

MORPHOLOGICAL AND PERFORMANCE ATTRIBUTES OF GLIDING MAMMALS

JOHN S. SCHEIBE AND JAMES H. ROBINS

*Department of Biology
Southeast Missouri State University
Cape Girardeau, MO. 63701*

ABSTRACT.—We compared the morphologies of 141 species of gliding, arboreal, and ground dwelling-mammals, and analyzed the cost effectiveness of gliding locomotion for *Glaucomys volans*. A canonical discriminant analysis revealed that ground dwelling forms have short tails, while gliding and arboreal forms have long tails. Gliders have shorter skulls and shorter upper tooth rows than arboreal forms. Tail length increases with body size more rapidly for gliders than nongliders, presumably because of the allometry of wing loading in large gliders. In spite of their longer tails, large gliders have higher wing loadings, glide faster, and appear to be less maneuverable than small gliders. While gliding conveys an energetic advantage to small animals like *Glaucomys*, it is expensive for *Petaurista*. Gliding is cost effective for *Petaurista petaurista* only if they climb trees rapidly, or if the cost of quadrupedal locomotion is increased.

INTRODUCTION

Recent work by Thorington and Heaney (1981) and Thorington and Thorington (1989) elucidated some of the appendicular adaptations associated with arboreal and glissant locomotion in sciurids. These papers, together with that of Peterka (1936), Polyakova and Sokolov (1965), Oxnard (1968), Bou et al. (1987), and Ando and Shiraishi (1991) constitute the bulk of our knowledge of the skeletal adaptations of gliding mammals. Studies on the myology of gliders (Peterka, 1936; Gupta, 1966; Johnson-Murray, 1987) have illustrated the unique ways in which the plagiopatagia of gliders are constructed and controlled to provide a flight structure. However, very little is known about the diversity of morphological adaptations on a faunal scale or across mammalian orders and families, or how size may have influenced the evolution of gliding.

Some progress has been made in functional research. Studies by Polyakova and Sokolov (1965), Nachtigall et al. (1974), Nachtigall (1979), Scholey (1986), and Ando and Shiraishi (1993) have provided information on the gliding abilities of gliding mammals and their aerodynamic qualities. Scholey (1986) used an energetics approach to study the cost effectiveness of gliding locomotion for *Petaurista petaurista*, but failed to generalize the model to include smaller gliders, or to explore constraints on the evolution of gliding.

Our understanding of the evolution of gliding is limited. Emerson and Koehl (1990) and Emerson (1991) have conducted detailed studies on gliding in rhacophorid frogs, but no such studies have been conducted for mammals. The distribution of gliding vertebrates has been used by Emmons and Gentry (1983) and Dudley and DeVries (1990) to propose several hypotheses about the evolution of gliding. Emmons and Gentry (1983) argued that forest structure, particularly liana densities and the prevalence of palm trees coincides with the diversity of gliding and vertebrates with prehensile tails, while Dudley and DeVries (1990) argued that the great height of oriental forest trees has played a significant role in the evolution of gliding. Other hypotheses for the evolution of gliding include foraging optimization (Norberg, 1985), predator avoidance, and controlled landing (Thorington and Heaney, 1981).

We know too little about the form, function, and ecology of gliders to discriminate between hypotheses for the adaptive significance of gliding locomotion. Also, it is unknown if the selective forces which led to the evolution of the Petauristinae are similar to those which produced the Anomaluridae, or if marsupial gliders have solved the gliding problem in the same way as eutherian gliders. In this paper we analyze some

basic morphological data on a wide variety of gliding mammals in an effort to add to what is already known about their morphological attributes. We then analyze laboratory and field glides of *Glaucomys volans* to provide a comparison with published data for larger gliders. Finally, we use the results of our glide analyses to evaluate and extend the model of Scholey (1986).

