

THE BURDEN OF MOTHERHOOD: GLIDING LOCOMOTION IN MAMMALS INFLUENCES MATERNAL REPRODUCTIVE INVESTMENT

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Body mass is usually positively associated with reproductive output in females, with larger females having more offspring. However, in gliding or flying species, large body mass is constrained as a result of wing loading, defined as the ratio of body mass to the surface area available to generate lift. Gliding animals may be particularly susceptible to increased wing loading resulting from added mass during pregnancy. We compiled reproductive and morphological data for gliding and related nongliding mammals in all extant taxa where this type of locomotion occurs to test the predictions that gliders will have proportionally lighter litters than related nongliders, and relative litter mass will be negatively associated with wing loading. Contrary to our 1st prediction, gliders had heavier offspring than did nongliders in all taxa examined. Consistent with our 2nd prediction, however, greater relative litter mass was associated with lower wing loading. Maintaining the ability to glide when pregnant may influence investment in reproduction. However, gliding locomotion appears to be associated with increased litter mass, perhaps because of smaller litters of heavy young. Thus, we suggest that gliders may be characterized by K-selected life-history traits such as low mortality, slow metabolism, and fewer offspring per litter, but increased investment in individual young. The findings of this comparative study highlight how major shifts in locomotor mode can have a profound influence on patterns of life history.

Key words: flying squirrel, glider, K-selection, life history, marsupial, phylogeny, reproduction, supertree

Reproduction is a costly endeavor for female mammals and is it widely accepted that within species, larger females tend to exhibit greater reproductive output than smaller individuals. Examples of costs associated with reproduction include increased energetic expenditure, increased risk of predation, and decreased longevity (Western and Ssemakula 1982). Another potential cost to individuals may be decreased locomotor performance and mobility associated with added mass or volume during pregnancy. Wing loading, defined as the ratio of body mass to the surface area available to generate lift, is an important determinant of flying or gliding ability (Hayssen and Kunz 1996; Shine 2003). Guillemette and Ouellet (2005) reported that prelaying female common eiders (*Somateria mollissima*) were temporarily flightless while gravid because they were unable to overcome gravity when faced with increased wing loading. Similarly, reproductive female brown long-eared bats (*Plecotus auritus*) exhibited a 2-fold increase in body mass and

wing loading 50 days before birth, thus requiring a predicted 3-fold increase in mechanical power to achieve flight (McLean and Speakman 2000).

Phylogenetic shifts in modes of locomotion may offer insight into potential costs of reproduction associated with novel forms of movement. Differential reproductive investment may be due to differences in the cost of reproduction among closely related taxa that differ in their modes of locomotion (Shine et al. 1998). Comparative analyses have assessed locomotor impairment resulting from gravidity in many taxa, including snakes (Shine 1988), lizards (Olsson et al. 2000; Shine 2003), raptors (Mueller and Meyer 1985), and bats (Hayssen and Kunz 1996). Of these studies, those examining flight are perhaps most interesting, because body mass imposes a strong constraint on the ability to attain the lift necessary to overcome gravity (Hayssen and Kunz 1996). Thus, maintaining aerodynamic performance during reproduction may be under strong selection (Guillemette and Ouellet 2005; Shine 2003). Indeed, several major aspects of reproduction in birds such as the lack of viviparity and sequential ovulation suggest that selection has acted to reduce the added mass of the female during reproduction (Blackburn and Evans 1986). Comparative studies of flying lizards (*Draco*, Agamidae) have found that the

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substantial interspecific variation in body size among these animals reflects differences in gliding performance associated with changes in wing loading (McGuire and Dudley 2005). Similar interspecific differences have been noted for flying fishes (Davenport 2003) and bats (Myers 1978). These interspecific differences in wing loading may influence patterns of reproduction, acting as a constraint on the physical burden that can be carried by a gliding female.

Thorington and Heaney (1981) examined the body proportions of flying squirrels and reported allometric relationships among morphological elements that influenced patagial area. Thus, larger squirrels had greater wing loading, suggesting that they would need to glide faster to maximize their glide ratio and would exhibit decreased variation in moments of inertia compared to smaller flying squirrels. These studies contrast with the findings of Rayner (1981), who found that wing loading varied little or exhibited functional similarity among a taxonomically broad set of glissant species, including gliding frogs and lizards, flying squirrels, and flying fish. Supplemental evidence of an association between gliding and reproduction is provided by the pattern of sexual dimorphism in gliding species of *Draco*, in which females are larger than males, which is the opposite of the pattern seen in other agamid lizards (Shine et al. 1998). Similar selection may be acting on the female-biased sexual size dimorphism found in southern flying squirrels (*Glaucomys volans*—Robins et al. 2000).

