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REPRODUCTION WITHIN MARMOTINE GROUND SQUIRRELS (SCIURIDAE, XERINAE, MARMOTINI): PATTERNS AMONG GENERA

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The sciurid tribe Marmotini has a distinctive, highly specialized reproductive profile characterized by annually produced litters of many offspring, each of small mass and fast growth rate. However, not all genera of marmotines follow the reproductive profile of the tribe. In fact, included in the tribe are squirrels with the highest and lowest energetic investment into reproduction of the entire family. Because of its large litter size, *Ammospermophilus* has the largest energetic investment into reproduction of nearly all squirrels. Also, *Ammospermophilus* is not limited to 1 litter per year. At the opposite extreme, *Marmota* has the smallest energetic investment into reproduction of all squirrels. Of the other 4 marmotine genera, reproduction in *Cynomys* is similar to that of *Marmota*, whereas that of *Tamias* is similar to that of *Ammospermophilus*; reproduction in *Sciurotamias* and *Spermophilus* may reflect their phylogenetic positions. Litter size in the basal *Sciurotamias* (2.5) is the lowest for all marmotines and is closest to that of other squirrel taxa. Consistent with the probable paraphyly of the genus, spermophiline data are the most variable and many reproductive characters sort along the probable clades within *Spermophilus*. For spermophilines, a litter size of 4 is probably basal and the larger litter sizes of 6–8 in some clades are derived. Two other derived features are the low offspring biomass in *Marmota* and a short time between conception and weaning in a spermophiline clade of predominantly New World species. Overall, reproductive investment within marmotines has followed 2 patterns: the larger marmotines (*Cynomys* and *Marmota*) have a reduced annual energetic investment compared with a higher reproductive investment in the smaller marmotines (*Ammospermophilus* and *Tamias*). Thus, body size is a key aspect in the diversification of reproductive patterns in the Marmotini.

Key words: allometry, gestation, ground squirrels, lactation, litter size, Marmotini, reproductive effort, reproductive investment

Patterns of reproductive investment for squirrels overall are dominated by marmotine ground squirrels (subfamily Xerinae, tribe Marmotini). Marmotines (Table 1) represent one-third of all sciurid species, but 48–72% of all available reproductive data (Hayssen 2008a). Ground squirrels, as a grade, do not have a distinct reproductive profile, because marmotine and nonmarmotine ground squirrels differ (Hayssen 2008a; Waterman 1996). Nonmarmotine ground squirrels have a reproductive pattern similar to that of tree squirrels, a pattern intermediate between those of marmotines and flying squirrels.

The reproductive profile of marmotines is distinctive and highly specialized (Hayssen 2008a). This speciose, well-studied, ground-dwelling tribe has large body size, often

hibernates, and has a reproductive profile characterized by an annually produced litter of many offspring each of small neonatal mass. Individuals at weaning are the smallest of all squirrels relative to adult body mass but total mass of litters at weaning is the highest. Gestation and lactation are very short, and growth rates are the highest for all squirrels. Many marmotines only produce a single litter per year. But do all marmotines follow this general pattern?

The taxonomic diversity of marmotines (Table 1) suggests that reproductive patterns may differ across genera. Previous studies (Armitage 1981; Levenson 1979; Lord 1960; Moore 1961; Morton and Tung 1971; Waterman 1996) on marmotines focused either on how the reproduction of a some marmotines matches a particular set of environmental or ecological constraints (life-history traits in 18 species of Marmotini versus length of active season [Armitage 1981] and growth rates of 18 species of Marmotini versus hibernation [Levenson 1979; Morton and Tung 1971]) or on how the reproduction of marmotines compares to other squirrels facing contrasting

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TABLE 1.—Geographic, taxonomic, and ecological diversity within Marmotini (Sciuridae, Xerinae) arranged by body size. Marmotines are a Northern Hemisphere taxon and most (*Tamias* excepted) live in open areas with sparse vegetation.

Tamias (chipmunks)
   North America and northern Asia; more forested areas than other marmotines
   25 species
   40−100 g
   Some hibernation, not colonial
Ammospermophilus (antelope ground squirrels)
   Primarily southwestern North America
   5 species
   100−150 g
   Active year-round, no hibernation, social
Sciurotamias (rock squirrels)
   China; rocky talus and cliffs
   2 species
   250−300 g
   Do not hibernate
Spermophilus (ground squirrels, susliks)
   North America, Eurasia
   Paraphyletic, 41 species
   100−800 g
   Hibernation common, some colonial
Cynomys (prairie dogs)
   Primarily central North America
   5 species
   500−1,000 g
   Colonial, some hibernation
Marmota (marmots, woodchucks)
   Northern North America and Eurasia
   14 species
   3,000−8,000 g
   Highly seasonal, long hibernation, some colonial

constraints (litter size versus latitude in 10 tree and flying squirrels, 7 chipmunks, and 15 ground squirrels from North America [Lord 1960]; and litter size in 17 tree squirrels from 4 climatic regions and litter size versus latitude in 25 species of nearctic Marmotini [Moore 1961]). No study to date has examined reproduction across the entire marmotine tribe.

The essence of natural selection is differential reproduction. Body size, ecological niche, and phylogenetic history are major evolutionary influences on reproductive investment. All marmotines are ground-dwelling squirrels with similar ecological profiles (compared with tree or flying squirrels) but marmotines live from hot, arid deserts to arctic plains. Unfortunately, no consistent data exist that categorize marmotine species with respect to ecological habitat. Previous studies of squirrels (Heaney 1984; Lord 1960; Moore 1961; Viljoen and Du Toit 1985; Waterman 1996) used latitude or broadly defined geographic units (neotropical, oriental, African, Ethiopian, tropical, temperate, nearctic, holarctic, and palearctic) to estimate the affect of climate on reproduction. Higher latitudes were correlated with increased litter size in squirrels (Lord 1960; Moore 1961). Also, squirrels in tropical, neotropical, Ethiopian, oriental, or African regions had smaller litter sizes and longer breeding seasons than those in palearctic, nearctic, or holarctic regions (Moore 1961; Viljoen and Du Toit 1985; Waterman 1996). Larger sample sizes would be expected

to confirm these trends, but did not (Hayssen 2008a). Thus, at the level of measurement available, climatic effects are not apparent on the reproduction of marmotines. However, reproductive investment within marmotines could exhibit patterns related to body size and ancestry. How do reproductive traits vary across marmotines?

