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Sexual Size Dimorphism and Allometry in Southern Flying Squirrels, *Glaucomys volans*

Abstract

*We explored sexual dimorphism and allometric variation in a large population of southern flying squirrels (*Glaucomys volans*) from South Carolina, USA. Body mass and 9 linear measurements were recorded for 257 squirrels. Sexual size dimorphism was assessed via non-parametric Mann-Whitney U tests, and multivariate allometry was evaluated using partial common and common principal components analysis. Across juveniles and adults, females had longer tails. Upper legs and head and body lengths tended to be longer as well, but females were not heavier than males. Among adults weighing more than 60 g, tail, upper leg, and head and body lengths were significantly longer in females. Percent dimorphism among all animals was greatest for tail length, but among adults, styliform and head and body lengths were dimorphic as well. Regressions of head and body length against mass revealed that light females were shorter than light males. However, above 52 g females were longer. *Glaucomys volans* appears to exhibit bimaturation in which males mature sexually at small size but continue to grow. However, few males attain the maximum size of females.*

Keywords

Glaucomys volans, sexual dimorphism, allometry

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1. Introduction

Sexual size dimorphism (SSD) is common among mammals. Usually, males are larger than females. However, some species exhibit reverse sexual size dimorphism (RSD), in which females are larger. The size disparity may reflect both internal and external selective pressures. Possible internal pressures leading to RSD include reproductive considerations, such as size of the pelvis in relation to infant head size (*sensu* [21]), or inter- and intrasexual competition for food, shelter, or mates [34]. External pressures may include thermoregulatory requirements for overwintering, constraints on locomotor morphology associated with habitat structure [37], or predation. These factors are not necessarily mutually exclusive, and are difficult to isolate and observe. Ralls [34,35] provided an extensive overview of causes and consequences of mammalian SSD and RSD, and Abouheif and Fairbairn [1] provided a more recent treatment across a broader taxonomic range.

Golley [12], Hoffmeister [14], and Madden [25] found RSD in southern flying squirrels, but Diersing [7] and Braun [4] did not (Table 1). We provide a preliminary assessment of SSD in *G. volans* and evaluate male/female size differences for several characters in an effort to resolve the contradictory findings. We present patterns of ontogenetic and static allometry [44] and explore possible reasons for observed dimorphisms.

2. Methods

Animals were collected in the Carolina Sandhills National Wildlife Refuge in an effort to control flying squirrel populations and enhance nesting opportunities for red-cockaded woodpeckers. Squirrels were trapped with Sherman live traps, and removed from nest cavities from the end of March to the first of July in 1994 and 1995. Since reproduction in *G. volans* has been reported for late winter, spring, and summer [12, 23] in South Carolina and Alabama, our samples were probably collected before, during, and after breeding periods.

Animals were weighed in the field, and reproductive conditions noted. Standard measurements were taken in the lab (head and body length, tail length, length of both ears, length of both fore feet and both hind feet). Animals were skinned, and lengths of all limbs determined to the nearest 0.1 mm using dial calipers. Thus, limb lengths include muscle and connective tissue. Both styliform cartilages were exposed by trimming away the patagium and associated musculature, and measured using dial calipers. All paired measurements were averaged to provide a more robust estimate of the metric.

Data were divided into two overlapping sets: a multiple-age series, and adult individuals weighing more than 60 g. Adulthood was determined on the basis of field data and external characteristics. In our study, reproductively active males (those with partially or fully descended testes) weighed as little as 29 g, but all reproductive females weighed more than 60 g. Suchland [52] reported a mean body mass of 56 g for non-reproductive males; 59 g for males with partially descended testes; 72.2 g for males with scrotal testes; and over

Table 1
Studies providing assessment of male/female sexual size dimorphism
(m = males, f = females).

Source	Location	n	Characters	Dimorphism
Braun [4]	Louisiana, USA	22	21 cranial	no*
	Oklahoma, USA	10	21 cranial	no*
	Texas, USA	25	21 cranial	no*
Diersing [7]	Chiapas, Mexico	8m, 8f	total length	no*
			tail length	no*
			head and body length	no*
			hind foot length	no*
			11 cranial	no*
Golley [12]	South Carolina, USA	52m, 71f	total length	yes†
			tail length	yes†
			hind foot length	yes†
			ear length	no
			body mass	yes†
Hoffmeister [14]	Illinois, USA	9m, 9f	total length	yes†
			tail length	yes†
			head and body length	no‡
			hind foot length	yes†
			11 cranial	yes†
Madden [25]	Massachusetts, USA	13m, 8f	2 cranial	no‡
			body mass	yes†
Ralls [34]	South Carolina, USA	52m, 71f	Total length from Golley [12]	yes*†

*. means compared statistically, otherwise means not tested

†. females larger

‡. males larger

60 g for all reproductive females. Thus, we designated animals over 60 g as adults. While using body mass to define adulthood is somewhat arbitrary, used in this way it provides information about overall size, not growth or SSD.