Although the physical burden of pregnancy on the gliding ability of females is straightforward, reproduction is also subject to selection due to numerous other factors that may work in concert with or in opposition to selection imposed by the mode of locomotion. For example, gliding locomotion is thought to have evolved in animals inhabiting mature forests, where a relatively open vegetation structure enables efficient gliding (Dial et al. 2004; Emmons and Gentry 1983). These mature forests are relatively stable in terms of temporal variation in resource abundance, particularly in tropical regions (Emmons and Gentry 1983), and, under these conditions, selection may favor the competitive ability of species that bear fewer, larger offspring (Roff 2002). Thus, the reproductive output of gliders may be influenced by their forest environment as well as, or in addition to, their mode of locomotion.

We examined the association between reproductive output (litter mass) and morphometry in gliding mammals and their nongliding relatives. In extant mammals, gliding is thought to have evolved on 8 separate occasions (Meng et al. 2006; Stafford et al. 2002) and is currently confined to 3 orders (Meng et al. 2006; Storch et al. 1996): Diprotodontia (Acrobatidae, Petauridae, and Pseudocheiridae), Dermoptera (Cynocephalidae), and Rodentia (Anomaluridae and Sciuridae). Although the exact nature of structural adaptations to gliding differ among these taxa, they all employ an airfoil created by a patagial membrane consisting of loose skin that stretches from forelimb to hind limb. We tested the following 2 predictions concerning the relationship between reproduction and structural components related to wing loading: gliding mammals will bear lighter litters than nongliding counterparts, and gliders with greater wing loading will bear proportionally lighter litters than those

with decreased wing loading. This study uses a comparative approach to elucidate patterns of reproduction associated with gliding locomotion and provides a conceptual framework from which future studies may examine the evolution of life-history traits of mammalian gliders.

MATERIALS AND METHODS

Morphometric and reproductive data.—We obtained reproductive and morphological data for gliders from primary research and secondary literature (Appendix I). Morphological data were available for most species but some species, particularly Asian flying squirrels, were known from only a few study skins. Thus, we included only species for which at least 3 intact specimens were available. Morphological measurements used were head and body length and body mass. Because multiple published sources may have reported morphological data from the same specimens, means generated from these sources would result in pseudoreplication. Thus, we calculated mid-point values based on the range of measurements obtained for each species, and used these values in subsequent analyses. Reproductive data included mean neonate mass and mean litter mass. When direct measures of litter mass were not available, this parameter was calculated as the product of litter size and neonate mass. For eutherian mammals, reproductive measurements were obtained from females at or near parturition. Although female eutherian gliders also transport their offspring postparturition, data for this portion of the reproductive cycle were not available for most species. Further, postpartum transport often involves 1 young at a time (Tyndale-Biscoe and Renfree 1987), making it more difficult to assess the cost of this behavior. For marsupial gliders and dermopterans, both of which bear altricial young (Wilson and Reeder 2005), we used the mass of offspring at weaning; this life-history event coincides with the cessation of transport of young by the female (Tyndale-Biscoe and Renfree 1987; Vaughan et al. 2000).

Because maternal body mass can also influence reproduction it was necessary to remove the potentially confounding effects of this variable from our analyses. To this end, we examined the residuals of a regression of litter mass on maternal body mass (Harvey and Pagel 1991). Specifically, we used reduced major axis regression (rather than ordinary least-squares regression) because reduced major axis regression considers error variance for both dependent and independent variables (Harvey and Pagel 1991). The resulting mass-corrected reduced major axis residuals (hereafter, litter residuals) were then used in subsequent analyses.