Three major components of reproductive investment are number of offspring produced (litter size), energetic input into offspring (neonatal or weaning mass, or litter mass at birth or at weaning), and time devoted to reproductive effort (gestation: time from conception to parturition; lactation: time from parturition to weaning; or total effort: time from conception or mating to weaning). These aspects of reproduction are commonly measured and provide a window to viewing reproduction in an evolutionary context. They also allow us to explore the evolution of reproduction in marmotines.

Finally, the genus *Spermophilus* is probably paraphyletic (Harrison et al. 2003; Herron et al. 2004). If evolutionary forces operated differently among the spermophiline clades then these clades might exhibit differences in reproductive investment. Examination of the data here can test this hypothesis. Thus, the goals of this paper are to assess the effects of allometry and phylogeny on reproductive investment in marmotine squirrels, to examine patterns of reproduction within marmotine genera, and to explore the evolution of reproduction in marmotines, especially spermophilines.

MATERIALS AND METHODS

Reproductive data.—Reproductive data, including litter size, gestation length (conception or mating to birth), neonatal mass, lactation length (birth to weaning), weaning mass, and litters per year, were obtained for 84 species (91% of 92 species) from 261 references in Hayssen et al. (1993) and 51 references in Hayssen (2008a). Not all reproductive variables were available for all species (Hayssen 2008a). No reproductive data were found for *Ammospermophilus insularis*, *Sciurotamias forresti*, *Spermophilus adocetus*, *Spermophilus atricapillus*, *Spermophilus brevicauda*, *Spermophilus musicus*, *Spermophilus pallidicauda*, and *Spermophilus ralli*.

Reproductive data include those for young females as well as adults. Primiparous females and females at the end of their reproductive lives may have litter sizes and reproductive investment patterns that differ from prime adult females. These are within-species, not across-species, effects. As such, variation due to age is not a confounding factor, although it will increase the variance of any given variable and hence make statistical significance more difficult to detect.

Litter-size values combine counts of corpora lutea, embryos, placental scars, neonates, offspring within a nest or at den emergence, as well as instances in which units were not given. Of the >400 litter-size values for marmotines in Hayssen et al. (1993), 46% were from in utero litter-size counts, 27% were from postnatal young, and 27% had unidentified units. Excluding measures without units, most (85%) marmotines with >2 estimates of litter size had both uterine and postnatal measures. The 15% of species with data for only 1 measure are spread

across the 6 genera. Thus, the use of different measures of litter size is not a confounding variable but will increase the variance and make detecting statistical significance more difficult.

Composite reproductive measures (with parenthetical units) were calculated as follows: duration of reproduction (days) = length of gestation + length of lactation; litter mass at birth (g) = litter size × neonatal mass; litter mass at weaning (g) = litter size × weaning mass; growth during gestation (g/days) = litter mass at birth/gestation length; growth during lactation (g/d) = (litter mass at weaning − litter mass at birth)/lactation length; overall growth during reproduction (g/days) = litter mass at weaning/duration of reproduction. Average litter size from both in utero and postbirth counts was used to estimate litter mass at weaning. Therefore, postbirth mortality is only partially included in litter mass at weaning.

Developmental state of neonates at birth (i.e., precocial or altricial) is an important component of reproductive investment. Unfortunately, consistent data on this facet of reproduction are not broadly available and this study does not address the precocial–altricial dimension.

Phylogeny.—Genera and species were classified according to Thorington and Hoffmann (2005). Clades of *Spermophilus* were from Harrison et al. (2003) as follows (clade identification of Herron et al. [2004] is given parenthetically): clade A (S-1): *adocetus* (no data) and *annulatus*; clade B (S-7): *atricapillus* (no data), *beecheyi*, *lateralis*, *madrensis*, *saturatus*, and *variegatus*; (clade C is *Marmota*); clade D (S-6): *alashanicus*, *citellus*, *dauricus*, *erythrogenys*, *fulvus*, *major*, *musicus* (no data), *pygmaeus*, *relictus*, *suslicus*, and *xanthoprymnus*; clade E (S-2): *armatus*, *beldingi*, *brunneus*, *canus*, *columbianus*, *elegans*, *mollis*, *parryii*, *richardsonii*, *townsendii*, *undulatus*, and *washingtoni*; clade F (S-3, S-4, and S-5): *franklinii*, *mexicanus*, *mohavensis*, *perotensis*, *spilosoma*, *tereticaudus*, and *tridecemlineatus*. Harrison et al. (2003) did not include *brevicauda*, *pallidicauda*, or *ralli*, but I found no reproductive data for these species.

For the purposes of this manuscript I will refer to Harrison et al.'s (2003) spermophiline clades as follows. Clade A is the *annulatus* clade because I only found data for *annulatus*. Species in both clades B and F are from Mexico or the southwestern United States, but they are placed in different subgenera (Thorington and Hoffmann 2005): *Otospermophilus* for clade B and *Ictidomys* or *Xerospermophilus* for clade F. I refer to clade B as *Otospermophilus* and clade F as *Ictidomys* (because that subgenus name is used for more species in this clade than *Xerospermophilus*). The subgenus name *Spermophilus* has been used for both clades D and E, but clade D has species primarily from Eurasia and those from clade E are predominantly from North America. I refer to clade D as the Old World clade and clade E as the New World clade. In sum, the monikers used here are: clade A, *annulatus*; clade B, *Otospermophilus*; clade D, Old World; clade E, New World; and clade F, *Ictidomys*.

Allometric analyses.—Body mass was used to investigate allometric effects on reproduction. Body mass of females was used whenever possible rather than mass of males or mass of adults of unknown sex. Body-mass data were available for 80

of the 84 species with reproductive data (Hayssen, 2008b). For the remaining 4 species, body mass was estimated from head–body length from the following equation (Hayssen 2008b): $\log_{10}$ mass = −4.30 + 2.91($\log_{10}$ head–body length). This equation is based on data from more than 4,000 squirrels from 233 species and has an R^2 of 97.2%. The estimates are: *Marmota camtschatica* (head–body length, 508 mm), estimated mass 3,764 g; *Spermophilus alashanicus* (head–body length, 199 mm), estimated mass 247 g; *Spermophilus major* (head–body length, 260 mm), estimated mass 537 g; and *Spermophilus relictus* (head–body length, 236 mm), estimated mass 404 g.