METHODS

We obtained morphological data for terrestrial, arboreal, and gliding sciurids and anomalurids from the literature (Miller, 1912; Allen, 1915; Ognev, 1940; 1947; Hall and Kelson, 1959; Rosevear, 1969; Lekagul and McNeely, 1977; Hoffmeister, 1986, 1989). Data for Acrobatids, burramyids, petaurids, and pseudocheirids were obtained at the Australian Museum in Sydney. Skeletal measurements were taken on specimens to the nearest 0.002 cm using dial calipers. External body measurements were taken from the specimen tags. All morphological data were log transformed. The data set included partial information for 155 species of mammals. We maximized sample size for the multivariate analysis by using only six variables: head and body length, tail length, hind foot length, greatest skull length, zygomatic width, and upper tooth row length. Because some of the data from the literature (Lekagul and McNeely, 1977) consisted of ranges rather than means, we used the midpoints of the ranges to estimate species means. For a few species it was necessary to subtract tail length from total length to obtain head and body length resulting in two measures which are not statistically independent. However, the general patterns explored here are probably not influenced strongly by these cases. The resultant data set contained 141 species. These are listed in Appendix I.

A canonical discriminant analysis was used to identify variables which discriminate between terrestrial, arboreal, and glissant mammals and to provide a measure of morphological overlap between the three locomotory modes. This was accomplished by computing mahalanobis distances between the three groups, and using the model of Harner and Whitmore (1977) and Whitmore and Harner (1980) to compute overlap of morphological groups.

The canonical analysis revealed the importance of tail length as a discriminatory variable. Therefore, we explored the allometry of tail length with head and body length and locomotor mode using a stepwise regression analysis with indicator variables (Neter and Wasserman, 1974). The indicator

variables were used both as main effects and interaction terms, and enabled us to investigate differences in the intercepts and slopes of flying, arboreal, and ground dwelling mammals. We used the regression model:

$$T_i = \beta_0 + \beta_1 H_i + \beta_2 X_{1i} + \beta_3 X_{2i} + \beta_4 H_i X_{1i} + \beta_5 H_i X_{2i} + \epsilon_i,$$

where $T = \ln(\text{tail length} + 1)$, $H = \ln(\text{head and body length} + 1)$, X_1 is an indicator variable for gliders (gliders = 1, otherwise $X_1 = 0$), X_2 is an indicator variable for arboreal mammals ($X_2 = 1$, otherwise $X_2 = 0$), β 's are regression coefficients and ϵ , is an error term. Thus, for a ground dwelling mammal the model is:

$$T_i = \beta_0 + \beta_1 H_i + \epsilon_i,$$

for gliding mammals,

$$T_i = (\beta_0 + \beta_2) + (\beta_1 + \beta_4) H_i + \epsilon_i,$$

and for arboreal mammals,

$$T_i = (\beta_0 + \beta_3) + (\beta_1 + \beta_5) H_i + \epsilon_i.$$

This approach permitted the use of one regression model to explore three potential relationships, and provided straightforward significance tests for differences between the three groups.

Phylogenetic effects were removed statistically using the regression approach of Miles and Dunham (1992). Indicator variables were used to define orders, and families nested within orders. These variables were then included in the tail length versus head and body length regression, and consequently removed residual variation associated with evolutionary history.

We analyzed glides of *G. volans* in the laboratory and field. The laboratory was an indoor handball court 14 x 7 m with a 7 m ceiling. We erected launching and landing poles consisting of 10.16 cm diameter schedule 40 PVC pipe, covered with astroturf. The launch and landing poles were 6.1 m and 3 m respectively, and each was embedded in a 20 l plastic bucket filled with concrete. The launch and landing poles were separated in the lab at varying distances in an effort to entice the squirrels to glide from one structure to the next. Usually, the animals failed to land on the landing pole and landed on the ground. The horizontal distance of each glide was measured to the nearest cm, and the height of the launch was determined by noting the exact launch point on the pole. In cases where the squirrels landed on the landing pole, the height of the landing point was determined as well. Two observers were used to time the glides and all other performance events. Their times were obtained using digital stopwatches to the nearest .01 sec, and the times averaged to reduce error. We obtained data for 115 glides by eight

squirrels in the laboratory. Climbing and running speeds were obtained for 60 climbing and running trials by six squirrels in the lab as well. For these trials the distances were measured directly.