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

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

where *g* is acceleration due to gravity. We used published regression equations derived from museum skins for marsupials (Diprotodontia—Jackson 2000) and flying squirrels (Thorington and Heaney 1981) to estimate patagial area for members of these taxa included in our analyses. This was done

because we had reproductive and body mass data for some species in these groups for which we did not have direct measures of the patagial surface area. Estimates of patagial area (A) were obtained by inserting data on body mass (M) into the equations shown below for marsupials:

$$\log(A) = 0.782 \log(M) + \log(2.5953),$$

and flying squirrels:

$$\log(A) = 0.766 \log(M) + \log(0.7874).$$

For anomalurids and dermopterans, we were unable to locate published estimates of patagial area or regressions from which we could estimate A . Therefore we used measurements of patagial surface area derived from museum specimens to generate the following regression equations for anomalurids:

$$\log(A) = 0.7556 \log(M) + \log(2.0195) \\ (R^2 = 0.759; P = 0.018),$$

and dermopterans:

$$\log(A) = 0.410 \log(M) + \log(0.6274) \\ (R^2 = 0.537; P = 0.033).$$

Again, data on body mass were then used to estimate patagial areas for members of these taxa for which we had reproductive data, but no direct estimates of A . Because we used body mass to calculate patagial surface area, we could not use wing loading as defined above, because M and A were not independent. Instead, we used the standardized residuals of a reduced major axis regression of patagial surface area on head and body length (hereafter, area residuals) to generate an index of surface area relative to head and body length. This approach allowed us to examine changes in surface area independently of those in body mass. To avoid the potentially confounding effects of sexual dimorphism in body size, for most analyses of patagial area, we used data from females only; for sexually monomorphic species, data from males also were included. For those taxa for which data on sexual dimorphism were not available, we used information from closely related species to determine whether data from both sexes could be included in our analyses.

Selection of study taxa.—To examine the influence of mode of locomotion on reproduction, we compared the closest possible nongliding relatives to the gliding taxa for which we had both information concerning litter masses and resolved phylogenetic relationships. For the Anomaluridae, little reproductive information was available for the nonvolant *Zenkerella insignis*. The classification of the anomalures is problematic, because several authors have suggested that the Pedetidae are the sister family to the Anomaluridae (Adkins et al. 2003; Montelgard et al. 2002). An alternative phylogenetic hypothesis (Landry 1999) places the anomalures within the Stegaulata, which includes the squirrels, aplodontids, and beavers. We chose to position the anomalures in the Stegaulata following the scheme of Landry (1999); however, we also included *Pedetes* as an outgroup for both the anomalures and squirrels in our analyses. The placement of the anomalures within the supertree did not influence subsequent

interpretation of the results on the relationship between gliding and reproduction.

With regard to the remaining taxa included in our analyses, no reproductive data were available for the nonvolant *Distoechurus pennatus* (Acrobatidae) and thus we used *Tarsipes rostratus* (Tarsipedidae) for comparisons with the gliding Acrobatidae. Similarly, although *Hemibelideus lemuroides* is considered a “semigliding” marsupial, the lack of available data on reproduction in this species precluded a comparison with the glider *Petauroides volans*. Thus, we compared the latter with all other marsupials for which we had reproductive data. Finally, there has been considerable debate concerning the phylogenetic placement of the order Dermoptera (Schmitz et al. 2002). Dermopterans have been placed as a “sister-group” to both the Primates (Arnason et al. 2002) and the Chiroptera (Novacek 1989). Because our study explores the relationship between gliding locomotion and reproduction, we opted to include the nonvolant primates in our comparisons. The primates represent a very diverse taxon; for simplicity, we used only the 5 species of primate that, according to Arnason et al. (2002), are most closely allied to the Dermoptera.

Construction of supertrees.—To control for potential phylogenetic autocorrelation in our comparative analyses, independent contrast analyses were employed (Felsenstein 1985), as described below. To execute these analyses, it was 1st necessary to construct a phylogenetic supertree for the mammal taxa in our data set. Supertrees are constructed by qualitatively concatenating the topologies of multiple, less-inclusive “source” trees for different lineages (Cardillo et al. 2004; Kennedy and Page 2002; Stoner et al. 2003). Thus, phylogenetic trees derived from multiple studies and compiled using different construction methods can be combined to provide a more comprehensive view of phylogenetic relationships (Kennedy and Page 2002).

Using previously published phylogenetic information we developed a supertree that included gliding mammals for which we had information concerning morphometry and litter mass. The nomenclature used for supertree generation was that of Wilson and Reeder (2005). Source trees were limited to recently published phylogenies (Arnason et al. 2002; Huchon et al. 2002; Landry 1999; Mercer and Roth 2003; Munemasa et al. 2006; Oshida et al. 2004; Schmitz et al. 2002; Steppan et al. 2004; Thorington et al. 2002; Yu et al. 2006) constructed using studies that had morphological or molecular data, or both. To avoid nonindependence among our source trees and the associated problem of pseudoreplication in our data matrices, we selected source trees using the criteria of Bininda-Emonds et al. (2003) and Cardillo et al. (2004). Source trees were redrawn using TreeView (Page 1996), which facilitated their storage in a common NEXUS file format. Using RadCon (Thorley and Page 2000), we then converted source tree topologies to data matrices using matrix representation with parsimony. Source trees were pruned to include only those species for which we had reproductive data. Removing species did not alter phylogenetic relationships among the remaining taxa.