The genera *Ammospermophilus*, *Cynomys*, and *Sciurotamias* individually have few species: 5, 5, and 2 respectively. Litter-size data are available for all *Cynomys*, 80% of the *Ammospermophilus*, and half the *Sciurotamias*. Fewer data are available for other reproductive parameters. In fact, only litter size is known for *Sciurotamias* although much more data are available for *Ammospermophilus* and *Cynomys*. One consequence of the low diversity is that genus-level allometric relationships are based on few data points and would be so even if data were available for all species. A 2nd consequence of the small number of data points is that a single datum may strongly influence a statistic. These issues do not negate the value of allometric relationships because the bivariate allometric equations are descriptive as well as analytical, just as statistical means are descriptive for univariate variables. The questions addressed here are descriptive (what is the pattern for each genus) as well as analytical (what do these patterns infer about the biology of marmotines). The statistics are exceptionally valuable in this context but individuals using them need to examine the individual data points before making conclusions about trends. In this manuscript, when a single data point has a large influence on a trend I have not concluded that the trend was biologically meaningful even if the trend was statistically significant. Thus, the interpretations from the statistical analyses are conservative.

Statistical analyses.—Common-log transformations were performed to improve symmetry of distributions across species, but even with these transformations gestation length, neonatal mass, and body mass are not normally distributed. Sample sizes are numbers of species. Both traditional statistical models and phylogenetic independent contrasts (PICs) were used for allometric analyses and are reported when samples sizes were >5 species.

Traditional statistical treatment was by a variety of general linear models (GLMs) using $n − 1$ genera as independent explanatory variables, with *Spermophilus* as the normative genus. The models included analysis of variance (when body mass has no effect), least-squares regression, multiple regression, or analysis of covariance, as appropriate (Hayssen and Lacy 1985; Snedecor and Cochran 1980). Results for these models are preceded by the label ''GLM.'' Interaction effects were tested by partial F-statistics and are reported if significant. If not significant, interaction effects were withdrawn from the models. Type III sums of squares were used to assess significance of individual genera. Deviations of residuals from a normal distribution are noted in the ''Results'' section. R^2
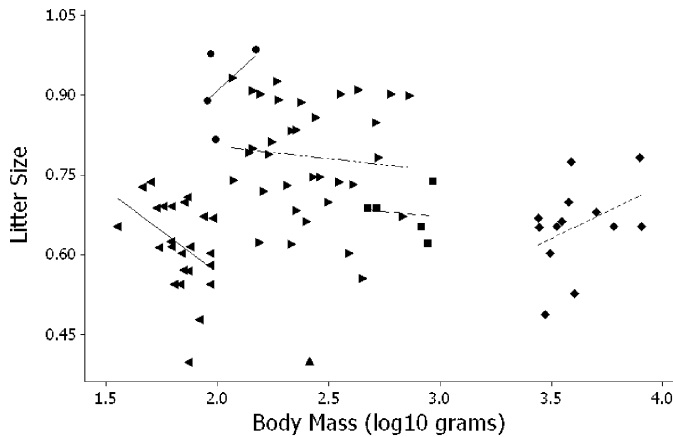
FIG. 1.—Allometry of litter size among genera of Marmotini (*n* = 82 species; *Tamias canipes* and *T. sonomae* superimposed). Key to genera from smallest to largest body mass: *Tamias* (left-facing triangles), *Ammospermophilus* (circles), *Spermophilus* (right-facing triangles), *Sciurotamias* (upright triangle), *Cynomys* (squares), *Marmota* (diamonds). All variables are in log10 units.

values are provided only for regression models with $P < 0.05$. To assess significance when doing multiple comparisons among genera for the same reproductive variable, nominal levels of significance were divided by the number of comparisons to maintain experiment-wide error rates of $\alpha < 0.05$ (Dunn 1961).

For all the major reproductive variables (litter size, gestation and lactation lengths, neonatal mass, litter mass at birth, weaning mass, and litter mass at weaning), phylogenetic independent contrasts were performed with Mesquite (Maddison and Maddison 2007) and PDAP (Milford et al. 2003) using the phylogeny in Herron et al. (2004). Branch lengths were assigned by the method of Pagel (1992). Results for these analyses are preceded by the label "PIC." Six species were not present in Herron et al. (2004) and were placed as follows. *Sciurotamias davidianus* was put basal to all other genera (Mercer and Roth 2003). *Tamias alpinus* was placed within the *minimus–panamintinus–quadrimaculatus* group (Clawson et al. 1994). *T. speciosus* was placed with *amoenus* (Best et al. 1994; Piaggio and Spicer 2001). *Spermophilus canus* was placed with *Sp. mollis* (Thorington and Hoffmann 2005). *Sp. alashanicus* was placed with *Sp. pallidicauda* (Harrison et al. 2003). *Ammospermophilus nelsoni* was placed with *A. interpres* (Best et al. 1990).

RESULTS

The reproductive profile of Marmotini (large litter size, and short gestation and lactation) is distinctive among squirrels, but like other squirrels, allometric effects strongly influence mass at birth and weaning, and phylogenetic effects have a prominent influence on litter size, gestation length, and lactation length. Within this broad pattern, genera differ (Figs. 1–3). Results are presented for each reproductive variable.
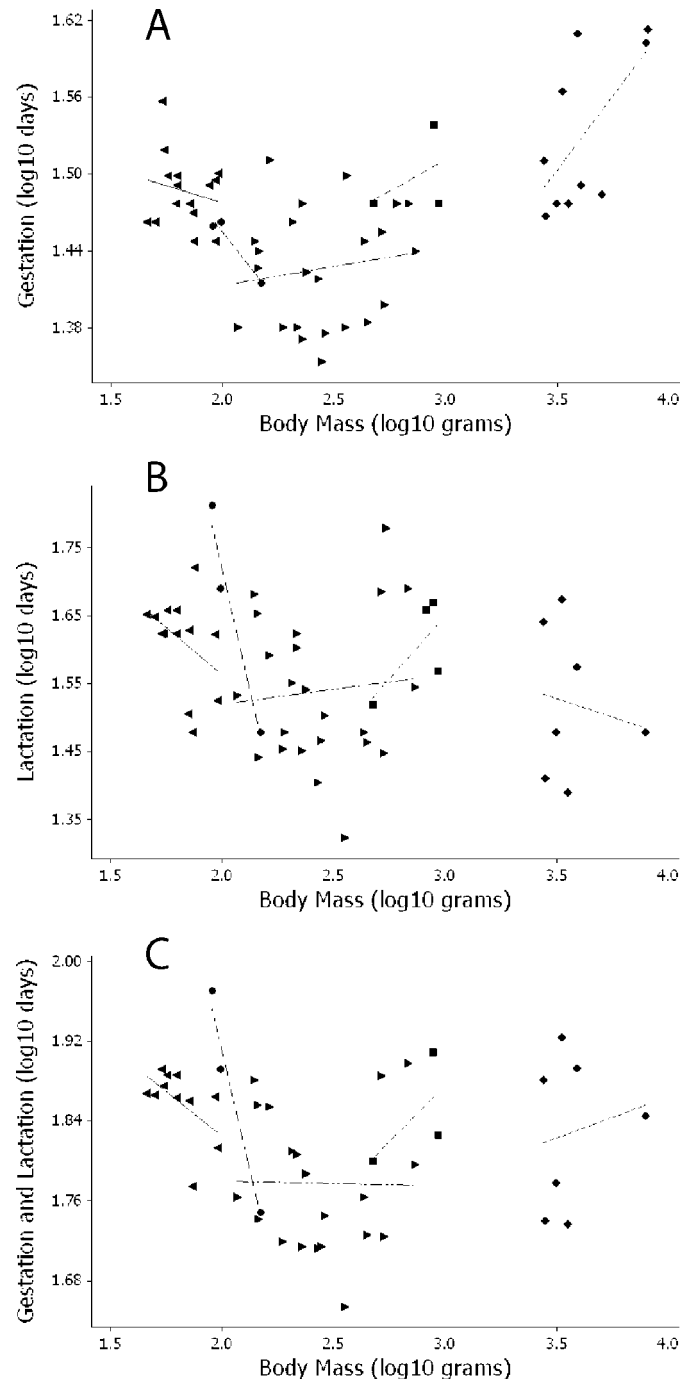