Field glide data were obtained from animals captured in nest boxes on two small mammal trapping grids in the I. R. Kelso Sanctuary, Cape Girardeau Co., Missouri. The site was characterized as a second growth forest dominated by oak (*Quercus alba*, *Q. stellata*, *Q. macrocarpa*, *Q. prinoides*, *Q. rubra*, *Q. velutina*) and hickory (*Carya ovata*). We visited the grids during the autumn of 1993 and spring of 1994, and obtained complete data for 26 glides by 12 animals. Animals were removed from the nest boxes and released on tree trunks. The animals climbed the trees and glided to another tree. We used a clinometer to estimate launch and landing heights (± 0.5 m), and measured horizontal distances of glides (± 5 cm) with a 100 m tape. Glide times were estimated using digital stopwatches to the nearest 0.01 sec.

The parameters for our analysis of Scholey's gliding model (Scholey, 1986) were estimated using linear regression. We regressed vertical drop against horizontal distance, and glide distance against glide time. We attempted to verify Scholey's graphical results using his data for *Petaurista* and discovered several inconsistencies. These were corrected by consulting Scholey's source for the energetics components of the model (Taylor, 1977).

Scholey's glide effectiveness model compares the energetic cost of an animal climbing and then gliding, to an animal using quadrupedal locomotion. The metabolic power consumption of an animal climbing is given as: $P_c = (f + mg/\eta)V_c + aP_b$, where f is a constant defined incorrectly by Scholey (1986) as $10.7^{0.6}$, and correctly by Taylor (1977) as $10.7m^{0.4}$, and where m = mass, gravitational acceleration = g (9.81 m/s/s), η = climbing efficiency, and V_c = the velocity of climbing. The power of metabolism is defined as P_b , and $a = 1.7$ (a constant derived from Taylor, 1977). Scholey (1986) defined the power of metabolism as $3.5m^{0.75}$, but this is the basal metabolic rate. Taylor (1977) gives the value as $3.5m^{0.25}$. For our analysis of *G. volans*, we used the relationship determined by Stapp (1992); $P_b = 3.42m^{0.25}$. The energetic cost of climbing, E_c , is simply $P_c T_c$, where T_c is the time required to climb to a specific height. We obtained this value from direct measures of climbing speed in the lab. The metabolic power consumption of gliding, P_g , is minimal relative to that of climbing, and is estimated by Scholey (1986) as $2P_b$. This figure seems reasonable, and was derived from work by

Scholey, 1986) on the herring gull. The energetic cost of gliding, E_g , is $2P_b T_g$, where T_g is the time of gliding. T_g can be derived from the regression analysis of horizontal distance against glide time. The total energetic cost of climbing and gliding, E_t , is $E_c + E_g$. The cost of gliding locomotion is thus: $C_g = E_t/mgD$, where D is the horizontal distance covered by the glide.

The cost of quadrupedal locomotion can be derived in a similar fashion. The metabolic power cost of running is: $P_r = fV_r + aP_b$, where V_r is the velocity of running. Scholey derived this value from estimates for *Callosciurus notatus*. Our values were derived from direct estimates of *G. volans* running in the lab. The energetic cost of running is given as: $C_r = P_r/mgV_r$.

Using the corrected relationships given above, we re-evaluated the results given by Scholey (1986). We then repeated the analysis specifically for *G. volans*. We investigated the effects of climbing efficiencies, climbing speeds, and running speeds on the cost effectiveness of gliding locomotion. Also, we explored the effects of glide ratios and initial drops on the cost effectiveness of gliding. These last two variables, although not independent, were treated as such. The results should be robust within small deviations of initial parameter estimates.

Table 1.—Total canonical structure for the canonical discriminant analysis of gliding, arboreal, and terrestrial mammals. Coefficients for the morphological variables are correlations of the log transformed original variables on the canonical discriminant functions.