Each node in a source tree was represented as a binary “pseudocharacter,” where “1” represented a descendent bearing the given pseudocharacter, and “0” represented a

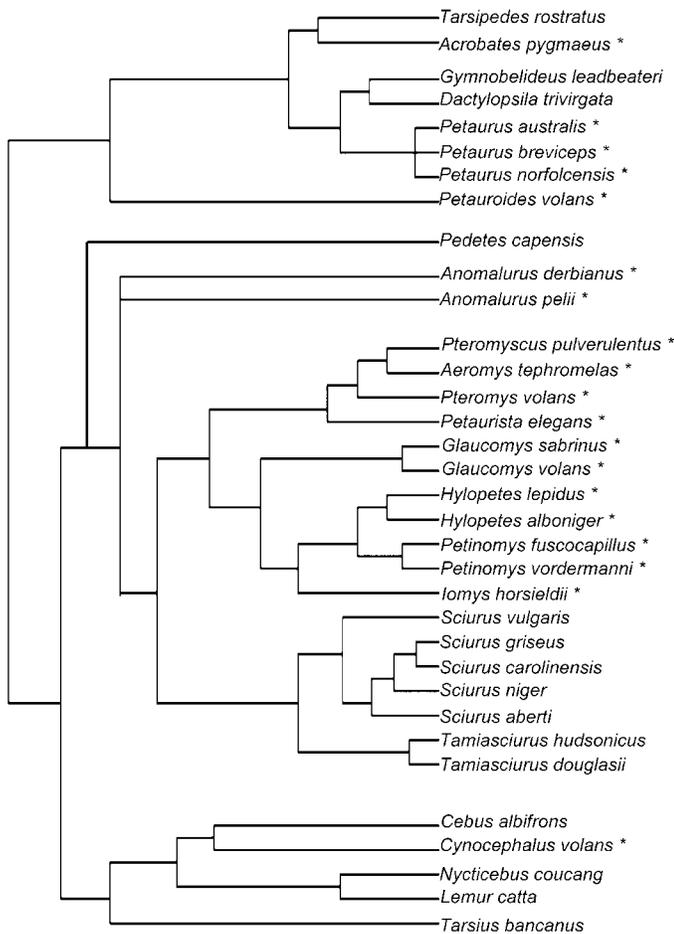


FIG. 1.—Unweighted supertree relationships among gliding (marked with an asterisk [*]) and nongliding mammalian taxa (taxonomy recognized by Wilson and Reeder [2005]) generated from 10 source trees (see text) following the methods of Cardillo et al. (2004). Branch lengths are not to evolutionary scale.

descendent without the pseudocharacter (Cardillo et al. 2004). Note that these pseudocharacters did not correspond to “real-life” characteristics of the animals. A total of 37 taxa and 48 pseudocharacters were included. Although source trees were constructed using different methods, we chose to make the pseudocharacters unweighted because weighting requires a priori assumptions regarding the relative importance of the different characters used to generate phylogenies, and because the use of weighted characters typically has only minor effects on supertree topology (Bininda-Emonds et al. 1999; Grenyer and Purvis 2003). Pseudocharacters were then analyzed and the supertree was constructed using PAUP* version 4b10 (Swofford 2002). The most-parsimonious supertree was obtained using a heuristic search method (Parsimony Ratchet—Nixon 1999) consisting of 10 runs of 500 iterations each; in each iteration, 25% of characters were randomly selected to receive a weighting factor of 2. The resulting trees were used to initiate a final search employing tree-bisection-reconstruction branch swapping. The resulting 10,000 most-parsimonious trees were combined into a conservative, strict consensus tree of phylogenetic relationships among the study taxa (Fig. 1).

