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REPRODUCTIVE EFFORT IN SQUIRRELS: ECOLOGICAL, PHYLOGENETIC, ALLOMETRIC, AND LATITUDINAL PATTERNS

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The distinctive features of reproduction in squirrels are the lack of allometric influences on the duration of reproductive investment; the strong allometric influences on offspring mass; and a trade-off between number and size of young, suggesting an important developmental component to reproduction. Lengths of gestation and lactation do not vary with body size but neonatal and weaning mass do. Apparently, the major constraint on reproduction in squirrels is not resources per se (food, calories, minerals, or water) but rather the length of time such resources are available. Squirrels adjust growth rate to fit the timing of resource abundance. Within the familial reproductive pattern, arboreal squirrels invest more into reproduction than do ground squirrels. Flying squirrels (Pteromyini) have a larger temporal investment into reproduction but a smaller energetic investment compared with other squirrels. Ground squirrels do not have a distinct reproductive profile, because marmotine and nonmarmotine ground squirrels differ. Marmotine ground squirrels have a small temporal investment and a large energetic investment on a per litter but not on an annual basis. Nonmarmotine ground squirrels have a reproductive pattern similar to that of tree squirrels, a pattern intermediate between marmotines and flying squirrels. Within this locomotor–ecological framework, reproductive patterns differ among subfamilies. Tribes differ in having few (2–4) versus many (4–8) young, and in the relative allocation of investment into gestation versus lactation. Specific environmental influences on reproduction in squirrels occur at lower taxonomic levels within the framework of a broad reproductive pattern set by earlier radiations into particular locomotor and nest-site niches.

Key words: flying squirrels, gestation, ground squirrels, lactation, litter size, reproduction, reproductive effort, reproductive investment, Sciuridae, tree squirrels

Differential reproduction is the essence of natural selection. Three major influences on reproduction are body size, ecological niche, and phylogenetic history. These factors operate in concert but may have greater or lesser effects in different groups. Three components of reproductive investment are number of offspring produced (litter size), energetic input into offspring (neonatal or weaning mass, litter mass at birth or at weaning), and time devoted to reproductive effort (gestation or lactation length, time from conception or mating to weaning). Selection will favor timing reproductive investment with patterns of energetic abundance and with patterns of mortality from animate (disease, predation) and inanimate (weather, climate) sources such that the largest number of healthy offspring result and the parent can produce subsequent litters.

The need versus the availability of energy is related to body size, thus reproductive measures often have an allometric component (Hayssen 1993; Hayssen and Kunz 1996; Hayssen et al. 1985; Jabbour et al. 1997). Natural selection has phylogenetic constraints because selection can only operate on traits present in the previous generation. Therefore, related species may show common reproductive patterns due to ancestry rather than adaptive evolution. Both allometric and phylogenetic constraints influence the evolution of reproduction in squirrels but the extent of these processes has not been assessed.

Previous studies (Armitage 1981; Emmons 1979; Heaney 1984; Levenson 1979; Lord 1960; Moore 1961; Morton and Tung 1971; Viljoen and Du Toit 1985; Waterman 1996) on reproduction in squirrels used few species and could not address phylogenetic constraints. These studies focused either on how the reproduction of a group of squirrels 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

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Tung 1971)) or on how the reproduction of a set of species compares to other squirrels facing contrasting constraints (litter size in 22 species from 5 geographic regions [Emmons 1979]; life-history traits in 6 species of Sciurini and 20 species of Marmotini versus climate [Heaney 1984]; litter size versus latitude in 10 species of tree and flying squirrels, 7 species of chipmunks, and 15 species of ground squirrels from North America [Lord 1960]; litter size in 17 species of tree squirrels from 4 climatic regions and litter size versus latitude in 25 species of nearctic Marmotini [Moore 1961]; neonatal and litter mass in 10 species of tree squirrels from 4 climatic regions [Viljoen and Du Toit 1985]; and reproductive biology of 26 species of nearctic and African tree and ground squirrels [Waterman 1996]). Although phylogenetic constraints could not be assessed in these taxonomically limited studies, the cogent analyses within each study were generalized to squirrels overall.

Here I present a broad investigation of reproduction in squirrels (Sciuridae) with reproductive data (chiefly litter size) available for 174 species. The family Sciuridae is a monophyletic lineage of 278 species with 3 distinct ecological profiles, 8 phylogenetic groupings, and body mass from 15 to 8,000 g. I explore how reproductive traits in squirrels (litter size, neonatal and weaning size, and gestation and lactation length) vary with respect to body size, ecological profile, phylogeny, and latitude. Specific predictions follow.

Allometric variation.—Adult squirrels range from 70 to 600 mm in head and body length and from 15 to 8,000 g in body mass (Hayssen 2008b). The smallest squirrels use all ecological niches and include 1 flying squirrel (lesser pygmy flying squirrel [*Petaurillus emiliae*]), 2 tree squirrels (African pygmy squirrel [*Myosciurus pumilio*] and least pygmy squirrel [*Exilisciurus exilis*]), and a ground squirrel (black-eared squirrel [*Nannosciurus melanotis*]). Of the very largest squirrels, only some flying squirrels (*Eupetaurus* and *Petaurista*) and some ground squirrels (*Marmota*) are >450 mm in head and body length. The largest tree squirrels are in the genus *Ratufa*. *Ratufa* and *Petaurista* (a flying squirrel) are of similar size and have comparable body mass; however, body mass within the genus *Marmota* (a ground squirrel) is greater than that of comparably sized flying squirrels, especially before hibernation.

Simple allometry suggests that larger squirrels should have larger neonates. If a trade-off exists between size and number of offspring then larger neonates may be part of smaller litters such that litter mass is constant. This trade-off has been found for mammals as a group (Charnov and Ernest 2006), but not specifically investigated in squirrels. All else being equal, larger neonates or weanlings or larger litter masses should take longer to produce and consequently larger squirrels should have longer periods of reproduction (gestation and lactation).

Ecological and energetic variation.—Sciurids occupy 3 major ecological or energetic niches with distinct profiles related to locomotion and location of nest site (Thorington and Ferrell 2006). Ground squirrels are diurnal, nest in burrows, reproduce in burrows, and forage on the ground. Ground squirrels have few adaptations for arboreal locomotion but can have significant adaptations for hibernation and torpor. Tree

squirrels are diurnal, nest in trees, reproduce in trees, and often forage in trees. Tree squirrels have strong adaptations for arboreal locomotion but fewer energetic adaptations for torpor compared with ground squirrels. Flying squirrels are nocturnal, nest in trees, reproduce in trees, and often forage in trees. Flying squirrels are the most adapted for arboreal and gliding locomotion and temperate forms have physiological adaptations for energy conservation in the form of torpor. Thus, the energetics, locomotion, and predation risk differ among the groups, but the 2 arboreal groups, tree and flying squirrels, have more similar ecological niches.

If ecological niche influences reproduction, the 3 ecomorphs would be expected to have distinct reproductive profiles. In addition, the 2 arboreal groups (tree and flying squirrels) should be more similar to each other in their energetic and temporal patterns of reproduction than either is to a reproductive pattern of ground squirrels.

Phylogenetic variation.—Phylogenetically, the 278 sciurid species are split into 8 groups: Callosciurinae, Marmotini, Protoxerini, Pteromyini, Ratufinae, Sciurillinae, Sciurini, and Xerini (Thorington and Hoffmann 2005). Phylogenetic influences on reproduction would be evident if individual tribes or subfamilies have distinctive reproductive profiles.

Latitude (climate).—Studies of squirrels (Heaney 1984; Lord 1960; Moore 1961; Viljoen and Du Toit 1985; Waterman 1996) have used latitude or broadly defined geographic units (neotropical, oriental, African, Ethiopian, tropical, temperate, nearctic, holarctic, or palearctic) to estimate the influence of climate on reproduction. Higher latitudes were correlated with increased litter size in squirrels (Lord 1960; Moore 1961). Also tropical, neotropical, Ethiopian, oriental, or African regions had smaller litter sizes and longer breeding seasons than palearctic, nearctic, or holarctic regions (Moore 1961; Viljoen and Du Toit 1985; Waterman 1996). Larger sample sizes would be expected to confirm these trends.

In sum, the goal of this paper is to assess the effects of allometry, ecology, phylogeny, and latitude on temporal and energetic components of reproductive investment in Sciuridae.

MATERIALS AND METHODS

Reproductive data.—Reproductive data were available for 173 species (62% of 278 species) but not all reproductive variables were available for all species (Appendix I). Litter size, gestation length, neonatal mass, lactation length, and weaning mass were obtained from Hayssen et al. (1993) supplemented by literature after 1992 and other sources (Appendix I). The litter size for *Funisciurus bayonii* has not been published and was obtained from a specimen label at the British Museum of Natural History (“3 emb”; BMNH 63.1081). Mean values were calculated, weighted by sample sizes when possible, after discarding obvious typographical errors and extreme estimates. Litter-size values combine counts of corpora lutea, embryos, placental scars, neonates, and offspring at nest or den emergence. Litter size at den emergence is more often available for marmotines than for other taxa. Reproductive data include those for yearling females as well as

adults. Composite reproductive measures were calculated as follows (with parenthetical units): duration of reproduction (days) = length of gestation + length of lactation; litter mass at birth (g) = litter size \times neonatal mass; litter mass at weaning (g) = litter size \times weaning mass; growth during gestation (g/day) = litter mass at birth/gestation length; growth during lactation (g/day) = (litter mass at weaning – litter mass at birth)/lactation length; overall growth during reproduction (g/day) = litter mass at weaning/duration of reproduction. Most data on litter size are from embryo counts, so litter mass at weaning using these litter-size data does not take postbirth mortality into consideration. Developmental state of neonates at birth, whether precocial or altricial, is a component of reproductive investment. Unfortunately, consistent data on this important facet of reproduction are not broadly available and this study does not address the precocial–altricial dimension.

The energetic component of reproduction (neonatal or weaning mass) is often assessed with greater precision than the temporal component (gestation or lactation length). For this study all temporal measures were converted to days. Neonatal and weaning mass are usually reported in grams and a single gram is usually a small percentage of the measured weight. In contrast, the units used to report gestation and lactation lengths are often weeks or months. Thus, a single unit (e.g., 1 week) may represent 25% of the reported measure (4 weeks). As units, weeks and months have little biological significance because most squirrels are unaware of our human measurement of time. The use of months is particularly awkward because a month can be 28–31 days. For this study, a month was converted to 30 days. Many gestation lengths of squirrels are reported as 4 weeks (which converts to 28 days) and suggest a uniformity and homogeneity in gestation length that is probably not natural. Measurement of reproductive stages with the units of weeks or months is not biologically meaningful and should be avoided.

Ecological classification.—Flying squirrels have gliding membranes between their limbs and their bodies. Tree and ground squirrels are classified according to the location of the nest in which young are most often born and raised. Species with fossorial nests were classified as ground squirrels. Species with arboreal nests were classified as tree squirrels.

Phylogeny.—No species-level phylogeny of the family Sciuridae has consensus. Taxonomy follows Harrison et al. (2003), Mercer and Roth (2003), Steppan et al. (2004), Herron et al. (2004), and Thorington and Hoffmann (2005). The following papers were used for particular groups: Heaney (1979—*Sundasciurus*), Harrison et al. (2003—ground squirrels), Herron et al. (2004—ground squirrels), Moore (1959—Sciurinae), and Thorington et al. (2002—Pteromyini). Analysis was across 8 taxa: Callosciurinae, Ratufinae, Sciurillinae, Sciurinae: Pteromyini, Sciurinae: Sciurini, Xerinae: Marmotini, Xerinae: Protoxerini, and Xerinae: Xerini. I use the term “tribal effects” to refer to phylogenetic effects across these 8 taxa.

Latitude.—Latitude was evaluated as the midpoint of the latitudinal range. This is a standard measure but is especially awkward for species with disjunct northern and southern distributions, for example, *Sciurus aberti*, for which the midpoint

lies outside the known distribution. An additional complication is that high-latitude areas generally lack arboreal habitats, thus ecomorph and latitude are confounded. Latitude was evaluated from range data in *Mammalian Species* accounts, Corbet and Hill (1992—Indomalaysia), Emmons (1990—Neotropics), Kingdon (1997—Africa), and Thorington and Hoffmann (2005).

Allometric analyses.—Body mass was used to investigate allometric effects on reproduction. Body-mass data were available for 166 (96%) of the 173 species with reproductive data (Hayssen 2008b). Mass of females was used preferentially ($n = 139$ species). If mass of females was not available, mass of adults was used ($n = 34$ species).

Body mass was not available for 7 species and was estimated from head–body length using the following equation (Hayssen 2008b): $\log_{10} \text{mass} = -4.30 + 2.91(\log_{10} \text{head–body length}) - 0.07$ (Pteromyini). This equation is based on data from more than 4,000 squirrels from 233 species and has an R^2 of 97.2%. The estimated body masses are as follows: *Funambulus sublineatus* (Callosciurinae; head–body length 110 mm, estimated mass 44 g), *Marmota camtschatica* (Xerinae, Marmotini; head–body length 508 mm, estimated mass 3,764 g), *Paraxerus flavovittis* (Xerinae, Protoxerini; head–body length 171 mm, estimated mass 157 g), *Spermophilus alashanicus* (Xerinae, Marmotini; head–body length 199 mm, estimated mass 247 g), *Spermophilus major* (Xerinae, Marmotini; head–body length 260 mm, estimated mass 537 g), *Spermophilus relictus* (Xerinae, Marmotini; head–body length 236 mm, estimated mass 404 g), and *Trogopterus xanthipes* (Sciurinae, Pteromyini; head–body length 310 mm, estimated mass 754 g). During the final preparation of this manuscript, body-mass data for *M. camtschatica* became available (Armitage and Blumstein 2002). The average mass of *M. camtschatica* at immergence and emergence from hibernation is 3,824 g. This value is 98.4% of the estimated value above. The close fit between the observed and estimated values leads support to validity of the above equation.

Statistical analyses.—Both traditional statistical models and phylogenetic independent contrasts (PICs) were used for allometric analyses and are reported when samples sizes were >5 species. Common-log transformations were performed to improve symmetry of distributions across species (Hoaglin et al. 1983). Some extreme outliers were not used but no more than 3% of the data was removed from a given analysis. The “Results” section lists any species excluded from an analysis. Sample sizes are numbers of species.

