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Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism

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Factors underlying the evolution of female-biased sexual size dimorphism in mammals are poorly understood. In an effort to better understand these factors we tested whether larger female southern flying squirrels, *Glaucomys volans*, gained reproductive advantages (larger litters or more male mates) and direct resource benefits, such as larger home ranges or access to more food (i.e. mast-producing trees). As dimorphism can vary with age in precocial breeding species, we compared females during their first reproduction and during a subsequent breeding attempt. Females were not significantly larger or heavier than males at first reproduction, but became about 7% heavier and 22% larger than males at subsequent breeding. Larger females produced larger litters and had home ranges containing a greater proportion of upland hardwood trees. Female body size was not associated with either multiple male mating or home range size, but females with larger home ranges had higher indexes of body condition. Females in precocial breeding flying squirrels initiate reproduction before sexual size dimorphism is evident, and thus, may be allocating resources to both reproduction and growth simultaneously, or delaying growth entirely. Larger females produce more pups and have access to more food resources. Thus, selection for increased female size may partly explain how female-biased sexual size dimorphism is maintained in this species.

Sexual size dimorphism (SSD) is a common characteristic of many animal taxa (Andersson 1994). The prevalence of SSD in numerous taxa suggests that its evolution and maintenance is possible through numerous mechanisms. Male-biased sexual size dimorphism (MSSD) is largely considered a product of sexual selection, often acting through male–male competition (Andersson 1994), which results in a strong coupling between body size and reproductive success in males that compete for mating opportunities. The result is often large intersexual differences in body size (Trivers 1972). Although sexual selection offers

a relatively satisfying explanation for MSSD, the factors underlying the evolution of female-biased sexual size dimorphism (FSSD), where females are larger than males, are less clear.

In mammals, FSSD has received little attention, despite a list of species compiled by Ralls (1976) that suggested its occurrence in mammalian taxa is widespread. Ralls (1976), and more recently, Isaac (2005a), proposed that unlike MSSD, there are probably multiple factors acting simultaneously on both sexes to select for larger size in females and smaller size in males. Several hypotheses attempting to explain the evolution of FSSD have been proposed, including selection for smaller body size and/or early reproduction in males (Ralls 1976), enhanced mobility of pregnant females (Myers 1978; Hayssen & Kunz 1996), greater female dominance and/or territoriality (Kruuk 1972; East et al. 2003), selection for increased fecundity in larger females (Howard et al. 1998; Schulte-Hostedde et al. 2004), intersexual differences in survival (Yoccoz & Mesnager 1998), and intersexual variation in growth

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patterns (Shine 1990; Badyaev et al. 2001). These explanations also suggest that reduced, direct male–male competition for females is a common trait among animals showing FSSD, and that sperm competition often explains a greater proportion of variance in male reproductive success than do traits usually associated with direct male–male competition (Isaac 2005a).

FSSD has been reported within several mammalian lineages, with the most prominent examples being the cetaceans, lagomorphs and bats (Ralls 1976). FSSD has also been noted in several members of the Sciuridae, including yellow-pine chipmunks, *Tamias amoenus* (Schulte-Hostedde & Millar 2000), and gliding mammals such as southern flying squirrels, *Glaucomys volans* (Robins et al. 2000) and giant flying squirrels, *Petaurista* spp. (Lee 1998). Indeed, FSSD may be more widespread in mammals than originally thought, since a common difficulty in accurately assessing SSD in the morphology of wild populations is variability in measurements associated with age, where often only adult divergence in size is considered (Badyaev et al. 2001). From the perspective of sexual selection, the implications of sexual dimorphism may be most important during breeding and thus consideration of adult morphology is most relevant. However, some species, such as small rodents, often initiate breeding precociously, even before having attained asymptotic growth (Dobson et al. 1999; Lambin & Yoccoz 2001; Broussard et al. 2005a). In these species, the degree or even direction of SSD may change with age along with the ecological implications of differential body size.

Southern flying squirrels are small nocturnal sciurids that show FSSD and have a short age to maturity relative to other tree squirrels (Dolan & Carter 1977). In this species, breeding often occurs within 6 months of birth, before growth of females is complete. Thus, SSD may not be evident during a female's first reproduction. This may have a marked influence on reproductive output, since individuals may allocate resources to growth and reproduction simultaneously, or delay growth entirely in favour of reproduction, which can constrain fecundity. Constraints of reproduction with age have been documented for female Richardson's ground squirrel, *Spermophilus richardsonii*, where somatic investment into growth and maintenance is greatest at primiparity (Broussard et al. 2005b). Increased fecundity with female age has been documented in several species, including red deer, *Cervus elaphus* (Clutton-Brock et al. 1987), white-footed mice, *Peromyscus leucopus* (Havelka & Millar 2004), common marmosets, *Callithrix jacchus* (Smucny et al. 2004), Columbian ground squirrels, *Spermophilus columbianus* (Risch et al. 1995; Broussard et al. 2003) and red-legged partridge, *Alectoris rufa* (Cabezas-Díaz et al. 2005). In many small mammals, larger females also show higher fecundity and overall higher reproductive success than smaller individuals (Schulte-Hostedde et al. 2004). However, age and breeding experience may play a confounding role, if the relationship between age, size and reproduction is not properly resolved.

Selection for larger body size in females of FSSD species may stem from reproductive advantages gained directly through increased fecundity or indirectly through advantages gained by mating with multiple males. Studies have suggested that mating with multiple males may increase a female's fitness through indirect genetic benefits attained from increasing the genetic diversity of offspring (Stockley et al. 1993; Zeh & Zeh 1996, 1997; Brown 1997; Kempenaers et al. 1997), or through direct benefits to fitness, such as access to territories, and avoidance of male aggression and infanticide (Krokene et al. 1998; Soltis & McElreath 2001; Li & Brown 2002; Garcia-Gonzalez et al. 2003; Wolff & MacDonald 2004). In both *T. amoenus* and Gunnison's prairie dogs, *Cynomys gunnisoni*, female reproductive success increases with the number of genetic mates (Hoogland 1998; Schulte-Hostedde et al. 2004). However, few studies have examined the association between female body size and number of genetic mates, despite associations with male body size being well documented (but see Fitze et al. 2005). Larger female body size may also be advantageous in species where females are the territorial sex, such as in *G. volans*, which are heavily dependent on hardwood mast, such as oak acorns (Dolan & Carter 1977), particularly during the autumn and winter months, which coincide with their breeding season. Additionally, cavities provide nesting sites, and these are typically in higher abundance in hardwood forests than in coniferous stands (Kahler & Anderson 2006). Thus, it is conceivable that larger females may defend larger territories and/or those with increased food and nesting resources, and this in turn may increase their reproductive success.