Data were natural log transformed, but measurements obtained from several characters were not normally distributed. Thus, we used Mann-Whitney U tests to evaluate SSD. Because the variables were not statistically independent, we used a Bonferroni adjustment [30] to protect against elevated

Type I error rates. A dimorphism ratio, D_r , was computed for each character [22] for all animals, and separately for all adult animals. The metric was calculated as the mean value of the character for females divided by the mean value for males. The percentage of dimorphism was calculated as the absolute value of $(D_r - 1) \times 100$, to provide information about relative female/male size differences for each character.

Multivariate techniques based on principal components analysis (PCA) were used to explore patterns of multivariate allometry in size and shape space. All multivariate analyses were computed using variance-covariance matrices of \ln transformed data. Analyses were performed using software provided by P. Phillips [32]. Standard errors for eigenvalues were computed using formulae presented in [2]. The first series included data from juvenile and adult animals (ontogenetic series), while the second series analyzed adult males and females (static series).

The jump-up approach [32, 33] to Flury's hierarchy of matrix relationships [11] was used to find an appropriate model for each analysis. This procedure evaluates several hypotheses about relationships between variance-covariance matrices. Equality of principal components across all matrices are compared. Each test involves construction of a pair of matrices that conform to constraints of the particular model being tested. One matrix resembles the model in question; the other resembles a matrix with arbitrary structure (as if from unrelated source matrices). A likelihood ratio statistic is computed to test the hypothesis that the data matrix matches the model better than the arbitrary matrix. The statistic follows a χ^2 distribution for approximately normal data and may be compared to values from a χ^2 table [2, 11]. Low p -values indicate rejection of the model [32, 33]. If all models are rejected, then PCAs should be performed separately for each variance-covariance matrix. If all models are accepted, the matrices are equal and Thorpe's multiple group PCA [55] should be performed on a pooled variance-covariance matrix of the sample data [2]. In the event some or all eigenvectors are shared, but eigenvalues differ, a partial common principal components model (PCPC) or full common principal components (CPC) model will be appropriate. These models are preferred over separate PCAs because they estimate fewer parameters [2, 11]. It should be noted that these tests are not independent. However, we are not testing an *a priori* hypothesis regarding structure of matrices. Instead, we are developing a parsimonious model that best summarizes the available data with the fewest parameter estimates.

Isometry values were computed and compared to coefficients of the first principal component for each multivariate analysis, allowing general comparison of allometric growth patterns in the population as a whole, and an assessment of differences in male/female growth strategies. Loadings different from the isometry value were considered to be either positively or negatively allometric. Isometry values were defined as $\sqrt{1/n}$ where n is the number of characters in the analysis. This value is equivalent to a condition in which coefficients of the first eigenvector are equal in magnitude, reflecting equal relative growth

rates in each character [16, 17, 18, 45]. In terms of the ln transformed original variables ($X_1 \dots X_n$), isometry is expressed in the linear form:

$$V_1 = C_1 \ln (X_1) + C_2 \ln (X_2) + \dots + C_n \ln (X_n),$$

where the C_i s are coefficients of the eigenvector (V_1) associated with the largest eigenvalue (by convention, the first), and all C_i s are equal [2, 16, 17].

We explored aspects of wing loading using regressions of ln transformed head and body length against the natural log of the cube root of body mass [56]. Separate regressions were computed for all males ($n = 145$), all females ($n = 112$), adult males (> 60 g, $n = 90$), adult females (> 60 g, $n = 71$), young males (< 60 g, $n = 55$), and young females (< 60 g, $n = 41$). We used head and body length as an index of patagial area since direct estimates of patagial area were not possible. This is reasonable since increased head and body length corresponds to increased limb length, thus increasing the dimensions of the patagium. This choice is robust in light of the allometric patterns presented below.