Traditional statistical treatment was by a variety of general linear models (GLMs; Minitab version 15.1, Minitab Inc., State College, Pennsylvania) including 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). Phylogeny was assessed either by analysis of variance with the 8 subfamilies and tribes as levels or using $n - 1$ taxa as independent explanatory variables, with Marmotini as the normative taxon (these 2 analyses yield the same sums of squares but provide different output in Minitab). Interaction effects were tested by

partial F -statistics and are reported if significant. If not significant ($P > 0.05$ or $R^2 < 3\%$), interaction effects were withdrawn from the models. Type III sums of squares or stepwise multiple regressions were used to assess significance of individual tribes and subfamilies ($\alpha = 0.05$). R^2 values are provided only for regression models with $P < 0.05$.

For all the major reproductive variables (litter size; gestation and lactation lengths; and 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 generic phylogeny in Mercer and Roth (2003) supplemented by species information from Herron et al. (2004), Thorington and Hoffmann (2005), and *Mammalian Species* accounts. Branch lengths were assigned by the method of Pagel (1992). Results for these analyses are preceded by the label “PIC.”

RESULTS

The goal of this paper was to assess patterns of reproduction in squirrels related to body size, ecological profile, phylogeny, and latitude. Overall, allometric effects strongly influence mass at birth and weaning, whereas phylogenetic effects have a prominent influence on litter size, gestation length, and lactation length (Figs. 1 and 2). Ecomorph and latitude have only slight effects on reproduction. The reproductive profile of Marmotini is distinctive (large litter size and short gestation and lactation) and dominates trends for squirrels overall. Marmotines often comprise a majority of the reproductive data for not only ground squirrels but for all sciurids. Thus, analyses on sciurids as a group and especially for ground squirrels as an ecomorph are strongly influenced by the reproductive character of marmotines. Specific details follow.

Reproductive Patterns: Allometric, Phylogenetic, Ecological, and Latitudinal Trends

The results for reproduction are presented in the following order: litter size; gestation length; lactation length; gestation plus lactation length; neonatal mass, litter mass at birth, and annual neonatal output; and weaning mass, litter mass at weaning, and annual weaning output. For each reproductive variable, the major quantitative results and descriptive statistics are summarized and followed by supporting statistical details for allometric, ecological, latitudinal, or phylogenetic effects. Results are put into a larger context in the “Discussion” section. Also in the “Discussion” section are reproductive profiles for individual taxa. More detailed analyses for Marmotini are given in Hayssen (2008a).

Litter size.—The major results from the analyses of litter size (Figs. 1A and 1B) are that marmotines have larger litter sizes than other sciurids; litter size in Pteromyini is negatively correlated with body mass; ecomorph does not influence litter size; and litter size increases with latitude in Callosciurinae and Sciurini.

Litter-size data were obtained for 171 species representing all 8 taxa (36–100% of the species within each taxon; Marmotini is 48% of the data). Average litter size varies from 1 to 9.7 and

is slightly right skewed with a median litter size of 3.5, a mean litter size of 3.8, and 2 outliers (*Ammospermophilus interpres*, 9.5; and *A. nelsoni*, 9.7). Fifty percent of squirrel species have litters of 2.2–4.9 offspring. Log₁₀ transformations produce a more symmetrical distribution with a slight left skew and no outliers.

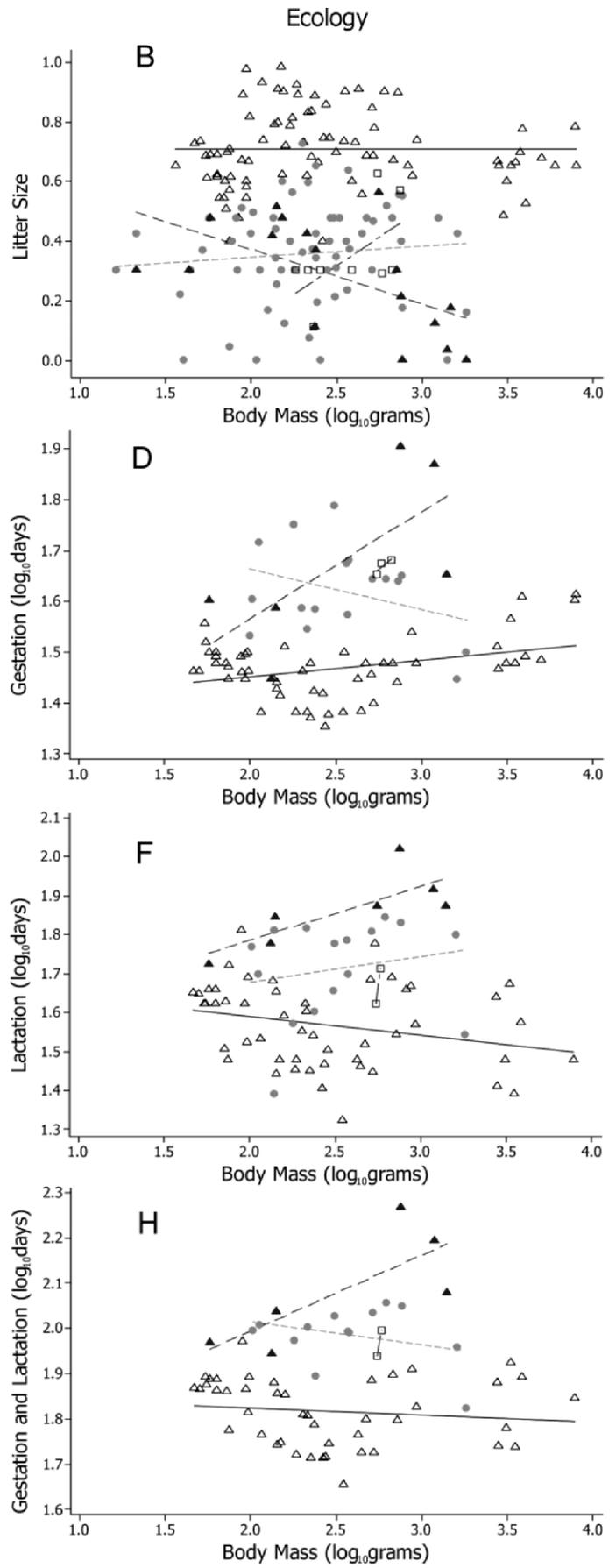
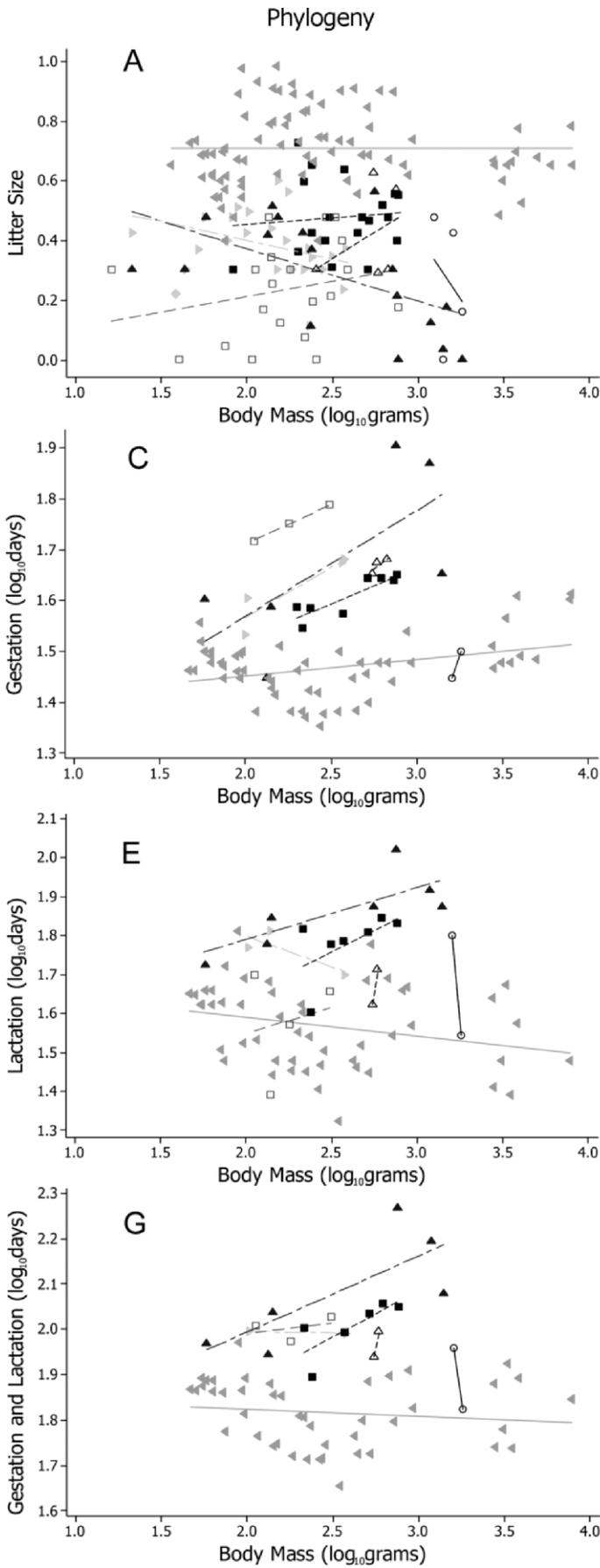
Allometric, phylogenetic, and ecological effects: Taxa differ (Fig. 1A). Analysis of litter size (Fig. 1; $n = 171$) indicates slight interaction effects between body mass and individual tribes (GLM: $P = 0.046$) that account for 2.6% of the variation in litter size. Litter size is not related to maternal mass (GLM: $P = 0.32$; PIC: $P = 0.72$). For the 5 taxa with litter sizes for 15 or more species, allometric relationships vary. Litter size has no relation with body mass for Sciurini ($n = 19$, $P = 0.7$), Protoxerini ($n = 20$, $P = 0.3$), and Marmotini ($n = 82$, $P = 0.96$) but is negatively correlated with body mass for Pteromyini ($n = 17$, $P = 0.016$, $R^2 = 29\%$) and perhaps Callosciurinae ($n = 23$, $P = 0.1$). Tribal effects account for 66.5% of the variation in litter size (GLM: $P < 0.0005$). Mean litter size for the tribe Marmotini (5.3, $n = 82$ species) is higher than that for other taxa. Overall, litter size for nonmarmotines ranges from 1.7 (Sciurillinae, $n = 1$ species) to 3.1 (Sciurini, $n = 19$ species).

Allometric effects with respect to ecomorph (Fig. 1B) are only those related to flying squirrels (Pteromyini, $n = 17$, negative correlation, $P = 0.016$, $R^2 = 29\%$); litter size and body mass are not correlated for tree ($n = 58$, $P = 0.3$) or ground ($n = 96$, $P = 1.0$) squirrels.

Latitude: Across all squirrels, litter size is higher at higher latitudes (regression: $n = 171$, $P < 0.0005$, $R^2 = 52\%$; PIC: $P = 0.009$, $R^2 = 4\%$). Marmotines have large litter sizes and are the predominant species at high latitudes. Thus, the litter size–latitude relationship is strongly influenced by marmotines. Without marmotines, the percent of variation in litter size explained by latitude drops from 52% to 21%. Across ecomorphs, litter size increases with latitude in tree ($n = 58$, $P < 0.0005$, $R^2 = 43\%$) and ground ($n = 96$, $P < 0.0005$, $R^2 = 45\%$) squirrels, but not flying squirrels ($n = 17$, $P = 1.0$). Within taxa, latitudinal gradients exist for Callosciurinae ($n = 23$, $P < 0.0005$, $R^2 = 42\%$) and Sciurini with a particularly tight correlation ($n = 19$, $P < 0.0005$, $R^2 = 75\%$), but not for Marmotini ($n = 82$, $P = 0.1$), Protoxerini ($n = 20$, $P = 0.6$), or Pteromyini ($n = 17$, $P = 1.0$).

The positive correlation of litter size with latitude is the only trend observed for squirrels overall but not observed for marmotines in particular. However, marmotines are responsible for the overall correlation because all the high-latitude ground squirrels are marmotines and marmotines have large litter sizes. Thus, the positive correlation of latitude and litter size in ground squirrels is influenced by marmotines, even though within marmotines latitude and litter size are not correlated.

Gestation length.—The major results for gestation length (Figs. 1C and 1D) are that taxonomic differences are significant (gestation length is short for Marmotini and Ratufinae but is longer for other taxa); gestation length increases with body mass for most taxa but not for squirrels overall because the largest squirrels (Marmotini and Ratufinae) have the shortest



gestations; ecomorph has no influence on gestation; and latitude has no influence on gestation.

Data were obtained from 80 species representing 7 of the 8 taxa (no data were available for Sciurillinae, 68% of the data are from marmotines). Gestation is known for only 4 of 64 Callosciurinae. Gestation length ranges from 22 to 80 days, with a mean of 34.6 days, and a median of 31 days.

Allometry: For gestation length ($n = 80$; Figs. 1C and 1D) interaction effects between body mass and individual genera are significant (GLM: $P = 0.02$, $R^2 = 6\%$) because *Ratufa* and *Marmota* are large squirrels with short gestation lengths. Without Ratufinae and Marmotini, gestation length increases with increasing mass (GLM: $n = 24$, $P = 0.014$, $R^2 = 21\%$) but if squirrels are taken as a whole the relationship is much reduced (GLM: $n = 80$, $P = 0.053$, $R^2 = 5\%$; PIC: $P = 0.027$, $R^2 = 6\%$). Thus, tribal effects are significant (GLM: $n = 80$, $P < 0.0005$, $R^2 = 64\%$).

Phylogenetic comparisons: Taxa vary in absolute body mass and in the extent to which gestation is related to body mass (Fig. 1C). Marmotini and Ratufinae have shorter gestation lengths ($\bar{X} = 29$ –30 days) than other taxa ($\bar{X} = 41$ –57 days), both absolutely and relative to body mass (Fig. 1B). Sciurini have the next shortest gestation lengths and they are tightly correlated with body mass. For Marmotini, body mass of females ($n = 54$, $P = 0.009$) accounts for only 11% of the variation in pregnancy length, whereas mass of females accounts for 74% of the variation in gestation length for Sciurini ($n = 8$, $P = 0.004$). Thus, gestation length is about 7 times more tightly related to body mass in Sciurini than in Marmotini.

The longest gestation lengths relative to body mass are in Protoxerini (Fig. 1C), but these 3 data points represent only 10% of the taxon. Data for the 6 flying squirrels (of a possible 44 Pteromyini) are disjunct because they represent 3 small-bodied species and 3 large-bodied species. The allometric regression from these disjunct data ($n = 6$, $P = 0.13$) is most similar to Callosciurinae, and both Pteromyini and Callosciurinae are intermediate between Protoxerini and Sciurini. The African ground squirrels in the tribe Xerini have gestation lengths slightly longer than those of similarly sized tree squirrels of the tribe Sciurini.