We tested whether female body size in southern flying squirrels is positively related to four parameters that are likely to influence reproductive success, and thus whether larger females show higher fitness. Specifically, we predicted that larger and heavier females would (1) have increased fecundity, (2) mate with a greater number of male sires, (3) have larger home ranges and (4) have home ranges with greater nesting and food resources, as determined by habitat composition. We also tested the prediction that FSSD in this species may be age dependent by comparing body size of females during their first reproductive attempt and during a subsequent litter to determine whether females begin breeding before they attain full size and whether SSD is expressed at age of first reproduction. This information may shed light on whether age-dependent changes in SSD result in differing size-dependent reproductive strategies and further our understanding of the nature of precocial breeding and of the selective factors that may influence the evolution of FSSD in mammals.

MATERIALS AND METHODS

Study Species and Field Site Description

The southern flying squirrel is a common and widespread arboreal inhabitant of primary and secondary hardwood deciduous forests of the eastern United States and southern Canada (Dolan & Carter 1977). The breeding season can largely be characterized as bimodal with a primary breeding season starting in the late summer/early autumn and

continuing through early winter, but if favourable conditions persist, breeding could occur throughout much of the year (Risch 1999). Mean litter size in *G. volans* is three to four, but can range from one to six (Dolan & Carter 1977). Females often breed precociously within 6 months of birth, during which time they may be simultaneously allocating resources to somatic and reproductive pathways or redirecting resources solely to reproduction, thereby delaying their growth.

This study was conducted on a population of *G. volans* located at the United States Department of Energy's Savannah River Site (SRS), near Aiken, South Carolina. The study area is located on the upper coastal plain ecoregion and is bordered to the south by the Savannah River, which separates South Carolina from Georgia. Although numerous habitats exist on the SRS, this study was conducted on two predominant forest types: upland deciduous forests dominated by water oak, *Quercus nigra*, and pignut hickory, *Carya glabra*, and plantations of slash pine, *Pinus elliottii*, loblolly pine, *P. taeda*, and longleaf pine, *P. palustris*, managed by the United States Forest Service. More detailed descriptions of the study area are available from Jones et al. (1981), Workman & McLeod (1990) and Risch & Brady (1996).

Field Data Collection

From 1991 to 1998, 993 southern flying squirrel nestboxes (for design see Sonenshine et al. 1973) were arranged in 10-by-10 grids with 40 m between adjacent boxes. Nestboxes were attached to trees about 4−5 m above the ground, following the protocol outlined in Brady et al. (2000) and Fokidis & Risch (2005). These nestboxes facilitated the trapping of females and offspring soon after parturition, as well as nonreproductive males and females. Flying squirrels were anaesthetized with Methoxyflurane (Metophane, Pitman-Moore, Inc., Channahon, Illinois, U.S.A.) upon first capture and individuals were marked with uniquely numbered paired eartags (Monel no. 1005) and PIT tags (Passive Integrated Transponders; AVID Marketing, Inc., Norco, California, U.S.A.) to ensure redundant identification of individuals throughout their lifetime, since there is often substantial loss of both external and internal markers (Fokidis et al. 2006). We recorded the reproductive condition of adult females (inactive, oestrus, pregnant, lactating and postlactating) and males (inactive and scrotal), according to Sollberger (1943). We measured body mass and seven linear measurements of body size (total length of body and tail (BTL), head to outstretched hind leg (HBL), body length (BL), skull length (SL), skull width (SW), foreleg length (FL) and hindleg length (HL)). Individuals with evidence of broken tails were excluded from analyses that involved tail length as a component measurement. Age was determined by examining the multi-year data set for females that were tagged as juveniles. For paternity analysis, we collected ear clippings from all females and their offspring, upon first capture, and these were stored at −70°C until DNA extraction. We did not use data from males for paternity analysis because they have substantially larger home ranges and are generally more mobile than females,

making it logistically difficult and costly to genotype the large numbers of males in each locality.

Ethical note

All procedures were approved by the Institutional Animal Care and Use Committee at Auburn University, Auburn, Alabama, U.S.A. Squirrels were retrapped several times to obtain information on home range size, in a manner that is commonly used in rodent studies (Ribble et al. 2002). There was no evidence of adverse effects of retrapping or repeated anaesthetizing on reproduction, survival, body mass, or body condition (T.S. Risch, unpublished data). Capture and handling time at first capture of an individual was about 20 min, and on subsequent captures, it was about 10 min, as eartagging, PIT tagging and collection of ear clips were not necessary. All sampling procedures were done under anaesthesia to minimize discomfort to the animal. Full recovery of each individual was observed before release at the site of capture.

Assessing Body Size

To determine the relationship between growth and breeding experience, we compared body size and mass of a subset of females at primiparity (within 6 months of birth) and during a subsequent breeding attempt, at least 1.5 years after birth. To document age-related changes in SSD, this subset of females was compared to all males captured from a female's locality within 10 days of expected conception, obtained by backdating 40 days from litter birth. This allowed us to compare females with potential suitors during oestrus and to avoid inclusion of pregnant or lactating females, which would bias weight. The seven linear measurements of size were tested for repeatability using individuals that had multiple measurements taken with 20 days, using general linear model analysis of variance (GLM ANOVA), and the most repeatable, noncomponent measurements were used. These body size components (BTL, SW, FL and HL) were log-transformed to satisfy normality and equal variance assumptions. To document both the magnitude and direction of SSD, we used discriminant function analysis (DFA) developed by Pimental (1979), in a manner outlined in Schulte-Hostedde & Millar (2000). Briefly, this procedure uses a multivariate analysis of variance (MANOVA) to determine differences between the sexes based on component measurements and then classifies each individual to the sex it most resembles. Mahalanobis distances between group centroids are calculated and canonical vectors that maximize variation in the component measurements are developed. The means and distributions of canonical scores are indications of the divergence of structural body size between the sexes. To quantify overall structure size and test predictions of individual variation in body size, we used principal component analysis (PCA) to generate structural size scores standardized to a mean of zero, for each individual, regardless of sex. To obtain values of body condition, we used the residuals of an ordinary least squares linear regression of body

mass on structural size. This 'body condition index' is considered an appropriate means to document increased fat and lean stores and body water in small mammals (Schulte-Hostedde et al. 2001, 2005; Parker & Krockenberger 2002). Where appropriate, we used either paired or two-sample t tests for comparisons.

Determining Home Range Size and Habitat Quality

Females often moved their litters to different nesting sites during the breeding season, allowing us to capture females repeatedly, so we obtained substantial spatial data using nestbox locations as fixes. We used these capture locations to determine home ranges during the breeding season. We only used females with litters for which we had obtained a minimum of 12 fixes. Using Universal Transverse Mercator (UTM) coordinates, we analysed home range using the Animal Movement Extension (Hooge & Eichenlaub 1997) of Arcview GIS 3.2 (Environmental Systems Research Institute, Inc., Redlands, California, U.S.A.). We used the adaptive kernel method (AKM) to determine home range size with 30%, 50% and 95% range use distributions. The 95% home range use distributions were overlaid on a detailed vegetation land-cover data set for the SRS, and the percentage of habitat within each range was calculated. The four habitat classifications were defined as upland and bottomland hardwoods, and dense and open canopy pine plantations. Pearson correlations were used to determine associations with female characteristics and reproduction.