3. Results

Mean values for 10 morphological variables are presented in Table 2. Using the Bonferroni adjustment, a critical value of 0.005 assured statistical significance at the 0.05 level. Among all animals, females were significantly larger than males with respect to tail length ($p < 0.005$), and tended to be larger than males with regard to head and body length and upper leg lengths ($p < 0.05$). When the sample was restricted to adult animals over 60 g, females had significantly longer tails, head and body lengths, and upper leg lengths than males ($p < 0.005$). Adult females tended to have longer lower legs, upper and lower arms, and fore feet than adult males ($p < 0.05$). Female mass was not greater than male mass, indicating females were proportioned differently than males.

Results of the matrix comparisons for the ontogenetic series indicated the data fit ($p = 0.102$) a model that assumed two common principal components (Table 3). The resulting PCPCA for the ontogenetic series of males and females is presented in Tables 4 and 5. The first two PCPCs summarized similarities between males and females, while the third PCPC provided an indication of how they differed. Results beyond the first three PCPCs are not presented. They accounted for little of the total variance in the data. The first PCPC reflected overall size and accounted for 62 % (males) and 82 % (females) of the total variance in the data. The second PCPC loaded most heavily for length of the styli-form cartilage, and accounted for 18 % (males) and 7 % (females) of the total variance. The third PCPC differed for males and females. It loaded most heavily for tail length, and accounted for 6 % (males) and 4.5 % (females) of the total variance. Comparison of the first PCPC coefficients with the isometry value (0.333) revealed head and body length and limb lengths were positively allometric, while tail, foot, and styli-form lengths were negatively allometric. Thus with inferred growth, head and body length and limb lengths were disproportionately longer, while tail, feet, and styli-form grew at a slower rate. There were notable differences between sexes in the ontogenetic series. Size (PCPC1)

Table 2

Means (standard deviations) and percent dimorphism (%D) for morphological characters. Results of Mann-Whitney U tests are also presented. Significance at the .05 level is indicated by *, while significance at the .005 level, consistent with the Bonferroni adjustment, is indicated by **.

Character	All Males n=145	All Females n=112	%D	U	Adult Males n=90	Adult Females n=71	%D	U
Mass (g)	62.1 (13.9)	62.0 (16.1)	0.2	8240.5	71.0 (6.5)	72.2 (8.1)	1.7	3387.0
Head-Body	121.1 (9.3)	122.0 (13.3)	0.7	9183.0*	125.8 (5.2)	129.0 (6.4)	2.5	4333.0**
Tail	109.4 (7.0)	111.5 (10.0)	1.9	9960.5**	110.7 (6.1)	114.2 (7.7)	3.2	4228.5**
Upper Leg	31.0 (2.8)	31.0 (3.8)	0.0	9184.0*	32.6 (1.0)	33.2 (1.1)	1.0	471.0**
Lower Leg	40.6 (2.8)	40.4 (3.9)	0.5	8781.5	42.1 (1.3)	42.5 (1.4)	1.0	3844.0*
Hind Foot	29.7 (1.0)	29.8 (1.4)	0.3	9047.5	30.0 (1.0)	30.1 (1.0)	0.3	3447.5
Upper Arm	27.4 (2.3)	27.4 (2.9)	0.0	8740.0	28.8 (1.0)	29.2 (1.2)	1.4	3791.5*
Lower Arm	33.6 (2.5)	33.5 (3.4)	0.3	8914.5	35.0 (1.1)	35.4 (1.1)	1.1	3933.0*
Forefoot	18.8 (0.9)	18.9 (1.0)	0.5	8982.5	19.0 (0.9)	19.2 (0.7)	1.0	3761.5*
Styliform	19.6 (2.0)	19.8 (2.2)	1.0	8768.5	19.9 (1.8)	20.4 (1.2)	2.5	3665.0

accounted for more morphological variance among females than males, and they had a noticeably different pattern of loadings for head and body, upper leg, and upper arm on PCPC3.

Analysis of adult animals greater than 60 g produced fundamentally different results. Matrix comparisons (Table 6) indicated the data fit CPC ($p = 0.394$) and PCPC ($p = 0.142$ to 0.543) models. We present the full common principal components (CPC) model because it involves fewer estimates of statistical parameters than either a PCPCA model or separate PCAs [2, 11].

The first CPC (Table 7) accounted for 43 % (males) and 39 % (females) of the total variance and loaded most heavily for styliform cartilage length (Table 8). In this case, a traditional size interpretation was rejected because of largely non-uniform patterns of coefficient loadings and little variance

Table 3

Flury hierarchy of matrix comparisons using Phillips' jump-up approach. Model matrices are built from the variance-covariance matrices of all males ($n = 145$) and all females ($n = 112$). Each depicted model is tested against a model of arbitrary structure.