Independent contrasts and statistical analyses.—Using our supertree, we calculated standardized independent contrasts for both litter residuals and patagium area residuals (Felsenstein 1985) using CAIC 2.62 (Purvis and Rambaut 1995). Although independent contrast methods require assumptions concerning the representation of branch lengths, our phylogenetic supertree did not provide us with accurate ages for nodes. The fossil record is relatively difficult to interpret with respect to some gliding taxa (Thorington et al. 2005) and thus we were unable to determine branch lengths using fossil data. Consequently, we assumed equal branch lengths (default = 2) for our final supertree, which corresponds to rapid character change and speciation at a node (i.e., punctuational model of evolution). Because of the broad range of mammalian taxa included in our study, the assumption of equal branch lengths is unlikely to have a significant effect on our contrast scores (Cardillo et al. 2004).

To test the hypothesis that gliding mammals bear relatively lighter litters than nongliding counterparts, we compared slopes and intercepts generated by regressing relative litter mass on maternal body mass for gliding and nongliding taxa. Ordinary least-squares regression analyses were used because they enabled us to distinguish between the coincidence and parallelism of regression slopes for these subsets of mammals; this was not possible with reduced major axis regression because this approach does not calculate the required confidence intervals for comparison of regression slopes. Regression analyses were conducted using both raw data and data corrected for phylogenetic effects. We examined the relationship between litter mass and wing-loading using reduced major axis regression, which takes into account the error variance in the dependent and independent variables expected when these are composed of residual values. With the exception of reduced major axis regressions, all statistical tests were performed using SPSS 13.0 (SPSS Inc., Chicago, Illinois); reduced major axis regressions were completed using *RMA: Software for Reduced Major Axis Regression* (<http://www.bio.sdsu.edu/pub/andy/RMA.html>).

RESULTS

Data on litter mass were obtained for 19 gliding and 15 closely related nongliding mammals (Appendix I). Regression analyses (Fig. 2A) suggested that gliders have proportionally heavier litters ($R^2 = 0.84$) than nongliding species ($R^2 = 0.73$); although slopes for these regression lines did not differ ($F = 0.27$, $d.f. = 1, 2$, $P = 0.13$), intercepts for gliders and nongliders were significantly different ($F = 11.20$, $d.f. = 1, 32$, $P = 0.008$). Controlling for phylogeny (Fig. 2B), the difference between intercepts for gliders ($R^2 = 0.81$) and nongliders ($R^2 = 0.90$) was even more pronounced ($F = 16.17$, $d.f. = 1, 32$, $P < 0.001$), although again slopes between regression lines did not differ ($F = 0.24$, $d.f. = 1, 2$, $P = 0.49$). Among gliding species, litter mass increased with area residuals (Fig. 3A) generated from a regression of patagial surface area on head and body length ($R^2 = 0.53$, $F = 7.23$, $d.f. = 1, 18$, $P = 0.032$). This suggests that species with a larger patagial surface area for their body length (i.e., longer “wings”) have proportionally heavier