Paternity Analysis

We extracted DNA from ear tissue using Qiagen DNeasy tissue kits (Qiagen Inc., Valencia, Califorina, U.S.A.) and used five microsatellite loci to test for paternity; three loci (SFS-04, SFS-07 and SFS-15) developed by Fokidis et al. (2003) for *G. volans* and two loci (GS-08, GS-10) developed by Zittlau et al. (2000) for *G. sabrinus*. Using this combination of loci we calculated a paternal exclusion probability using CERVUS 2.0 (Marshall et al. 1998), described as the probability of these loci excluding a nonfather from paternity based on results where the genotype of one parent and all offspring were known. Our methodology is outlined in detail in Fokidis et al. (2003). Briefly, we amplified samples in 25-μl polymerase chain reactions (PCR) using the touchdown 60°C thermocycling protocol. PCR products were resolved using polyacrylamide gels on an ABI 377-96 sequencer run at 70 W. Product sizes were determined as compared to a commercially available known size ladder (Gensize ROX 500 ladder, Genpak, Boston, Massachusetts, U.S.A.). Samples from mothers were run alongside that of their offspring to facilitate direct comparison. PCR products were scored using ABI Genotyper version 2.5 (Fostercity, California), and observed heterozygosity (H_o), expected heterozygosity (H_e) and allele frequencies for all loci were calculated with CERVUS 2.0. We tested maternal allele frequencies for deviations from Hardy−Weinberg equilibrium and tested pairs of loci for linkage disequilibrium using a Markov chain algorithm in GENEPOP 3.3 (Raymond & Rousset 1995).

We only had access to maternal genotypes and thus we determined multiple paternity using two approaches. The first involved manual identification of paternal alleles based on the three novel allele approach. In some situations, either allele for a locus could be inherited from the mother in two or more offspring within a litter. The resulting genotype of the father was unclear, and we could not distinguish whether one or two paternal alleles were present. In these cases, we used the conservative estimate of only one paternally inherited allele. The second approach involved paternal reconstruction using the likelihood estimator GERUD 2.0 (Jones 2001). This program determines the paternally inherited alleles within a litter for all loci and reconstructs possible paternal genotypes, providing a minimum number of sires for each litter (Jones 2001). The resulting paternal genotypes are ranked in order of likelihood based on known allele frequency distributions for each locus. To determine the minimum number of fathers required to explain variation within a litter, we used the highest ranked genotypes that explained all the variation in offspring genotype. The minimum number of sires was related to female structural size and mass, body condition and age. In addition, for each litter, we calculated both mean heterozygosity (H_L) and mean allele diversity (AD_L). All statistical comparisons were conducted using either SAS (Cary, North Carolina, U.S.A.) or SigmaStat (San Jose, California) statistical software and data were either log-transformed or arcsine-square-root-transformed where necessary to satisfy normality assumptions. Subsamples for various components of this study were obtained from a large data set for *G. volans*, and thus, sample sizes varied throughout the study.

RESULTS

The DFA and PCA were performed using a sample of 1391 adults (544 females and 847 males) and the MANOVA indicated a significant difference in body size between the sexes (Wilk's $\lambda = 0.9015$, $F_{4,1387} = 114.555$, $P < 0.0001$). The squared Mahalanobis distance between female and male centroids was 0.5499 ($P < 0.0001$), and 76.1% of individuals were correctly classified as to sex (87.7% of males and 73.7% of females). All four measurements were positively correlated with the canonical vector, suggesting intersexual differences in body size (Table 1). PC1 explained 67.9% of the variation in body size, whereas PC2 and PC3 only explained 21.3% and 6.4% of the variation, respectively. PC1 had moderate positive loadings for each component variable, and thus seemed an appropriate index of overall structural body size (Table 1). We compiled data for 16 females at primiparity, at 6 months (75%) to 1 year (25%) of age, and at a subsequent breeding attempt from 1.5 years (63%) to 2 years (37%) after birth. Females were about 7.1% heavier and 18.1% structurally larger in their latter breeding attempt than at the time of first reproduction (body mass: $t_{12} = 2.165$, $P = 0.047$; body size: $t_{12} = 2.77$, $P = 0.014$; Fig. 1). Experienced females also had forelegs that were about 6.5% longer

Table 1. Four body size components obtained from 1391 adult (544 females and 847 males) southern flying squirrels, *Glaucomys volans*

		Principal components		
	Canonical structure	PC1	PC2	PC3
BTL	0.979	0.898	−0.360	−0.102
SW	0.299	0.655	0.192	−0.084
FL	0.450	0.853	0.387	0.240
HL	0.414	0.679	0.190	−0.063
% Cumulative variance explained		67.9	89.1	95.6

Discriminant function analysis factor structures for canonical vectors are shown along with principal component (PC) loadings for the first three axes. Measurements include total length of body and tail (BTL), skull width (SW), foreleg length (FL) and hindleg length (HL).

($t_{12} = 2.181$, $P = 0.045$) and hindlegs that were about 6.9% longer ($t_{12} = 2.66$, $P = 0.018$). Body condition did not differ between primiparity and subsequent breeding ($t_{12} = 0.20$, $P = 0.844$).

Intersexual differences in body mass and body size were not statistically significant at primiparity (body mass: 4.2%, $t_{12} = 0.97$, $P = 0.127$; body size: 10.8%, $t_{12} = 1.39$, $P = 0.1862$; Fig. 1). However, these differences were statistically significant at subsequent breeding attempts (body

Figure 1. Mean (a) body mass and (b) body size for 16 female southern flying squirrels, *Glaucomys volans*, breeding at primiparity and during a subsequent reproductive attempt, relative to the number of males present in the locality during expected conception ($N = 38$, and 52 males, respectively). ○: females; ●: males.

mass: 6.9%, $t_{12} = 5.17$, $P = 0.0041$; body size: 22.1%, $t_{12} = 4.38$, $P = 0.0009$; Fig. 1). Females were also larger than males in several univariate comparisons of linear measurements, which became consistently more pronounced in older, experienced females (Table 2).

Litter size was influenced by both maternal body size ($F_{5,80} = 1.433$, $P = 0.0413$; Fig. 2) and body mass ($F_{5,80} = 1.925$, $P = 0.038$; Fig. 3), with larger and heavier females bearing larger litters. The interaction of body size and body mass was also associated with litter size (ANCOVA: $F_{1,84} = 3.02$, $P = 0.003$), indicating differences in the slope of the regression line between body mass and body size. Independent of both body size and body mass, older females consistently bore larger litters and 64% of first-time breeders produced only two offspring (body size: $F_{1,47} = 6.21$, $P = 0.034$; Fig. 2; body mass: $F_{1,47} = 2.95$, $P = 0.042$; Fig. 3). However, an ANCOVA indicated no significant difference between the slope of the regression lines for younger and older females ($F_{1,84} = 0.74$, $P = 0.083$), suggesting that maternal body size and mass are more important predictors of reproductive output than is female age. In contrast, maternal body condition was not associated with litter size ($F_{5,80} = 0.894$, $P = 0.684$).

