



Female-biased sexual size dimorphism: ontogeny, seasonality, and fecundity of the cliff chipmunk (*Tamias dorsalis*)

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Female-biased sexual dimorphism is uncommon in mammals and is usually attributed to increased fecundity of large females. Moreover, sexual dimorphism is usually described for adults, and the ontogeny of sex differences is poorly documented. We studied cliff chipmunks (*Tamias dorsalis*), a small mammal with female-biased sexual dimorphism, to describe development of sexual dimorphism in juveniles and to measure sexual dimorphism and seasonal body mass in adults. To test the fecundity hypothesis, we compared body mass of females to litter size and body mass of offspring. Juveniles were not sexually dimorphic at emergence from the nest and did not differ in body mass 2 months after emergence. Adult chipmunks maintained a relatively stable body mass in March–October with females consistently larger than males. Maternal mass did not have an effect on litter size or mass of juveniles. Because females were consistently larger than males, the ontogeny of sexual dimorphism may provide insights into selection pressures that lead to female-biased sexual dimorphism.

Key words: Arizona, body mass, cliff chipmunk, litter size, small mammal, *Tamias dorsalis*

Although males are generally larger than females in mammals (Eisenberg 1981), many counter examples exist (Ralls 1976). Female-biased sexual size dimorphism may result from selective pressures favoring larger females than males or favoring smaller size in males (Ralls 1976; Isaac 2005). Larger females may have increased survival and reproductive success compared to smaller females, leading to selection for female-biased size dimorphism (Schulte-Hostedde et al. 2002; Edelman and Koprowski 2006; Fokidis et al. 2007).

An oft-cited hypothesis to explain selection for large females is the fecundity hypothesis, which predicts that larger females produce more offspring than smaller females do. Evidence to support the fecundity hypothesis is found for lizards, insects, fishes, and anurans with female-biased sexual dimorphism (Fairbairn 1997). However, for mammals, the evidence is mixed. For example, larger female yellow-pine chipmunks (*Tamias amoenus*—Schulte-Hostedde et al. 2002) and Siberian flying squirrels (*Pteromys volans*—Selonen et al. 2013) produce larger litters than smaller females do. In contrast, body size of females and fecundity were only weakly correlated in a comparison of species within the rabbit genus *Sylvilagus* (Davis and Roth 2008). However, females experience many selection pressures, and fecundity may already be optimized

(Isaac 2005). Instead of simply producing more offspring, females with larger body mass may be in better body condition (e.g., greater fat reserves) or have a larger body size, thereby increasing reproductive success through provisions to young (Olsson and Shine 1997; Keech et al. 2000).

Most often, sexual dimorphism is described for adults (Bondrup-Nielsen and Ims 1990; Levenson 1990; Schulte-Hostedde et al. 2002). However, in some species, sexual dimorphism in body mass occurs before or soon after birth (Kovacs and Lavigne 1986; Wheelwright et al. 1994), whereas other species develop sexual dimorphism as animals approach sexual maturity (Festa-Bianchet et al. 1996; Funakoshi et al. 2010), and some species do not develop dimorphism until after the 1st reproductive event (Fokidis et al. 2007). In species with sexual dimorphism in body mass, tracking seasonal body mass changes of adults and juveniles can elucidate the ontogeny of sexual dimorphism in juveniles and generate insights into selective pressures for female-biased sexual dimorphism.

We studied cliff chipmunks (*Tamias dorsalis*), a species with female-biased body mass dimorphism (Levenson 1990; Hart 1992), to investigate the ontogeny of sexual dimorphism in juveniles and the effect of female body mass on fecundity. First, we hypothesized that juveniles are sexually dimorphic

at emergence. We predicted that females are larger than males at emergence because cliff chipmunks at our study site have a short time (≤ 4 months) to grow before winter hibernation and being sexually dimorphic at emergence alters the timing of growth for females compared to males. Second, we hypothesized that male and female cliff chipmunks show seasonal changes in body mass but females remain consistently larger. We predicted that all adults gain mass in fall before winter hibernation because cliff chipmunks are not known to larder hoard food (Hoffmeister 1956), but we predicted that females always are larger than males (i.e., no seasonal changes in sexual dimorphism). Finally, we hypothesized that body mass of females affects litter size and body mass of juveniles (Schulte-Hostedde et al. 2002; Selonen et al. 2013). Specifically, we predicted that litter size and body mass of juveniles are greater for larger females than for smaller females.