VARIABLE	CAN 1	CAN 2
Head and body length	0.0102	0.1371
Tail length	0.8221*	0.2204
Hind foot length	-0.1604	0.1848
Greatest skull length	-0.0528	0.3549*
Zygomatic width	-0.0246	0.1751
Upper tooth row length	0.1642	0.3579*
Canonical correlation	0.7997	0.3925
Canonical R^2	0.6396	0.1541
P value	0.0001	0.0013

RESULTS

Morphological Analysis.—Two canonical axes provide significant discrimination between the three modes of locomotion. The first axis is dominated by tail length (Table 1) and discriminates between ground dwelling forms and arboreal/gliding forms. The second axis is correlated most strongly with greatest skull length and upper tooth row length and discriminates between arboreal and gliding mammals. Glissant mammals have the longest tails, short skulls, and short upper tooth rows, while arboreal forms have long tails, long skulls, and long tooth rows (Fig. 1). The greatest morphological overlap occurs between gliding and arboreal mammals (69.28%), while the least occurs between gliding and ground dwelling forms (53.72%). Overlap between arboreal and ground dwelling mammals is 58.62%.

The overall regression of tail length against head and body length is significant (Table 2). Marsupials and eutherians differ significantly in tail length. Within the marsupials, differences exist between four families. Across taxonomic groups, the indicator variable and interaction term for gliding mammals is significant. Thus, the regression line for gliding mammals has a steeper slope than the lines for arboreal and ground dwelling forms (Fig. 2). The regression for the arboreal mammals

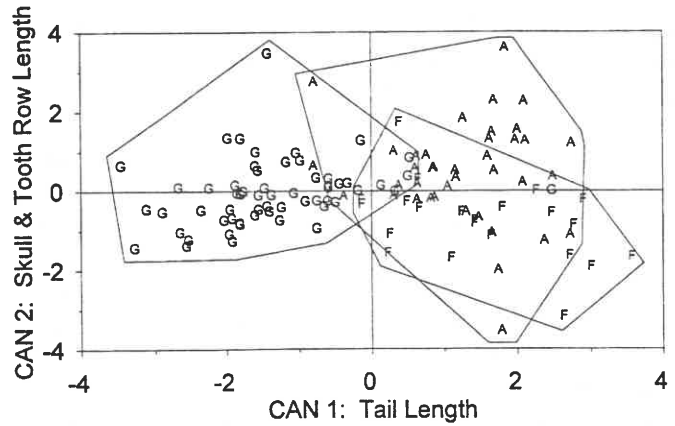


Fig. 1.—The distribution of gliding (F), arboreal (A), and ground dwelling (G) mammals in the canonical discriminant space.

does not have an intercept different from the ground dwelling mammals. However, the interaction term is significant and thus the slope for the regression line of arboreal species is greater than that for ground-dwelling species, but less than that for gliding species. Overall, small gliders have shorter tails than small arboreal mammals, but larger gliders (head and body length > 172.3 mm) have longer tails than larger arboreal mammals.

Table 2.—Stepwise regression results for log tail length against log head and body length (HB) and indicator variables for order, family, gliding, arboreal, and ground-dwelling mammals.

SOURCE	d.f.	SS	MS	F	P
MODEL	8	50.3075	6.2884	30.89	0.0001
ERROR	142	28.9066	0.2036		
TOTAL	150	79.2140			

PARAMETER	\$	SE	Type II SS	F	P
INTERCEPT	4.5754				
Order	-3.3416	0.3234	21.7402	106.80	0.0001
Acrobatidae	3.3494	0.4614	10.7296	52.71	0.0001
Burramyidae	2.9048	0.3781	12.0155	59.02	0.0001
Petauride	3.6513	0.3599	20.9488	102.91	0.0001
Pseudocheiridae	3.6460	0.3468	22.5041	110.55	0.0001
Glider	-4.5318	1.2003	6.4964	14.25	0.0002
HB x Glider	0.9986	0.2238	9.0748	19.91	0.0001
HB X Arboreal	0.1195	0.0227	12.5970	27.64	0.0001