Home ranges of the 16 females varied in size and percentage of habitat cover (Table 3). Females with larger home ranges (95% AKM) had higher body condition indexes ($F_{1,14} = 6.13$, $P = 0.027$; Fig. 4), but did not differ in body size ($F_{1,14} = 2.21$, $P = 0.160$) or body mass ($F_{1,14} = 3.36$, $P = 0.088$) from females with smaller home ranges. Larger females had a significantly higher proportion of upland hardwood within their 95% AKM home ranges than did smaller females ($F_{1,14} = 12.36$, $P = 0.003$; Fig. 5). The percentage of upland hardwood forest within a female's home range was also positively correlated with increased litter size (Pearson correlation: $r_{14} = 0.69$, $P = 0.035$).

Genetic data at primiparity and subsequent reproduction were available for 11 females. Our sample size was limited, so we conducted a power analysis, using G-power (Faal & Erdfelder 1992), to determine whether it was sufficient to detect a medium or large effect for the minimum number of sires ($\omega = 0.3$ and 0.5, respectively). The sample size had sufficient power to detect both medium and large differences ($1 - \beta = 0.81$ and 0.84, respectively), which we considered most biologically relevant if access to mating opportunities was a primary proximate mechanism in the evolution of FSSD. Details on allele characteristics for this population of *G. volans* are available from Fokidis et al. (2003), and for this study, the combination of markers used provided a paternal exclusion probability of 0.995. All loci were in Hardy−Weinberg equilibrium and linkage disequilibrium was not detected among any pair of loci used. From a total of 22 litters, only two were sired by a single father. However, this difference was not significant (Wilcoxon sign test: $B = 0.5$, $N = 11$, $P = 0.28$), and thus, female breeding experience did not influence multiple mating behaviour. The majority of litters were sired by at least two fathers, however, the calculated percentage paternal contributions to each litter varied according to the likelihood estimator GERUD 2.0.
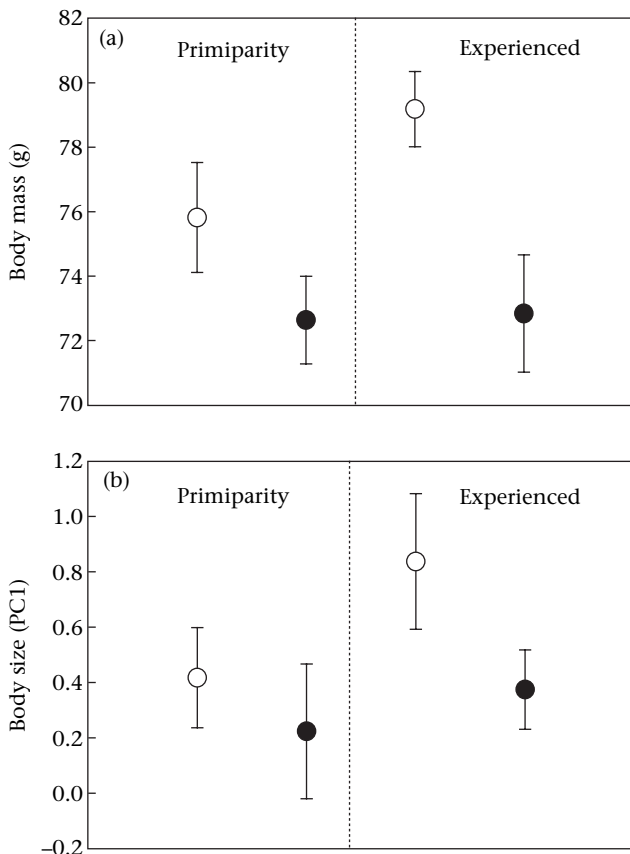
Table 2. Comparison of seven structural body size measurements (mm) of 16 female flying squirrels, *Glaucomys volans*, breeding at primiparity and during subsequent breeding attempts, with measures taken from adult males ($N = 38$, and 52, respectively) present in the area within 10 days of expected conception

	Primiparity				Experienced			
	Females Mean±SD	Males Mean±SD	t	P	Females Mean±SD	Males Mean±SD	t	P
BTL	251.12±6.32	244.70±4.25	3.32	0.034*	258.91±7.22	245.17±3.24	3.51	0.022*
B	144.29±5.11	139.52±2.03	1.93	0.092	149.18±3.93	135.98±2.35	6.12	0.0008*†
HBL	212.46±4.58	204.24±5.31	4.01	0.007*†	218.71±4.93	211.09±3.20	8.04	<0.0001*†
SL	39.23±0.64	38.10±0.52	1.61	0.096	40.12±5.52	36.84±1.12	2.14	0.0414*
SW	23.91±0.44	24.86±1.31	1.55	0.071	27.77±0.89	24.39±0.76	2.76	0.0375*
FL	51.78±1.27	49.32±1.67	0.97	0.326	53.16±2.01	50.61±1.30	3.88	0.0031*†
HL	26.31±2.55	25.81±2.35	0.42	0.625	29.26±1.36	28.97±1.01	0.95	0.3657

Measurements include total length of body and tail (BTL), head to outstretched hind leg (HBL), body length (B), skull length (SL), skull width (SW), foreleg length (FL), and hindleg length (HL).
*Indicates significance at $P < 0.05$.
†Indicates significance with Bonferroni correction at $P < 0.0071$.

There were no discrepancies between direct observation of paternal alleles or GERUD 2.0 in terms of number of potential sires. The two females that bore singly sired litters did not appear to differ in body size, body mass or body condition from females of comparable age that bore multiply sired litters. Females at primiparity and in subsequent breeding attempts did not differ in the minimum number of sires ($t_{12} = 0.74$, $P = 0.319$). There was a significant correlation between H_L and AD_L ($r_9 = 0.37$, $P = 0.034$), but neither variable was correlated with body size (H_L: $r_9 = 0.41$, $P = 0.118$; AD_L: $r_9 = 0.27$, $P = 0.802$), body mass (H_L: $r_9 = 0.10$, $P = 0.721$; AD_L: $r_9 = 0.16$, $P = 0.488$) or body condition (H_L: $r_9 = 0.17$, $P = 0.217$; AD_L: $r_9 = 0.31$, $P = 0.091$) of females.

DISCUSSION

We examined age-dependent variation in female body size within the context of female-biased sexual size dimorphism and the potential benefits of large body size to fitness in female southern flying squirrels. First-time breeding females were not significantly larger or heavier than males, but became so on subsequent breeding attempts, about 1 year after birth. However, despite female growth continuing beyond first reproduction, increased body size and body mass in females was positively associated with litter size, independent of age. Contrary to our predictions, larger females did not have more mates or larger home ranges than smaller females, but their home ranges did contain a greater proportion of upland hardwood tree species, as predicted, suggesting that larger females have greater food and nesting resources available to them.