Ecological comparisons (Fig. 1D): All Xerini and Marmotini are ground-dwelling squirrels but gestation length in Xerini is more than 50% longer (47 versus 30 days) than in marmotines, and xerine gestation lengths are similar to those of arboreal (tree or flying) squirrels of the same size. Ratufinae, Protoxerini, and Sciurini are composed primarily of tree squirrels but mean gestation length in Protoxerini ($n = 3$, 57

TABLE 1.—Lactation as a percentage of the time from conception to weaning. Average for all 65 species is 55.8%.

	n	\bar{X} (%)	Median (%)
Taxon			
Ratufinae	2	60.9	60.9
Sciurillinae	0		
Sciurinae			
Sciurini	6	59.9	60.8
Pteromyini	6	60.2	59.7
Callosciurinae	2	55.1	55.1
Xerinae			
Xerini	2	50.2	50.2
Protoxerini	3	43.8	42.5
Marmotini	44	55.5	56.0
Ecomorph			
Ground	46	55.3	55.6
Tree	13	55.6	59.3
Flying	6	60.2	59.7

days) is 40% longer than in Sciurini ($n = 8$, 41 days), and that for Ratufinae ($n = 2$, 30 days) is 40% shorter than for Sciurini. Also, gestation lengths for Marmotini (ground squirrels) and Ratufinae (tree squirrels) are the same. Gestation lengths for flying squirrels are intermediate. Thus, no ecological patterns are present in gestation length.

Latitude: Latitude does not have an independent influence on gestation length (GLM: $P_{\text{latitude}} = 0.64$; PIC: $P = 0.43$). Using stepwise regression with gestation length as the dependent variable and body mass (common log), latitude (absolute value), and individual tribes as possible predictors, the order of significant predictors is Marmotini (high latitude, short gestation), Ratufinae (low latitude, short gestation), body mass, Protoxerini (low latitude, long gestation), and Sciurini (high latitude, intermediate gestation). Thus, short and long gestations are found at both high and low latitudes.

Lactation length.—The major results for lactation length (Figs. 1E and 1F) are that lactation is short in Marmotini and Protoxerini and long in Pteromyini; for Sciurini (*Sciurus*) and Pteromyini, heavier species have longer lactation; flying squirrels (Pteromyini) have long lactations tied to body mass but no other ecomorph trends are significant; and lactation is not related to latitude.

Data were obtained from 75 species representing 7 of the 8 taxa (no data were available for Sciurillinae; two-thirds of the data are from marmotines). Lactation length ranges from 21 to 105 days, with a mean of 45.0 days, and a median of 42.0 days. Across tribes, lactation is 44–61% of the time from conception to weaning (Table 1).

←

FIG. 1.—Litter size (top row, A, B; \log_{10} , $n = 171$), gestation length (2nd row, C, D; \log_{10} days, $n = 80$), lactation length (3rd row, E, F; \log_{10} days, $n = 75$), and gestation plus lactation (bottom row, G, H; \log_{10} days, $n = 65$) versus body mass (\log_{10} g) illustrating phylogenetic (left) or ecological (right) trends. Key to taxa: Callosciurinae (gray right-facing triangles), Marmotini (black left-facing triangles), Protoxerini (open squares), Pteromyini (black upright triangles), Ratufinae (open circles), Sciurillinae (gray diamond), Sciurini (black squares), Xerini (open triangles). Key to ecomorphs: marmotine ground squirrels (open triangles), nonmarmotine ground squirrels (open squares), tree squirrels (closed circles), flying squirrels (closed triangles).

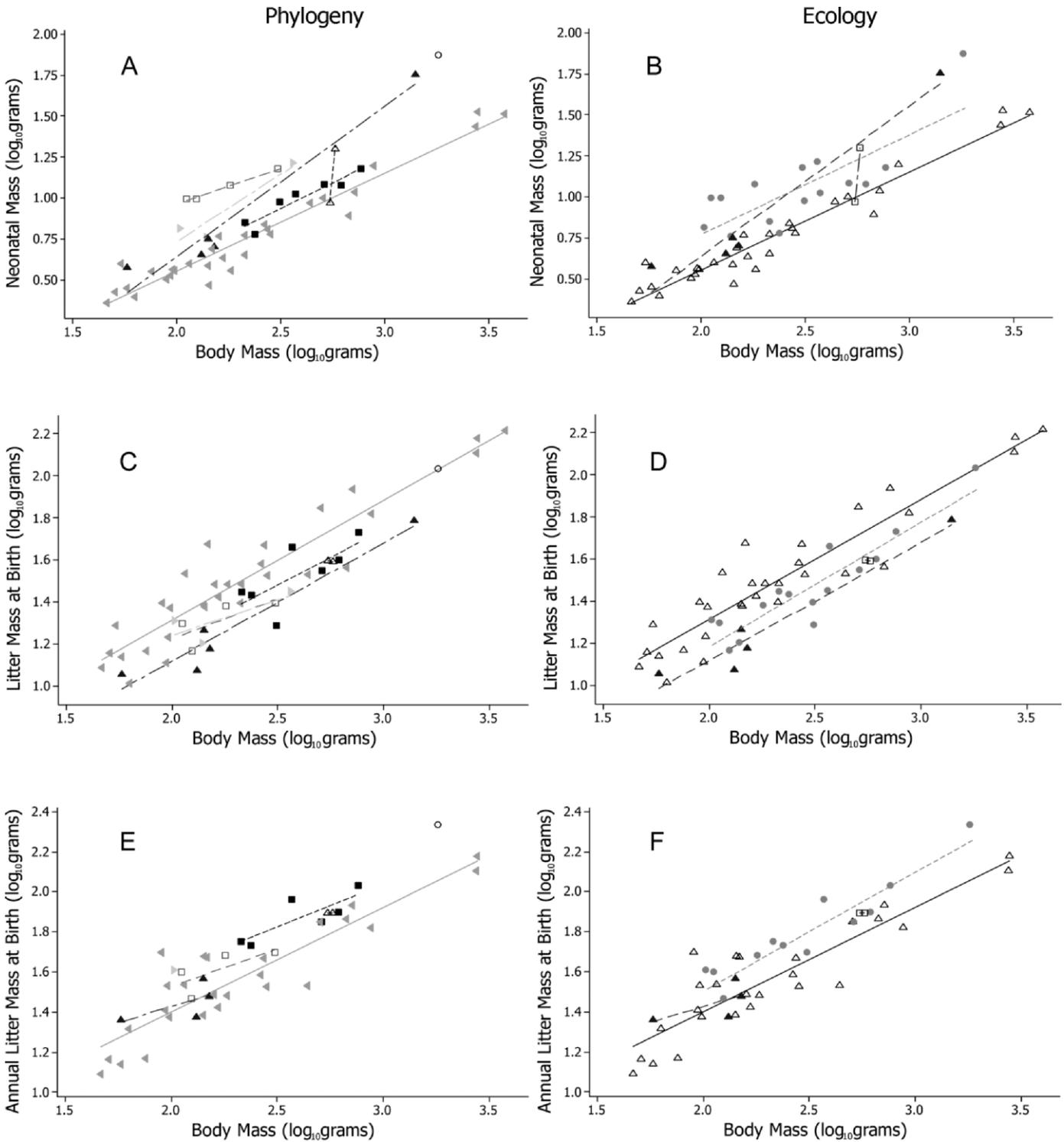


FIG. 2.—Neonatal mass (top row, A, B; $n = 52$), litter mass at birth (middle row, C, D; $n = 52$), and annual litter mass at birth (bottom row, E, F; $n = 44$) versus body mass (all in \log_{10} g) illustrating phylogenetic (left) or ecological (right) trends. Key to taxa: Callosciurinae (gray right-facing triangles), Marmotini (black left-facing triangles), Protoxerini (open squares), Pteromyini (black upright triangles), Ratufinae (open circles), Sciurillinae (gray diamond), Sciurini (black squares), Xerini (open triangles). Key to ecomorphs: marmotine ground squirrels (open triangles), nonmarmotine ground squirrels (open squares), tree squirrels (closed circles), flying squirrels (closed triangles).

Allometry and phylogenetic comparisons: For lactation (Figs. 1E and 1F) neither interaction (GLM: $P = 0.23$) nor body mass (GLM: $P = 0.23$; PIC: $P = 0.12$) effects are significant, but tribal effects (GLM: $P < 0.0005$, $R^2 = 51\%$)

are significant ($n = 75$ species). Lactation in most squirrel taxa is 47–61 days. However, short lactations typify marmotines ($\bar{X} = 38.0$, median = 37.2, $n = 50$, 54% of marmotines) and protoxerines ($\bar{X} = 39.3$, median = 41.3, $n = 2$, 50% of proto-

xerines), whereas long lactations are characteristic for Pteromyini ($\bar{X} = 74.3$, median = 74.7, $n = 7$, 16% of Pteromyini). Lactation in Sciurini and Pteromyini is positively correlated with body mass and may have a slight negative correlation with mass in Marmotini (Sciurini: $n = 5$ species of *Sciurus* after removing *Sciurus lis* and *Tamiasciurus hudsonicus*, $P = 0.028$, $R^2 = 79\%$; Pteromyini: $n = 7$, $P = 0.039$, $R^2 = 53\%$; Marmotini: $n = 50$, $P = 0.071$, $R^2 = 4.7\%$).

Ecological comparisons (Fig. 1F): Marmotines are ground squirrels and have short lactation lengths ($\bar{X} = 38$ days) and pteromyines are flying squirrels and have long lactation lengths ($\bar{X} = 74$ days). But ground squirrels do not uniformly have short lactations. Xerines are ground-dwelling squirrels and mean lactation length for the 2 xerines is longer (47 days) than that for marmotines (38 days). In addition, protoxerines are tree squirrels and the short lactation lengths for these 4 species ($\bar{X} = 39$ days) are exactly within the range of variation of marmotine ground squirrels of similar size. Lactations in other taxa of tree squirrels, Ratufinae ($n = 2$; 35 and 63 days) and Sciurini ($n = 7$, $\bar{X} = 61$ days), are intermediate to those of marmotines and pteromyines. Callosciurinae is a speciose subfamily with 64 species that include ground- and tree-nesting ecomorphs; unfortunately, lactation data are only available for 3 species ($\bar{X} = 58$ days). Thus, flying squirrels have long lactation lengths, but no other ecological trends are apparent.

Latitude: Overall lactation is shorter at higher latitudes in squirrels ($n = 75$, $P = 0.012$, $R^2 = 7\%$) but not when phylogeny is taken into consideration (GLM: $P_{\text{latitude}} = 0.37$; PIC: $P = 0.28$). The overall effect is primarily because marmotines have short lactation lengths and are predominately found at higher latitudes. Without Marmotini, lactation is longer at higher latitudes (GLM: $n = 25$, $P = 0.035$, $R^2 = 14\%$) and protoxerines have a great influence because they have short lactations and are from lower latitudes. In fact, removing a single protoxerine, the equatorial African *Paraxerus ochraceus* with a 24.5-day lactation, removes the significance (GLM: $n = 24$, $P = 0.14$). Within taxa, lactation has no relation to latitude in Sciurini (GLM: $n = 7$, $P = 0.93$) or Pteromyini (GLM: $n = 7$, $P = 0.54$). Lactation is negatively correlated with latitude in Marmotini (GLM: $n = 50$, $P = 0.041$) but removing the highest latitude species, *Spermophilus parryii* from 65°N, removes the significance (GLM: $n = 49$, $P = 0.09$). Thus, lactation lengths characteristic for individual taxa generate higher-level (e.g., tribal) latitudinal trends that do not reflect patterns for component taxa (e.g., genera).

Gestation length compared with lactation length.—Across squirrel taxa, gestation length is from 30% shorter to 30% longer than lactation length. For most squirrel taxa, gestation is shorter than lactation (Callosciurinae: gestation 42 days, $n = 4$, lactation 58 days, $n = 3$; Ratufinae: gestation 30 days, $n = 2$, lactation 49 days, $n = 2$; Pteromyini: gestation 51 days, $n = 6$, lactation 74 days, $n = 7$; Sciurini: gestation 41 days, $n = 8$, lactation 61 days, $n = 7$; Marmotini: gestation 30 days, $n = 54$, lactation 38 days, $n = 50$). Thus, gestation is two-thirds the length of lactation in Ratufinae, Pteromyini, and Sciurini and 80% the length of lactation in Callosciurinae and Marmotini. Xerini have equal gestation and lactation lengths (47 days, $n = 2$

or 3). Protoxerini are distinct because gestation is 30% longer than lactation (gestation: 57 days, $n = 3$, lactation 39 days, $n = 2$).

Gestation plus lactation length.—The total time devoted by a female to offspring is the length of gestation plus the length of lactation, that is, the time between conception and weaning. The major results (Figs. 1G and 1H) for this interval are that marmotines devote the least and pteromyines (flying squirrels) devote the most time to reproduction; the time invested in reproduction does not have a consistent relationship with body mass for squirrels overall but Sciurini and Pteromyini exhibit a small positive correlation with body mass; arboreal squirrels have longer reproductive intervals than ground squirrels (except for Ratufinae); and for most squirrels latitude does not influence the time devoted to reproduction, but within Marmotini reproduction is shorter at higher latitudes.

Data were obtained from 65 species representing 7 of the 8 taxa (no data were available for Sciurillinae; 44 of the 65 species are marmotines). Gestation plus lactation length ranges from 45 to 185 days, with a mean of 79.0 days, and a median of 75.0 days.

Allometry and phylogenetic trends: Across squirrels, the time between conception and weaning is not related to body mass (regression: $n = 65$, $P = 0.66$; PIC: $P = 0.16$; Figs. 1G and 1H). Marmotini have the shortest interval ($\bar{X} = 66.5$ days, median = 66 days, range 45–94 days, $n = 44$) and Pteromyini have the longest interval ($\bar{X} = 125.2$ days, median = 114 days, range 88–185 days, $n = 6$). The 2 *Ratufa* have intervals of 66 and 91 days ($\bar{X} = 79$ days). The 2 xerines have intervals of 87 and 99 days ($\bar{X} = 93$ days). Callosciurines are represented by only 2 species of a possible 64; these 2 devote 98–99 days to gestation and lactation. On average, Sciurini and Protoxerini devote 101 and 102 days to reproduction, respectively (Sciurini, range 78–114 days, median = 105 days, $n = 6$; Protoxerini, range 94–107 days, median = 102 days, $n = 3$). Only 3 taxa have sufficient species for regression against body mass. Data exist for 6 Sciurini: 5 *Sciurus* and 1 *Tamiasciurus*. For these 6, gestation plus lactation length may increase with increasing body mass (GLM: $n = 6$, $P = 0.08$, $R^2 = 48\%$), for the 5 *Sciurus* alone this trend is definitive (GLM: $n = 6$, $P = 0.012$, $R^2 = 88\%$). For Pteromyini, the 6 species representing 4 genera suggest that time devoted to offspring increases with body mass (GLM: $P = 0.08$, $R^2 = 48\%$). However, for marmotines, the length of reproduction has no relationship with body mass (GLM: $n = 44$, $P = 0.40$).