MATERIALS AND METHODS

Study area and species.—We studied cliff chipmunks in 200 ha of mixed-conifer forest at $> 3,000$ m elevation on Mt. Graham, an isolated 3,267-m peak in the Pinaleno Mountains, Graham County, Arizona ($32^{\circ}42'5.87''\text{N}$, $109^{\circ}52'18.87''\text{W}$). Dominant trees include Douglas fir (*Pseudotsuga menziesii*), southwestern white pine (*Pinus strobiformis*), and corkbark fir (*Abies lasiocarpa* var. *arizonica*), mixed with Engelmann spruce (*Picea engelmannii*), aspen (*Populus tremuloides*), and ponderosa pine (*Pinus ponderosa*—Sanderson and Koprowski 2009).

The cliff chipmunk is a granivorous rodent that ranges from Mexico to Utah, with populations located as far east as New Mexico and west into Nevada (Hart 1992). Although this species is considered semifossorial, the Mt. Graham population climbs trees to forage and often steals food cached by the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*—Edelman et al. 2005), nests in tree cavities, and uses tree cavities for maternal nests (Hoffmeister 1956; Kilanowski 2015). This species exhibits female-biased sexual size dimorphism across its range; females weigh more than males, and females are larger than males in all morphological measurements (Levenson 1990).

The cliff chipmunk reportedly hibernates from approximately November to March with some variation due to temperature and snowfall (Hoffmeister 1956; Hart 1992). On Mt. Graham, we observed cliff chipmunks out of the burrow during warm winter days (A. L. Kilanowski, pers. obs.); this population likely does not hibernate but enters torpor for short periods of time, similar to other chipmunk species at high elevation (Best et al. 1992; Sutton 1992, 1993). During torpor, cliff chipmunks can emerge to forage and maintain body mass during winter.

Cliff chipmunks exit torpor and begin breeding in April–May, depending on winter conditions (Hart 1992). On Mt. Graham, males possess scrotal testes from April to July, and litters are born as late as July (A. L. Kilanowski, pers. obs.). Females produce litters of 2–6 young, and reproductive success is highly

variable with some females producing no litters in a given year (Hart 1992). No evidence exists that female chipmunks in Arizona produce multiple litters within a single breeding season (Hart 1992), and juveniles do not reproduce until the next breeding season in the subsequent year (A. L. Kilanowski, pers. obs.).

Trapping.—From March to September 2013 and May to October 2014, we captured adults and juveniles ($7.62 \times 8.89 \times 22.86$ cm Large Folding Galvanized Sherman Traps; H.B. Sherman Traps, Tallahassee, Florida), affixed ear tags (Monel #1; National Band and Tag, Newport, Kentucky) and colored washers, and recorded body mass with a Pesola scale (± 1 g; Pesola AG, Schindellegi, Switzerland). We obtained body mass data for 1,120 captures (2013: $n = 308$; 2014: $n = 812$) of 257 unique individuals (2013: $n = 132$; 2014: $n = 125$). In 2013, we trapped 61 males (adult: $n = 51$; juvenile: $n = 10$) and 71 females (adult: $n = 58$; juvenile: $n = 13$). In 2014, we trapped 50 males (adult: $n = 47$; juvenile: $n = 3$) and 75 females (adult: $n = 65$; juvenile: $n = 10$).

Ontogeny of female-biased sexual dimorphism.—For all analyses, we pooled data from 2013 and 2014 because mean mass of chipmunks did not differ between years (Welch 2-sample t -test, $t_{243.33} = -0.21$, $P = 0.84$). To avoid pseudoreplication from multiple measurements on an individual, we calculated an arithmetic mean using measurements from all trapping events within the specified time period (month or year) for each unique individual before conducting t -tests. We did not recapture any juveniles after their 1st year; therefore, pooling data across years did not combine measures of individuals across life stages. Because data sets for adult males and females had unequal variances and were approximately normally distributed, we used all measurements from 2013 and 2014 to perform an unpaired Student's t -test with a Welch approximation to confirm that adult males and females in our population are sexually dimorphic (Sokal and Rohlf 1995; R package “stats”; R Core Team 2016).

To determine when sexual dimorphism occurs in juveniles, we examined data for 2 months after emergence from the nest. To determine when juveniles emerge, we radiocollared (SOM 2070; Wildlife Materials, Murphysboro, Illinois) 8 nursing females (2013: $n = 2$; 2014: $n = 6$) and observed maternal nests on multiple days (mean: 2.6 days; range: 1–6 days) at sunrise. Once we observed juveniles, we initiated trapping to obtain body mass of juveniles. We could not use calendar months because some litters emerged in June, whereas others emerged in July or August. Therefore, we considered 1 month after emergence as month 1, 2 months after emergence as month 2, and so on. For juvenile females, we have data for 4 months after emergence, and for juvenile males we have 2 months of data.

