Does gliding when pregnant select for larger females?

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Abstract

For terrestrial vertebrates, gliding imposes unique constraints on the interaction of body mass and structural size, particularly with reference to minimizing wing loading. Females of gliding animals experience increases in wing loading during pregnancy or gravity, and selection may favour increased structural size to compensate for the added mass. We tested whether pregnant southern flying squirrels *Glaucomys volans* had similar wing loading as males, and whether females with lower wing loading bore heavier litters, than those with greater wing loading. Males had greater wing loading than females, regardless of the latter's reproductive state (males: $38.4 \pm 3.62\,\mathrm{N\,m^{-2}}$, pregnant females: $30.7 \pm 4.21\,\mathrm{N\,m^{-2}}$ and non-pregnant females: $26.8 \pm 5.13\,\mathrm{N\,m^{-2}}$). The slope of the linear relationship between planar surface area and body mass was similar between pregnant females and males, however ($F = 0.383$, $P = 0.322$). Thus female flying squirrels may optimize their litter mass to minimize wing loading during pregnancy. Contrary to our prediction, females with greater wing loading had heavier litters than those with lower wing loading, which suggests reproductive output may be influenced by other ecological factors.

Introduction

Sexual size dimorphism (SSD) is attributed to differential selection acting separately, but concurrently on each sex (Andersson, 1994). Intersexual divergence in body size may be associated with female fecundity (Darwin, 1874; Howard et al., 1998; Reeve & Fairburn, 1999), ecological niche separation (Slatkin, 1984; Shine, 1989; Temeles et al., 2000), sexual selection (Darwin, 1874; Webster, 1997) or differences in survival (Yoccoz & Mesnager, 1998; Schulte-Hostedde, Millar & Gibbs, 2002). Male-biased SSD is usually explained in the context of sexual selection acting on male body size during mate competition; however, selection could act to decrease female body size (Loison et al., 1999; Karubian & Swaddle, 2001).

Hypotheses concerning the evolution of female-biased SSD vary and include: selection for smaller males (Ralls, 1976), female dominance (Kruuk, 1972), increased female fecundity (Howard et al., 1998; Schulte-Hostedde, Millar & Gibbs, 2004), intersexual differences in survival (Yoccoz & Mesnager, 1998) and enhanced mobility of pregnant or gravid females (Myers, 1978; Shine, 1988; Hayssen & Kunz, 1996). The latter hypothesis may be particularly relevant for organisms where body size are major determinants of locomotor efficiency, such as in flying, gliding and swimming species (McGuire & Dudley, 2005). Increases in body mass with reproduction can potentially interfere with selection for lighter or more aerodynamic body forms, which generally increases efficiency of locomotion (Shine, 1988).

In numerous studies, potential constraints on reproduction may have resulted from shifts towards novel locomotory modes (Hayssen & Kunz, 1996; Davenport, 2003; McGuire & Dudley, 2005; Fokidis & Risch, 2008). Evidence for a reproductive constraint come from studies that have assessed locomotor impairment during gravity in snakes (Shine, 1988), lizards (Olsson, Shine & Bak-Olsson, 2000; Shine, 2003), raptors (Mueller & Meyer, 1985) and bats (Hayssen & Kunz, 1996). In flying species, increased body mass means an individual must generate more lift to overcome gravity (Hayssen & Kunz, 1996; Guillemette & Ouellet, 2005), and thus added mass during reproduction may be particularly important in these species. Indeed, this 'wing loading hypothesis' may explain adaptations in birds, such as sequential ovulation and oviparity that can result from the need to minimize mass associated with reproduction (Blackburn & Evans, 1986).