Female flying squirrels often breed within a few months of birth, before they have reached their full body size. Whether female *G. volans* simultaneously allocate resources to growth and reproduction, or whether they delay growth entirely to reproduce is unknown, but either strategy may constrain litter size. Indeed, a large majority of first-time breeding females produce only two offspring (64% of first-time litters), which may indicate a physiological constraint on reproduction at this age. Lambin &
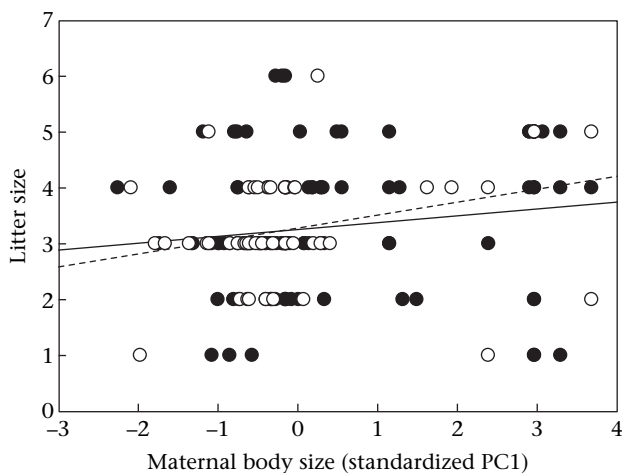
Figure 2. The relationship between litter size and maternal body size, as determined by principal component analysis of four linear measurements in southern flying squirrels, *Glaucomys volans*. −○−: at primiparity; —●—: at subsequent breeding.
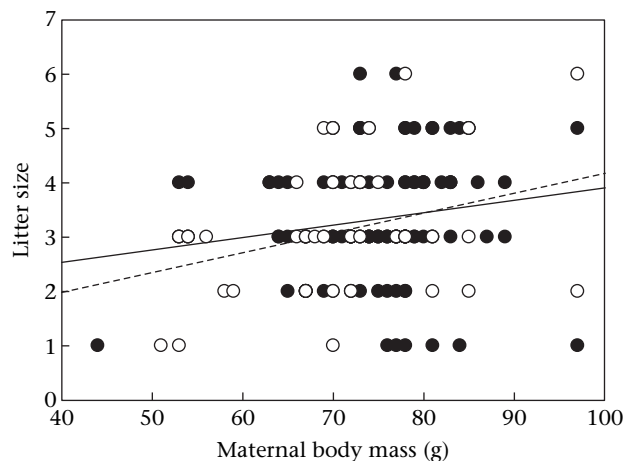

Figure 3. The relationship between litter size and female body mass in southern flying squirrels, *Glaucomys volans*. −○−: at primiparity; —●—: at subsequent breeding.

Table 3. Home ranges (ha) and percentage of habitat cover for 16 female southern flying squirrels, *Glaucomys volans*, calculated using adaptive kernel methods (AKM)

Home range estimation	Mean	SE	Range	Mean % Habitat cover			
				UH	BH	OCP	DCP
AKM 95%	6.09	0.67	2.46–10.46	58	13	38	15
AKM 50%	1.95	0.33	0.53–5.59	42	11	31	11
AKM 30%	1.22	0.31	0.26–5.59	51	16	28	6

Habitats include upland hardwood forest (UH), bottomland hardwood forest (BH), open canopy pine (OCP) and dense canopy pine (DCP).

Yoccoz (2001) examined precocially breeding female Townsend's voles, *Microtus townsendii*, and reported increases in structural mass during pregnancy, suggestive of simultaneous allocation, yet growth rates did not differ from those of nonprecocial cohorts. However, litter size at primiparity also did not differ for precocial and nonprecocial females. We did not test differences in litter size at age of first reproduction between precocial and nonprecocial breeding females, because litter size can vary substantially across seasons, and data for nonprecocial breeding females are scant (T. S. Risch, unpublished data), which could make analysis and interpretation difficult. Although the proximate determinants of age at first reproduction in small mammals remain poorly known, Kraus et al. (2005) suggested that high adult mortality rates could select for early onset of reproduction to maximize fitness. An additional element is that of resource availability and its fluctuation in seasonal environments. Tkadlec & Zejda (1995) found that, in common voles (*M. arvalis*), which show one of the most extreme examples of precocial breeding in mammals, older females produced smaller litters than first-time precocial breeders, a pattern opposite to that of other studies, including this one. They reasoned that precocial reproduction, in concert with maturation and growth, might induce energetic costs that decrease overwinter survival and thus favour maximal reproduction early in life. In
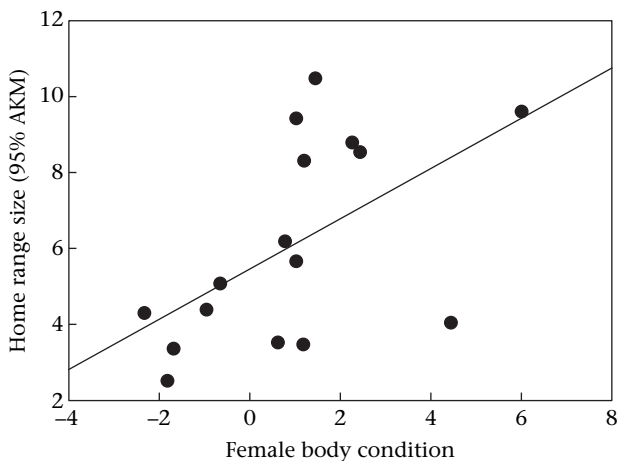
Figure 4. Home range size, determined with a 95% adaptive kernel estimate, (AKM) as a function of female body condition in southern flying squirrels, *Glaucomys volans*.
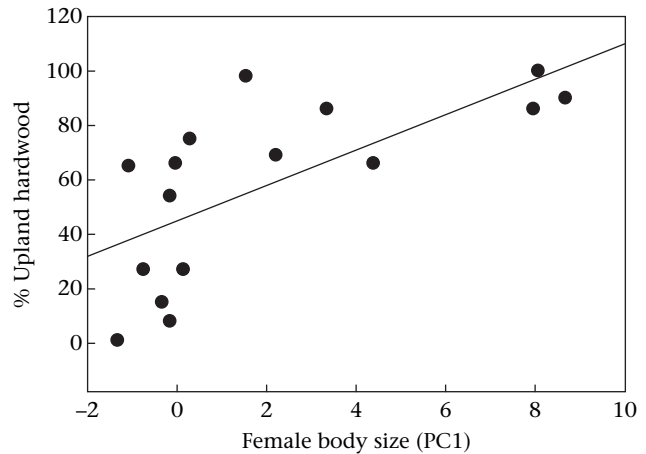
Figure 5. The association between body size and the percentage upland hardwood forest within the home range of female southern flying squirrels, *Glaucomys volans*.

longer-lived *G. volans*, mortality of adults is probably lower than that of juveniles, and thus, precocially breeding females may hedge their bets in favour of future reproductive attempts, and thus limit litter sizes. However, it is unknown whether offspring survival varies between age of first reproduction and subsequent attempts, and whether survival covaries with litter size. Long-term demographic data on this species may shed light on these issues.