To determine when juveniles become sexually dimorphic after emergence, we used a generalized linear mixed model with fixed effects of sex (male or female), months after emergence (1st or 2nd), and the interaction between sex and month, with a random effect of individual (R package “nlme” and “car”). To determine the magnitude of the effect of sex and month on body mass, we calculated Cohen's D , and we estimated 95% confidence intervals using bootstrapping (R package “bootES”).

Because our data set on juveniles limited our model to 2 months after emergence, we used multiple *t*-test comparisons and a visual analysis of the data to determine when juveniles reached adult mass (knowing that adults are sexually dimorphic, this approach allows us to estimate when juveniles become sexually dimorphic). We used an unpaired Wilcoxon rank-sum test to compare body mass of male and female juveniles each month to mean body mass of female and male adults to determine how many months after emergence elapsed until juveniles reached adult mass (Sokal and Rohlf 1995; R package “stats”). Because body mass of adults changes over time, we calculated the arithmetic average of body mass for males or females for a single month to compare mass of juveniles to that of adults more accurately. For both male and female juveniles, the majority of individuals first emerged in July, so we compared body mass of adults in July to body mass of juveniles in month 1 (month 2 was compared to August, etc.).

Seasonal body mass.—To determine if adult females are consistently larger than adult males and to determine if body mass of adults changes seasonally, we used a generalized linear mixed model with sex (male or female), month (March–October), and their interaction as fixed effects, and individual as a random effect (Zuur et al. 2009; R package “nlme” and “car”). We also included reproductive status for males (0: no sign of testes; 1: testes enlarged and visible) and females (0: not pregnant; 1: pregnant) as covariates because small mammals that are reproductive have an increased body mass compared to nonreproductive individuals. To determine the magnitude of the effect of sex and month on body mass, we calculated Cohen’s *D*, and we estimated 95% confidence intervals using bootstrapping (R package “bootES”).

Fecundity of females.—For each focal female ($n = 8$), we calculated body mass by calculating an arithmetic mean using all capture weights from the same month that the juveniles of that female emerged (i.e., if juveniles emerged in July, we averaged all capture weights from July for the adult female). While observing emergence of juveniles, we counted the number of juveniles in each litter ($n = 8$ litters; mean litter size: 2; range: 1–4; $n = 17$ juveniles).

To determine if body mass of females influenced litter size, we performed a linear regression that included average mass of juveniles per litter (arithmetic mean weight for all juveniles

belonging to a single female) as a covariate (R package “stats”—Sokal and Rohlf 1995). Instead of investing in larger litter size, females may invest in fewer numbers of heavier offspring. Therefore, to determine if body mass of females influenced body mass of juveniles, we performed a generalized linear mixed model with maternal mass as a fixed effect, litter size as a covariate, and maternal identity as a random effect (R package “nlme”). For comparisons of sexual dimorphism in body mass, we used a conservative Bonferroni-corrected significance level of $\alpha = 0.005$, and for all other analyses, we used a significance level of $\alpha = 0.05$. All results are presented as mean \pm SD.

All animal handling methods were approved by the Institutional Animal Care and Use Committee at the University of Arizona (Protocol #08-024) and conform to the guidelines of the American Society of Mammalogists (Sikes et al. 2011). Field methods were conducted under permits from the United States Department of Agriculture Forest Service (Special Use Permit, Coronado National Forest) and Arizona Game and Fish Department (SP654189).

RESULTS

Ontogeny of female-biased sexual dimorphism.—Adult females averaged 13% larger than males (Table 1). Juvenile males and females did not develop sexual dimorphism during the 1st 2 months after emergence (interaction of sex and month after emergence: $\chi^2_1 = 0.88$, $P = 0.35$; Fig. 1A). Body mass of juveniles increased from the 1st to 2nd month after emergence ($\chi^2_1 = 37.31$, $P < 0.0001$; Fig. 1B), but females were not larger than males ($\chi^2_1 = 1.47$, $P = 0.23$; Fig. 1B). Due to the small sample size, we compared juveniles to adults to estimate when juveniles reached adult mass. In the 1st 2 months after emergence, female juveniles had a lower body mass than adult females in July and August, whereas in the 3rd month after emergence, female juveniles did not differ from adult females in September (Table 1). Juvenile males were smaller than adult males during the 1st month after emergence (Table 1).