FIG. 2.—Allometry of the temporal investment into reproduction among genera of Marmotini: A) gestation length (*n* = 54), B) lactation length (*n* = 50; *Tamias palmeri* and *T. panamintinus* superimposed), C) gestation plus lactation (*n* = 44). Key to genera from smallest to largest body mass: *Tamias* (left-facing triangles), *Ammospermophilus* (circles), *Spermophilus* (right-facing triangles), *Cynomys* (squares), *Marmota* (diamonds). All variables are in log10 units.

Comparisons by Reproductive Variable

Litter size.—Analysis of litter size (*n* = 82; Fig. 1) indicated no interaction effects between body mass and individual genera (GLM: $P = 0.28$). Litter size was not related to maternal mass
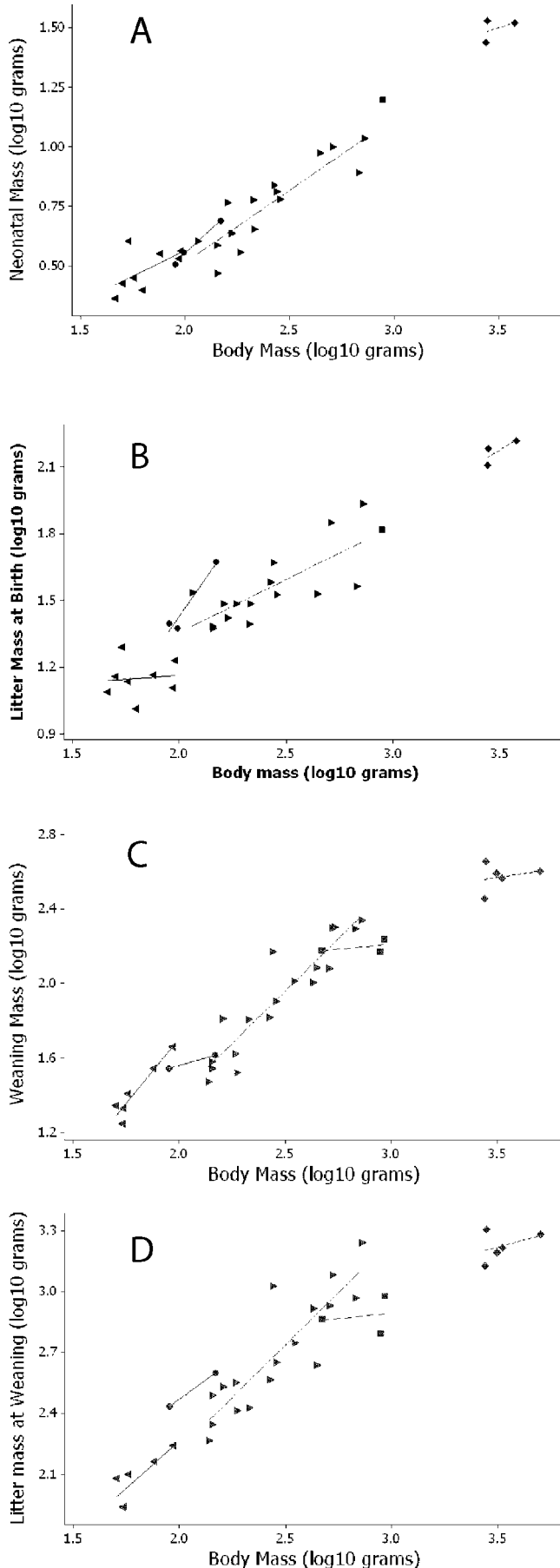
TABLE 2.—Gestation and lactation lengths (days), by genus and for spermophiline clades.

Genus	Gestation length			Lactation length		
	n	$\bar{X}$	Range	n	$\bar{X}$	Range
Ammospermophilus	3	27.9	26−29	3	47.9	30−65
Cynomys	3	31.5	30−35	4	40.5	33−47
Marmota	10	34.1	29−41	7	34.1	24−47
Sciurotamias	0			0		
Spermophilus	23	26.8	23−32	23	35.6	21−60
annulatus	0			0		
Ictidomys	5	26.8	24−28	5	38.1	28−48
New World	9	24.6	23−27	10	29.2	21−35
Old World	6	28.4	23−31	4	39.6	29−60
Otospermophilus	3	30.3	28−32	4	44.6	39−49
Tamias	15	30.7	28−36	13	41.4	30−52

(GLM: $P = 0.96$; PIC: $P = 0.26$); however, genera had significantly different litter sizes (GLM: $P < 0.0005$, $R^2 = 53\%$) and for *Tamias* litter size and body mass were correlated (GLM: $n = 25$, $P = 0.046$, $R^2 = 16\%$). Litter size in *Ammospermophilus* was significantly different from that of all genera but *Spermophilus*; that of *Spermophilus* differed from those of *Marmota*, *Tamias*, and *Sciurotamias*; and litter sizes of *Cynomys*, *Marmota*, *Tamias*, and *Sciurotamias* did not differ from each other (GLM: $P < 0.003$ for each significant comparison). *Sciurotamias* had the smallest litter size (2.5). Generally litter size was 4 or 5 for *Cynomys*, *Marmota*, and *Tamias* and >6 ($\bar{X} = 8.3$) for *Ammospermophilus*. Litter size was 2–5 for 8 of 34 *Spermophilus* and >5 for the remaining 26 species. Clades within *Spermophilus* had roughly different litter sizes (GLM: $n = 34$, $P = 0.087$).