Most mammals exhibit male-biased SSD, however Ralls (1976) compiled data on mammals exhibiting female-biased SSD and suggested that, although less common, female-biased SSD is widespread in mammals (documented in c. 178 species from 13 orders). Ralls (1976) reasoned that female-biased SSD likely resulted from a variety of ecological factors that are not necessarily mutually exclusive, as opposed to direct sexual selection favouring large females. In mammals, the wing loading hypothesis has been applied to some bat species, where litter size and mass increase with the degree of female-biased SSD in forearm length and hence wing area (Myers, 1978). The mass gained during pregnancy increases wing loading. Thus, when females are

larger than males they have an enlarged planar surface area of the airfoil, so that the lift to drag ratio is increased and the effects of this added mass are minimized (Hayssen & Kunz, 1996). Although, these ideas were developed initially for bats, recent work has suggested similar constraints of pregnancy on species that engage in gliding locomotion. In the flying lizard *Draco melanopogon*, selection for the locomotor ability of egg-burdened females may have been responsible for the larger size of females compared with males, which is a pattern not observed in most agamid lizards (Shine *et al.*, 1998). Several species of mammalian gliders exhibit female-biased SSD including; southern flying squirrels *Glaucomys volans* (Madden, 1974; Robins, Scheibe & Laves, 2000; Fokidis, 2004; Fokidis, Risch & Glenn, 2007), and red giant flying squirrels *Petaurista petaurista* (Lee, Lin & Progulske, 1993; Lee, 1998). Gliding mammals are known to have longer gestation periods, slower development and generally larger offspring when compared with similarly size non-gliding mammals (Stapp, 1992; Holmes & Austad, 1994; Fokidis & Risch, 2008). These observations suggest that wing loading may be an important factor during reproduction.

To test the hypothesis that wing loading influences female reproductive output, we used morphological and reproductive data collected from southern flying squirrels, a species that exhibits female-biased SSD (Fokidis, 2004; Fokidis *et al.*, 2007). Female *G. volans* typically produce two litters a year (litter size varies from 1 to 5), with smaller litter sizes in the spring than in late summer–early fall (Risch, 1999). Female *G. volans* are reproductively precocious and thus may be under selection for early breeding, before female-biased SSD becomes conspicuous (Fokidis *et al.*, 2007). Adult non-reproductive females can be up to 13% heavier than males, and litter size increases with female breeding experience (Fokidis *et al.*, 2007).

We tested three predictions concerning the relationship of wing loading to reproduction: (1) when pregnant, female wing loading would be similar to that of males; whereas non-pregnant females would have lower wing loading than males; (2) females with lower wing loadings would bear heavier litters; (3) females breeding for the first time would bear proportionally lighter litters than at subsequent reproductive attempts, but wing loading values not differ.

Methods

Field data collection

Our study was conducted on a population of *G. volans* at the US Department of Energy's Savannah River Site, near Aiken, SC. The habitat on the study can be characterized as a mixture of upland hardwood forests and managed pine stands (Brady, Risch & Dobson, 2000; Fokidis & Risch, 2005). Eleven grids of 100 nest boxes each (modified from Sonenshine *et al.*, 1973) were established with at least 3 km between grids and 40 m between adjacent boxes. Nest boxes were checked for pregnant females every 2 weeks during the breeding season (August–May). Pregnancy was assessed

using the criteria of Sollberger (1943). Pregnant females were housed at the Savannah River Ecology Laboratory's animal care facility until the date of parturition. At parturition, litter size, offspring sex and offspring mass (to the nearest 0.1 g) were recorded. Because females had usually been captured before, we consulted a dataset on this population to obtain measurements taken within 15 days of expected conception (backdated 40 days gestation from the parturition date). We used measurements for: head and body length (HB), head or skull length (SL), hindleg length (HF), foreleg length (FL) and body mass. All measurements were repeatable ($R^2 \geq 0.80$) as determined via analysis of variance. Comparisons of breeding experience were done using the mark–recapture history of females. Females previously observed with offspring or in breeding condition were labelled experienced breeders, whereas first-time breeders were those captured as juveniles in the previous season. Data on male body size were obtained from a randomly selected subset of a larger dataset compiled as part of a study on the reproductive biology of free-living flying squirrels (Risch, 1999). All live capture procedures followed ASM guidelines and were approved by the Institutional Animal Care and Use Committee at Auburn University, AL.