Seasonal body mass.—Adult cliff chipmunks maintained a relatively stable body mass from March to October (interaction of sex and month: $\chi^2_7 = 2.78$, $P = 0.90$; Fig. 1C) with females consistently larger than males ($\chi^2_1 = 53.22$, $P < 0.0001$; Fig. 1D). Pregnant females and scrotal males were heavier than

Table 1.—Summary of all body mass (g) comparisons for adult and juvenile cliff chipmunks (*Tamias dorsalis*) on Mt. Graham, Arizona, from March to October 2013 and 2014. Groups are categorized as adult males (AM), adult females (AF), juvenile males (JM), and juvenile females (JF). The 95% CI corresponds to the difference between group means. Bold values indicate a statistically significant result (Bonferroni-corrected $\alpha = 0.005$). Sample size is the number of individuals.

| Group 1 (sample size) | Group 2 (sample size) | Group 1 mean (\pm SD) | Group 2 mean (\pm SD) | Test name | Test statistic | <i>P</i> value | 95% CI (lower, upper) |
|---------------------------|---------------------------|-----------------------------|-----------------------------|----------------------|--------------------|--------------------|--------------------------|
| AM ($n = 98$) | AF ($n = 123$) | 64 (± 5) | 73 (± 7) | Welch <i>t</i> -test | 11.40 ^a | < 0.0001 | (7, 10) |
| JM—1st month ($n = 13$) | JF—1st month ($n = 23$) | 52 (± 5) | 54 (± 9) | Wilcoxon | 171.50 | 0.48 | (−4, 8) |
| JF—1st month ($n = 23$) | AF ($n = 59$) | 54 (± 9) | 74 (± 5) | Wilcoxon | 1308.00 | < 0.0001 | (15, 23) |
| JF—2nd month ($n = 9$) | AF ($n = 32$) | 65 (± 6) | 73 (± 6) | Wilcoxon | 249.50 | < 0.0001 | (3, 11) |
| JF—3rd month ($n = 4$) | AF ($n = 17$) | 69 (± 4) | 72 (± 5) | Wilcoxon | 46.50 | 0.28 | (−3, 9) |
| JM—1st month ($n = 13$) | AM ($n = 46$) | 52 (± 5) | 65 (± 4) | Wilcoxon | 575.50 | < 0.0001 | (9, 16) |

^a*d.f.* = 214.38.