Ecological comparisons (Fig. 1H): Generally, arboreal squirrels spend more time on reproduction than ground squirrels and flying squirrels have longer intervals than tree squirrels. But most ground squirrels are marmotines with exceptionally short reproductive intervals. Two nonmarmotine ground squirrels, *Xerus*, have shorter reproductive intervals for their body mass than arboreal squirrels. So the result still holds. However, the trend does not hold for the 2 giant tree squirrels, *Ratufa*. These arboreal squirrels have much shorter reproductive intervals than expected for their body mass based on reproductive lengths for other tree or flying squirrels.

Latitude: Overall, squirrels spend less time on their offspring at higher latitudes (GLM: $n = 65$, $P < 0.0005$, $R^2 = 18\%$), but when phylogenetic effects are removed the pattern is not present (GLM: $P_{\text{latitude}} = 0.36$; PIC: $P = 0.61$). The high-latitude Marmotini with short intervals strongly influences the result. Excluding Marmotini, latitude does not influence the time between conception and weaning in squirrels (GLM: $n = 21$, $P = 0.20$). Latitude is not significantly correlated with the reproductive interval in Sciurini (GLM: $n = 6$, $P = 0.71$) or Pteromyini (GLM: $n = 6$, $P = 0.47$). In Marmotini, the interval between conception and birth is shorter at higher latitudes (GLM: $n = 44$, $P = 0.002$, $R^2 = 19\%$; *Tamias* is an exception with equal or longer intervals at higher latitudes).

Neonatal mass, litter mass at birth, and annual neonatal output.—The major results (Fig. 2) are as follows. Body mass accounts for most (80–90%) of the variation in neonatal and litter mass at birth and across all squirrels ($n = 52$; Figs. 2A–2D), individual neonates are approximately 3.5% and litters approximately 14.2% of the mass of females. Larger species have relatively smaller litter mass at birth (Table 2). Taxonomic units (subfamilies or tribes and genera within them) have idiosyncratic neonatal and litter mass (Figs. 2A and 2C). Sciurini, Marmotini, and Xerini have the smallest neonates and Protoxerini has the largest. Marmotini has the highest litter mass and Pteromyini the lowest. Median litters per year for Marmotini is less than other taxa, but annual output at birth relative to the mass of the female does not differ across taxa or ecomorphs (Figs. 2E and 2F). Ratufinae and Xerini have the lowest annual output, whereas Callosciurinae has the highest. Overall, arboreal squirrels tend to have larger neonates but smaller litter mass than ground squirrels (Figs. 2B and 2D). In addition, arboreal squirrels tend to have larger annual output because more often they attempt >1 litter per year (Fig. 2F). Latitude has no consistent relationship with neonatal mass.

Data for neonatal mass were obtained from 52 species representing 7 of the 8 taxa (no data were available for Sciurillinae; 30 of the 52 species are marmotines). Data on number of litters per year were available for 44 (26 of which are marmotines) of the 52 species allowing calculation of annual energetic output (litter mass \times litters/year).

Allometric and phylogenetic trends: Unlike gestation and lactation, allometric relationships for neonatal mass are similar for squirrels overall and for individual taxa (Fig. 2A). Across squirrels (Figs. 2A and 2B), neonatal mass and the mass of females are strongly and positively correlated (regression: $n = 52$, $P < 0.0005$, $R^2 = 78\%$; PIC: $P < 0.0005$, $R^2 = 75\%$), as are litter mass at birth and the mass of females (regression: $n = 52$, $P < 0.0005$, $R^2 = 81\%$; PIC: $P < 0.0005$, $R^2 = 63\%$) and annual output (litter mass \times litters/year; regression: $n = 44$, $P < 0.0005$, $R^2 = 80\%$; PIC: $P < 0.0005$, $R^2 = 57\%$). Phylogeny has a significant but smaller effect after removing maternal mass (GLM: neonatal mass, $P_{\text{phylogeny}} < 0.0005$, $R^2 = 14\%$; litter mass, $P_{\text{phylogeny}} = 0.002$, $R^2 = 7\%$; annual litter mass, $P_{\text{phylogeny}} = 0.024$, $R^2 = 6\%$).

Strong and positive relations are observed within taxa between neonatal and maternal mass (Fig. 2A). Neonatal mass and the mass of females are tightly correlated for the 3 taxa

TABLE 2.—Neonatal mass and litter mass at birth as percentages of the mass of female sciurids. Neonatal mass and litter mass at birth are strongly correlated with maternal mass but exhibit no clear patterns relative to ecomorph or taxonomy.

Taxon	Neonatal mass			Litter mass at birth		
	<i>n</i>	\bar{X} (%)	Median (%)	<i>n</i>	\bar{X} (%)	Median (%)
Ratufinae	1	4.2	4.2	1	6.0	6.0
Sciurillinae	0			0		
Sciurinae						
Sciurini	7	2.6	2.5	7	9.1	7.0
Pteromyini	5	4.3	4.0	5	11.2	9.9
Callosciurinae	3	5.0	4.5	3	13.0	11.5
Xerinae						
Xerini	2	2.6	2.6	2	7.0	7.0
Protoxerini	4	7.1	7.3	4	12.7	12.5
Marmotini	30	3.0	2.6	30	17.0	16.5
Ecomorph						
Ground	32	2.9	2.6	32	16.4	16.1
Tree	15	4.4	4.2	15	10.6	11.4
Flying	5	4.3	4.0	5	11.2	9.9

with data for at least 5 species, but Pteromyini has a much steeper slope (0.93), about 50% greater than that of Sciurini (0.63) or Marmotini (0.60; Pteromyini: $n = 5$, $P = 0.005$, $R^2 = 93\%$; Sciurini: $n = 7$, $P = 0.001$, $R^2 = 87\%$; Marmotini: $n = 30$, $P < 0.0005$, $R^2 = 94\%$). Allometry of litter mass (Figs. 2C and 2D) is nearly identical (slopes 0.5–0.6) across taxa but the correlation is less tight for Sciurini and not significant (Pteromyini: $n = 5$, $P = 0.007$, $R^2 = 91\%$; Sciurini: $n = 7$, $P < 0.068$, $R^2 = 42\%$; Marmotini, $n = 30$, $P < 0.0005$, $R^2 = 94\%$). Pteromyini have the smallest litters relative to body size and Marmotini have the largest. Only Sciurini and Marmotini had sufficient data for analysis of annual output. Allometry was similar (slopes 0.4–0.5) for the 2 taxa but Sciurini had a larger annual output, which was less tightly correlated with the mass of females (Sciurini: $n = 6$, $P = 0.042$, $R^2 = 60\%$; Marmotini: $n = 26$, $P < 0.0005$, $R^2 = 80\%$).

Latitude: The significance of latitude in explaining neonatal and litter mass in squirrels is not robust. Overall, neonatal mass is smaller at higher latitudes (multiple regression: $n = 52$, $P_{\text{latitude}} < 0.0005$, $R^2 = 8\%$) but this is due to phylogenetic effects because the phylogenetic independent contrasts analysis is not significant (PIC: $P = 0.74$). Protoxerini have heavy neonates and are equatorial, whereas Marmotini have small neonates and are from high latitudes. Removing Marmotini reduces the significance to 0.014 (multiple regression: $n = 22$, $R^2 = 6\%$). Removing both groups eliminates the significance (multiple regression: $n = 18$, $P_{\text{latitude}} = 0.1$). Although individual neonates are smaller, litters at birth are heavier at higher latitudes (multiple regression: $n = 52$, $P_{\text{latitude}} < 0.0005$; PIC: $P = 0.017$, $R^2 = 11\%$). As with neonatal mass, Marmotini strongly influences the result because marmotines have the heaviest litters and are the predominate species at higher latitudes. Removing marmotines reduces the significance to 0.015 ($n = 18$). Sciurini may have larger litter mass at birth at higher latitudes ($n = 7$, $P_{\text{latitude}} = 0.006$), but the data are

influenced by the sole equatorial squirrel (*Sciurus granatensis*) and removing this species removes the significance ($n = 6$, $P_{\text{latitude}} = 0.08$).

Relative neonatal or litter mass: Because small sample sizes for most taxa make allometric analysis by regression unreliable, percentage of neonatal or litter mass relative to the mass of females was evaluated (Table 2). Neonatal mass ranges from 2.3 to 75.3 g and represents 0.9–8.9% of the mass of females. Mean neonatal mass is 10.9 g (median = 6.3 g). Mean percent relative to the mass of females is 3.5% (median = 3.3%). Litter mass ranges from 10.3 to 165 g and represents 4.4–36.0% of the mass of females. Mean litter mass is 38.3 g (median = 27.6 g). Mean percent of litter mass relative to the mass of females is 14.2% (median = 13.1%). Relative litter mass at birth is smaller for larger species (GLM: $n = 52$, $P < 0.0005$, $R^2 = 58\%$), such that litter mass is 20% of adult mass for a 100-g squirrel but only 7% of adult mass for a 1,000-g squirrel.

Taxa vary (Table 2): Several taxa have small neonates, Sciurini and Xerini (2.6%) and Marmotini (3.0%). Only 1 tribe has larger neonates, Protoxerini (7.2%). The smallest litter masses at birth occur in Ratufinae (6.0%) and Xerini (7.0%), whereas the largest litter mass occurs in Marmotini (17%). For most taxa neonatal mass and litter size appear to trade off (i.e., species with smaller neonates have a larger litter size). Xerini is an exception with both the smallest neonates and smallest litter mass. Many squirrels can attempt >1 litter per year. Thus, annual reproductive output can be estimated by litter mass \times litters/year. Across squirrels, mean annual neonatal output is 21.4% (median = 19.2%, $n = 44$) of the mass of females and is not statistically different across taxa (GLM: $n = 44$, $P = 0.38$). Ratufinae ($n = 1$, 12.0%) and Xerini ($n = 2$, 13.9%) have lower annual output, whereas Callosciurinae ($n = 1$, 39.7%) has a higher output. Reproductive output for the other 4 taxa is 19.1–25.4% of the mass of females with wide variation.

Ecological differences in relative neonatal or litter mass (Figs. 2B, 2D, and 2F): Ecomorph comparisons are confounded by phylogeny because most ground squirrels are marmotines and flying squirrels are in their own tribe. The ecomorph comparison does indicate that low neonatal and litter mass in Sciurini may be characteristic of the tribe rather than of tree squirrels in general because adding other tree squirrels increases the overall average. In addition, ground-dwelling squirrels exhibit no pattern because the ecomorph includes taxa with both very low (Xerini) and very high (Marmotini) litter mass. Even within the Marmotini, genera vary widely (Hayssen 2008a). Annual output is 20%, 22%, and 26% of the mass of females in ground ($n = 28$), tree ($n = 12$), and flying squirrels ($n = 4$), respectively, but these values are not statistically different ($P = 0.59$). Given these caveats, the tendency is for arboreal squirrels to have larger neonates but smaller litter mass and larger annual output because they may have >1 litter per year.

Litter size versus neonatal mass: Across all squirrels, larger litters have smaller neonates (GLM: $n = 52$, $P < 0.0005$, $R^2 = 29\%$). This effect holds when the effects of maternal mass are removed (GLM: $n = 52$, $P < 0.0005$), but the percent of

variation due to litter size is reduced to 15%. Marmotines have the largest litter sizes and have small neonates, but the results hold for the remaining sciurids when marmotines are removed from the analyses (neonatal size versus litter size: $n = 22$, $P = 0.024$, $R^2 = 19\%$; neonatal size versus the mass of females and litter size: $n = 22$, $P < 0.0005$, partial $R^2 = 20\%$ for litter size without effects of maternal mass).

Weaning mass, litter mass at weaning, and annual output at weaning.—The major results (Fig. 3) are as follows. Body mass accounts for most (76–84%) of the variation in weaning mass and litter mass at weaning (Figs. 3A–3D). Taxa vary. Marmotini have the smallest mass of individual weanlings but the highest litter mass. Pteromyini have average weaning mass but the lowest litter mass at weaning. The single protoxerine has the larger weaning mass but its litter mass at weaning is similar to that of other tree squirrels (Figs. 3A and 3C). Tree squirrels have larger individual weanlings and greater annual output than ground and flying squirrels (Figs. 3B, 3D, and 3F). Latitude has little correlation with reproductive output at weaning.

Data for weaning mass were obtained from 47 species representing 5 of the 8 taxa (no data were available for Ratufinae, Sciurillinae, and Xerini; 34 of the 47 species are marmotines; Protoxerini are represented by 1 species). No litter-size data were available for *Speromophilus major*. Data on number of litters per year were available for 40 (29 of which are marmotines) of the 47 species, allowing calculation of annual energetic output (litter mass \times litters/year).

Weaning mass ranges from 17.7 to 451.8 g and represents 8–77% of the mass of females. Mean weaning mass is 133.8 g and median weaning mass is 102.5 g (about one-third of maternal mass). Litter mass at weaning ranges from 86.2 to 2,025.2 g and represents 15–390% of maternal mass. Mean litter mass at weaning is 608.1 g and median litter mass at weaning is 405.7 g (about 1.5 times maternal mass). Relative litter mass at weaning is smaller for larger species (GLM: $n = 46$, $P < 0.0005$, $R^2 = 34\%$), such that litter mass is $\sim 200\%$ of adult mass for a 100-g squirrel but only 113% of adult mass for a 1,000-g squirrel.

Taxa vary: Individual mass of weanlings ranges from 29% to 72% of the mass of females across taxa (Table 3). Litter mass at weaning ranges from 117% to 163% of maternal mass across taxa. Marmotines ($n = 33$ or 34) have the smallest individual weanlings (29% of maternal mass) but the largest litter mass at weaning (163% of maternal mass). Pteromyines ($n = 4$) have average weanlings (42% of maternal mass) but the smallest litter mass at weaning (about 117% of maternal mass). Annual reproductive output (litter mass \times litters/year) at weaning is about 300% of maternal mass for taxa that may attempt >1 litter per year (Callosciurinae, 299%, $n = 1$; Pteromyini, 302%, $n = 3$; Sciurini, 300%, $n = 6$; Protoxerini, 290%, $n = 1$), but only 200% for marmotines (201%, $n = 29$) for which >1 litter per year is uncommon.