Defining wing loading

Wing loading (WL) is the ratio of body mass (M) to the lift-generating surface area (A), and can be defined as

$$WL = \frac{Mg}{A}$$

where g is the acceleration due to gravity. We calculated planar surface area of the patagium as a hypothetical trapezoidal shape with the mean length of the body (calculated from HB−SL), multiplied by the average of $4 \times HF$ and $4 \times FL$. Planar surface area is isometric with the appendicular and axial skeleton (Thorington & Heaney, 1981), and although this method provides only an approximation, it is a reasonable index of the minimal airfoil area. To avoid statistical difficulties associated with the use of ratios (Packard & Boardman, 1987), such as a ratio of body mass to airfoil area we used standardized residuals of a regression of body mass on planar surface area to assess wing loading, hereafter referred to as *wing loading residuals*. Thus, individuals with greater wing loading have larger residual values. However, we also analysed and present the 'traditional measure' of wing loading, as body mass versus airfoil area (Newtons of force per unit of airfoil area; $N m^{-2}$), assuming gravity remains constant during glided flight, to facilitate comparisons between sexes and reproductive states, using unpaired Wilcoxon's tests for male versus female comparisons.

Statistical analysis

To obtain wing loading residuals we used ordinary least-squares (OLS) regression. Although, the use of OLS regression has been contested in situations where both the

independent and dependent variables are subject to error, as a result of measurement (Harvey & Pagel, 1991), a study by Schulte-Hostedde *et al.* (2005) has demonstrated that OLS regression satisfies critical assumptions about body size to a degree more favourable than other regression analyses. All linear measurement data were natural logarithm (ln) transformed to satisfy normality assumptions, as tested by Kolmogorov–Smirnov tests. Wing loading residuals were generated using a regression analysis including all individuals in a large dataset collected over several years ($n = 1877$). We were interested in examining how planar surface area varied with body mass, sex and female reproductive status. Residuals for pregnant and non-pregnant females were compared with those of males using two-sample *t*-tests. We also wanted to examine how planar surface area and body mass were associated within the three groups, this was done using analysis of covariance (ANCOVA) where planar surface area was the response variable and body mass and sex/status (group: males, pregnant females and non-pregnant females) were factors. To test differences in intercepts and slopes between groups, we included the interaction body mass × reproductive group in the model. Because the same females during both stages (pregnant and non-pregnant) were used, we adjusted the degrees of freedom in the ANCOVA model, by using the residual error of the model as the denominator in subsequent *F*-tests, to address potential concerns about independence of the data.

We determined mass while pregnant for each female by using the summed masses of individual offspring in a litter (litter mass) and adding this sum to each female's original body mass, providing us with a measure of female body mass during near-term pregnancy. We were interested in testing the relationship between wing loading, breeding experience and reproductive output (litter mass). However, body mass and more importantly body condition, are known to strongly influence reproduction in many species. Because both body condition and wing loading are influenced by body mass separating out their effects on reproduction can be statistically troublesome due to potential violation of independence assumptions. To attempt to separate the contributions of wing loading we used three methods. First, we used ANCOVA with litter mass as a response variable and female body mass, breeding experience and wing loading residuals (generated from OLS regression of all individuals) as factors. This enabled us separate the contribution of both wing loading and body mass to overall variation in reproductive output. The degrees of freedom were again adjusted to minimize effects of pseudoreplication. Second, we used litter mass residuals based on OLS regressions of litter mass on maternal (non-pregnant) body mass which provides a reproductive measure adjusted for the effects of body mass. Then we tested these litter mass residual values against the wing loading residual values and breeding experience. Lastly, we calculated the traditional measure of wing loading and it was related to the litter mass residuals, which were corrected for maternal body mass, and these were analysed separately for experienced and first-time breeding females. These

approaches enable us to consider the influence of wing loading on reproduction independent of the affect that body mass or condition may impart. All statistics were performed using SPSS version 13.0® software and all values are reported as mean ± standard error.