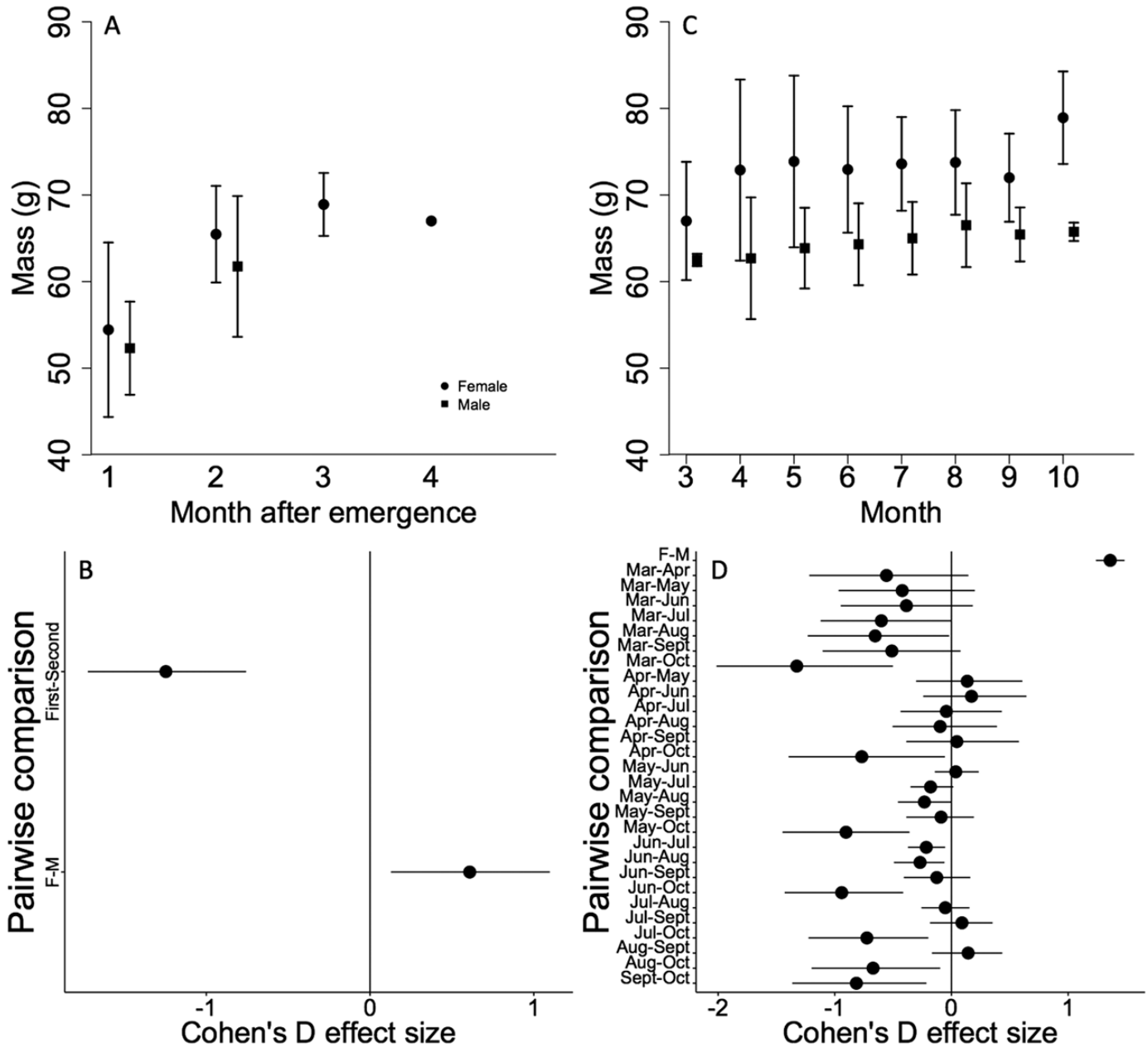


Fig. 1.—Mean \pm 95% CI body mass of A) juvenile and C) adult female (circles) and male (squares) cliff chipmunks (*Tamias dorsalis*) on Mt. Graham, Arizona, from March (month 3) to October (month 10) 2013 and 2014 (adult females: $n = 123$; adult males: $n = 98$; juvenile females: $n = 23$; juvenile males: $n = 13$) and model effect sizes for B) juveniles and D) adults. We could not collect data in months 3 and 4 for juvenile males. Chipmunks emerge from torpor in March and breed in March–August. Juveniles emerge in June–August and do not breed their 1st year. Chipmunks initially enter torpor in November.

nonreproductive individuals of the same sex (female covariate: $\chi^2_1 = 46.72$, $P < 0.0001$; male covariate: $\chi^2_1 = 3.89$, $P = 0.04$). Body mass of adults varied during the year ($\chi^2_7 = 67.14$, $P < 0.0001$), generally increasing over time with mass of chipmunks in October larger than mass in all other months, but body masses in other months were comparable (Fig. 1D).

Fecundity of females.—Larger females did not produce larger litter sizes than smaller females did ($\beta = 0.03$, $F_{1,5} = 0.67$, $P = 0.44$, $R^2 = 0.25$; Fig. 2A), and the juvenile mass covariate did not account for a significant amount of variation ($\beta = -0.07$, $F_{1,5} = 1.43$, $P = 0.28$). Similarly, larger females did not produce

heavier juveniles than smaller females did ($\chi^2_1 = 0.20$, $P = 0.66$; Fig. 2B) even when accounting for litter size ($\chi^2_1 = 0.48$, $P = 0.49$).

DISCUSSION

Similar to other populations of cliff chipmunks, the study population exhibits female-biased sexual dimorphism (Levenson 1990; Best et al. 1992; Hart 1992; Sutton 1993; Verts and Carraway 2001; Schulte-Hostedde et al. 2002). Larger females are more dominant in conspecific interactions, which could