Gestation length.—For gestation length ($n = 54$; Fig. 2A; Table 2) interaction effects between body mass and individual genera were not significant (GLM: $P = 0.14$). Body mass had no significant affect on gestation length (GLM: $P = 0.13$; PIC: $P = 0.061$), but genus effects were significant (GLM: $n = 54$, $P < 0.0005$, $R^2 = 48\%$). Gestation in *Spermophilus* differed significantly from that in *Marmota* and *Tamias* (GLM: $P < 0.005$), but other pairwise comparisons among genera were not significant. Overall, the shortest gestation lengths were in *Spermophilus* (3–4 weeks). Within *Spermophilus*, gestation length broke down by clade (GLM: $n = 23$, $P = 0.002$, $R^2 = 47\%$). *Tamias* species were smaller in size but had longer gestation lengths (4–5 weeks) than those in *Spermophilus*. Groundhogs and marmots (*Marmota*) are much larger than

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FIG. 3.—Allometry of energetic investment into reproduction among genera of Marmotini: A) neonatal mass ($n = 30$), B) litter mass at birth ($n = 30$; *Spermophilus tereticaudus* and *S. tridecemlineatus* superimposed), C) weaning mass ($n = 34$), and D) litter mass at weaning ($n = 33$; *Tamias palmeri* and *T. panamintinus* superimposed) versus body mass. Key to genera from smallest to largest body mass: *Tamias* (left-facing triangles), *Ammospermophilus* (circles), *Spermophilus* (right-facing triangles), *Cynomys* (squares), *Marmota* (diamonds). All variables are in log10 units.

TABLE 3.—Litter size and neonatal or litter mass as percentage of mass of females, by genus and for spermophiline clades.

Genus	Litter size			Neonatal mass			Litter mass		
	n	$\bar{X}$	Range	n	$\bar{X}$	Range	n	$\bar{X}$	Range
Ammospermophilus	4	8.38	6.6−9.7	3	3.51	3.3−3.7	3	27.90	24.1−31.9
Cynomys	5	4.78	4.2−5.5	1	1.78		1	7.47	
Marmota	13	4.57	3.1−6.1	3	1.03	0.8−1.2	3	4.82	4.4−5.4
Sciurotamias	1	2.50		0			0		
Spermophilus	34	6.26	3.6−8.6	15	2.35	1.2−3.6	15	14.90	5.5−29.7
annulatus	1	4.00		0			0		
Ictidomys	7	6.88	6.2−8.1	4	2.36	2.0−2.7	4	15.99	14.4−17.1
New World	12	6.64	3.6−8.6	7	2.31	1.5−3.5	7	15.62	7.7−29.7
Old World	9	6.19	4.6−8.0	0			0		
Otospermophilus	5	5.07	4.2−7.1	4	2.40	1.2−3.6	4	12.54	5.5−19.1
Tamias	25	4.21	2.5−5.4	8	4.81	3.6−7.4	8	22.73	13.7−36.0

other marmotines and had 4- to 6-week gestation lengths with positive allometry (GLM: $n = 10$, $P = 0.043$, $R^2 = 42\%$).

Lactation length.—For lactation (Fig. 2B; Table 2) neither interaction (GLM: $P = 0.13$), body mass (GLM: $P = 0.94$; PIC: $P = 0.79$), nor individual genus (GLM: $P = 0.29$) effects were significant ($n = 50$ species). For lactation, the 3 genera with the most species (*Marmota*, $n = 7$, $\bar{X} = 34$ days; *Spermophilus*, $n = 23$, $\bar{X} = 36$ days; and *Tamias*, $n = 12$, $\bar{X} = 42$ days) had very similar lactation lengths. Within *Spermophilus*, lactation length breaks down by clade (GLM: $n = 23$, $P = 0.009$, $R^2 = 36\%$).

Conception to weaning.—Within Marmotini, gestation was shorter than lactation for all genera except *Marmota*. In *Marmota*, gestation was often equal to or longer than lactation. At 58 days, *Spermophilus* ($n = 20$) had the shortest median time from conception to weaning. In contrast, most (8 of 11) *Tamias* species had reproductive intervals of 70–80 days. Overall, the time devoted to reproduction (60–80 days) was similar across genera (Fig. 2C) but that of the New World *Spermophilus* clade was shorter (range, 45–62 days; all Marmotini, GLM: $n = 44$, $P = 0.014$, $R^2 = 27\%$; *Spermophilus* clades only, GLM: $n = 20$, $P = 0.001$, $R^2 = 64\%$).

Neonatal mass and litter mass at birth.—For both neonatal mass ($n = 30$; Fig. 3A; Table 3) and litter mass at birth ($n = 30$; Fig. 3B; Table 3) interaction effects between body mass and

individual genera were not significant (neonatal mass, GLM: $P = 0.63$; litter mass at birth, GLM: $P = 0.62$). For both neonatal mass and litter mass at birth, body mass was highly significant (GLM, neonatal mass: $P < 0.0005$, $R^2 = 94\%$; PIC: $P < 0.0005$; litter mass at birth, GLM: $P < 0.0005$, $R^2 = 88\%$; PIC: $P < 0.0005$). Genus effects were not significant for neonatal mass (GLM: $P = 0.11$), but were significant for litter mass at birth (GLM: $P = 0.035$, additional $R^2 = 3\%$ after the effects of body mass were removed). For all genera with sufficient data, neonatal mass and body mass were strongly correlated. For most genera, litter mass at birth also was strongly correlated with body mass. The exception was *Tamias*, for which larger species had smaller than expected litter mass.

Weaning mass and litter mass at weaning.—For weaning mass ($n = 34$; Fig. 3C; Table 4), interactions effects were nearly significant (GLM: $P = 0.057$) and accounted for 2% of the variation in the mass of individual weanlings; genus effects were significant (GLM: $P = 0.02$) but accounted for only 3% of the variation in weaning mass; whereas body mass was highly significant (GLM: $P < 0.0005$) and accounted for 91% of the variation (PIC: $P < 0.0005$) . The interaction and genus effects were due to the nearly flat relationship with body mass for *Cynomys* ($n = 3$) and *Marmota* ($n = 5$). Larger species of *Spermophilus* and *Tamias* had larger offspring mass at weaning, but for *Marmota* such a trend was not distinct.