$F^2 = 0.6351$

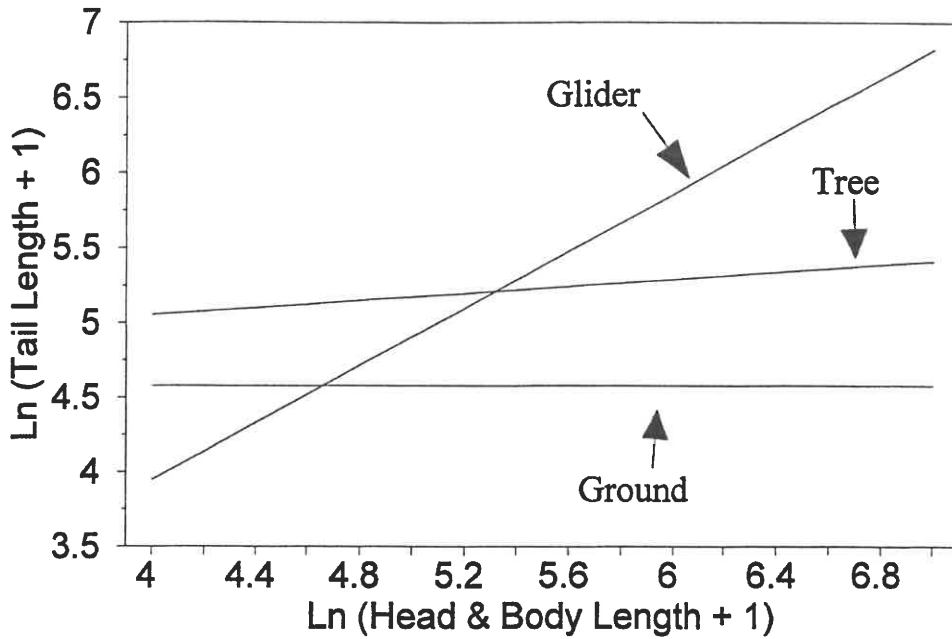


Fig. 2.—Regression lines for log tail length against log head and body length for gliding, arboreal, and ground dwelling mammals.

Performance Analysis.—The regression results of the glide analyses for *G. volans* are presented in Tables 3, 4, and 5. The regression for vertical drop against horizontal distance of the glide is significant and explains 54% of the variance in the glide data. Vertical drop increases with increasing horizontal distance, as expected. The model presented here has a steeper slope than that published by Scholey (1986) for *Petaurista petaurista* (Fig. 3). Thus, for glides greater than 18.62 m, *G. volans* experiences a greater loss in altitude for each additional horizontal m than does *P. petaurista*. The

regression also shows that while the initial vertical drop for *P. petaurista* as reported by Scholey (1986) is 7.45 m, that for *G. volans* is only 1.85 m. Thus, *G. volans* appears to reach gliding speed much sooner than does *Petaurista*. *Petaurista* attains a glide speed of about 15.1 m/s in Scholey's analysis, while *Glaucomys* reaches a terminal glide speed of about 8.27 m/s in our study. The minimum glide speed exhibited by *G. volans* was 4.12 m/s and the maximum was 8.85 m/s. Across all glides, the average glide speed, including the launch phase, was 6.37 m/s ($SE = 0.20$).

Table 3.—Regression results for vertical drop (m) against glide distance (sec) for laboratory and field glides of *Glaucomys volans*.

SOURCE	d.f.	SS	MS	F	P
MODEL	1	633.3024	633.3024	95.67	0.0001
ERROR	134	887.0722	6.6199		
TOTAL	135	1520.3746			
PARAMETER	ESTIMATE	T	P	SE	
INTERCEPT	1.8479	3.55	0.0005	0.5206	
TIME	0.5108	9.78	0.0001		0.0522