Results

Reproduction in flying squirrels

We measured 91 newborn litters from different females between 20 November 1994 and 25 March 1998: 66 spring-born litters and 25 fall-born litters. We estimated wing loading for 91 adult males, randomly selected from a larger dataset. Using information from a mark–recapture study, known females breeding for the first-time accounted for 24 litters and 67 were from females with previous breeding experience. Mean litter size was 3 ± 0.41, with range from 1 to 5. Mean neonate mass was 5.53 ± 0.24 g and mean litter mass was 15.41 ± 0.73 g. Litter size was positively correlated with litter mass ($r = 0.85$, $P < 0.0001$) and negatively correlated with mean neonatal mass ($r = -0.39$, $P = 0.0009$). Season did not influence litter size ($F_{1,89} = 136.749$, $P = 0.897$) or litter mass ($F_{1,89} = 72.525$, $P = 0.601$).

Sex and reproductive status effects on wing loading

The results of the OLS regression of female body mass on airfoil area that was used to generate the wing loading residuals are presented in Table 1. Although analyses were done using regression residuals we depict a graphical representation of sex and reproductive status differences in airfoil area and body mass (Fig. 1). Both sex and reproductive status influenced wing loading (interaction term: group - mass; $F_{1,8} = 7.46$, $P = 0.016$). Wing loading in males was heavier than that for pregnant and non-pregnant females (comparison of intercepts; pregnant: $F_{1,90} = 8.537$, $P = 0.009$; non-pregnant: $F_{1,90} = 6.151$, $P = 0.021$; Fig. 1). The relationship between airfoil area and body mass differed significantly between males and non-pregnant females (comparison of slopes: $F_{1,90} = 10.950$, $P = 0.035$); however, the slope of the lines did not differ between males and

Table 1 Results of ordinary least squares (OLS) regression analyses of body mass on planar airfoil area for male and female southern flying squirrels *Glaucomys volans* at different reproductive stages

	n	R^2	Slope (SE)	Intercept (SE)
Complete model	1877	0.683	0.97 (0.24)	47.28 (9.23)
Sex and reproductive stages				
Males	91	0.781	5.72 (0.29)	39.22 (4.28)
Non-pregnant females	91	0.814	3.04 (0.61)	33.07 (3.32)
Pregnant females	91	0.790	5.60 (0.57)	18.75 (2.08)

Complete model indicates analyses using all individuals in a large dataset. OLS regression parameters for sex and reproductive stage exclusive analyses also shown for comparison. All are significant with $P < 0.05$.
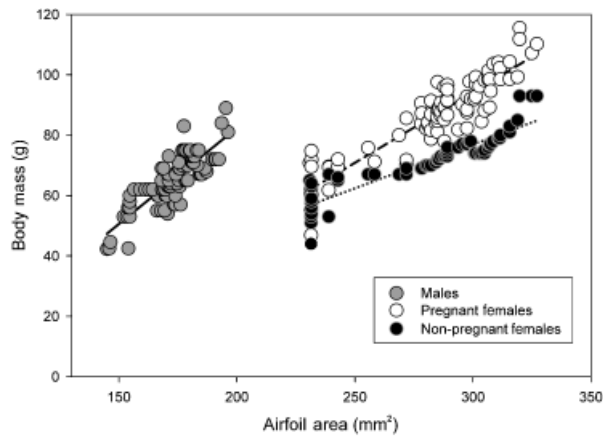
Figure 1 Relationships between body mass and airfoil area for male, pregnant female and non-pregnant female southern flying squirrels *Glaucomys volans*. Solid line (males, $n=91$), long dash line (pregnant females, $n=91$), and dotted line (non-pregnant females, $n=91$).
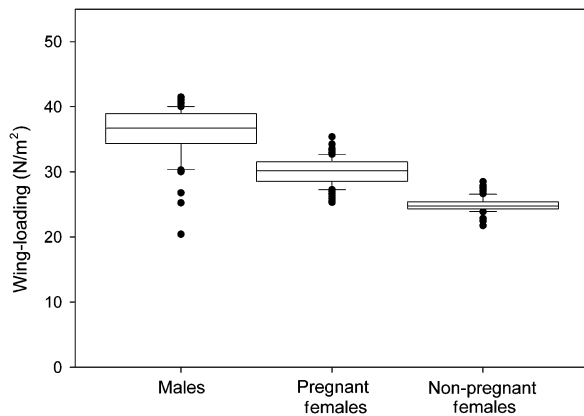