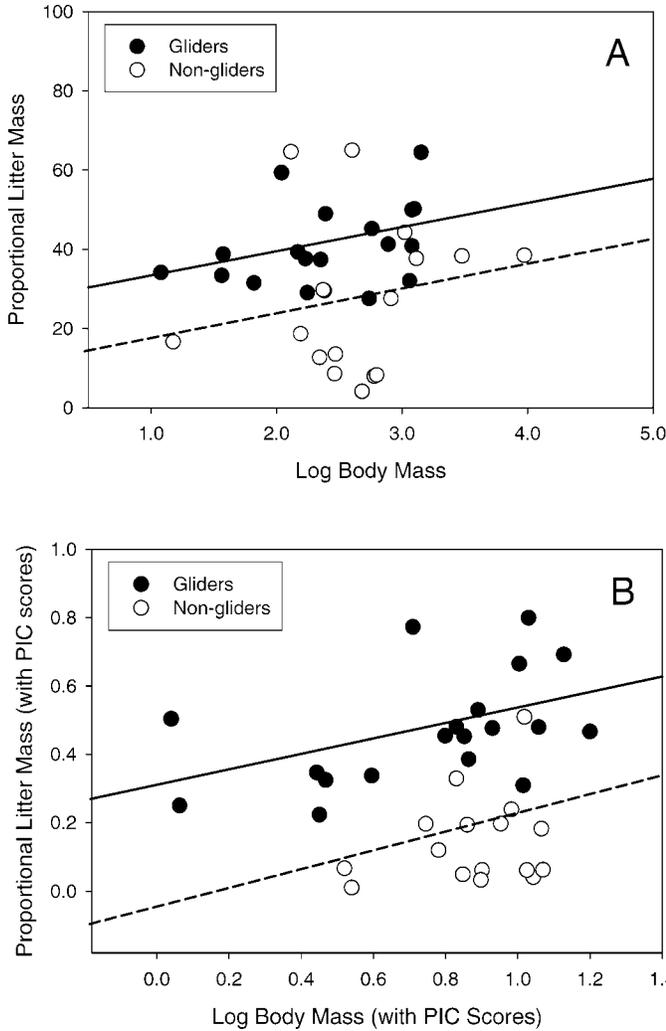


FIG. 2.—Differences in proportional litter mass as a function of body mass for both gliding (solid line) and nongliding mammals (dashed line). A) Data uncorrected for phylogeny and B) data corrected using phylogenetic independent contrast scores (Felsenstein 1985).

litters. This association also was evident when data points were phylogenetically corrected (Fig. 3B; $R^2 = 0.41$, $F = 3.18$, $df = 1, 18$, $P = 0.041$).

To determine whether our estimates of patagial surface area (A) were robust, we repeated the regression analysis using only those species for which the patagial surface area was obtained from measurements of museum skins (Dermoptera and anomalures), from Thorington and Heaney (1981—flying squirrels), or from Jackson (2000—marsupials). A positive relationship between litter mass and area residuals appeared to be present, but was not significant ($R^2 = 0.74$, $F = 8.48$, $df = 1, 13$, $P = 0.057$). This suggests that even without the estimations of A, the relationship between litter mass and area residuals may still be present because the directionality of the association is similar. Although the association was not significant, the small sample size for these analyses ($n = 14$) and associated high probability of type II error may have contributed to this outcome. Before phylogenetic correction (Fig. 3A),

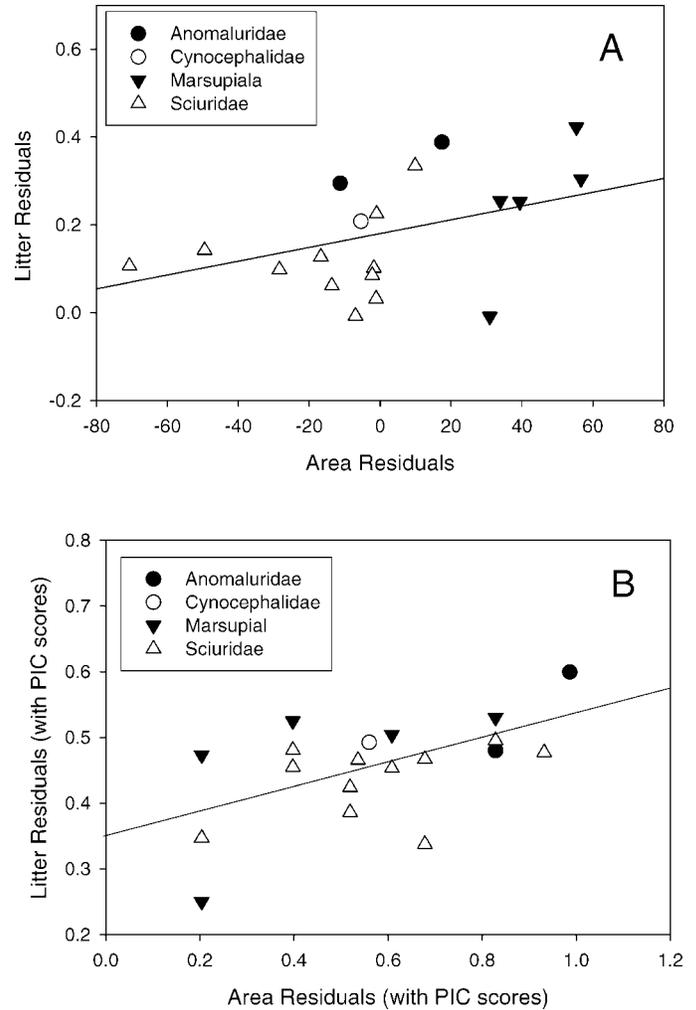


FIG. 3.—The relationship between patagial surface area and litter mass residuals for 19 species of gliding mammals from 3 orders (6 families). A) Data uncorrected for phylogeny and B) data corrected using phylogenetic independent contrast scores (Felsenstein 1985). See text for details concerning calculation of area and litter mass residuals.

marsupials had proportionally larger surface areas for their body lengths than other taxa but varied widely with respect to litter mass. Also before correction, the 2 species of anomalures examined, *A. derbianus* and *A. pelii*, had proportionally heavier litters compared to most flying squirrels of comparable patagial area (Fig. 3). However, these tendencies were not evident when analyses were repeated using phylogenetically corrected values for area and litter residuals (Fig. 3B), suggesting that although phylogenetic history is important, it alone cannot account for the differences in reproductive patterns between gliders and nongliders reported here.