Allometry and relative weaning mass: Across squirrels, weaning mass and mass of females are strongly correlated (regression: $n = 47$, $P < 0.0005$, $R^2 = 84\%$; PIC: $P < 0.0005$, $R^2 = 65\%$; Figs. 3A and 3B), as are litter mass at weaning and

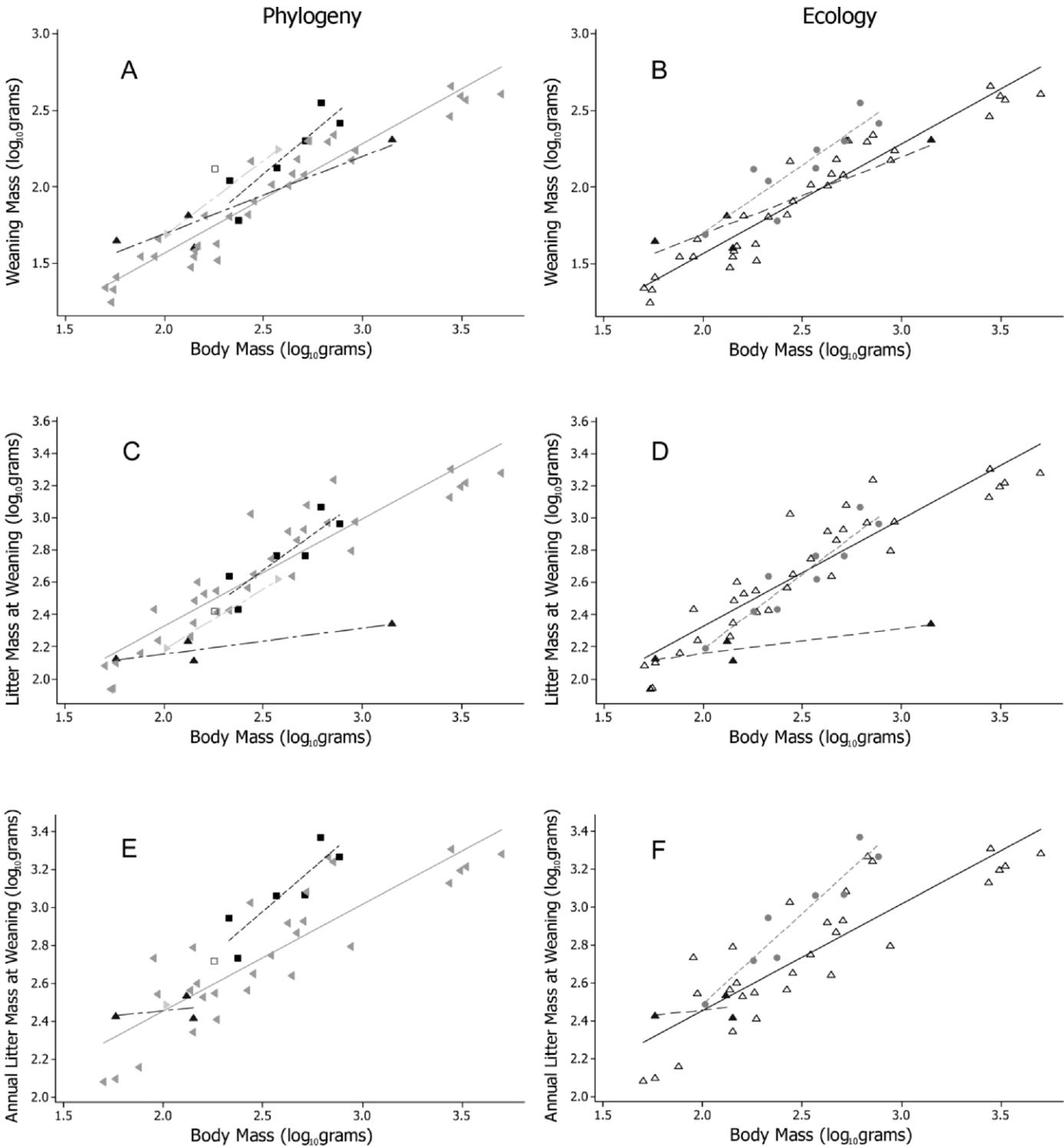


FIG. 3.—Weaning mass (top row, A, B; $n = 47$), litter mass at weaning (middle row, C, D; $n = 46$), and annual litter mass at weaning (bottom row, E, F; $n = 40$) versus body mass (all in \log_{10} g) illustrating phylogenetic (left) or ecological (right) trends. Key to taxa: Callosciurinae (gray right-facing triangles), Marmotini (black left-facing triangles), Protoxerini (open squares), Pteromyini (black upright triangles), Ratufinae (open circles), Sciurillinae (gray diamond), Sciurini (black squares), Xerini (open triangles). Key to ecomorphs: marmotine ground squirrels (open triangles), nonmarmotine ground squirrels (open squares), tree squirrels (closed circles), flying squirrels (closed triangles).

maternal mass ($n = 46$, $P < 0.0005$, $R^2 = 76\%$; PIC: $P < 0.0005$, $R^2 = 54\%$; Figs. 3C and 3D), and annual output (litter mass \times litters/year) and maternal mass ($n = 40$, $P < 0.0005$, $R^2 = 70\%$; PIC: $P < 0.0005$, $R^2 = 45\%$; Figs. 3E and 3F).

Only 2 taxa, Sciurini and Marmotini, have weaning data for >5 species.

The data on Sciurini are for 5 *Sciurus* and *Tamiasciurus hudsonicus*. *Tamiasciurus* weanlings are much larger than

TABLE 3.—Weaning mass and litter mass at weaning as percentages of the mass of female sciurids. Weaning mass and litter mass at weaning are strongly correlated with maternal mass but exhibit no clear patterns relative to ecomorph or taxonomy.

Taxon	Weaning mass			Litter mass at weaning		
	<i>n</i>	\bar{X} (%)	Median (%)	<i>n</i>	\bar{X} (%)	Median (%)
Ratufinae	0			0		
Sciurillinae	0			0		
Sciurinae						
Sciurini	6	40.5	37.4	6	150	139
Pteromyini	4	42.2	38.8	4	117	111
Callosciurinae	2	47.1	47.1	2	130	130
Xerinae						
Xerini	0			0		
Protoxerini	1	72.2	72.2	1	145	145
Marmotini	34	28.7	27.9	33	163	158
Ecomorph						
Ground	34	28.7	27.9	33	163	158
Tree	9	45.5	46.7	9	145	145
Flying	4	42.2	38.8	4	117	111

those of *Sciurus* (52% versus 38% of maternal mass). With or without *Tamiasciurus*, reproductive output at weaning scales strongly with maternal mass but the relationship is tighter without *Tamiasciurus* (GLM with *Tamiasciurus*: weaning mass, $n = 6$, $P = 0.017$, $R^2 = 74\%$; litter mass at weaning, $n = 6$, $P = 0.023$, $R^2 = 70\%$; and annual litter mass, $n = 6$, $P = 0.023$, $R^2 = 70\%$; GLM without *Tamiasciurus*: weaning mass, $n = 5$, $P = 0.015$, $R^2 = 86\%$; litter mass at weaning, $n = 5$, $P = 0.026$, $R^2 = 80\%$; and annual litter mass, $n = 6$, $P = 0.026$, $R^2 = 80\%$).

Weaning data are available for 34 marmotines representing 5 of the 6 genera (2 *Ammospermophilus*, 3 *Cynomys*, 5 *Marmota*, 18 *Spermophilus*, and 6 *Tamias*). Weaning mass has a tight correlation with maternal mass; annual litter mass at weaning

is less tightly related to maternal mass (weaning mass, GLM: $n = 34$, $P < 0.0005$, $R^2 = 91\%$; litter mass at weaning, GLM: $n = 33$, $P < 0.0005$, $R^2 = 85\%$; annual litter mass, GLM: $n = 29$, $P < 0.0005$, $R^2 = 74\%$).

Ecomorph comparisons: Tree squirrels have larger individual weanlings and greater annual output than ground and flying squirrels (Figs. 3B and 3F). For their body mass, tree squirrels have larger weanlings than ground squirrels and flying squirrels are intermediate (GLM: $n = 47$, $P < 0.0005$). Litter mass at weaning is smallest for flying squirrels, but tree and ground squirrels overlap (GLM: $n = 46$, $P = 0.003$; Fig. 3D). Tree squirrels tend to have higher annual output at weaning compared with ground and flying squirrels (GLM: $n = 40$, $P = 0.01$; Fig. 3F).

Latitude: Reproductive output at weaning has little relation to latitude after removing body-mass effects. Latitude is not correlated with weaning mass (multiple regression: $n = 47$, $P_{\text{latitude}} = 0.43$; PIC: $P = 0.16$) or annual litter mass at weaning (multiple regression: $n = 40$, $P_{\text{latitude}} = 0.71$; PIC: $P = 0.13$), but is positively correlated with litter mass at weaning (multiple regression: $n = 46$, $P_{\text{latitude}} = 0.004$, $R^2 = 9\%$; PIC: $P = 0.04$, $R^2 = 9\%$). Removing marmotines from the analysis removes the correlation of latitude with litter mass at weaning (multiple regression: $n = 13$, $P_{\text{latitude}} = 0.2$).

Growth rates.—Growth during gestation, growth during lactation, and growth over the entire reproductive interval were calculated (Table 4). Dividing growth rate by adult body mass (relative growth rate) allows comparison across taxa of different body size. The relative measure also compensates for the fact that larger species invest proportionally less into litter mass than do smaller species. Absolute growth rate during gestation is slower than that during lactation but relative to adult body mass gestational growth rates are faster.

Gestational growth rates were calculated for 44 species representing 7 of the 8 taxonomic groups (no data were available for Sciurillinae; 26 species were marmotines). Mean growth rate during gestation was 1.21 g/day ($n = 44$, median =

TABLE 4.—Absolute growth rates (g/day; see “Materials and Methods” for calculations). These rates do not adjust for body size.

Taxon	During gestation			During lactation			Overall		
	<i>n</i>	\bar{X}	Median	<i>n</i>	\bar{X}	Median	<i>n</i>	\bar{X}	Median
Ratufinae	1	3.454	3.454	0			0		
Sciurillinae	0			0			0		
Sciurinae									
Sciurini	6	0.940	0.853	6	9.780	8.620	6	6.260	5.630
Pteromyini	4	0.636	0.488	4	2.158	2.197	4	1.597	1.626
Callosciurinae	2	0.552	0.552	1	2.277	2.277	2	2.890	2.890
Xerinae									
Xerini	2	0.849	0.849	0			0		
Protoxerini	3	0.403	0.404	1	6.363	6.363	1	2.787	2.787
Marmotini	26	1.445	1.246	22	15.29	11.52	29	10.95	8.020
Ecomorph									
Ground	28	1.402	1.083	22	15.29	11.52	29	10.95	8.020
Tree	12	0.951	0.751	8	8.410	7.430	9	5.129	4.334
Flying	4	0.636	0.488	4	2.158	2.197	4	1.597	1.626

0.87 g/day, range 0.28–5.16 g/day), about one-tenth the growth rate during lactation ($n = 34$, $\bar{X} = 12.13$ g/day, median = 8.18 g/day, range 1.59–73.0 g/day, no data for Ratufinae, Sciurillinae, or Xerini). Mean growth rate over the entire reproductive interval was 8.81 g/day ($n = 42$, median = 6.31 g/day, range 1.11–36.82 g/day, no data for Ratufinae, Sciurillinae, or Xerini). Relative to body mass, growth rates during gestation (4.7 mg litter per day per gram adult) are much slower than those during lactation (36.8 mg litter per day per gram adult). Phylogenetic effects are significant for relative growth rate during gestation ($n = 44$, $P = 0.005$) but not during lactation ($n = 34$, $P = 0.12$) or over the entire reproductive interval ($n = 42$, $P = 0.09$). Marmotines have the fastest growth rates during both gestation (6.3 mg of litter mass per day per gram adult mass; Xerini 1.5, Ratufinae 1.9, Protoxerini 2.4, Sciurini 2.4, Pteromyini 3.1, and Callosciurinae 3.3) and lactation (44.6 mg of litter mass per day per gram adult mass; Pteromyini 18.2, Callosciurinae 22.1, Sciurini 23.0, and Protoxerini 35.3).

Ecomorph has little influence on growth rates. Ground squirrels have both the fastest (Marmotini) and the slowest (Xerini) growth rates during gestation. Tree squirrels have both slow (Ratufinae) and fast (Protoxerini) growth rates. Flying squirrels (Pteromyini) have fast gestational growth rates but slow growth rates during lactation.

DISCUSSION

Most of the reproductive data available for squirrels are from a single taxon, the tribe Marmotini. Much of the data on Marmotini are from high-latitude or high-altitude squirrels with a distinctive reproductive pattern of large litter size, short temporal investment, and a single annual litter. This pattern characterizes many, but not all, Marmotini (Hayssen 2008a) and does not distinguish ground squirrels as a group. In other words, although most ground squirrels are marmotines, the marmotine reproductive pattern does not characterize ground squirrels. As a result, comparisons of ecomorphs (e.g., tree versus ground squirrels) using marmotines as the only ground squirrels have a phylogenetic bias. Similarly, most data for tree squirrels in North America are from the genus *Sciurus* in the tribe Sciurini and present similar challenges to ecological comparisons. Finally, all flying squirrels are in the tribe Pteromyini, thus completely confounding phylogeny and ecomorph for this group.

The following discussion of squirrel reproduction is in 5 parts. First, I summarize reproductive investment patterns in squirrels overall with separate discussions of litter size, energetic investment, temporal investment, and number of litters per year. Second, I examine effects of latitude on sciurid reproduction. Third, I review differences in ground, tree, and flying squirrels. Fourth, I provide reproductive profiles of the major squirrel taxa. Finally, I review the results of this study compared with the predictions in the introduction.

Reproductive Investment

The length of gestation and lactation and the mass of offspring at birth and weaning are strongly influenced by

natural selection. For sciurids, the temporal component of reproduction is influenced by the environment and the energetic component is influenced by body size.