Figure 2 Comparisons of traditional 'wing loading' measurements, assuming constant gravity, for male, pregnant female and non-pregnant female southern flying squirrels *Glaucomys volans*. Box plots indicate median lines and the 25th and 75th percentiles and error bars indicate 10th and 90th percentiles. Filled circles indicate outlying data. All comparisons are statistically significant at $P<0.05$.

pregnant females (comparison of slopes: $F_{1,90} = 0.383$, $P = 0.322$). For non-pregnant females, the slope of the line of airfoil area on body mass was shallower, but became steeper when litter mass was added. A similar relationship was observed when comparing the traditional measure of wing loading ($N\,m^{-2}$), with greater wing loading in males compared to both non-pregnant (Wilcoxon's test: $P = 0.027$; Fig. 2) and pregnant females (Wilcoxon's test: $P = 0.041$; Fig. 2).

Wing loading, breeding experience and reproductive output

We used ANCOVA to explore the relationships between maternal body mass, breeding experience and wing loading residuals on litter mass (Table 2). Breeding experience of the

Table 2 ANCOVA results and effect sizes for the influence of maternal body mass, breeding experience and wing loading on litter mass

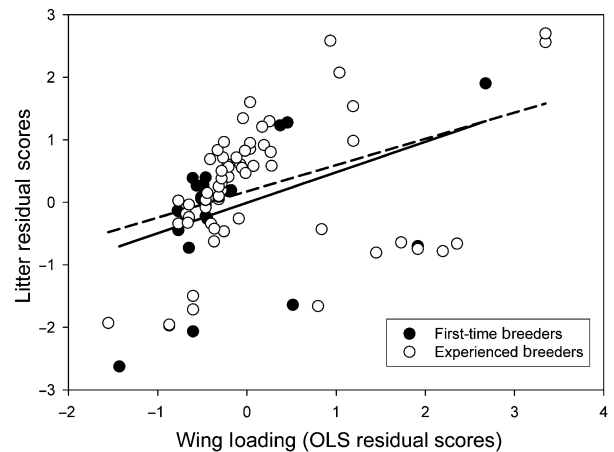| Variable	F	d.f.	P	Partial ε^2
Model	3.04	1, 87	0.0053	
Comparisons of intercepts	9.21	1, 1	≤ 0.0001	0.112
Breeding experience	0.628	1, 1	0.2864	0.07
Wing loading residuals	17.17	1, 41	≤ 0.0001	0.181
Maternal body mass	33.48	1, 41	≤ 0.0001	0.762

Figure 3 Relationship between female wing loading, breeding experience and litter mass in the southern flying squirrel *Glaucomys volans*. Both wing loading and litter mass are expressed as the residuals of an ordinary least squares regression. Solid line indicates first-time breeders (primiparous, $n=24$) and dashed line indicates experienced females ($n=67$).

mother was not associated with litter mass. However, both maternal body mass and wing loading were associated with litter mass (Table 2). Females with greater wing loading than predicted by their body size ($R^2 = 0.421$, $F_{1,90} = 2.92$, $P = 0.023$) generally bore heavier litters regardless of breeding experience (Table 2). We also investigated the relationship between maternal wing loading and reproduction by controlling for maternal body mass effects on litter mass using litter mass residuals (Table 2). Females with greater wing loading beyond that expected for their body size bore heavier litters ($F_{1,90} = 14.002$, $P \leq 0.001$; Fig. 3), but litter mass did not differ between 24 first-time and 67 experienced breeders (comparison of slopes: $F_{1,89} = 0.62$, $P = 0.311$; comparison of intercepts: $F_{1,89} = 0.9342$, $P = 0.235$; Fig. 3). Using the traditional measure of wing loading, as $N\,m^{-2}$, females with greater wing loading bore larger litters ($R^2 = 0.329$, $F_{1,89} = 4.31$, $P = 0.025$), but females with breeding experience did not differ in wing loading from first time breeders (Wilcoxon's test: $P = 0.414$; Fig. 4).

