tools: BDJ. Wrote the paper: BDJ JAJ.

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