At age of first reproduction, there was no evidence of FSSD, however, FSSD becomes considerable later in the life of female flying squirrels. This age-related difference in body size coupled with the precocial breeding and smaller litters of younger females may reflect different reproductive strategies between young and old females. Variation in mating strategies with age has been well documented in male mammals (Lacey & Wieczorek 2001; Weingrill et al. 2003; Isaac 2005b) but much less so in females. A study of swift foxes, *Vulpes velox*, showed that older females were more likely to be involved in breeding groups, which could consist of either two females and one male or one female and two males (Kitchen et al. 2006). Similarly, age influences multiple mating behaviour of female common lizards, *Lacerta vivipara* (Richard et al. 2005). Although multiple male mating by females is common in *G. volans*, we did not find evidence of an age-dependent mating strategy involving polyandry. This suggests that mating with multiple males is beneficial to females, regardless of body size or age, and this is supported by the generally high incidence of the behaviour in our study population. Schulte-Hostedde et al. (2004) also failed to detect a relationship between female body size and multiple paternity in *T. amoenus*, but they found a high incidence of multiple paternity in litters (91.7%) in their study population. Among mammals showing FSSD, polyandry may be a common mating strategy for females, but competition for males is unlikely to be a major factor underlying the evolution of FSSD.

Regardless of age, maternal body size influenced litter size, consistent with results of other studies from a variety of taxa (Iason 1990; Olsson & Shine 1996). Body size in gliding mammals may be under selection because efficient

gliding locomotion imparts the need for an optimal relationship between body mass and structural size to minimize wing loading. For females of gliding species, mass gained during pregnancy (which would increase wing loading) may favour an increase in structural size and, thus, patagial surface area relative to body mass. In bats, the need to minimize wing loading of gravid females has been suggested as an explanation for FSSD, where larger female structural size is associated with larger litter sizes (Myers 1978; Hayssen & Kunz 1996). Similar constraints have been proposed for *G. volans* (Robins et al. 2000) and flying lizards of the genus *Draco*, which also show FSSD (Shine et al. 1998; McGuire 2003). Although data on SSD are scarce for many gliding mammals, some species, such as the northern flying squirrel, *G. sabrinus*, do not show FSSD (Wells-Gosling & Heaney 1984). However, an age-dependent FSSD may be occurring in this species, as in *G. volans*, and thus, the timing of sampling may influence whether SSD is detected.

An interesting finding of our study was the association between female body size and the proportion of the home range containing upland hardwood forest. *Glaucomys volans* are secondary cavity nesters, and hardwood forests provide more cavities than do pine forests, the other major habitat type encountered (Kahler & Anderson 2006). Similarly, Fridell & Litvaitis (1991) found that, although home ranges of females were smaller than those of males, they contained a greater abundance of snags. These findings suggest that competition for nest sites may be an important resource for which females compete. However, Brady et al. (2000) found that manipulation of cavity availability did not correspond to changes in population density of *G. volans*, suggesting that nest site availability is not a limiting resource in this species. Another potential source of competition among females is tree mast, which is available in hardwood forests and is a major food resource, particularly during the breeding season (Dolan & Carter 1977). Female territoriality, as reported in this species (Madden 1974), may allow monopolization of access to food, so it is conceivable that larger females have greater access to resources within their territory, allowing them to raise larger litters. This notion is supported by our observation that females with larger home ranges had higher scores of body condition, although we did not detect a correlation with litter size. Food supplementation experiments have demonstrated increased litter sizes in other squirrel species (Dobson & Kjelgaard 1985). In a study of *S. vulgaris*, Wauters & Dhondt (1995) found that larger females had larger home ranges with greater resource availability and were typically more fecund. However, an important consideration is whether offspring survival varies with the presence of upland hardwood habitat. Fridell & Litvaitis (1991) suggested that female *G. volans* may move to areas with lower food resources when rearing young, although the reasons for this behaviour remain unclear. Clearly, more studies are needed to determine the extent to which habitat composition affects various parameters of reproductive success, namely, offspring survival, home range size and female body size.

Although we examined the relationship between female body size and a number of parameters that could influence reproductive success to determine whether selection favours larger females in a species with female-biased sexual size dimorphism, an explanation for the evolution of SSD must consider not only why the larger sex is larger, but also why the smaller sex is smaller. The mating system of *G. volans* is similar to that of other tree squirrels where many males engage in active mate chases in pursuit of a female (Koprowski 1998), which tests male manoeuvrability. Aerial agility and flight efficiency have been proposed as selective factors for small male size in shorebirds (Jehl & Murray 1986) and raptorial birds (Andersson & Norberg 1981). Increased mobility in males may allow differential access to females during oestrus. Schulte-Hostedde & Millar (2002a) found that smaller *T. amoenus* males dominated larger males in staged dyadic encounters, by generally being more aggressive. However, they also found that smaller males had slower running speeds than larger males (Schulte-Hostedde & Millar 2002b), which suggests a trade-off between two body size variables that could influence access to mating opportunities during a mate chase.

Further studies examining the degree to which selection on size and age in both sexes influences reproductive success could help to elucidate patterns of SSD in an otherwise understudied group of mammals, those showing FSSD.

References

Andersson, M. 1994. *Sexual Selection.* Princeton, New Jersey: Princeton University Press.

Andersson, M. & Norberg, R. A. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds with a size scaling of flight performance. *Biological Journal of the Linnean Society*, **15**, 105–130.

Badyaev, A. V., Whittingham, L. A. & Hill, G. E. 2001. The evolution of sexual size dimorphism in the house finch. III. Developmental basis. *Evolution*, **55**, 176–189.

Brady, M. J., Risch, T. S. & Dobson, F. S. 2000. Availability of nest sites does not limit population size of southern flying squirrels. *Canadian Journal of Zoology*, **78**, 144−1149.

Broussard, D. R., Risch, T. S., Dobson, F. S. & Murie, J. O. 2003. Senescence and age-related reproduction of female Columbian ground squirrels. *Journal of Animal Ecology*, **72**, 212−219.

Broussard, D. R., Michener, G. R., Risch, T. S. & Dobson, F. S. 2005a. Somatic senescence: evidence from female Richardson's ground squirrels. *Oikos*, **108**, 591−601.

Broussard, D. R., Dobson, F. S. & Murie, J. O. 2005b. The influence of capital and income on reproductive strategies of female Columbian ground squirrels. *Canadian Journal of Zoology*, **83**, 546−552.

Brown, J. L. 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology*, **8**, 60−65.