DISCUSSION

We tested the prediction that gliders with greater wing loading bear proportionally lighter litters. In accordance with this prediction, we found a positive relationship between differences in patagial surface area and proportional litter mass

across gliding species. Although all mammalian gliders depend on the patagium to attain lift, there are differences among taxa in terms of the design of both the patagium (Thorington et al. 1998) and other important anatomical structures such as the tail (Jackson 2000). These interspecific differences can alter the surface area and shape of the patagium, an individual's center of mass, and the ability to control moments of inertia during a gliding event (Jackson 2000; Thomas and Taylor 2001; Thorington et al. 1998). For example, larger and heavier species of flying squirrel need to glide at faster speeds to maximize their glide ratio and hence have less time to steer, thus decreasing overall aerodynamic maneuverability (Thorington and Heaney 1981). However, more interspecific comparisons in gliding ability are required before generalizations can be extended to nonsciurid gliding species and the separate effects of gliding components on reproduction can be discerned.

We also examined whether litter mass differed between gliding and nongliding mammals. Contrary to our prediction, we found that litter mass was proportionally greater in glissant species compared to nongliding relatives. Litter mass is a function of both litter size and the mass of individual neonates. Litter size was not considered in our study because it can be influenced by multiple ecological factors (Fokidis et al. 2007; Risch et al. 1995, 2007). Nevertheless, although data on litter size are lacking for some gliding species, in particular the anomalurids and Southeast Asian flying squirrels, we note that many glissant species bear only a single offspring per reproductive attempt (Goldingay 2000), which may be indicative of a K-selected (slow) life-history strategy (Promislow and Harvey 1990; Read and Harvey 1989; Roff 2002). Several lines of evidence suggest different life-history strategies for gliders and nongliders. In general, flying squirrels exhibit nocturnality, increased longevity, increased survivorship, decreased annual fecundity, and smaller litter sizes compared to diurnal tree squirrels (Holmes and Austad 1994; Stapp 1992, 1994). Further, basal metabolic rate in the southern flying squirrel (*G. volans*) is substantially lower than predicted from data for similarly sized tree squirrels. This metabolic difference has energetic implications, including costs of gliding and nocturnality that may contribute to the more K-selected life-history traits of gliders (Stapp 1992, 1994). Holmes and Austad (1994) proposed an alternative hypothesis that argues that gliding locomotion reduced mortality due to predation, leading to selection for increased longevity and associated life-history traits. Indeed, bats are the longest-lived mammals relative to their body mass (Austad and Fischer 1991), have a low annual reproductive rate (Barclay et al. 2004), and have slow growth rates (Jones and MacLarnon 2001), indicating a high level of investment in individual young. Our study provides evidence that independent of phylogeny, mammalian gliders have heavier litters than their nongliding relatives. Coupled with evidence suggesting that litter size is also smaller for gliding mammals (Goldingay 2000), these data lead us to suggest that gliders may have more K-selected life histories than predicted by their body mass.

Gliding locomotion has evolved independently multiple times in mammals as well as in other vertebrates such as fish,

amphibians, and reptiles. At present, little is known about how gliding locomotion relates to reproduction and other life-history traits in these lineages. Research that explores relationships between gliding and reproductive output in these taxa is needed to determine how the evolution of novel modes of locomotion influence major life-history patterns.

ACKNOWLEDGMENTS

We are grateful to A. Smith for allowing access to his extensive literature collection. We are grateful to M. Toomey, E. Lacey, and 2 anonymous reviewers for useful comments on the manuscript. We also thank J. Dines at the Natural History Museum of Los Angeles County, and M. Schulenberg at the Field Museum for providing morphometric measurements of anomalures and colugos. We thank S. Landry for assistance with phylogenetic contrasts. This study was funded in part by contract DE-FC09-96SR18546 between the United States Department of Energy and the Savannah River Ecology Laboratory, and by a reassignment time grant to TSR from the Environment Sciences Program at Arkansas State University.

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Submitted 16 April 2007. Accepted 15 October 2007.

Associate Editor was Eileen A. Lacey.