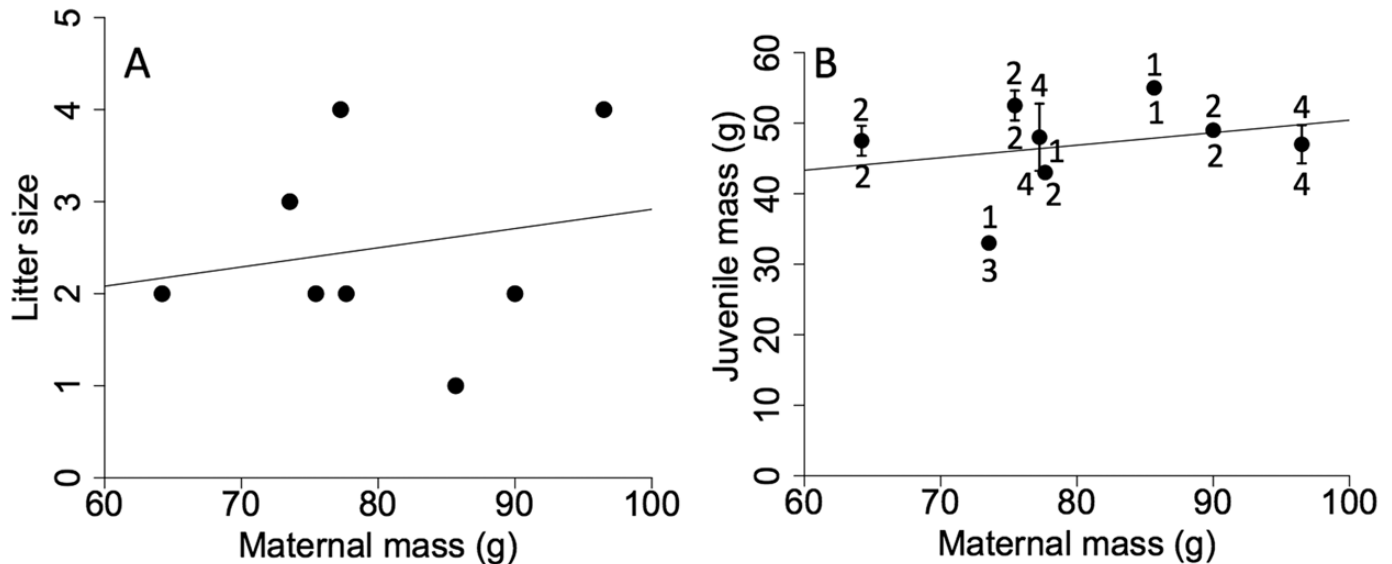


Fig. 2.—A) Litter size (number of juveniles in a litter) and B) juvenile mass (mean mass 1 month after emergence \pm SD) in relation to maternal mass (calculated as mean of all capture weights from the same month in which the juveniles for a female emerged) for female cliff chipmunks (*Tamias dorsalis*; $n = 8$) and their juveniles ($n = 17$) on Mt. Graham, Arizona, 2013 and 2014. Lines represent linear models fit to each data set. Numbers above error bars in B) represent the number of juveniles weighed per litter and numbers below error bars indicate total litter size.

lead to larger females acquiring more resources and having increased reproductive success than smaller females do (Edelman and Koprowski 2006). Alternatively, larger females could produce larger litters and juveniles with better body condition than those of smaller females (Schulte-Hostedde et al. 2002; Fokidis et al. 2007; Stuart-Smith et al. 2007).

We weighed juveniles immediately after emergence from the nest, continuing throughout the 1st 4 months of life. Contrary to our prediction, juveniles were not sexually dimorphic at emergence. Instead, juveniles did not develop body mass dimorphism during the 1st 2 months after emerging from the nest, but by the 3rd month (for females), body mass of juveniles did not differ from body mass of adults. Although sample size was small, our data suggest that juveniles take 3 months to develop sexual dimorphism. Cliff chipmunks may follow a similar ontogeny as bighorn sheep (*Ovis canadensis*), where juveniles are identical in size at birth, but within 3 months, males become heavier than females (Festa-Bianchet et al. 1996). We predicted that juveniles would be sexually dimorphic at emergence because the peak growing season on Mt. Graham is short (approximately 4–5 months; A. L. Kilanowski, pers. obs.). However, availability of food (mushrooms and conifer seeds) on Mt. Graham in 2013 and 2014 was above average (J. L. Koprowski, pers. obs.), and elevated food resources may have reduced the influence of the short growing season.

We examined monthly changes in body mass of adult males and females to look for changes in sexual dimorphism over time. Because cliff chipmunks do not larder hoard food (Hoffmeister 1956) and because we observed active chipmunks during winter, we predicted that chipmunks would gain mass before winter to increase survival during the low-food period that coincides with torpor. Male and female cliff chipmunks maintained a relatively constant body mass throughout the seasons and gained a small amount of weight before winter.

Most western chipmunk species hoard food for winter in a burrow (*T. canipes*—Best et al. 1992; *T. amoenus*—Sutton 1992; *T. cinereicollis*—Hilton and Best 1993; *T. townsendii*—Sutton 1993; *T. speciosus*—Best et al. 1994; *T. rufus*—Burt and Best 1994; *T. minimus*—Verts and Carraway 2001), and chipmunks that hoard food do not increase body mass in fall (Best et al. 1992; Sutton 1992; Hilton and Best 1993; Sutton 1993). Although cliff chipmunks have not been observed to hoard food (Hoffmeister 1956), the minimal increase in body mass might be due to unobserved hoarding behavior. Cliff chipmunks on Mt. Graham have access to food year-round by taking cones from middens of Mt. Graham red squirrels (Posthumus et al. 2015), which may provide a winter food source that reduces the need to gain weight in fall (Edelman et al. 2005). Thus, chipmunks on Mt. Graham may rely on a combination of their hoarded food and larder hoards from Mt. Graham red squirrels. The combination of chipmunk food hoards and red squirrel larder hoards may also account for nonseasonal changes in body mass. Body size of males can change seasonally due to reproductive costs. Many males spend large amounts of energy on reproduction, with minimal time spent foraging, which leads to a decrease in body mass of males throughout the breeding season (Koprowski 2005; Welbergen 2011). In cliff chipmunks, we did not see an increase in body mass of males before the breeding season or a decrease in body mass of males during the breeding season. A closer examination of male behavior during the breeding season could provide information on time budgets and explain why male chipmunks do not follow the same seasonal patterns in body mass as other small mammals.