Cabezas-Díaz, S., Virgos, E. & Villafuerte, R. 2005. Reproductive performance changes with age and laying experience in the red-legged partridge *Alectoris rufa*. *Ibis*, **147**, 316−323.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. *Journal of Animal Ecology*, **56**, 857−871.

Dobson, F. S. & Kjelgaard, J. D. 1985. The influence of food resources on life-history in Columbian ground squirrels. *Canadian Journal of Zoology*, **63**, 2105−2109.

Dobson, F. S., Risch, T. S. & Murie, J. O. 1999. Increasing returns in the life history of Columbian ground squirrels. *Journal of Animal Ecology*, **68**, 73−86.

Dolan, P. G. & Carter, D. C. 1977. *Glaucomys volans. Mammalian Species*, **78**, 1−6.

East, M. L., Burke, T., Wilhelm, K., Greig, C. & Hofer, H. 2003. Sexual conflicts in spotted hyenas: male and female mating tactics and their reproductive outcome with respect to age, social status and tenure. *Proceedings of the Royal Society of London, Series B*, **270**, 1247−1254.

Faal, F. & Erdfelder, E. 1992. *GPOWER: a Priori, Post-hoc, and Compromise Power Analysis*. Bonn, Germany: Bonn University.

Fitze, P. S., Le Galliard, J. F., Federici, P., Richard, M. & Clobert, J. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. *Evolution*, **59**, 2451−2459.

Fokidis, H. B. & Risch, T. S. 2005. The use of nest boxes to sample arboreal vertebrates. *Southeastern Naturalist*, **4**, 447−458.

Fokidis, H. B., Schable, N. A., Hagen, C., Glenn, T. C. & Risch, T. S. 2003. Characterization of microsatellite DNA loci for the southern flying squirrel (*Glaucomys volans*). *Molecular Ecology Notes*, **3**, 616−618.

Fokidis, H. B., Robertson, C. & Risch, T. S. 2006. Keeping tabs: are redundant marking systems needed for rodents? *Wildlife Society Bulletin*, **34**, 764−771.

Fridell, R. A. & Litvaitis, J. A. 1991. Influence of resource distribution and abundance on home-range characteristics of southern flying squirrels. *Canadian Journal of Zoology*, **69**, 2589−2593.

Garcia-Gonzalez, F., Nunez, Y., Ponz, F., Roldan, E. R. S. & Gomendio, M. 2003. Sperm competition mechanisms, confidence of paternity, and the evolution of paternal care in the golden egg bug (*Phyllomorpha laciniata*). *Evolution*, **57**, 1078−1088.

Havelka, M. A. & Millar, J. S. 2004. Maternal age drives seasonal variation in litter size of *Peromyscus leucopus*. *Journal of Mammalogy*, **85**, 940−947.

Hayssen, V. & Kunz, T. H. 1996. Allometry of litter mass in bats: maternal size, wing morphology, and phylogeny. *Journal of Mammalogy*, **77**, 476−490.

Hooge, P. N. & Eichenlaub, B. 1997. *Animal Movement Extension to ARCVIEW. Version 1.1*. Anchorage: Alaska Biological Science Center, U.S. Geological Survey.

Hoogland, J. L. 1998. Why do female Gunnison's prairie dogs copulate with more than one male? *Animal Behaviour*, **55**, 351−359.

Howard, R. D., Martens, R. S., Innis, S. A., Drnevich, J. M. & Hale, J. 1998. Mate choice and mate competition influence male body size in Japanese medaka. *Animal Behaviour*, **55**, 1151−1163.

Iason, G. R. 1990. The effects of size, age and a cost of early breeding on reproduction in female mountain hares. *Holarctic Ecology*, **13**, 81−89.

Isaac, J. L. 2005a. Sexual dimorphism in mammals: a review of potential causes and consequences. *Mammal Review*, **35**, 101−115.

Isaac, J. L. 2005b. Mass loss during the mating system in male common brushtail possums (*Trichosurus vulpecula*): implications for age-specific variation in mating strategy. *Journal of Zoology*, **266**, 181−185.

Jehl, J. R. & Murray, B. G., Jr. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. *Current Ornithology*, **3**, 1−86.

Jones, A. G. 2001. GERUD1.0: a computer program for the reconstruction of parental genotypes from progeny arrays using multilocus DNA data. *Molecular Ecology Notes*, **1**, 215−218.

Jones, S. M., Van Lear, D. H. & Cox, S. K. 1981. *Major Forest Community Types of the Savannah River Plant: a Field Guide*. Aiken, South Carolina: Savannah River National Environmental Research Park Program.

Kahler, H. A. & Anderson, J. T. 2006. Tree cavity resources for dependent cavity-using wildlife in West Virginia forests. *Northern Journal of Applied Forestry*, **23**, 114−121.

Kempenaers, B., Verheyen, G. R. & Dhondt, A. A. 1997. Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behavioral Ecology*, **8**, 481−492.

Kitchen, A. M., Gese, E. M., Waits, L. P., Karki, S. M. & Schauster, E. R. 2006. Multiple breeding strategies in the swift fox, *Vulpes velox*. *Animal Behaviour*, **71**, 1029−1038.

Koprowski, J. L. 1998. Conflict between the sexes: a review of social and mating systems of the tree squirrels. In: *Ecology and Evolutionary Biology of Tree Squirrels* (Ed. by M. A. Steele, J. F. Merritt & D. A. Zegers), pp. 33−41. Martinsville: Virginia Museum of Natural History.

Kraus, C., Thomson, D. L., Künkele, J. & Trillmich, F. 2005. Living slow and dying young? Life-history strategy and age-specific survival rates in a precocial small mammal. *Journal of Animal Ecology*, **74**, 171−180.

Krokene, C., Rigstad, K., Dale, M. & Lifjeld, J. T. 1998. The function of extrapair paternity in blue tits and great tits: good genes or fertility insurance? *Behavioral Ecology*, **9**, 649−656.

Kruuk, H. 1972. *The Spotted Hyaena: a Study of Predation and Social Behaviour*. Chicago: University of Chicago Press.

Lacey, E. A. & Wieczorek, J. R. 2001. Territoriality and male reproductive success in Arctic ground squirrels. *Behavioral Ecology*, **12**, 626−632.

Lambin, X. & Yoccoz, N. G. 2001. Adaptive precocial reproduction in voles: reproductive costs and multivoltine life-history strategies in seasonal environments. *Journal of Animal Ecology*, **70**, 191−200.

Lee, P. F. 1998. Body size comparison of two giant flying squirrel species in Taiwan. *Acta Zoologica Taiwanica*, **9**, 51−57.

Li, S. H. & Brown, J. L. 2002. Reduction of maternal care: a new benefit of multiple mating? *Behavioral Ecology*, **13**, 87−93.

McGuire, J. A. 2003. Allometric prediction of locomotor performance: an example from Southeast Asian flying lizards. *American Naturalist*, **161**, 337−349.