Armitage (1981) reported that the mass of a single young at weaning was positively correlated with gestation length and not correlated with lactation. For *Cynomys*, *Marmota*, and *Spermophilus* taken together, weaning mass correlated with gestation length (weaning mass versus gestation length, $n = 23$, $P = 0.023$; log weaning mass versus log gestation length, $n = 23$, $P = 0.045$) but no correlation existed for marmotines overall (weaning versus gestation, $n = 30$, $P = 0.27$; log weaning versus log gestation, $n = 30$, $P = 0.88$; litter mass at weaning versus gestation, $n = 30$, $P = 0.66$; log litter mass at weaning versus log gestation, $n = 30$, $P = 0.57$). In addition, for *Spermophilus* and *Marmota* alone, gestation and weaning mass were not correlated (*Spermophilus*: weaning mass versus gestation length, $n = 14$, $P = 0.91$; log weaning mass versus log gestation length, $n = 14$, $P = 0.74$; *Marmota*: weaning

TABLE 4.—Weaning and litter mass at weaning as a percentage of mass of females, by genus and for spermophiline clades.

Genus	Weaning mass			Litter mass at weaning		
	n	$\bar{X}$	Range	n	$\bar{X}$	Range
Ammospermophilus	2	33.33	27.7−39.0	2	285.2	268−303
Cynomys	3	22.50	16.8−31.9	3	109.6	70−156
Marmota	5	11.62	8.0−16.2	5	51.8	38−73
Sciurotamias	0			0		
Spermophilus	18	29.45	17.7−53.9	17	181.5	98−390
annulatus	0			0		
Ictidomys	4	24.16	21.5−26.6	4	174.6	133−216
New World	9	30.31	17.7−53.9	9	194.0	98−390
Old World	1	37.22		0		
Otospermophilus	4	30.85	23.6−40.2	4	160.4	126−211
Tamias	6	42.27	32.7−48.7	6	191.1	158−237

TABLE 5.—Growth rates by genus and for spermophiline clades (overall is from conception to weaning). Upper: Absolute growth rates (g/day; see "Materials and Methods" for calculations). Lower: Growth rate relative to adult mass as percent of adult mass gained per day (= (absolute growth rate/adult mass) × 100).

Genus	During gestation			During lactation			Overall		
	n	$\bar{X}$	Range	*n*	$\bar{X}$	Range	*n*	$\bar{X}$	Range
Absolute rate									
Ammospermophilus	3	1.17	0.8−1.8	2	7.73	3.8−11.6	2	4.99	2.9−7.1
Cynomys	1	1.91		1	11.9		3	11.14	7.6−14.2
Marmota	2	4.56	4.0−5.2	2	50.3	27.6−73.0	4	25	17.6−36.8
Sciurotamias	0			0			0		
Spermophilus	13	1.53	0.9−3.1	12	16.3	4.4−47.1	15	11.09	2.4−27.8
annulatus	0			0			0		
Ictidomys	3	1.02	0.9−1.3	2	7.33	4.4−10.3	4	6.32	2.4−14.2
New World	7	1.74	1.3−3.1	6	22.18	11.4−47.1	8	14.19	6.8−27.8
Old World	0			0			0		
Otospermophilus	3	1.55	0.9−2.5	4	11.98	5.8−18.2	3	9.17	4.7−11.8
Tamias	7	0.45	0.3−0.5	5	2.54	1.6−3.8	5	1.58	1.1−2.4
Relative rate									
Ammospermophilus	3	1.01	0.1−1.2	2	6.05	4.2−7.9	2	4.01	3.2−4.8
Cynomys	1	0.22		1	1.35		3	1.62	0.9−2.5
Marmota	2	0.16	0.1−0.2	2	1.81	1.0−2.6	4	0.84	0.6−1.3
Sciurotamias	0			0			0		
Spermophilus	13	0.58	0.2−1.2	12	5.16	2.7−12.7	15	3.22	1.7−7.5
annulatus	0			0			0		
Ictidomys	3	0.61	0.6−0.6	2	5.14	3.1−7.2	4	2.79	1.7−3.9
New World	7	0.64	0.3−1.2	6	6.35	3.1−12.7	8	3.79	1.8−7.5
Old World	0			0			0		
Otospermophilus	3	0.42	0.2−0.6	4	3.38	2.7−4.9	3	2.29	1.7−3.0
Tamias	7	0.74	0.4−1.0	5	3.84	2.9−4.7	5	2.55	2.0−3.2

mass versus gestation length, $n = 5$, $P = 0.42$; log weaning mass versus log gestation length, $n = 5$, $P = 0.43$). In fact, for *Marmota*, if the trend were significant, the effect would be negative, heavier weanlings and shorter gestations.

For litter mass at weaning ($n = 33$; Fig. 3D; Table 4), interaction effects were not significant (GLM: $P = 0.41$), but genus (GLM: $P = 0.0018$) and body mass (GLM: $P < 0.0005$; PIC: $P = 0.0005$) effects were. Body mass accounted for 85% of the variation in litter mass at weaning compared with 7% accounted for by differences among genera. Again, the relationship between body mass and litter mass at weaning was nearly flat for the larger-bodied marmotines (*Cynomys*, $n = 3$, and *Marmota*, $n = 5$).

Growth rates.—Marmotine genera differed in growth rate (Table 5). These differences are in part related to body mass because larger species have slower growth rates, but genera differed even when body mass was taken into account (growth during gestation: GLM: $n = 26$, $P_{\text{mass}} = 0.003$, $P_{\text{genus}} = 0.021$; growth during lactation: GLM: $n = 21$, $P_{\text{mass}} = 0.001$, $P_{\text{genus}} = 0.087$; growth from conception to weaning: GLM: $n = 29$, $P_{\text{mass}} < 0.0005$, $P_{\text{genus}} = 0.006$). On average, *Tamias* species put 7% of adult mass into offspring per day of gestation compared with 1% for *Ammospermophilus*. However, during lactation, *Ammospermophilus* put 6% of adult mass into offspring compared with 4% for *Tamias*. Between conception and weaning, *Cynomys* and *Marmota* invested the least in reproduction (0.8–1.6% of adult mass per day). These growth-

rate data represented, on average, only 30% of the species in each genus; thus, the results are tentative.