$R^2 = 0.7428$

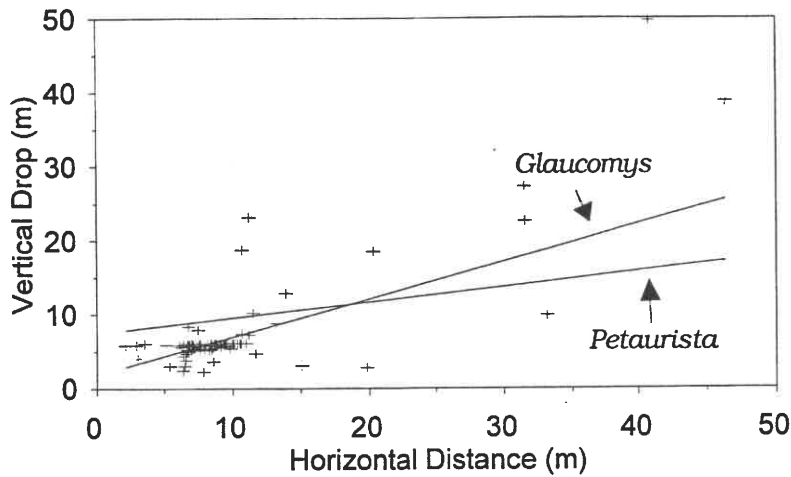


Fig. 3.—Regression line for total vertical drop (m) against horizontal glide distance (m) for *Glaucomys volans*. The line with the shallow slope represents the regression line determined by Scholey (1986) for *Petaurista petaurista*.

The mean glide ratio for *G. volans* in our study is 1.53. That is, the animals travel 1.53 m for every 1 m loss in altitude. The maximum glide ratio is 6.93, and the minimum is 0.36. Clearly, a glide ratio less than one indicates parachuting rather than gliding. These values are based on the direct glide angles. Estimates using actual glide angles would be somewhat higher. Nevertheless, the mean values reported here are lower than those reported by Nowak (1991), and Thorington and Heaney (1981).

The regression of glide distance against glide time is significant (Table 4). The slope for this equation is less than that reported by Scholey for *Petaurista* (Fig. 4). Thus for glides longer than 3.5 seconds, *G. volans* covers shorter distances than does *Petaurista*. There is a significant increase in glide speed with glide distance (Table 5), indicating that *Glaucomys* accelerates throughout the glide. However, the low R^2 for this regression (0.289), together with our observations of repeated glides by individuals (including complete rolls and 180 degree turns), suggests the animals exhibit considerable control over their glides.

Table 4.—Regression results for glide distance (m) against glide time (sec) for laboratory and field glides of *Glaucomys volans*.

SOURCE	d.f.	SS	MS	F	P
MODEL	1	2596.7046	2596.7046	386.90	0.0001
ERROR	134	899.3567	6.7116		
TOTAL	135	3496.0614			
PARAMETER	ESTIMATE	T	P	SE	
INTERCEPT	-3.5420	-4.52	0.0001	0.7842	
TIME	8.0920	19.67	0.0001	0.4114	

$R^2 = 0.7428$

SCHEIBE AND ROBINS—ATTRIBUTES OF GLIDING MAMMALS

Table 5.—Regression results for glide speed (m/sec) against direct glide distance (m).

SOURCE	d.f.	SS	MS	F	P
MODEL	1	78.2302	78.2302	61.84	0.0001
ERROR	134	169.5155	1.2650		
TOTAL	135	247.7457			
PARAMETER	ESTIMATE	T	P	SE	
INTERCEPT	4.4377	18.91	0.0001	0.2347	
GLIDE DISTANCE	0.5100	7.86	0.0001	0.0190	

$R^2 = 0.3158$

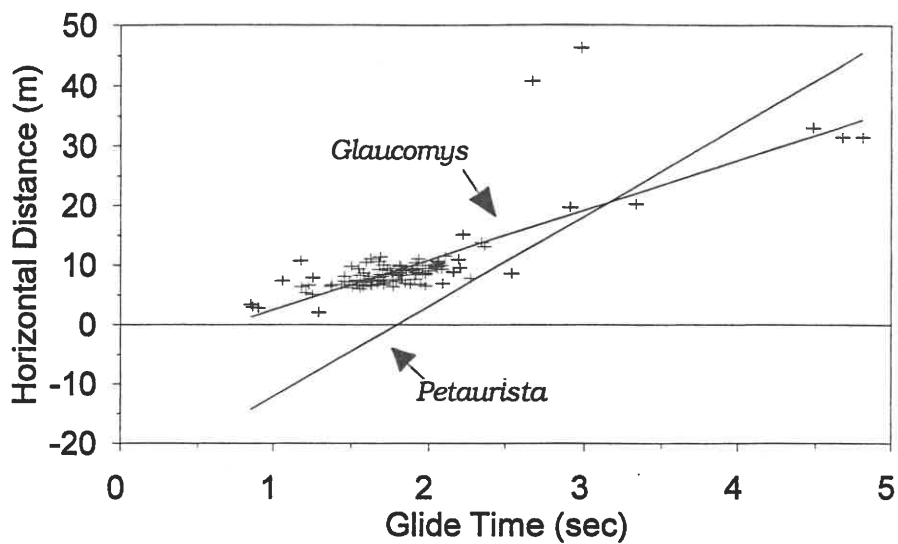


Fig. 4.—Regression line for horizontal glide distance (m) against total glide time (sec) for *Glaucomys volans*. The line with the steeper slope represents the regression line computed by Scholey (1986) for *Petaurista petaurista*.