MODEL	χ^2	DF	P-VALUE
Equality	142.086	45	< 0.0001
Proportional	120.541	44	< 0.0001
CPC	58.648	36	0.0088
CPC(7)	57.880	35	0.0099
CPC(6)	54.031	33	0.0119
CPC(5)	50.340	30	0.0114
CPC(4)	48.581	26	0.0046
CPC(3)	34.584	21	0.0313
CPC(2)	22.246	15	0.1015
CPC(1)	16.798	8	0.0323

Table 4

Estimated eigenvalues (λ s) and their standard errors in parentheses (both multiplied by 10^4) under the assumption of 2 common principal components for all males and all females. Additionally, proportions of the total variance accounted for by each λ are presented.

	Males		Females	
	λ	Proportion	λ	Proportion
I	359.960 (42.422)	0.623	810.690 (108.820)	0.820
II	102.660 (12.100)	0.178	73.500 (9.866)	0.074
III	33.543 (3.953)	0.058	44.955 (6.034)	0.045
IV	22.249 (2.650)	0.039	21.884 (2.938)	0.022
V	10.513 (1.239)	0.018	16.504 (2.215)	0.017
VI	5.800 (0.684)	0.010	8.639 (1.160)	0.009
VII	3.715 (0.438)	0.006	6.187 (0.830)	0.006
VIII	3.079 (0.363)	0.005	4.216 (0.566)	0.004
IX	2.308 (0.272)	0.004	2.195 (0.295)	0.002

Table 5

Eigenvectors (PCPCs) corresponding to the 3 largest eigenvalues under the assumption of 2 common principal components for all males and all females. The sign in parentheses represents the type of allometric change in the original variable based on a comparison of the first principal component loadings with the isometry value 0.3333.

Variable	Allometry	PCPC1	PCPC2	PCPC3 MALES	PCPC3 FEMALES
Head and Body	+	0.3881	-0.0188	-0.0531	0.2966
Tail	-	0.2445	-0.0153	-0.8700	-0.9099
Upper Leg	+	0.4766	-0.1828	0.2132	0.0920
Lower Leg	+	0.3600	-0.1240	0.0328	-0.0270
Hind Foot	-	0.1204	0.0525	-0.2478	-0.2005
Upper Arm	+	0.4098	-0.2319	0.2649	0.1332
Lower Arm	+	0.3879	-0.1148	0.0770	0.0872
Fore foot	-	0.1290	0.0426	-0.1997	-0.0726
Styliform	-	0.2885	0.9376	0.1286	0.0636

Table 6

Flury hierarchy of matrix comparisons using Phillips' jump-up approach. Constrained matrices are built from the variance covariance matrices of adult males (> 60 g, n = 90) and adult females (> 60 g, n = 71). Each model is tested against a model of arbitrary structure.

Model	χ^2	DF	P-VALUE
Equality	70.785	45	0.0084
Proportional	64.594	44	0.0232
CPC	37.645	36	0.3938
CPC(7)	37.253	35	0.3658
CPC(6)	36.947	33	0.2915
CPC(5)	29.209	30	0.5066
CPC(4)	25.917	26	0.4677
CPC(3)	19.663	21	0.5427
CPC(2)	15.249	15	0.4336
CPC(1)	12.202	8	0.1424

accounted for by the first axis. The second axis accounted for 26 % (males) and 21 % (females) of total variance, and contrasted tail length with styliform length. The third axis accounted for 11 % (males) and 14 % (females) of total variance, and contrasted tail length with upper and lower limb lengths. Among adults, tail length exhibited significant RSD (3.2 %, Table 2). Mean female styliform length was longer than male styliform length, and exhibited a dimorphism ratio of 2.5 %. Additionally, mean limb lengths tended to be longer for females than males, in some cases significantly.

Table 7

Eigenvalues (λ s) and their standard errors in parentheses (both multiplied by 10^4) under the assumption of common principal components for adult males and adult females. Additionally, proportions of the total variance accounted for by each λ are presented.