Discussion

To investigate the hypothesis that increased wing loading during pregnancy imposes constraints on reproduction we
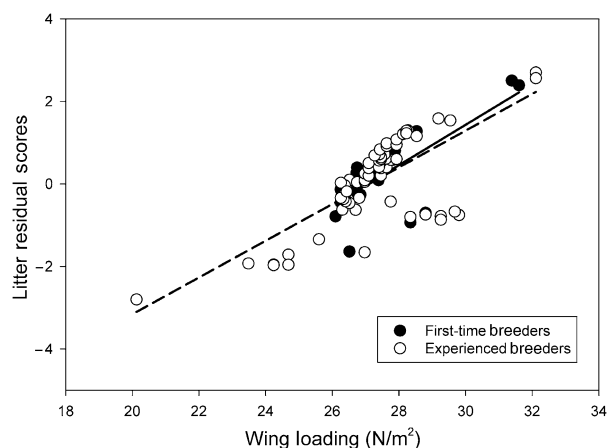
Figure 4 Relationship between female wing loading (as $N m^{-2}$), breeding experience and litter mass (expressed as residuals of an ordinary least squares regression) in the southern flying squirrel *Glaucomys volans*. Solid line indicates first-time breeders (primiparous, $n=24$) and dashed line indicates experienced females ($n=67$).

tested three predictions concerning intersexual variation in wing loading and its relationship to reproductive output in southern flying squirrels. Although males on average weighed less than females, they had greater wing loadings than either pregnant or non-pregnant females. However, the association of body mass and airfoil area was similar between males and pregnant females. Heavier females gave birth to heavier litters, and females with greater wing loading, than would be expected from their body mass, also bore heavier litters. This result does not support the wing loading hypothesis, which predicted an opposite relationship.

Intersexual variation in wing loading

Intersexual differences in wing loading were most apparent when comparing males to non-pregnant females. Comparisons of males to females when litter mass was added (i.e. pregnant females) resulted in similar regression slopes. This suggests that larger structural size in females may easily accommodate the added mass during pregnancy without having a negative effect on gliding locomotion. Such an association was also reported by Robins *et al.* (2000) for *G. volans*. Flight imposes unique and strict constraints on structural morphology, and minimizing wing loading is a central tenet behind many of the adaptations to both gliding and flight. For instance, to minimize wing loading, bats have reduced the size of the anterior and posterior regions of the body, so that the centre of mass is pectoral (Myers, 1978). Heavier bat species have proportionally longer wings (Myers, 1978; Hayssen & Kunz, 1996) and in species exhibiting female-biased SSD, females also have proportional longer wings than males (Hayssen & Kunz, 1996). Intersexual differences in planar surface area resulting from sex-specific factors designed to optimize aerial locomotion have also been proposed for some bird species, such as wandering albatross *Diomedea exulans* (Shaffer, Weimers-

kirch & Costa, 2001), some shorebirds (Jehl & Murray, 1986) and raptors (Andersson & Norberg, 1981). Another line of evidence for intersexual differences related to gliding is provided by female-biased sexual dimorphism in gliding species of *Draco*, which differs from the predominant male-biased dimorphism seen in other agamid lizards (Shine *et al.*, 1998).

Gliding and reproduction: a trade-off?

Maternal investment in reproduction is influenced by a myriad of ecological and physiological factors including body condition (Festa-Bianchet, 1998; Dobson, Risch & Murie, 1999; King & Allaine, 2002), predation risk (Fontaine & Martin, 2006), bet-hedging or restraint strategies (James & Whitford, 1994; Broussard *et al.*, 2003), direct assessment of future reproductive opportunities (Hanssen, 2006) and breeding experience (Fokidis *et al.*, 2007). In our study, female *G. volans* with greater wing loading produced heavier litters, and this pattern persisted using three methods to account for the effects of maternal body mass. This contradicts our *a priori* prediction that females with lower wing loading would have larger litters because they could accommodate increased mass.