Litter size versus neonatal mass.—A trade-off exists between litter size and neonatal mass for the tribe as a whole. A significant, negative coefficient for litter size resulted when regressing neonatal mass against litter size using maternal mass as a covariate and taking genus into account (log-transformed variables; GLM: $n = 31$, $P_{\text{maternal mass}} = 0.006$, $P_{\text{litter size}} = 0.043$, $P_{\text{genus}} = 0.9$). Thus, across marmotines higher litter sizes were associated with lower neonatal mass. The data are predominantly from *Tamias* and *Spermophilus*. The data on *Tamias* included an outlier (low litter size and high neonatal mass) that would strongly leverage a regression on *Tamias* alone, but did not affect the regression across the tribe because the 3 *Marmota* species also had low litter size and heavy neonates. *Spermophilus* is paraphyletic but the sample sizes for individual clades were too small and the data were too idiosyncratic (individual data points that strongly influence relationships) for cogent analysis. Thus, trade-offs between neonatal size and litter size could be documented across the tribe but not within genera or clades.

DISCUSSION

Three questions focus this discussion. First, across marmotines how do different reproductive traits vary with body size and phylogeny? Second, how do genera within Marmotini vary in their reproduction? Third, what do the current analyses

indicate about the evolution of reproduction in marmotines, especially spermophilines?

How Do Reproductive Traits Vary Across Marmotine Genera?

The present study supports and extends the work of Lord (1960), Moore (1961), Morton and Tung (1971), Levenson (1979), and Armitage (1981). Armitage's work is the most extensive and other comparisons of marmotines with tree squirrels (Heaney 1984) or nonmarmotine ground squirrels (Waterman 1996) have used Armitage's analysis and data as their foundation.

Armitage (1981) examined reproduction in 18 species of North American Marmotini from the 3 genera with the largest-bodied squirrels: *Cynomys* (3 species), *Marmota* (3 species), and *Spermophilus* (12 species). His results are not directly comparable because he used geographically isolated populations of some species as independent data points and he did not consistently use log transformations. Nevertheless, for *Cynomys*, *Marmota*, and *Spermophilus*, Armitage (1981) concluded that weaning mass was smaller for larger females. This result was supported across marmotine genera. Larger genera had relatively smaller young. So *Marmota* produced relatively smaller young than *Spermophilus*, which produced relatively smaller young than *Tamias*. Within *Ammospermophilus*, *Cynomys*, and *Marmota*, this trend was not apparent but small sample sizes prevented conclusive analysis. Within *Tamias* and *Spermophilus* the trend was reversed, larger females had larger weanlings.

Armitage (1981) also suggested that weaning mass was positively correlated with gestation length. This result was not supported for marmotines overall or for any individual genus. Why the mass of a single offspring after lactation would be related to the length of pregnancy is not clear. Perhaps a more interesting comparison would be to see if the mass of a litter at weaning is related to the length of gestation and lactation. In other words, does producing a larger litter mass at weaning take longer? For marmotines, the answer is no. The length of gestation plus lactation was not related to litter mass at weaning. If anything, larger litters had a shorter time between conception and weaning (negative, but not significant, coefficient) and this was after removing the effects of body mass. Lactation length also was not related to litter mass at weaning. Again, if anything, larger litters were associated with shorter lactation lengths (negative, but not significant, coefficient and after removing the effects of body mass). Thus, in the present study, weaning mass was not related to the temporal component of reproductive investment but was strongly related to maternal mass both across the tribe and within genera.

Levenson (1979) and Morton and Tung (1971) examined growth rates of 5 species of *Tamias*, 1 species of *Ammospermophilus*, and 12 species of *Spermophilus*. Their calculations of growth rate differed from those used here but are most similar to the ''absolute growth rates'' in Table 5 for the entire reproductive interval (conception to weaning). For both their calculations and those presented here, the increase in offspring biomass per day was smallest in *Tamias*, intermediate in *Ammospermophilus*, and largest in *Spermophilus*. Thus, the larger the mother, the faster the absolute growth rate. However, an absolute 10-g/day increase in offspring biomass represents a relatively larger investment from a 100-g mother than from a 500-g mother.

Relative growth rate takes maternal mass into consideration and presents a different picture. *Tamias* still had the slowest growth rate but *Ammospermophilus* and *Spermophilus* were reversed. The smaller *Ammospermophilus* had a faster growth rate. The largest marmotines, *Cynomys* and *Marmota*, were not included in the previous work but were included in this study. Relative growth rates in both these genera were much slower those in *Ammospermophilus*, *Spermophilus*, and *Tamias*. Thus, the daily investment into offspring biomass during reproduction was a smaller proportion of maternal mass in larger females. The larger the mother, the slower the relative growth rate.

What is the Reproductive Profile of Each Marmotine Genus?

The reproductive profile of Marmotini, with their large litter size and short gestation and lactation, is distinctive among squirrels. Within this broad pattern, genera differ. Squirrels with the highest (*Ammospermophilus*) and lowest (*Marmota*) energetic investment in reproduction of the entire family are included within the tribe.

Sciurotamias is not well studied. All that is known of its reproduction is that its litter size is 2.5. Given the phylogenetically basal position of *Sciurotamias* (Mercer and Roth 2003) and the fact that litter sizes for nonmarmotine squirrels range from 1.7 to 3.1 (Hayssen 2008), the ancestral litter size for all marmotine squirrels may be 2 or 3 but increased to 4 early in the evolution of the tribe.

Tamias is the most arboreal genus in the tribe. How, or if, these reproductive traits might relate to a more arboreal life is not clear. *Tamias* was 2nd only to *Ammospermophilus* among marmotines in energetic investment. Litter size was only half that of *Ammospermophilus* but, relative to adult mass, litter mass at birth and weaning were nearly as high. Thus, *Tamias* had fast growth rates. The fact that more aspects of reproduction in chipmunks were influenced by body mass, combined with the high growth rates, suggests that chipmunks might be reproducing closer to their physiological limit than other genera of marmotines.

Reproduction in *Ammospermophilus* was specialized along several dimensions. Because of its large litter size, *Ammospermophilus* had the largest energetic investment in reproduction. This high litter mass could be achieved either by increasing the lengths of gestation or lactation or by speeding up growth rate; *Ammospermophilus* did both. Before birth, increased investment was achieved by increasing growth rate, not gestation length. After parturition, *Ammospermophilus* both lengthened lactation and increased growth rate. In addition, although both *Ammospermophilus* and *Tamias* had fast growth rates, that of *Ammospermophilus* was 40–60% faster. *Ammospermophilus* does not usually hibernate and can produce >1 litter in a year. Therefore, energy saved by not fattening up for

hibernation can be channeled into offspring. *Ammospermophilus* excels at putting resources into offspring.

At the opposite extreme, *Marmota* had the smallest energetic investment of all squirrels. Neonatal mass was only 1% of adult mass and litter mass only 5%. Litter mass at weaning was only 50% of adult mass and growth rates were slow. *Marmota* relies extensively on hibernation over long winters and energetic investment may be channeled into winter survival rather than reproduction.