We predicted that female-biased sexual size dimorphism might be adaptive because larger females produce larger litters and heavier offspring than smaller females do. The data suggest that larger female cliff chipmunks do not produce a larger number of offspring or heavier offspring than smaller females; however,

our sample size was small. A review of mammals with female-biased sexual dimorphism found a similar lack of strong evidence for larger females having a reproductive advantage in the form of increased litter size or increased offspring size compared to smaller females (Ralls 1976; Lu et al. 2014). However, contrary results have been reported in other sciurids (Schulte-Hostedde et al. 2002; Selonen et al. 2013). Currently, the relationship between fecundity and body size in mammals is not clear.

Female-biased dimorphism in cliff chipmunks may not be driven by female fecundity, but alternatively by female–female competition for mates (Ralls 1976; Isaac 2005). Most mammalian species engage in polygynous or promiscuous mating, meaning that females do not compete for mates, as in polyandrous mating systems (Isaac 2005). Cliff chipmunks have a promiscuous mating system (Broadbrooks 1999); therefore, we conclude that female–female competition for mates is not likely. However, female–female competition may occur over other resources such as territory or food (Isaac 2005; Edelman and Koprowski 2006; Selonen et al. 2013). Cliff chipmunks den communally and do not guard territories (Kilanowski and Koprowski 2016); however, females may compete for other resources such as seasonally available food.

We provide evidence that suggests female-biased sexual size dimorphism in mammals may not be due to selection for increased fecundity of females (Ralls 1976; Isaac 2005). Cliff chipmunks are sexually dimorphic year-round, with females consistently larger than males. This difference is particularly evident when we examined the ontogeny of sexual dimorphism of juveniles. Females and males are the same size at emergence, but within 2 months, a clear difference is evident between sexes. Understanding the ontogeny of sexual dimorphism generates insights into the selective pressures across the lifetime of an individual that lead to female-biased size dimorphism.

ACKNOWLEDGMENTS

We thank T&E, Inc., the American Society of Mammalogists, Arizona Agricultural Experiment Station, and the University of Arizona for financial support for this project. We also thank 3 anonymous reviewers, A. Brokman, P. Crowley, C. Mendes, B. Slabach, and A. Veals for feedback on early drafts of this manuscript. Special thanks to J. Dillard and L. Dunoyer for statistical consultation.