	MALES		FEMALES	
	λ	PROPORTION	λ	PROPORTION
I	88.555 (13.275)	0.434	87.139 (14.729)	0.393
II	52.142 (7.816)	0.256	46.109 (7.793)	0.208
III	21.612 (3.240)	0.106	31.110 (5.258)	0.140
IV	17.512 (2.625)	0.086	24.031 (4.062)	0.108
V	9.775 (1.465)	0.048	16.247 (2.746)	0.073
VI	6.118 (0.917)	0.030	6.760 (0.114)	0.030
VII	2.964 (0.444)	0.014	4.164 (0.704)	0.019
VIII	2.730 (0.409)	0.013	3.946 (.671)	0.018
IX	2.583(0.387)	0.013	2.263 (0.382)	0.010

Overall, adults varied considerably with respect to styliform length. Additionally, styliform length varied differently than tail length, and tail length tended to vary in a manner opposite that of limb lengths. However, loading patterns and standard errors for the three axes indicated some sphericity in the data, and suggested instability in the underlying variance-covariance matrices.

Results of the head and body length vs. mass regressions are presented in Table 9 and Figs. 1-3. The regression for all males had a significantly different slope than the regression for all females. Females had a steeper slope than males (t-test, $p < 0.05$), although the intercept for females was smaller. Thus, at small mass, females tended to be shorter than males, but after about 51.8 g, females were longer than males. For animals < 60 g, the regression slopes of males and females were significantly different (t-test, $p < 0.05$). Here, females increased in length with increasing body mass faster than males. The slopes of the regressions for adult males and adult females were not different (t-test,

Table 8

Eigenvectors (CPCs) corresponding to the 3 largest eigenvalues under the assumption of common principal components for adult males and adult females.

VARIABLE	CPC1	CPC2	CPC3
Head and Body	0.2486	0.1564	0.1887
Tail	0.3050	0.5930	-0.7174
Upper Leg	0.1619	0.2612	0.3050
Lower Leg	0.1621	0.2748	0.2722
Hind Foot	0.1690	0.2000	0.0557
Upper Arm	0.1368	0.2919	0.4307
Lower Arm	0.1695	0.2336	0.2991
Fore foot	0.1157	0.1630	0.0397
Styliform	0.8386	-0.5232	-0.0540

Table 9

Least-squares regression analyses of the relationship between the natural logarithm of head and body length (mm) and the natural logarithm of the cube root of body mass ($g^{1/3}$). All regressions are significant at $p = 0.001$.

GROUPS	N	SLOPE	INTERCEPT	R ²
All animals				
Males	145	0.788*	3.717	0.68
Females	112	0.994*	3.446	0.83
Animals < 60 g				
Males	55	0.900*	3.576	0.55
Females	39	1.237*	3.136	0.82
Animals > 60 g				
Males	90	0.727	3.801 [†]	0.28
Females	71	0.521	4.120 [†]	0.15
Females +16.1g [‡]	71	0.636	3.912 [†]	0.15

*. Within each group, slopes significantly different from each other ($p < 0.05$).

†. Intercepts for Females and Females + 16.1 g are significantly different from the intercept for Males.

‡. See Discussion for details.

$p > 0.05$), but the intercepts were (t-test, $p < 0.05$). Adult females were significantly longer at any adult mass (> 60 g) than males.