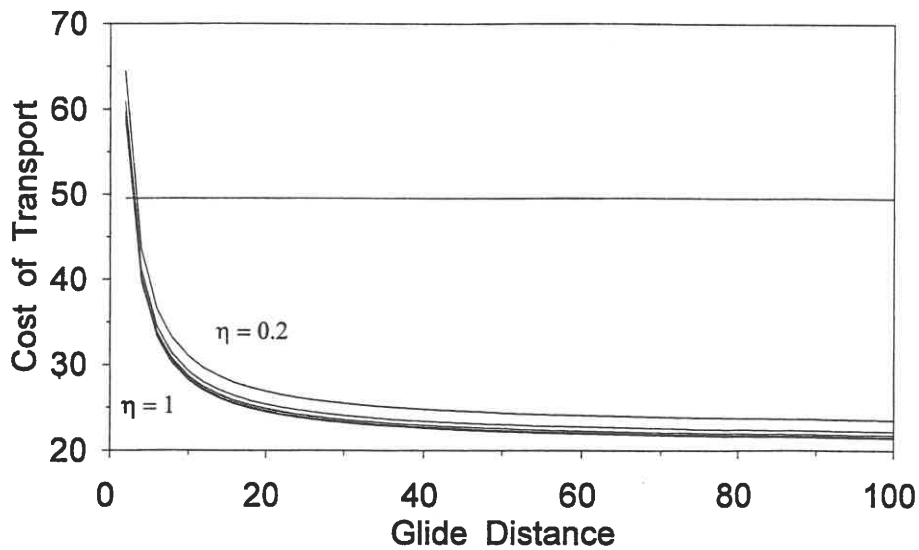


Fig. 5.—Results of the glide cost analysis for *Glaucomys volans*. Increasing climbing efficiencies from 20 to 100% results in a small decrease in the overall cost of the glides. The cost of quadrupedal locomotion is indicated by the horizontal line.

Our reanalysis of Scholey's (1986) work on the cost effectiveness of gliding in *P. petaurista* shows that his results are incorrect. That is, gliding does not become cost effective for *P. petaurista* at horizontal glide distances less than 100 m. This result is based on climbing efficiencies of 0.4 and 0.2, use of metabolic power rather than metabolic rate, and assumptions concerning climbing speeds, and running speeds of *Petaurista* (Scholey, 1986). However, when applied to *G. volans* the Scholey model produces results markedly different from those for *Petaurista*. Glide cost decreases rapidly with horizontal glide distance, especially up to 10 m, and is less than the cost of quadrupedal transport after about 3 m when mean running and climbing speeds are used (Fig. 5).

The distance at which gliding becomes cost effective is dependent on climbing and running speeds. Reducing running speed to 50% of the average for *Petaurista* reduces the cost effective glide distance to less than 40 m. Increasing climbing speed to 200% of the mean reduces the cost effective glide distance to 74 m (Fig. 6). Thus, for gliding to be cost effective in *Petaurista*, the animals must climb quickly and/or run slowly. If quadrupedal locomotion is fast and climbing slow, it is cheaper for *Petaurista* to move quadrupedally than to glide.