Reproduction in *Cynomys* was similar to that of *Marmota* but was otherwise not distinctive. *Cynomys* was intermediate in every reproductive character, suggesting reproduction in *Cynomys* is not specialized.

Overall, the distinctive marmotine reproductive profile was primarily that of the genus *Spermophilus*. That genus had the largest sample size, the greatest variability, and is paraphyletic (Harrison et al. 2003; Herron et al. 2004).

Evolution of Reproduction in Spermophiline Taxa

Three marmotine genera are nested within the paraphyletic *Spermophilus*: *Ammospermophilus*, *Cynomys*, and *Marmota* (Harrison et al. 2003). Thus, we can compare the reproduction of clades in *Spermophilus* with their sister taxa. The divergence of all these clades from earliest to most derived is *annulatus* (with *Ammospermophilus* as a sister taxon), the *Otospermophilus* clade, *Marmota*, the Old World clade, the New World clade, and finally the *Ictidomys* clade with *Cynomys*. These patterns of divergence allow hypotheses regarding the evolution of reproduction in these groups.

The basal *annulatus* clade is a sister taxon to *Ammospermophilus*. The only reproductive information on *Sp. annulatus* was a litter size of 4, whereas that for *Ammospermophilus* was 8. Given that smaller litter sizes are probably basal for sciurids overall (Hayssen 2008), and that the *Otospermophilus* clade also has smaller litter sizes, the large litter size in *Ammospermophilus* is probably derived.

The genus *Marmota* is the outgroup to the Old World, New World, and *Ictidomys* clades. With respect to litter size, nearly all of spermophilines in the *Ictidomys* clade, many in the New World clade, and some in the Old World clade had larger litters than those of *Marmota*, but most of the litter sizes in earlier lineages (*Otospermophilus* and *annulatus* clades) were similar to those of *Marmota*. Thus, the higher litter sizes in the Old World, New World, and *Ictidomys* clades are derived.

Cynomys is nested in the *Ictidomys* clade. Litter size in *Cynomys* (4 or 5) was smaller than that of the *Ictidomys* clade (6–8) and is probably plesiomorphic. The duration of reproduction was similar in *Cynomys* and the *Ictidomys* clade although gestation lengths were longer in *Cynomys*. For offspring mass, too few neonatal data ($n = 1$) were available to make comparisons for *Cynomys*. Individual weanlings were a similar percentage of maternal mass in *Cynomys* (22%) and the *Ictidomys* clade (24%), but litter mass at weaning was lower in *Cynomys* (110% versus 175%).

Like *Cynomys* and *Tamias*, *Marmota* tended to have long gestation lengths but the overall duration of reproduction in *Marmota* was similar to the later Old World and *Ictidomys* clades as well as the earlier *Otospermophilus* clade. The New World clade had decidedly shorter reproductive periods, both in gestation and lactation and hence overall. The distinctiveness of this short reproduction suggests that the trait is derived for the New World clade.

Comparisons of offspring size in *Marmota* versus the spermophiline clades were thwarted by sample size problems. Neonatal mass data were only available for 3 species of *Marmota* and no species in the Old World clade. Weaning mass data were available for 5 species of *Marmota* and 1 species in the Old World clade. Also, *Marmota* had the lowest energetic investment into offspring of the entire tribe suggesting that the way *Marmota* invests resources into reproduction is a derived trait.

In sum, comparisons across the spermophiline clade suggested 3 hypotheses. First, a litter size of 4 is probably basal for the group and thus the larger litter sizes in *Ammospermophilus* and the Old World, New World, and *Ictidomys* clades are derived. Second, the shorter reproduction of the New World clade is distinct and probably derived. Finally, the distinctly low investment into offspring biomass in *Marmota* is derived.

Overall Reproductive Patterns and Evolution

The 92 species of marmotines are all ground squirrels with similar locomotion, foraging, and habitat requirements, but with distinct reproductive strategies among genera. For instance, by not hibernating *Ammospermophilus* can channel resources into offspring and thus has the highest output of all marmotines. *Tamias* can hibernate and *Tamias* also has a high energetic investment into reproduction. *Tamis* is the only genus for which gestation length is influenced by body mass. Thus, *Tamias* is probably closer to the physiological limit of resource turnover than other genera.

Arctic and many temperate-zone marmotines live in areas with very short growing seasons. During this short season, they must reproduce and fatten up for the long winter. During the 1st half of the growing season, most of these squirrels devote their energy to reproduction. They then spend the 2nd half of the active season in efforts to fatten up for hibernation. The large-bodied *Marmota* exemplifies this pattern. *Marmota* is sharply seasonal and has few offspring with slow growth rates while under maternal care. Survival over the long hibernation period is clearly paramount for *Marmota*.

Reproduction in the highly social *Cynomys* does not stand out. Litter size is average; gestation and lactation are of average length. Growth rates and the energetic aspects of reproduction are most similar to those of large *Marmota*. Although all 5 species are large, *Marmota* are much larger and some *Spermophilus* are as large as *Cynomys*. Also, hibernation is a critical feature of marmot biology but is variable in *Cynomys*. Thus, body mass and seasonal climate patterns are not constraints to reproduction in *Cynomys*.

Reproductive investment in *Cynomys* and *Marmota* contrasts strongly with that in *Ammospermophilus* and *Tamias*. The energetic component of reproductive investment is much smaller in the larger prairie dogs and marmots than in the smaller

antelope ground squirrels and chipmunks. Reproduction is more expensive for the smaller genera.

Spermophilus is paraphyletic and *Ammospermophilus*, *Cynomys*, and *Marmota* are nested within spermophiline trees. For the group, litter size of 4 is probably basal and the larger litter sizes in *Ammospermophilus* and the Old World, New World, and *Ictidomys* clades are derived. Two other derived features are the low offspring biomass in *Marmota* and the short time between conception and weaning in the New World clade of *Spermophilus*.

In sum, marmotines are all ground squirrels with similar selection pressures. Like other squirrels, the energetic component of reproduction is more tightly tied to body mass than the temporal component. Marmotine genera differ in the number of offspring and the rate at which resources are put into these offspring. Basal litter size was 2 or 3 but increased to 4 early in the evolution of the group. Subsequent reproductive investment within marmotines followed 2 patterns: the larger *Cynomys* and *Marmota* reduced annual energetic investment, whereas the smaller *Ammospermophilus* and *Tamias* increased their investment into reproduction. Thus, body size is a key aspect in the diversification of reproductive patterns within Marmotini.

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