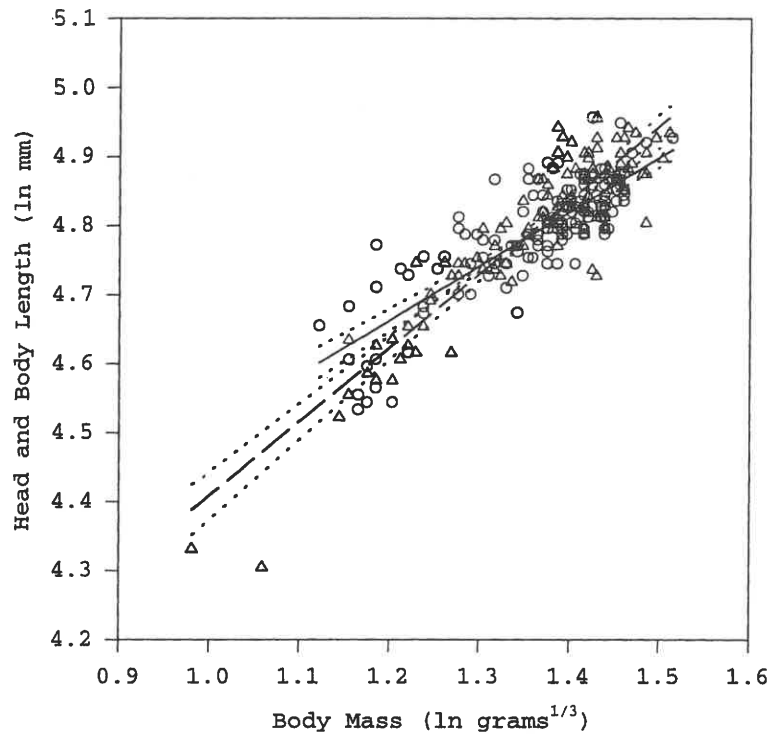


Fig. 1. Regression lines with 95 % confidence limits for the complete samples of 145 males and 112 females. Head and body length is expressed in ln mm, body mass is expressed in $\ln(\text{grams}^{1/3})$. Males are indicated by the solid line and circles, females are indicated by the broken line and triangles. Regression slopes are significantly different at the .05 level.

4. Discussion

In our sample of *G. volans* there was significant RSD for tail length in the total sample of 257 animals, and for lengths of head and body, tail, and upper leg in the sample of 161 adults (Table 2). Dolan and Carter [8] reported no evidence of SSD in *G. volans*. Diersing [7], used standard museum and 11 cranial measures and found no evidence of dimorphism (Table 1). Braun's [4] analysis of 21 cranial measures also revealed no dimorphism. However, Madden [25] found significant RSD with respect to mass, and Golley [12] and Hoffmeister [14] provided data which suggested RSD. Ralls' [34] analysis of Golley's data for total

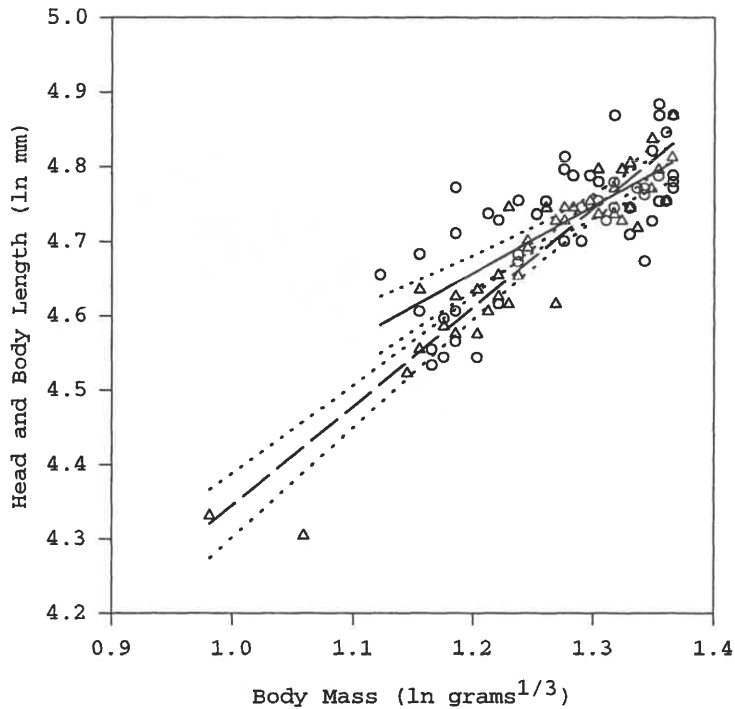


Fig. 2. Regression lines with 95 % confidence limits for the subsamples of 55 small (< 60 g) males and 39 small females. Head and body length is expressed in ln mm, body mass is expressed in $\ln(\text{grams}^{1/3})$. Males are indicated by the solid line and circles, females are indicated by the broken line and triangles. Regression slopes are significantly different at the .05 level.

length revealed significant RSD. Some of these studies relied on relatively small sample sizes and used t-tests for data which may not have been normally distributed. Furthermore, the contradictory results may reflect clinal or subspecific variation in the presence and direction of SSD in *G. volans*. Intraspecific variation in SSD and RSD has been documented in chipmunks [22] and pocket gophers [5], and may be present in *G. volans*.

Several non-exclusive hypotheses may explain RSD in *G. volans*. If natural selection favors larger females, two possible proximate causes are: 1) females may compete with males for resources [34] and 2) females may face reproductive constraints in that they are more sensitive to wing loading problems associated with pregnancy and gliding transport of offspring from nest to nest.