One interpretation is that increased wing loading during pregnancy may not constrain reproduction directly, but indirectly. For example, increased wing loading may influence reproduction, by affecting how efficiently a female can gather food resources, and maintain high energetic stores. Females with increased wing loading (increased body mass relative to structural size) could have greater energy reserves that could increase capacity for reproduction. In many species, measures of body condition correlate with reproductive output (Festa-Bianchet, 1998; Dobson *et al.*, 1999; King & Allaine, 2002) and studies manipulating nutritional availability demonstrate correlated responses in reproduction (Ylonen & Eccard, 2004). In sciurids, annual changes in female mass correlate with annual changes in litter size (Risch, Dobson & Murie, 1995; Risch, Michener & Dobson, 2007). Conceivably a trade-off may exist between maintaining gliding ability and having to increase energy reserves in preparation for reproduction in gliding animals, such as *G. volans*. Thus maximizing fecundity may compromise gliding efficiency.

An alternate explanation concerns our derivation of wing loading based on the assumption of a static trapezoidal planar gliding surface and positive allometry of the fore and hind limbs. Although this method is useful, it is only an index of the 'minimal area' of the airfoil available to an individual to obtain lift. Studies of the kinematics of gliding transport have demonstrated that gliding is far from a passive process, and depending on the stages of a glide, environmental conditions or behaviour of the glider, the airfoil area can change in shape and size (Addington, Scheibe & Hendershott, 2000; Jackson, 2000; Keith, Scheibe & Hendershott, 2000; Bishop, 2004, 2006). Thus, our measure of wing loading does not accommodate these other factors, which may strongly influence gliding performance.

Wing loading and other factors in the evolution of female-biased SSD

Studies of other volant taxa have cited natural or sexual selection on wing loading as a major driving force in the evolution of female-biased SSD (Myers, 1978; Jehl & Murray, 1986; Shine *et al.*, 1998; Shaffer *et al.*, 2001). Although, we tested a possible mechanism of selection acting on female fecundity through wing loading constraints, patterns of SSD represent selection acting on both sexes. In considering intersexual differences in wing loading and body size one must also consider why males are smaller. Selection may be acting on male body size to increase mobility during the 'mate chase' characteristic of arboreal sciurids (Koprowski, 1993). Schulte-Hostedde & Millar (2002*a,b*) in a study of yellow-pine chipmunks *Tamias amoenus* hypothesized that body size in males influenced mating tactics, with larger individuals attaining greater running speeds, but smaller males being more aggressive. Both tactics might be effective at gaining mating opportunities during male–male competition for females. In *G. volans*, which exhibits a similar mating system to *T. amoenus*, smaller males (i.e. those with lower wing loading) may be more effective gliders which may in turn result in greater mating success.

Additionally, larger body size may provide other benefits exclusive of wing loading and gliding performance for female *G. volans*. Larger females may be capable of defending larger territories or those with increased food resources and thus exhibit higher fecundity. In our population, larger females have home ranges that contain a greater proportion of mast-producing trees, which are a major food resource during the breeding season (Fokidis *et al.*, 2007). This increased resource availability within a home range may translate to increased fecundity, as documented in the Eurasian red squirrel *Sciurus vulgaris* (Wauters & Dhondt, 1995). Another important resource to *G. volans* are snags and tree cavities and these may be more easily exploited by larger individuals as suggested by larger female *G. volans* having a larger proportion of cavity producing hardwood trees in their home range (Fokidis *et al.*, 2007). Female *G. volans* often maintain three or more nesting sites, and transfer offspring between them during the rearing period (Dolan & Carter, 1977). Thus access to multiple cavities may be an important resource. However, a study in which tree cavity availability was manipulated failed to demonstrate a change in population densities of *G. volans*, suggesting that cavity availability may not be a limiting resource in our study population (Brady *et al.*, 2000).

Conclusion

Our study provides some support that intersexual differences in wing loading, and specifically the larger structural size of females, may result from the need to minimize the effect of pregnancy on gliding ability. However, the degree to which the burden of gliding while pregnant influences reproduction is unclear, largely due to the difficulty of statistically separating the effects of wing loading from those of body mass, which is known to influence reproduction in many taxa. Species exhibiting specialized locomotory modes could provide useful models for assessing the costs of reproduction and provide much needed insight concerning the evolution of life-history patterns.

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