APPENDIX I

Morphological and reproductive characteristics for mammalian gliders (marked with an asterisk *) and associated outgroup taxa. Offspring mass is either the weight at birth (rodents and primates) or mass at weaning (Diprotodontia marsupials and dermopterans). HB length refers to head and body length.

	Body mass (g)	HB length (mm)	Litter mass (g)	Mean litter size	Offspring mass (g)	References ^a
Diprotodontia						
Tarsipedidae						
<i>Tarsipes rostratus</i>	15	75	5	3	1.7	1
Acrobatidae						
<i>Acrobates pygmaeus</i> *	12	73	6.5	3	—	2, 3, 4, 5
Petauridae						
<i>Gymnobelideus leadbeateri</i>	130	160	56	2	28	1
<i>Dactylopsila trivirgata</i>	400	273	160	2	80	1
<i>Petaurus australis</i> *	575	285	285	1	285	6, 7, 8
<i>Petaurus breviceps</i> *	110	185	66	2	33	2, 6, 9, 10
<i>Petaurus norfolcensis</i> *	245	245	120	2	60	5, 11
Pseudocheiridae						
<i>Petauroides volans</i> *	1,200	400	600	1	600	2, 12
Rodentia						
Anomaluridae						
<i>Anomalurus derbianus</i> *	775	325	320	2	160	3, 13
<i>Anomalurus pelii</i> *	1,418	430	630	3	210	3, 13
Pedetidae						
<i>Pedetes capensis</i>	3,000	400	276	1	276	1
Sciuridae						
<i>Pteromyscus pulverulentus</i> *	225	247	84	1	—	14, 15, 16, 17
<i>Aeromys tephromelas</i> *	1,148	391	368	1	—	14, 15, 16, 18
<i>Pteromys volans</i> *	170	174	64	3	—	19
<i>Petaurista elegans</i> *	1,200	351	490	2	—	14, 15, 16, 18, 20
<i>Glaucomys sabrinus</i> *	148	308	58	3	—	16, 21
<i>Glaucomys volans</i> *	66	215	34	4	—	16, 22, 23
<i>Hylopetes lepidus</i> *	37	134	20	3	—	14, 15, 17, 18
<i>Hylopetes alboniger</i> *	240	200	71	3	—	15, 18, 19
<i>Petinomys fuscocapillus</i> *	547	285	151	2	—	15
<i>Petinomys vordermanni</i> *	38	106	18	2	—	14, 15, 16
<i>Iomys horsfieldii</i> *	176	189	51	2	—	14, 15, 16
<i>Sciurus carolinensis</i>	600	490	48	3	16	1
<i>Sciurus granatensis</i>	480	240	20	2	10	1
<i>Sciurus niger</i>	1,050	520	45	3	15	1
<i>Sciurus vulgaris</i>	295	210	40	4	10	1
<i>Sciurus griseus</i>	815	285	225	3	75	24
<i>Tamiasciurus douglasii</i>	290	325	25	5	5	1
<i>Tamiasciurus hudsonicus</i>	220	190	28	4	7	1
Dermoptera						
Cynocephalidae						
<i>Cynocephalus volans</i> *	1,250	355	378	1	378	25, 26
Primates						
Lorisidae						
<i>Nycticebus coucang</i>	626	340	52	1	52	1
Lemuridae						
<i>Lemur catta</i>	235	385	70	1	70	1
Tarsiidae						
<i>Tarsius bancanus</i>	155	145	29	1	29	1
Cebidae						
<i>Cebus albifrons</i>	1,300	510	230	1	230	1

^a References are: 1, Hayssen et al. 1993; 2, Jackson 2000; 3, Nowak 1999; 4, Fleming and Frey 1984; 5, Ward 1990; 6, Tate 1945; 7, Goldingay 1992; 8, Goldingay and Kavanagh 1993; 9, Smith 1973; 10, Suckling 1984; 11, Quin 1995; 12, Henry 1984; 13, Kingdon 1997; 14, Payne et al. 1994; 15, Corbet and Hill 1992; 16, Thorington and Heaney 1981; 17, Muul and Liat 1974; 18, Lekagul and McNeely 1977; 19, Allen 1940; 20, Muul and Liat 1978; 21, Wells-Gosling and Heaney 1984; 22, Dolan and Carter 1977; 23, T. S. Risch, in litt.; 24, Carraway and Verts 1994; 25, Parker 1990; 26, Wischusen et al. 1992.