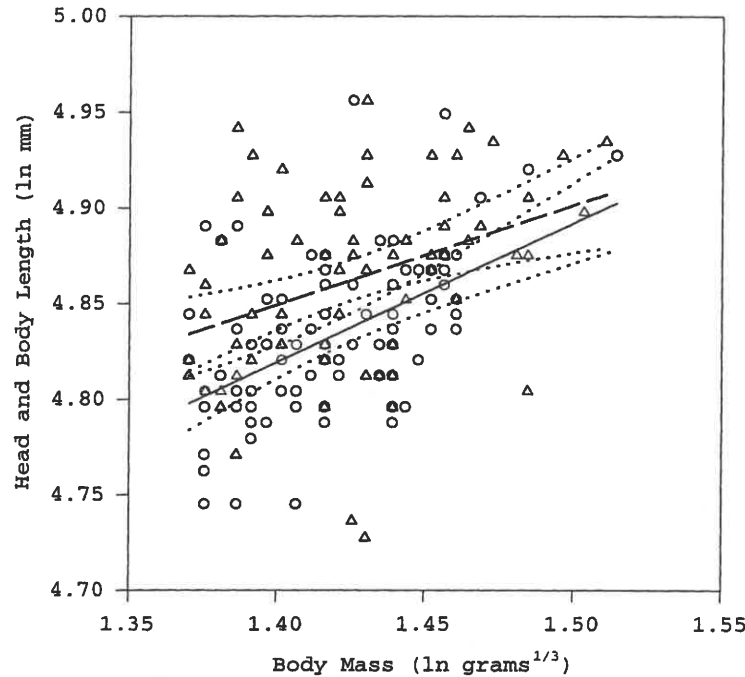


Fig. 3. Regression lines with 95 % confidence limits for the subsamples of 90 adult (> 60 g) males and 71 adult females. Head and body length is expressed in ln mm, body mass is expressed in ln(grams^{1/3}). Males are indicated by the solid line and circles, females are indicated by the broken line and triangles. Regression slopes are not significantly different at the .05 level. The intercepts are significantly different.

It seems likely that tree cavities are a limiting resource for flying squirrels, and may result in inter- and intraspecific competition. Several studies [6, 13, 15, 24, 48] have identified *G. volans* as a potential competitor with red-cockaded woodpeckers and other cavity nesters. Intraspecifically, females exhibit increased aggressiveness toward males before and after parturition [19, 28, 46]. Also, males tend to have larger home ranges [47] and/or core habitat areas [10] than females. Furthermore, home range overlap between males and conspecifics is greater than overlap between females [10], suggesting females maintain more exclusive core areas. Additionally, Fridell and Litvaitis [10] noted that male core areas had more large mast-producing trees, but core areas of females contained more tree cavities. Finally, Stapp et al. [51] noted

that tree cavities may be critical for overwintering females since pregnant individuals tend not to form aggregates with other flying squirrels prior to first spring parturition. These findings suggest nest cavities are limiting, and that females compete for access to nest sites. If females compete for access to nest cavities, we can expect selection for increased female size.

Vespertilionid bats exhibit RSD [29]. Large female size has been attributed to reductions in proportional loading of offspring on the female during flight. Also, larger mothers are able to provide more nutrients to embryos, which may promote development and reduce time necessary for offspring to achieve flight [29]. Female *G. volans* may face similar reproductive constraints. In light of the slower development rate and longer gestation period of *G. volans* relative to similar sized mammals [49, 50], wing loading may be an important factor.

There is some support for the hypothesis that increased female size accommodates wing loading problems associated with pregnancy and juvenile transport. Small females tend to be heavier than small males, but overtake males in length relative to mass at about 51.8 g (Table 9, Figs. 1 and 2). Large females tend to be longer than large males, although this difference decreases in the largest individuals (Tables 2, 9, and Fig. 3). The slope for females in this analysis is probably an underestimate since 27 of the 71 females were in reproductive condition when collected, but the 6 heaviest females were not. Lee and Zucker [20] reported an average increase of 16.1 g in mass seven days prior to parturition for *G. volans*, and females have been observed carrying “half grown” juveniles while gliding [27]. Masses of “half grown” juveniles are probably 30–40 g [20, 36], and juveniles begin to experiment with gliding at about 6 to 8 weeks or 40–50 g [20, 27, 36].

To test the wing loading hypothesis, we added 16.1 g to the mass of adult females. For non-pregnant females, this approximated the increased mass of unborn offspring, and for pregnant females, this approximated the mass associated with transport of a juvenile. The resultant regressions for males and females did not differ in slope, but differed with respect to intercept (Table 9). More importantly, females tended to become heavier than males, and wing loading increased. The greater linear dimensions of females minimizes increased wing loading.