LITERATURE CITED

- BEST, T. L., J. L. BARTIG, AND S. L. BURT. 1992. *Tamias canipes*. Mammalian Species 411:1–5.
- BEST, T. L., R. G. CLAWSON, AND J. A. CLAWSON. 1994. *Tamias speciosus*. Mammalian Species 478:1–9.
- BONDRUP-NIELSEN, S., AND R. A. IMS. 1990. Reversed sexual size dimorphism in microtines: are females larger than males or are males smaller than females? *Evolutionary Ecology* 4:261–272.
- BROADBROOKS, H. 1999. Cliff chipmunk (*Tamias dorsalis*). Pp. 363–365 in *The Smithsonian book of North American mammals* (D. Wilson and S. Ruff, eds.). The Smithsonian Institution Press, London, United Kingdom.
- BURT, S. L., AND T. L. BEST. 1994. *Tamias rufus*. Mammalian Species 460:1–6.
- DAVIS, C. M., AND V. L. ROTH. 2008. The evolution of sexual size dimorphism in cottontail rabbits (*Sylvilagus*, Leporidae). *Biological Journal of the Linnean Society* 95:141–156.
- EDELMAN, A. J., AND J. L. KOPROWSKI. 2006. Influence of female-biased sexual size dimorphism on dominance of female Townsend's chipmunks. *Canadian Journal of Zoology* 84:1859–1863.
- EDELMAN, A., J. L. KOPROWSKI, AND J. EDELMAN. 2005. Kleptoparasitic behavior and species richness at Mt. Graham red squirrel mid-dens. Pp. 395–398 in *Connecting mountain islands and desert seas: biodiversity and management of the Madrean Archipelago II* (G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. B. Edminster, comps.). United States Department of Agriculture, Forest Service, Proceedings RMRS-P-36:1–631.
- EISENBERG, J. F. 1981. *The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior*. University of Chicago Press, Chicago, Illinois.
- FAIRBAIRN, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 28:659–687.
- FESTA-BIANCHET, M., J. T. JORGENSEN, W. J. KING, K. G. SMITH, AND W. D. WISHART. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. *Canadian Journal of Zoology* 74:330–342.
- FOKIDIS, H. B., T. S. RISCH, AND T. C. GLENN. 2007. Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. *Animal Behaviour* 73:479–488.
- FUNAKOSHI, K., E. NOMURA, M. MATSUKUBO, AND Y. WAKITA. 2010. Postnatal growth and vocalization development of the lesser horseshoe bat *Rhinolophus cornutus*, in the Kyushu district, Japan. *Mammal Study* 35:65–78.
- HART, E. B. 1992. *Tamias dorsalis*. Mammalian Species 399:1–6.
- HILTON, C. D., AND T. L. BEST. 1993. *Tamias cinereicollis*. Mammalian Species 436:1–5.
- HOFFMEISTER, D. F. 1956. Mammals of the Graham (Pinaleno) mountains, Arizona. *American Midland Naturalist* 55:257–288.
- ISAAC, J. L. 2005. Sexual dimorphism in mammals: a review of potential causes and consequences. *Mammal Review* 35:101–115.
- KEECH, M. A., R. T. BOWYER, J. M. VER HOEFT, R. D. BOERTJE, B. W. DALE, AND T. R. STEPHENSON. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management* 64:450–462.
- KILANOWSKI, A. L. 2015. Individual behavioral phenotypes of the cliff chipmunk (*Tamias dorsalis*): effects on female reproductive success and juvenile habitat selection. M.S. thesis, University of Arizona, Tucson.
- KILANOWSKI, A. L., AND J. L. KOPROWSKI. 2016. Communal denning of cliff chipmunks (*Tamias dorsalis*). *Southwestern Naturalist* *In Press*.
- KOPROWSKI, J. L. 2005. Annual cycles of body mass and reproduction of endangered Mt. Graham red squirrel. *Journal of Mammalogy* 86:309–313.
- KOVACS, K. M., AND D. M. LAVIGNE. 1986. Maternal investment and neonatal growth in phocid seals. *Journal of Animal Ecology* 55:1035–1051.
- LEVENSON, H. 1990. Sexual size dimorphism in chipmunks. *Journal of Mammalogy* 71:161–170.
- LU, D., C. Q. ZHOU, AND W. B. LIAO. 2014. Sexual size dimorphism lacking in small mammals. *Northwestern Journal of Zoology* 10:53–59.

- OLSSON, M., AND R. SHINE. 1997. The limits to reproductive output: offspring size vs number in the sand lizard (*Lacerta agilis*). *American Naturalist* 149:179–188.
- POSTHUMUS, E. E., J. L. KOPROWSKI, AND R. J. STEIDL. 2015. Red squirrel middens influence abundance but not diversity of other vertebrates. *PLoS ONE* 10:e0123633.
- RALLS, K. 1976. Mammals in which females are larger than males. *Quarterly Review of Biology* 51:245–276.
- R CORE TEAM. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 10 March 2016.
- SANDERSON, H. R., AND J. L. KOPROWSKI. 2009. The Mt. Graham red squirrel and its last refuge: ecology of endangerment. University of Arizona Press, Tucson.
- SCHULTE-HOSTEDDE, A. I., J. S. MILLAR, AND H. L. GIBBS. 2002. Female-biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. *Evolution* 56:2519–2529.
- SELONEN, V., J. N. PAINTER, S. RANTALA, AND I. K. HANSKI. 2013. Mating system and reproductive success in the Siberian flying squirrel. *Journal of Mammalogy* 94:1266–1273.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry: the principles and practices of statistics in biological research*. 3rd ed. W. H. Freeman and Company, New York.
- STUART-SMITH, J., R. SWAIN, R. D. STUART-SMITH, AND E. WAPSTRA. 2007. Is fecundity the ultimate cause of female-biased size dimorphism in a dragon lizard? *Journal of Zoology* 273:266–272.
- SUTTON, D. A. 1992. *Tamias amoenus*. *Mammalian Species* 390:1–8.
- SUTTON, D. A. 1993. *Tamias townsendii*. *Mammalian Species* 435:1–6.
- VERTS, B. J., AND L. N. CARRAWAY. 2001. *Tamias minimus*. *Mammalian Species* 653:1–10.
- WELBERGEN, J. A. 2011. Fit females and fat polygynous males: seasonal body mass changes in the grey-headed flying fox. *Oecologia* 165:629–637.
- WHEELWRIGHT, N. T., G. TRUSSELL, J. P. DEVINE, AND R. ANDERSON. 1994. Sexual dimorphism and population sex ratios in juvenile savannah sparrows. *Journal of Field Ornithology* 65:520–529.
- ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SVELIEVE, AND G. M. SMITH. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York.

Submitted 23 December 2015. Accepted 4 October 2016.

Associate Editor was Christine Maher.