For squirrels, the energetic component of reproduction has a strong allometric component but the temporal component does not. These results suggest that the major constraint on reproduction in squirrels is not food, calories, minerals, or water per se but rather the length of time such resources are available. This result confirms that of Waterman's (1996) exemplary study of 26 nearctic and African tree and ground squirrels. Waterman (1996) concluded that climate, specifically the time available when resources are abundant, was the most critical factor influencing reproduction and allometry was less important. When resources are available, they are available in abundance, but resources are not available for very long. The epitome of this pattern is the high-latitude or high-altitude marmotines. These species may hibernate for up to 8 months and then allocate their short summer energetic investment 1st to reproduction and then to fattening up for the winter underground. For many squirrels, energetic resources are not limiting, but time is. As a result, natural selection alters growth rate to synchronize reproductive investment to resource availability.

Litter size.—Because most squirrels have litter sizes of 2 or 3, litter size is relatively homogenous across squirrels. Marmotini, with a litter size of more than 5, is distinctive. These large litter sizes in part reflect the single litter most marmotines have per year. Thus, the annual number of offspring produced by marmotines and other sciurids is similar. Other taxonomic idiosyncrasies are that litter size in Pteromyini is negatively correlated with body mass and that litter size increases with latitude in Callosciurinae and Sciurini. These trends are based on small sample sizes or single genera and deserve more focused study.

Energetic investment.—Reproductive output has a strong allometric component. Most of the variation in neonatal and litter mass is related to body size as is variation in the mass of individual weanlings and litter mass at weaning.

Ecological effects on reproductive output are apparent. Per reproductive attempt, Pteromyini (flying squirrels) have the lowest energetic investment of all squirrels, with other groups having similar output. Although Pteromyini (flying squirrels) have average-sized individual neonates, litter mass at birth and weaning are lower relative to other squirrels. This suggests that flying squirrels have smaller litters to lower "wing loading" and improve the aerodynamics of gliding during gestation or when carrying suckling young.

Similar aerodynamic constraints are not apparent for tree squirrels. Most data for tree squirrels are for temperate zone or African forms. More information on tropical tree squirrels especially in the Callosciurinae is needed. At present, tree squirrels have the largest annual reproductive output, suggesting that they have fewer energetic constraints than either flying or ground squirrels.

For ground squirrels, neonatal and weaning mass are not subject to arboreal locomotor constraints but many species (especially marmotines) have severely restricted breeding

seasons. As a result, most marmotines have small individual neonates and weanlings relative to other squirrels. However, the mass of their litters at birth and weaning is larger relative to other squirrels because they have much larger litter sizes. Thus, marmotines opt for smaller but many more offspring in their single reproductive effort. Nonmarmotine ground squirrels do not share this distinction.

Temporal investment.—For squirrels the energetic component of reproductive effort is closely tied to the mass of females, but the temporal component is not. Gestation and lactation length are not related to body mass. Thus, the duration of reproduction is not related to energetics per se.

The independence of gestation and lactation from body mass is distinctive. In a study of lactation across all mammals, body mass accounted for 43% of the variation in lactation length and if exceptionally short or long lactation lengths were excluded, body mass accounted for 75% of the variation (Hayssen 1993). Looking just at rodents, body mass accounted for less (30%) of the variation in lactation length (Hayssen 1993), but in squirrels body mass and lactation are not correlated at all. Thus, the independence of lactation, and presumably gestation, from body mass may be characteristic of squirrels. Alternatively, this independence may be a function of small body size, because gestation and lactation have little correlation with body mass in bats (Hayssen and Kunz 1996).

Although larger species of ground and tree squirrels have bigger neonates, larger litter masses at birth, bigger weanlings, and larger litter masses at weaning, these trends do not translate into longer lengths of gestation or lactation. Thus, growth rates must be faster for larger species because larger species produce larger young in the same amount of time that smaller species produce smaller young.

Litters per year.—Annual reproductive output (litter mass \times litter/year) is influenced by the number of litters produced in a year. High-latitude marmotines are constrained by their long hibernations to separate the time they are active into an initial reproductive phase followed by a fattening up phase. Hibernation occurs only in Marmotini and a number of species hibernate for 8 months out of the year. This imposes severe constraints on resource use during the active season. High-latitude marmotines cannot extend reproduction late into the season. If their 1st reproductive attempt fails they do not have time for a 2nd. Arboreal species and lower-latitude ground squirrels are not constrained by extended hibernation. Thus, if an initial reproductive attempt fails they can try again. They can let preparations for periods of low food availability overlap with reproduction. So high-latitude, hibernating marmotines cannot attempt >1 litter per year. Other squirrels are not constrained to a single reproductive attempt per year. What litters-per-year does not measure is the number of litters that fail completely. I have not seen figures, but would guess that the proportion of females with no successful reproduction per year is higher in high-latitude, hibernating marmotines. Ideally, one would like to know the number (or percent) of females with 0, 1, or 2 litters to estimate annual reproductive effort.

The larger litter size of marmotines may compensate for the constraint on the number of reproductive attempts. Marmotines

are reproducing at a time of year with high food availability. Other squirrels reproduce at optimal times but also attempt reproduction at less optimal times, something that marmotines cannot do. Thus, each marmotine litter has a higher probability of success and the greater food availability allows a larger litter size. Squirrels attempting reproduction later in the season when food is less abundant may have smaller litters. This option is not available to species with an obligate single litter per year.

Latitude

Latitude has been used to investigate the effects of climate on reproduction (chiefly litter size) in squirrels (Heaney 1984; Lord 1960; Moore 1961; Viljoen and Du Toit 1985; Waterman 1996). In these studies, squirrels from tropical, neotropical, Ethiopian, oriental, or African regions (which are generally at lower latitudes) are reported to have smaller litter sizes and longer breeding seasons than those from palearctic, nearctic, or holarctic regions (which are generally at higher latitudes—Moore 1961; Viljoen and Du Toit 1985; Waterman 1996). Also, higher latitudes have been correlated with increased litter size across squirrels (Moore 1961). However, these observations are confounded by the fact that most high-latitude (palearctic, nearctic, and holarctic) squirrels are marmotines and marmotines have large litter sizes. What happens if marmotines are excluded?

The data set presented here has information on litter size for 171 species, 82 marmotines and 89 nonmarmotines. The positive correlation of litter size and latitude both with and without marmotines is significant but the amount of variation explained by latitude falls from 52% to 21% when marmotines are excluded. Thus, across taxa of squirrels, the litter size–latitude relationship holds but is much weaker without marmotines. Does the relationship hold within tribes or within genera?

Looking at individual tribes, litter size is related to latitude only in 2 taxa, Callosciurinae and Sciurini, both tree squirrels. For marmotines overall, litter size and latitude are not related, although within marmotines litter sizes within some genera are related to latitude (Hayssen 2008a). In addition, the largest litter size is that of *Ammospermophilus*, a genus that generally lives in Mexico and southwestern United States, not at high latitudes. Other studies have explored litter-size relationships across smaller taxonomic units.

Lord (1960) examined litter size versus latitude in 3 groups of North American squirrels (usually genera) rather than across all squirrels. Lord found significant positive correlations with latitude for tree squirrels (*Sciurus*, *Tamiasciurus*, and possibly including *Glaucomys*), but not chipmunks (*Tamias*) or ground squirrels (*Spermophilus*). Using more species, I confirmed 2 of Lord's 3 conclusions. I found a tight and positive correlation of litter size with latitude in Sciurini (*Sciurus* and *Tamiasciurus*), but, unlike Lord, and using a much larger data set (25 versus 7 species) also found that litter size increases with latitude in *Tamias*. Use of a larger data set for *Spermophilus* (34 versus 15 species) confirmed Lord's finding of no correlation with latitude.

If litter size varies with latitude, so might neonatal size or gestation length. If litter size increases, neonatal mass may decrease to compensate and thus leave the total energetic investment the same across latitudes. Or an increase in litter size may increase litter mass if neonatal mass remains constant, requiring a large energetic input at higher latitudes. In this case, the duration of gestation may increase to compensate. Thus, either the temporal or the energetic component of reproduction may change with latitude.

For sciurids as a group, latitude has little influence on either the temporal or the energetic component of reproduction. Long and short gestation lengths occur at both high and low latitudes. Lactation is either higher or lower at high latitudes depending on which groups are included. Thus, sciurids as a group change litter size without compensatory changes in gestation or lactation length; however, at lower taxonomic levels such trade-offs exist. Similarly, energetic aspects of reproduction (the mass of neonates, weanlings, or litters of either) are distinctive for lower-level taxa and relationships for sciurids overall are dependent on the weighting of individual taxa. Thus, the interplay between the elements of reproduction and latitude is occurring at lower taxonomic levels and a characteristic pattern for sciurids is not apparent.

Previous work suggested that lower-latitude squirrels had longer reproductive seasons (Moore 1961; Viljoen and Du Toit 1985; Waterman 1996). The length of a breeding season has 2 components, the length of an individual reproductive bout (gestation plus lactation) and the number of reproductive bouts per season. Thus, longer breeding seasons at lower latitudes may be associated with an increase in the number of litters produced or by an increase in the duration of the time between conception to weaning. Examination of the data on squirrels indicates that longer breeding seasons are produced by increasing the number of litters rather than increasing the temporal component of a single reproductive bout.

Overall, the major correlation of latitude with reproduction in sciurids is that litter size is larger at higher latitudes. However, this relationship is characteristic of only some squirrel taxa, chiefly Callosciurinae, Sciurini, and *Tamias*. Thus, the predominant effect of broad environmental constraints on squirrels is to alter litter size in some taxa.

Ground Versus Tree Versus Flying Squirrels

Investigations of squirrels often focus on Sciurini and Marmotini and use these groups to represent tree and ground squirrels, respectively. This approach is flawed because both Sciurini and Marmotini have reproductive specializations that are not shared by other tree and ground squirrels. For instance, both groups have litter sizes that are much higher than average for other squirrels. To use marmotine patterns as typical for ground squirrels is especially difficult because marmotine reproduction is the most specialized of all squirrels. The fact that reproductive data of marmotines constitute the bulk of the reproductive data on all squirrels, and especially ground squirrels, is an additional complication.

For this study, a species was classified as a ground, tree, or flying squirrel depending on behavior. Overall, arboreal squirrels invest more into reproduction than do ground squirrels. Although ecomorph has no influence on litter size or gestation length, flying squirrels have long lactations with an allometric component, in contrast to ground or tree squirrels, whose lactations are shorter and are not tied to body mass. Thus, arboreal squirrels generally have a larger temporal investment into reproduction than ground squirrels. With respect to energetic investment, arboreal squirrels tend to have larger neonates but smaller litter mass than ground squirrels. In addition, arboreal squirrels tend to have larger annual output because more often they attempt >1 litter per year. This is not possible in those ground squirrels (marmotines) with long periods of hibernation. Finally, tree squirrels have larger individual weanlings and greater annual output than either ground or flying squirrels.

The conclusion that arboreal squirrels invest more into reproduction than ground squirrels is not robust because phylogeny so closely matches ecomorph. The best exploration of the effects of ecomorph on reproduction or any other physiological process in ground squirrels would be to compare ecomorphs in a single taxon. No single squirrel taxon has all 3 ecomorphs, but several taxa have 2. The subfamily Sciurinae is composed of tree squirrels (Sciurini) and flying squirrels (Pteromyini). The subfamily Callosciurinae includes 5 genera of ground squirrels and 9 genera of tree squirrels. The African subfamily Xerinae includes the tribe Xerini, which are predominately ground squirrels, and the tribe Protoxerini, which are predominately tree squirrels. Finally, the genus *Funisciurus* in the tribe Protoxerini has species that are either tree or ground squirrels. Most of these comparisons are with Old World species and the sciurid data we have is nearly all from New World animals. We need more data on Old World species especially from Callosciurinae and from the genus *Funisciurus* (Protoxerini).

Comparisons between New World and Old World groups can lead to different conclusions. For instance, comparing North American tree squirrels (Sciurini) and ground squirrels (Marmotini) suggests that ground squirrels have faster growth rates than tree squirrels, but the same comparison with African tree squirrels (Protoxerini) and ground squirrels (Xerini) suggests the reverse, that ground squirrels have slower growth rates than tree squirrels. These comparisons are preliminary at best.

To the extent possible, ecological comparisons are detailed in the phylogenetic profiles below, but the tentative conclusions are that reproduction in flying squirrels reflects internal constraints (physiology and morphology), whereas that for tree squirrels reflects external constraints (climate and habitat), and that differences in reproduction between tree and ground squirrels reflect phylogenetic or geographic constraints rather than ecological ones.

Phylogenetic Profiles

Some high-level mammalian taxa have characteristic reproductive profiles. For instance, Metatheria, the infraclass that

includes marsupials, has an extremely short gestation with tiny, embryonic neonates and long periods of lactation (Hayssen et al. 1985) and Chiroptera, the order that includes bats, has long gestations with very large singleton offspring and long lactations (Hayssen and Kunz 1996). Reproduction in squirrels cannot be so simply characterized. Squirrels are only a family within the order Rodentia, yet squirrels have no obvious reproductive profile. In fact, each subtaxon of squirrels has a distinctive reproductive pattern and each taxon contributes to our understanding of how reproduction in squirrels is integrated with their biology.

Basal squirrels.—Basal squirrels may have remnants of the ancestral reproductive pattern for squirrels. The 2 phylogenetically basal taxa are Sciurillinae (South American pygmy squirrels) and Ratufinae (giant tree squirrels of southern Asia). Both Sciurillinae and Ratufinae have litter sizes of 2; thus, small litter size may be ancestral for squirrels.

The oldest squirrel taxa, Sciurillinae (1 genus, 1 species) and Ratufinae (1 genus, 4 species), are both ecologically tree squirrels but differ widely in size from the small *Sciurillus* (35–45 g) to the giant *Ratufa* (1.5–2 kg). *Sciurillus* lives in Amazonian rain forests and has a morphologically specialized skull (Moore 1959) associated with a diet of bark (Emmons 1990). A modal litter size of 2 is all that is known of its reproduction (Olalla 1935). Thus, *Sciurillus* appears morphologically and physiologically specialized and the paltry data on reproduction give little insight into possible ancestral reproductive patterns.

More is known of Ratufinae. *Ratufa* are large-bodied tree squirrels primarily from southern latitudes in Asia. Ratufinae may put the least effort into reproduction of all squirrels. Although *Ratufa* may reproduce throughout the year, litter size is only 2 and, relative to their large body size, litter mass is small, growth rates are slow, and gestation and lactation are short. Thus, the reproductive strategy of *Ratufa* is to put a small but continuous effort into reproduction throughout the year.