Overall, females become longer faster than males (Table 9, Fig. 1 and 2) and males and females become heavier relative to length after maturity (see also [23]). Interestingly, females (Fig. 2) appear to outgrow males in length relative to mass just prior to the age and dimension at which they become mature and learn to glide. Further study is needed to determine the size and age at which females stop carrying young, and possible sex differences in juvenile motor development. These factors may be important in the dispersal strategies and resource utilization of males and females, especially during the transition from juvenile to adult.

It is possible that selection is operating on males rather than females. As in many other mammals, males use larger home ranges and travel greater distances, perhaps in an effort to encounter potential mates [41]. It is possible that

small size enhances maneuverability (see below). Alternatively, small size may reduce the cost of mate procurement by lowering the cost of gliding transport. Small gliding squirrels have shorter cost effective glide distances than larger forms [43], although intraspecific comparisons have not been made.

Traditionally, the second and third axes of a PCA based on the variance-covariance matrix reveal more information about shape than size. If the first axis is loaded relatively evenly for all variables, and accounts for the majority of the variance in the data, it can be interpreted as a size axis. Remaining axes contain morphological ("shape") information with a component of size variation removed [26]. The PCPCA of the ontogenetic series (Tables 4 and 5) appears consistent with this traditional interpretation. However, the CPCA of adult animals (Tables 7 and 8) did not summarize directly the non-linear variation in size. In the adult only sample, styliform length loaded heavily on CPC1 and relatively little variance was accounted for by this first axis, presumably because there was little variance associated with size in adults heavier than 60 g.

Large gliding mammals have longer limbs than non-gliding mammals, presumably an adaptation to decrease wing loading [39, 54]. Our univariate analyses (Table 2) indicate that females tend to be larger than males with regard to body and limb lengths. This pattern seems to be the result of differences in growth strategies. Females exhibit a larger degree of positive allometry in the head and body and limbs than males on PCPC1 (Tables 4 and 5). This result, combined with the lack of difference in male vs. female mass, results in larger patagia and less wing loading for females. Larger loadings for males should decrease gliding maneuverability but increase speed.

However, males may compensate for decreased patagial area between their shorter limbs. In the ontogenetic series, PCPC2 is dominated by styliform length and it accounts for more morphological variation in males than females (Tables 4 and 5). In the static series, CPC1 is dominated by styliform length and accounts for more variation in males than females (Tables 7 and 8). This result may indicate a difference in the shapes of male and female wingtips. Increased wingtip area, and styliform control of its leading edge, should result in greater maneuverability and increased resistance to yaw [31]. Thorington et al. [53] documented the importance of the styliform cartilage in the evolution and aerodynamics of pteromyines.

Scheibe and Robins [43] showed that tail length increases faster than head and body length in mammalian gliders compared to non-gliders. The tail is known to play a role as a rudder, and controls pitch in flying vertebrates [31]. Our univariate analyses indicate females have longer tails than males (Table 2). However, in the multivariate analyses tail length is often contrasted with styliform length and limb lengths (Tables 4-5 and 7-8). This result may indicate contrasts in morphology to accommodate differences in male and female gliding strategies. A better understanding of tail and wingtip dimensions and their contributions to patagial area and gliding performance is needed to evaluate these results.

Sexual dimorphism in *G. volans* may have evolutionary implications. Our study revealed significant RSD, and illustrated important locomotory consequences. Roth [38] described a relatively large amount of morphological integration in the crania of sciurids, suggesting that sciurid crania do not evolve as assemblages of independent units. Essner and Scheibe [9] and Scheibe and Essner [42] distinguish pteromyine species using postcranial material, although there may be integration in postcranial elements as well. It is important to note that skeletal components associated with locomotion may respond very differently to adaptive landscapes than cranial components associated with feeding. Whereas crania may be highly integrated, we have no evidence to suggest that the appendicular skeleton as a whole is highly integrated. Clearly, elucidation of evolutionary trends associated with dimorphic aspects of locomotion will require detailed study of many additional pteromyine species.

Acknowledgements

We thank S. Loeb for providing us with a freezer full of specimens, N. Blackstone and R. King for ideas and discussion, P. Phillips for access to a pre-publication manuscript, and V. Naples and two anonymous reviewers for comments on an earlier draft of the manuscript.

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