Madden, J. R. 1974. Female territoriality in a Suffolk County, Long Island, population of *Glaucomys volans*. *Journal of Mammalogy*, **55**, 647−652.

Marshall, T. C., Slate, J., Kruuk, L. & Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, **7**, 639–655.

Myers, P. 1978. Sexual dimorphism in size of vespertilionid bats. *American Naturalist*, **112**, 701–711.

Olsson, M. M. & Shine, R. 1996. How and why does reproductive success increase with age? A case study using sand lizards (*Lacerta agilis*). *Oecologia*, **105**, 175–178.

Parker, A. K. & Krockenberger, A. K. 2002. Sometimes the simple way is best: an evaluation of total body electrical conductivity (TOBEC) and a morphological index as predictors of total body water in the northern brown bandicoot, *Isodon macrourus*. *Wildlife Research*, **29**, 135–140.

Pimental, R. A. 1979. *Morphometrics: the Multivariate Analysis of Biological Data*. Dubuque, Iowa: Kendall/Hunt.

Ralls, K. 1976. Mammals in which females are larger than males. *Quarterly Review of Biology*, **51**, 245–276.

Raymond, M. & Rousset, F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.

Ribble, D. O., Wurtz, A. E., McConnell, E. K., Buegge, J. J. & Welch, K. C., Jr. 2002. A comparison of home ranges of two species of *Peromyscus* using trapping and radiotelemetry data. *Journal of Mammalogy*, **83**, 260–266.

Richard, M., Lecomte, J., De Fraipont, M. & Clobert, J. 2005. Age-specific mating strategies and reproductive senescence. *Molecular Ecology*, **14**, 3147–3155.

Risch, T. S. 1999. Significance of litter size and costs of reproduction in small mammals. Ph.D. thesis, Auburn University, Auburn, Alabama.

Risch, T. S. & Brady, M. J. 1996. Trap height and capture success of arboreal small mammals: evidence from southern flying squirrels (*Glaucomys volans*). *American Midland Naturalist*, **136**, 346–351.

Risch, T. S., Dobson, F. S. & Murie, J. O. 1995. Is mean litter size the most productive? A test in Columbian ground squirrels. *Ecology*, **76**, 1643–1654.

Robins, J. H., Scheibe, J. S. & Laves, K. 2000. Sexual size dimorphism and allometry in southern flying squirrels, *Glaucomys volans*. In: *Biology of the Gliding Mammals* (Ed. by R. Goldingay & J. Scheibe), pp. 229–248. Furth: Filander-Verlag.

Schulte-Hostedde, A. I. & Millar, J. S. 2000. Measuring sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*). *Canadian Journal of Zoology*, **78**, 728–733.

Schulte-Hostedde, A. I. & Millar, J. S. 2002a. 'Little chipmunk' syndrome? Male body size and dominance in captive yellow-pine chipmunk (*Tamias amoenus*). *Ethology*, **108**, 127–137.

Schulte-Hostedde, A. I. & Millar, J. S. 2002b. Effects of body size and mass on running speed of male yellow-pine chipmunks (*Tamias amoenus*). *Canadian Journal of Zoology*, **80**, 1584–1587.

Schulte-Hostedde, A. I., Millar, J. S. & Hickling, G. J. 2001. Evaluating body condition in small mammals. *Canadian Journal of Zoology*, **79**, 1021–1029.

Schulte-Hostedde, A. I., Millar, J. S. & Gibbs, H. L. 2004. Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism. *Behavioral Ecology*, **15**, 351–356.

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S. & Hickling, G. J. 2005. Restitution of mass/size residuals: validating body condition indices. *Ecology*, **86**, 155–163.

Shine, R. 1990. Proximate determinants of sexual differences in adult body size. *American Naturalist*, **135**, 278–283.

Shine, R., Keogh, S., Doughty, P. & Giragossyan, H. 1998. Costs of reproduction and the evolution of sexual dimorphism in a 'flying lizard' *Draco melanopogon* (Agamidae). *Journal of Zoology*, **246**, 203–213.

Smucny, D. A., Abbott, D. H., Mansfield, K. G., Schultz-Darken, N. J., Yamamoto, M. E., Alencar, A. I. & Tardif, S. D. 2004. Reproductive output, maternal age, and survivorship in captive common marmoset females (*Callithrix jacchus*). *American Journal of Primatology*, **64**, 107–121.

Sollberger, D. E. 1943. Notes on the breeding habits of the eastern flying squirrel (*Glaucomys volans volans*). *Journal of Mammalogy*, **24**, 163–173.

Soltis, J. & McElreath, R. 2001. Can females gain extra paternal investment by mating with multiple males? A game theoretic approach. *American Naturalist*, **158**, 519–529.

Sonenshine, D. E., Cerretani, D. G., Enlow, G. & Elisberg, B. L. 1973. Improved methods for capturing wild flying squirrels. *Journal of Wildlife Management*, **37**, 588–590.

Stockley, P., Searle, J. B., MacDonald, D. W. & Jones, C. S. 1993. Female multiple mating behaviour in the common shrew as a strategy to reduce inbreeding. *Proceedings of the Royal Society of London, Series B*, **254**, 173–179.

Tkadlec, E. & Zejda, J. 1995. Precocious breeding in female common voles and its relevance to rodent fluctuations. *Oikos*, **73**, 231–236.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Wauters, L. A. & Dhondt, A. A. 1995. Lifetime reproductive success and its correlates in female Eurasian red squirrels. *Oikos*, **72**, 402–410.

Weingrill, T., Lycett, J. E., Barrett, L., Hill, R. A. & Henzi, S. P. 2003. Male consortship behaviour in chacma baboons: the role of demographic factors and female conceptive probabilities. *Behaviour*, **140**, 405–427.

Wells-Gosling, N. & Heaney, L. R. 1984. *Glaucomys sabrinus*. *Mammalian Species*, **229**, 1–8.

Wolff, J. O. & MacDonald, D. W. 2004. Promiscuous females protect their offspring. *Trends in Ecology and Evolution*, **19**, 127–134.

Workman, S. W. & McLeod, K. W. 1990. *Vegetation of the Savannah River Site: Major Community Types*. Aiken, South Carolina: Savannah River National Environmental Research Park Program.

Yoccoz, N. G. & Mesnager, S. 1998. Are alpine bank voles larger and more sexually dimorphic because adults survive better? *Oikos*, **82**, 85–98.

Zeh, J. A. & Zeh, D. W. 1996. The evolution of polyandry 1: intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London, Series B*, **263**, 1711–1717.

Zeh, J. A. & Zeh, D. W. 1997. The evolution of polyandry 2: postcopulatory defenses against genetic incompatibility. *Proceedings of the Royal Society of London, Series B*, **264**, 69–75.

Zittlau, K. A., Davis, C. S. & Strobeck, C. 2000. Characterization of microsatellite loci in the northern flying squirrel (*Glaucomys sabrinus*). *Molecular Ecology*, **9**, 817–829.