Callosciurinae.—Callosciurinae is a large group (64 species) of ecologically diverse squirrels from primarily southern latitudes in southeast and southern Asia. With 9 genera (55 species) of tree squirrels and 5 genera (9 species) of ground squirrels, this is an ideal group to investigate how reproduction is related to nest site. Unfortunately, detailed reproductive data are known for only 2–4 species, so the comparisons cannot be made. Litter size is known for 23 species and is positively correlated with latitude. Thus, litter size increases farther from the equator. Apart from this trend, examination of the few data suggests no particular reproductive strategy. Both temporal and energetic investments into reproduction are average for squirrels. Gestation and lactation are similar in length. Growth rate during gestation may be on the fast side. However, with so few data, the reproduction of Callosciurinae is essentially unknown. With more data, a starting point for further investigation would be to see if the increase in litter size away from the equator is correlated with changes in neonatal mass, litter mass, or gestation and lactation lengths.

Sciurinae.—Comparing the 2 subgroups of the subfamily Sciurinae (Sciurini, tree squirrels; Pteromyini, flying squirrels)

allows investigation of the influence of a highly specialized mode of locomotion (gliding) on reproduction. Both Sciurini and Pteromyini have wide latitudinal ranges and thus live in diverse habitats and climates. They have similar numbers of species and the extent of documented reproductive data is similar. Most of the Sciurini data are from 1 genus (*Sciurus*), which has differentiated widely. In contrast, data from Pteromyini represent different genera. Thus, the comparison between subgroups is essentially *Sciurus* versus Pteromyini, rather than Sciurini versus Pteromyini.

Flying squirrels have smaller litters than tree squirrels. Litter size in flying squirrels ranges from 1 to 4 with a mean of 2, whereas litter size in tree squirrels ranges from 2 to 5 with a mean of 3. Litter size in tree squirrels is larger at higher latitudes but has no correlation with body size. Heaney (1984) found a similar result using populations rather than species of *Sciurus*. In contrast, for flying squirrels litter size is smaller for larger species but has no correlation with latitude. Thus, in flying squirrels litter size is related to body mass (internal physiological factors), but in tree squirrels litter size is related to climate (external environmental factors).

The temporal component of reproduction has some tie to body mass in both tree and flying squirrels, but is tied to latitude only in tree squirrels. Gestation is two-thirds the length of lactation for both groups, but gestation and lactation are 10–15 days longer in flying squirrels. For tree squirrels, gestation is longer for larger species and shorter at higher latitudes, whereas gestation in flying squirrels is independent of body mass and latitude. Lactation reverses these trends. Lactation in flying squirrels increases with increasing adult body mass (but has no relationship with latitude), whereas lactation in tree squirrels is not related to body mass or to latitude. However, for *Sciurus* alone, larger species have longer lactations. Overall, the temporal investment into reproduction is higher for flying squirrels.

Tree and flying squirrels differ in the energetic component of reproduction. Flying squirrels have faster growth rates during gestation than tree squirrels but slower growth rates during lactation. Although litters of flying squirrels at birth are a larger proportion of maternal mass than those of tree squirrels, at weaning, litter mass of flying squirrels is a smaller proportion of maternal mass. Thus, for flying squirrels reproductive investment is more concentrated in the 1st part of reproduction and then more gradual during a long lactation, whereas tree squirrels have a constant energetic investment throughout reproduction.

Overall, flying squirrels take longer to produce fewer young compared with tree squirrels of similar mass. So temporal investment is larger in flying squirrels and energetic investment is smaller. Also, flying squirrels have front-end-loaded reproduction, with faster growth rates during gestation. Finally, external environmental factors (latitude) influence the reproduction of tree squirrels but reproduction in flying squirrels is more closely tied to physiological factors.

How does reproduction reflect the biology of flying squirrels? First, if gliding is more difficult to master than climbing then a longer lactation will give offspring time to achieve sufficient skill to glide effectively. Giving birth to larger but

fewer offspring suggests that flying squirrels have less predator pressure or other mortality than tree squirrels. The fact that physiological not environmental factors influence reproduction also suggests that flying squirrels are surviving closer to their carrying capacity.

Xerinae.—*Xerinae* is a fascinating subfamily with 2 African taxa, African tree squirrels (Protoxerini; includes some ground-dwelling squirrels) and African ground squirrels (*Xerini*), and 1 large, diverse, and highly successful group, the Northern Hemisphere ground squirrels (*Marmotini*). Comparisons of Protoxerini and *Xerini* allow comparisons of tree and ground squirrels on the same continent, whereas comparisons between *Xerini* and *Marmotini* allow comparisons of ground squirrels adapted to very different habitats. The 9 species in the protoxerine genus *Funisciurus* are of special interest because 5 are ground nesters and 4 nest in trees or shrubs. Unfortunately, except for the excellent work of Emmons (1979) and Viljoen and Du Toit (1985), little is known of reproduction in *Funisciurus*.

Protoxerini is a mix of ground and tree squirrels; however, except for litter size the reproduction of ground-nesting Protoxerini is unknown. Protoxerines have small litters of large neonates. Relative to adult size, neonatal mass is the largest of all squirrels and gestation length is the longest. Protoxerines are the only squirrels for which gestation is longer than lactation. Growth rate during gestation is the same as that for sciurine tree squirrels, but growth rate during lactation is much faster and litter mass at weaning is average; however, individual weanlings are large. Thus, protoxerine squirrels have long gestations that produce few but large neonates; they then speed up growth during lactation. These results extend those of Emmons (1979) and Viljoen and Du Toit (Viljoen 1981; Viljoen and Du Toit 1985), who studied litter size and growth rates in *Epixerus*, *Funisciurus*, *Heliosciurus*, *Myosciurus*, *Paraxerus*, and *Protoxerus* and found that offspring were more precocial than those of other tree squirrels. Thus, production of small litters with large neonates after a long gestation is related to precocial development of the young at birth. These southern African squirrels may “conceive at a postpartum estrus” (Viljoen and Du Toit 1985:126). This may be another reason why gestation is longer than lactation. If it were shorter, females would be giving birth to a 2nd litter before the 1st litter was weaned. If these traits are true of the taxon, the protoxerine (African tree squirrels) reproductive strategy is opposite to that of New World ground squirrels, the marmotines. Protoxerines have the potential for continuous (potentially overlapping) production of small litters of young throughout the year.

Xerini (African ground squirrels) have more but smaller offspring than Protoxerini (African tree squirrels). Litter mass at birth is also smaller and gestation length is shorter. So *xerines* invest less in the early phase of gestation than protoxerines, and growth rates are much slower. No data on weaning mass exist, but lactation length is equal to that of gestation. Waterman (1996) suggested that *Xerini* have small litter sizes and long periods of gestation and lactation. This is true when compared to North American tree (*Sciurini*) and ground

(*Marmotini*) squirrels, but not the case when compared with squirrels overall. *Sciurini* and *Marmotini* have unusually high litter sizes, whereas that of *Xerini* is about average. Compared with other squirrels, gestation and lactation lengths of *Xerini* are intermediate. What is unusual about *Xerini* is the small neonatal mass and litter mass at birth. Thus, what appears to be characteristic of *Xerini* is a slow growth rate during gestation. This may be the feature that facilitates “reproductive success during a long active season in an unpredictable environment” (Waterman 1996:143). The slow growth rates of African ground squirrels are opposite the fast growth rates of North American ground squirrels.

Marmotini (Northern Hemisphere ground squirrels) have a distinctive, highly specialized reproductive profile. 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. Arctic and many temperate-zone marmotines concentrate their reproductive effort into the 1st half of a seasonal activity period and fatten up for hibernation during the 2nd half. Details across marmotine genera in reproductive patterns are available (Hayssen 2008a).

Observations Versus Predictions

Simple allometry suggests larger squirrels should have larger young and longer periods of reproductive investment. Larger squirrels do have larger young but the duration of reproductive investment is independent of body size. A difficulty with the data for reproductive stages is that the units most researchers use to measure the duration of gestation and lactation (weeks or months) are imprecise and lead to an artificial homogeneity. Thus, the independence of gestation and lactation with respect to body size may in part be due to measurement error. Nonetheless, for squirrels energetic investment into reproduction has an allometric component but temporal investment does not.

Squirrels with smaller neonates tend to also have larger litters. This suggests that development of neonates at birth, the altricial-precocial dimension, may have a significant role in reproduction in squirrels (Emmons 1979; Viljoen and Du Toit 1985; Waterman 1996).

Ecomorph influences reproduction because ground, tree, and flying squirrels have distinct reproductive profiles and the 2 arboreal groups are more similar to each other. Arboreal squirrels invest more into reproduction than do ground squirrels and flying squirrels take longer to produce fewer young compared with tree squirrels of similar mass. These results have a very strong phylogenetic component and this suggests that the early radiation of squirrels probably had a strong ecological-locomotor component. Thus, reproductive patterns for different groups probably were established early in the history of the group and then evolved in response to ground-nesting, tree-nesting, and gliding locomotion.

Phylogenetic influences on reproduction would be evident if individual tribes or subfamilies have distinctive reproductive profiles. In fact, the phylogenetic component of reproduction in squirrels is more distinctive than either allometric or ecological influences. Taxa of squirrels have distinct reproductive profiles. This is true at the subfamily and tribe level, but also true at the level of genus. Differential reproduction is the essence of natural selection and the differentiation of taxa of squirrels has a reproductive component.

The effects of latitude and climatic region on reproduction were expected to conform to previous studies and the results here do support those studies. Litter size increases as latitude increases. However, the more extensive analysis here failed to find any new effects of latitude on reproduction and latitude has little influence on reproduction in squirrels at broad taxonomic levels.

For sciurids overall, differences in reproduction are primarily related to phylogenetic history and secondarily influenced by the locomotor–ecological position of the group. Allometric effects are strong for the energetic component of reproduction but not the temporal component and latitude–climatic regions have little effect on the pattern of reproduction.

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APPENDIX I

Reproductive data, including neonatal and weaning mass in grams, and lengths of gestation and lactation in days. Body mass (in grams) is from Hayssen (2008).

	Body mass	Litter size	Neonatal mass	Gestation	Lactation	Weaning mass	Litters per year	References ^a
Sciurillinae								
<i>Sciurillus pusillus</i>	38.50	1.67						1, 2, 3
Ratufinae								
<i>Ratufa affinis</i>	1,236.88	3.00						4
<i>Ratufa bicolor</i>	1,807.52	1.44	75.33	31.50	35.00		2	1, 5
<i>Ratufa indica</i>	1,391.71	1.00						1
<i>Ratufa macroura</i>	1,600.00	2.67		28.00	63.00		2	1, 6
Callosciurinae								
<i>Callosciurus adamsi</i>	150.00	2.00						1
<i>Callosciurus caniceps</i>	312.87	2.22						1, 7, 8
<i>Callosciurus erythraeus</i>	375.09	2.37		48.00	50.00	175.00		1, 9, 10, 11, 12
<i>Callosciurus finlaysonii</i>	278.00	2.00						8
<i>Callosciurus nigrovittatus</i>	239.38	2.20						1
<i>Callosciurus notatus</i>	227.87	2.37						1
<i>Callosciurus prevostii</i>	361.95	1.73	16.35	47.20				1
<i>Dremomys lokriah</i>	172.50	3.67						1
<i>Dremomys pernyi</i>	150.90	4.00						9
<i>Exilisciurus exilis</i>	21.30	2.67						1, 13
<i>Funambulus layardi</i>	168.00	2.50						1
<i>Funambulus palmarum</i>	99.20	2.67		34.00				1
<i>Funambulus pennanti</i>	102.87	3.14	6.50	39.75	58.60	49.00	2	1, 14, 15, 16
<i>Funambulus sublineatus</i>	44.10	2.00						1
<i>Funambulus tristriatus</i>	139.00	2.75	5.81		65.00			17
<i>Lariscus hosei</i>	215.00	2.00						4
<i>Lariscus insignis</i>	182.06	2.00						2
<i>Rhinosciurus laticaudatus</i>	232.50	1.30						1
<i>Sundasciurus lowii</i>	76.41	2.50						4
<i>Sundasciurus tenuis</i>	81.37	3.00						1
<i>Tamiops maccllellandii</i>	51.80	2.33						1, 18
<i>Tamiops maritimus</i>	56.50	3.00						10
<i>Tamiops swinhoei</i>	87.88	3.25					2	1, 9
Sciurinae, Pteromyini								
<i>Eoglaucomys fimbriatus</i>	560.13	3.67			75.00		2	1
<i>Glaucomys sabrinus</i>	141.34	3.27	5.60	38.67	70.00	39.74	2	1, 19
<i>Glaucomys volans</i>	57.60	3.00	3.79	40.00	53.00	44.35	2	1, 20
<i>Hylopetes alboniger</i>	240.00	2.33						1
<i>Hylopetes lepidus</i>	43.32	2.00						1
<i>Iomys horsfieldii</i>	209.83	2.67						1
<i>Petaurillus hosei</i>	21.10	2.00						21, 22
<i>Petaurista alborufus</i>	1,454.29	1.50					2	8, 9
<i>Petaurista elegans</i>	759.75	1.00						1
<i>Petaurista leucogenys</i>	1,178.89	1.33		74.00	82.33		2	1, 23, 24, 25, 26
<i>Petaurista magnificus</i>	1,800.00	1.00						1
<i>Petaurista petaurista</i>	1,405.30	1.08	56.65	45.00	74.67	201.00		1, 27, 28, 29
<i>Petinomys fuscocapillus</i>	712.00	2.00						1
<i>Pteromys momonga</i>	151.80	3.00	5.00				2	1, 23, 26
<i>Pteromys volans</i>	131.25	2.63	4.50	28.00	60.00	65.00	2	1, 26
<i>Pteromyscus pulverulentus</i>	235.02	1.30						1
<i>Trogoxerus xanthipes</i>	753.79	1.64		80.30	105.00			1
Sciurinae, Sciurini								
<i>Microsciurus flaviventer</i>	82.57	2.00						30
<i>Sciurus aberti</i>	618.56	3.31	12.00	44.00	70.00	355.00	2	1
<i>Sciurus aestuans</i>	200.00	2.30						2
<i>Sciurus alleni</i>	472.99	3.00						1
<i>Sciurus arizonensis</i>	667.00	3.00					1	31
<i>Sciurus aureogaster</i>	505.38	2.00						1
<i>Sciurus carolinensis</i>	512.69	2.92	12.13	44.10	64.50	200.00	2	1
<i>Sciurus colliaei</i>	440.84	2.67						1
<i>Sciurus deppei</i>	287.28	2.50						1
<i>Sciurus granatensis</i>	311.67	2.04	9.50		60.00			1, 30
<i>Sciurus griseus</i>	727.49	3.60		43.67			1	1

APPENDIX I.—Continued.

	Body mass	Litter size	Neonatal mass	Gestation	Lactation	Weaning mass	Litters per year	References ^a
<i>Sciurus lis</i>	237.00	4.50	6.00	38.50	40.00	60.00	2	26
<i>Sciurus nayaritensis</i>	756.18	2.50					1	31
<i>Sciurus niger</i>	764.35	3.56	15.08	44.67	67.64	260.50	2	1, 32, 33
<i>Sciurus richmondi</i>	239.30	2.67						1
<i>Sciurus vulgaris</i>	371.00	4.36	10.55	37.44	61.00	132.50	2	1, 34, 35
<i>Sciurus yucatanensis</i>	302.40	3.00						1
<i>Tamiasciurus douglasii</i>	199.26	5.36		38.67			2	1
<i>Tamiasciurus hudsonicus</i>	212.97	3.97	7.08	35.10	65.64	110.00	2	1, 30, 36, 37, 38
Xerinae, Marmotini								
<i>Ammospermophilus harrisi</i>	98.32	6.57	3.60	29.00	49.00		1	1, 31
<i>Ammospermophilus interpres</i>	93.06	9.50					2	1
<i>Ammospermophilus leucurus</i>	89.79	7.77	3.21	28.80	64.83	35.00	2	1
<i>Ammospermophilus nelsoni</i>	148.15	9.68	4.88	26.00	30.00	41.00	1	1, 31
<i>Cynomys gunnisoni</i>	470.16	4.88		30.00	33.00	150.00	1	1, 39, 40
<i>Cynomys leucurus</i>	923.54	5.48		30.00	37.00	173.33		1, 39, 41
<i>Cynomys ludovicianus</i>	881.28	4.18	15.75	34.54	46.59	148.25	1	1, 39
<i>Cynomys mexicanus</i>	820.45	4.50			45.50			1
<i>Cynomys parvidens</i>	516.00	4.87						1
<i>Marmota baibacina</i>	7,850.00	6.07		40.00	30.00		1	1, 9, 42
<i>Marmota bobak</i>	3,875.00	5.95		40.67	37.50		1	1, 43
<i>Marmota broweri</i>	3,180.00						1	31
<i>Marmota caligata</i>	3,515.25	4.60		30.00	24.50		1	1
<i>Marmota camtschatica</i>	3,763.87	5.00	33.00					1
<i>Marmota caudata</i>	5,000.00	4.78		30.50		400.00	1	1, 9, 44, 45
<i>Marmota flaviventris</i>	2,791.69	4.48	33.80	29.33	25.67	451.81	1	1
<i>Marmota himalayana</i>	6,000.00	4.50					1	9
<i>Marmota marmota</i>	3,324.00	4.50		36.69	47.22	366.00	1	1, 46
<i>Marmota menzbieri</i>	2,966.00	3.07						1, 44
<i>Marmota monax</i>	2,754.36	4.67	27.43	32.35	43.70	285.96	1	1, 39
<i>Marmota olympus</i>	3,120.00	4.00		30.00	30.00	390.00	1	39, 47
<i>Marmota sibirica</i>	8,000.00	4.50		41.00			1	1
<i>Marmota vancouverensis</i>	4,000.00	3.36		31.00				1, 31, 48, 49
<i>Sciurotamias davidianus</i>	260.00	2.50					2	9
<i>Spermophilus alashanicus</i>	247.25	4.60						50
<i>Spermophilus annulatus</i>	386.26	4.00						1, 51
<i>Spermophilus armatus</i>	347.32	5.45		24.00	21.00	102.50	1	1, 39, 52
<i>Spermophilus beecheyi</i>	508.52	7.06	10.00	28.50	48.33	120.08	1	1, 39, 52
<i>Spermophilus beldingi</i>	265.24	5.57	6.87	26.20	25.33	65.87	1	1, 19, 39, 53, 54
<i>Spermophilus brunneus</i>	116.80	5.50					1	31
<i>Spermophilus canus</i>	154.00	8.00						55
<i>Spermophilus citellus</i>	202.29	5.38		29.00	35.50		1	1, 56, 57, 58
<i>Spermophilus columbianus</i>	441.39	3.60	9.41	24.20	29.00	120.83	1	1, 39, 53, 59, 60, 61, 62, 63
<i>Spermophilus dauricus</i>	223.79	4.82		30.00			1	1, 64
<i>Spermophilus elegans</i>	284.29	5.57	6.02	23.75	31.83	80.00	1	1, 31, 39, 65
<i>Spermophilus erythrogenys</i>	355.00	8.00		31.50			1	1, 9
<i>Spermophilus franklinii</i>	424.86	8.12		28.00	30.00	101.33	1	1, 39, 53
<i>Spermophilus fulvus</i>	596.00	7.99		30.00			1	1, 44
<i>Spermophilus lateralis</i>	159.68	5.25	5.83	32.44	39.00	64.27	1	1, 19, 39, 66
<i>Spermophilus madrensis</i>	152.00	4.20						1
<i>Spermophilus major</i>	537.43				60.00	200.00	1	1
<i>Spermophilus mexicanus</i>	167.25	6.15	4.31				1	1, 31, 67
<i>Spermophilus mohavensis</i>	213.00	6.80	4.50	24.00	40.00			1
<i>Spermophilus mollis</i>	115.31	8.57	4.00	24.00	34.00		1	1, 31
<i>Spermophilus parryi</i>	524.28	6.05		25.00	28.00	199.00	1	1, 39, 53, 68, 69
<i>Spermophilus perotensis</i>	174.00	6.50						1
<i>Spermophilus pygmaeus</i>	235.20	7.70		26.50	34.75		1	1
<i>Spermophilus relictus</i>	403.64	5.40						44
<i>Spermophilus richardsonii</i>	273.43	7.23	6.47	22.56	29.23	147.50	1	1, 39, 53, 70
<i>Spermophilus saturatus</i>	212.32	4.16	5.97		42.00	64.07		1, 71, 72
<i>Spermophilus spilosoma</i>	137.29	6.19		28.00	48.00	29.57	2	1, 31, 73
<i>Spermophilus suslicus</i>	224.00	6.83		23.50	28.25		1	1, 74
<i>Spermophilus tereticaudus</i>	142.09	6.31	3.85	26.71	45.00	35.00	1	1, 39
<i>Spermophilus townsendii</i>	183.28	8.43	3.61	24.00	28.40	41.99	1	1, 39, 75
<i>Spermophilus tridecemlineatus</i>	142.78	8.11	2.93	27.50	27.63	38.00	2	1, 39, 53
<i>Spermophilus undulatus</i>	718.14	7.93	10.86	27.50	35.00	218.80	1	1, 76

APPENDIX I.—Continued.

	Body mass	Litter size	Neonatal mass	Gestation	Lactation	Weaning mass	Litters per year	References ^a
<i>Spermophilus variegatus</i>	672.60	4.70	7.80	30.00	49.00	197.46	2	1, 77
<i>Spermophilus washingtoni</i>	186.50	7.80			30.00	33.00	1	1, 31
<i>Spermophilus xanthoprymnus</i>	311.00	5.00						1
<i>Tamias alpinus</i>	35.85	4.50						19, 28
<i>Tamias amoenus</i>	50.60	5.45	2.65	29.00	44.40	22.00	1	1, 78
<i>Tamias bulleri</i>	74.89	2.50						1
<i>Tamias canipes</i>	70.00	4.00						31
<i>Tamias cinereicollis</i>	72.03	5.00		30.00	42.50			1, 31
<i>Tamias dorsalis</i>	74.37	5.10		29.50	30.00		2	1
<i>Tamias durangae</i>	83.75	3.00						79
<i>Tamias merriami</i>	71.30	3.72			32.00			80
<i>Tamias minimus</i>	46.42	5.33	2.30	29.00	44.80		1	1, 31
<i>Tamias obscurus</i>	69.00	3.50						81
<i>Tamias ochrogenys</i>	94.10	3.50						31
<i>Tamias palmeri</i>	55.19	4.11		33.00	42.00	21.22		1
<i>Tamias panamintinus</i>	54.09	4.88	4.00	36.00	42.00	17.68		1, 31
<i>Tamias quadrimaculatus</i>	87.43	4.69		31.00			1	1, 19
<i>Tamias quadrivittatus</i>	62.96	4.13	2.50	31.50	45.50		2	1, 31
<i>Tamias ruficaudus</i>	63.16	4.91		31.00	42.00		1	1, 31
<i>Tamias rufus</i>	57.59	4.90	2.80	31.50	45.50	25.55	1	31, 82
<i>Tamias senex</i>	94.00	4.00		28.00			1	19, 31, 83
<i>Tamias sibiricus</i>	96.17	4.66	3.64	31.63	33.43		2	1, 9, 26, 84, 85
<i>Tamias siskiyou</i>	75.00	3.71		28.00			1	83
<i>Tamias sonomae</i>	70.00	4.00					1	31
<i>Tamias speciosus</i>	62.70	4.21		30.00			1	1, 19, 31
<i>Tamias striatus</i>	93.90	3.81	3.38	31.25	41.91	45.69	2	1
<i>Tamias townsendii</i>	76.11	4.13	3.55		52.50	35.00	1	1
<i>Tamias umbrinus</i>	64.56	3.50						1
Xerinae, Protoxerini								
<i>Epixerus ebii</i>	388.00	2.00						1
<i>Funisciurus anerythrus</i>	217.78	1.19						1
<i>Funisciurus bayonii</i>	135.00	3.00						86
<i>Funisciurus congicus</i>	111.23	2.00	9.91	52.00	50.00		2	1
<i>Funisciurus isabella</i>	107.12	1.00						1
<i>Funisciurus lemniscatus</i>	140.88	1.80						1
<i>Funisciurus leucogenys</i>	251.86	1.00						1
<i>Funisciurus pyrropus</i>	240.30	1.57						1
<i>Heliosciurus gambianus</i>	328.63	3.00						1
<i>Heliosciurus rufobrachium</i>	360.63	2.50						1, 87
<i>Heliosciurus ruwenzorii</i>	291.00	3.00						1
<i>Myosciurus pumilio</i>	16.11	2.00						1
<i>Paraxerus alexandri</i>	40.17	1.00						1
<i>Paraxerus boehmi</i>	74.83	1.11						1
<i>Paraxerus cepapi</i>	180.17	2.01	11.92	56.50	37.33	130.00	2	1, 88
<i>Paraxerus flavovittis</i>	156.95	1.33						1
<i>Paraxerus ochraceus</i>	137.51	2.20			24.50			1, 87
<i>Paraxerus palliatus</i>	307.43	1.63	15.21	61.33	45.25		2	1
<i>Paraxerus poensis</i>	125.00	1.48	9.91				2	1
<i>Protoxerus stangeri</i>	760.84	1.50						1
Xerinae, Xerini								
<i>Spermophilopsis leptodactylus</i>	548.33	4.23	9.30	45.00	42.00		2	1, 44, 89
<i>Xerus erythropus</i>	741.68	3.73						1, 90
<i>Xerus inauris</i>	579.73	1.95	20.00	47.33	51.67		2	1, 91, 92
<i>Xerus princeps</i>	665.20	2.00		48.00				93
<i>Xerus rutilus</i>	252.00	2.00						1

^a 1, Hayssen et al. 1993; 2, Emmons 1979; 3, Olalla 1935; 4, Davis 1962; 5, Payne 1979; 6, Paulraj and Kasinathan 1993; 7, Blanford 1888; 8, Lekagul and McNeely 1977; 9, Helin et al. 1999; 10, Allen 1940; 11, Tamura 1999; 12, Tamura and Terauchi 1994; 13, Heaney 1985; 14, Bishnupuri and Haldar 1999; 15, Purohit et al. 1966; 16, Bhat and Mathew 1984; 17, Sahi and Sharma 2004; 18, Tien 1966; 19, Grinnell and Storer 1924; 20, Stapp and Mautz 1991; 21, Tate 1947; 22, Thomas 1900; 23, Ando and Shiraishi 1984a; 24, Kawamichi 1997; 25, Ando and Shiraishi 1984b; 26, Kawamichi 1996; 27, Lee et al. 1993; 28, Lee et al. 1992; 29, Kloss 1916; 30, Eisenberg 1989; 31, Wilson and Ruff 1999; 32, Nixon et al. 1991; 33, Brown and Yeager 1945; 34, Macdonald and Barrett 1993; 35, P. Lurz, in litt.; 36, Boutin and Larsen 1993; 37, Larsen et al. 1997; 38, Larsen and Boutin 1994; 39, Armitage 1981; 40, Rayor 1985; 41, Clark 1977; 42, Yang et al. 1988; 43, Beskrovnyi 1970; 44, Davydov 1974; 45, Blumstein 1997; 46, Allainé et al. 1998; 47, Edelman 2003; 48, Bryant 1996; 49, Graham et al. 2003; 50, Chen 1991; 51, Moore 1961; 52, Sauer and Slade 1987; 53, Boag and Murie 1981; 54, Nunes and Holekamp 1996; 55, Davis 1939; 56, Huber et al. 1999; 57, Millesi et al. 1999b; 58, Millesi et al. 1999a; 59, Moore 1937; 60, Hare and Murie 1992; 61, Festa-Bianchet and King 1991; 62, Neuhaus 2000; 63, Risch et al. 1995; 64, Wang et al. 1992; 65, Stanton et al. 1994; 66, Phillips 1981; 67, Valdez and Ceballos 1991; 68, Karels et al. 2000; 69, Boonstra et al. 2001; 70, Dobson and Michener 1995; 71, Kenagy et al. 1990; 72, Geiser and Kenagy 1990; 73, Blair 1942; 74, Trunova et al. 1999; 75, Van Home et al. 1997; 76, Mayer and Roche 1954; 77, Ortega 1991; 78, Broadbooks 1958; 79, Best et al. 1993; 80, Best and Granai 1994b; 81, Best and Granai 1994a; 82, B. Patterson, in litt.; 83, Sutton and Patterson 2000; 84, Lu 1993; 85, Kawamichi and Kawamichi 1993; 86, this study; 87, Kingdon 1974; 88, Viljoen 1975; 89, Ružić 1967; 90, Böhme and Hutterer 1978; 91, Waterman 1996; 92, Herzig-Straschil 1978; 93, Herzig-Straschil and Herzig 1989.

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