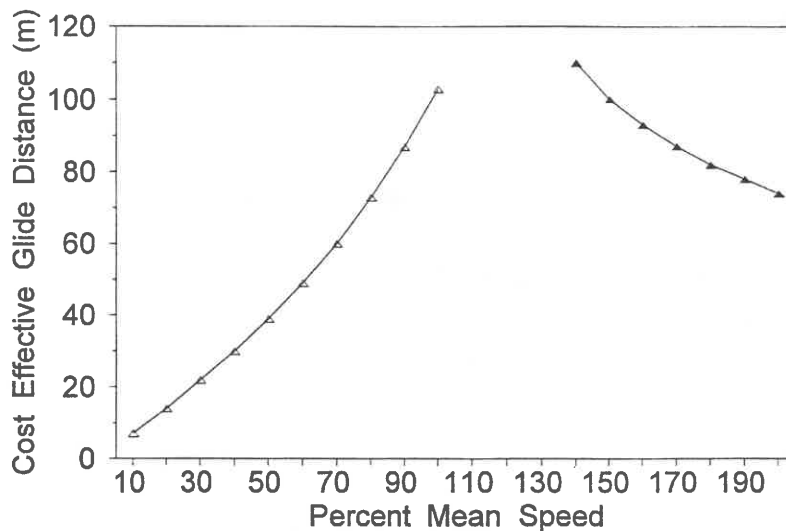


Fig. 6.—The effect of running speeds (open triangles) and climbing speeds (closed triangles) on the distance at which gliding becomes cost effective for *Petaurista petaurista*. Values on the abscissa are percentages of the mean climbing and running speeds (m/sec) reported by Scholey (1986).

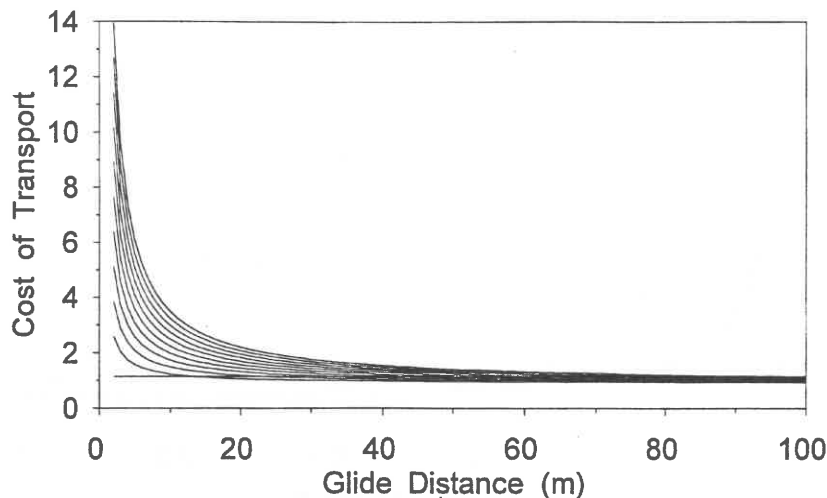


Fig. 7.—The cost of gliding in *Petaurista petaurista* as a function of reductions in the initial vertical drop of the glides. Each lower line represents a 10% reduction in the distance of the initial vertical drop. The cost of quadrupedal locomotion is indicated by the horizontal line.

Two parameters of the vertical drop/horizontal distance regression are subject to selection, and influence the cost effectiveness of gliding. The initial drop and the glide ratio are not independent variables, but we are interested only in the general behavior of the system near the initial parameter estimates. Reducing the initial vertical drop (the intercept of the vertical drop/horizontal distance regression) of a glide by *Petaurista* had the greatest effect on the early portions of the glide (Fig 7), reducing the cost of the glide. During this portion of the glide, the animals accelerate to speeds sufficient to obtain lift for the latter part of the glide. Thus, reducing the initial vertical drop will result in a slower glide with less lift, and consequently, a shorter glide. Increasing the glide ratio (equivalent to decreasing the slope of the regression between vertical drop and horizontal distance) results in reduced glide costs during the later portions of the glides. In fact, increasing the glide ratio by only 20% results in glides which are cost effective relative to quadrupedal locomotion at about 60 m (Fig. 8).

DISCUSSION

Tail length is an important morphological component of gliding. Thorington and Heaney (1981) hypothesized that since the tail is important for steering and balance, flying squirrels should have longer tails than tree squirrels. Based on their sample of 28 squirrels, they rejected the hypothesis, and found that small tree squirrels have shorter tails than small flying squirrels, and that large tree squirrels have longer tails than large flying squirrels. Our larger data set, which includes sciurids, anomalurids, acrobatids, burramyids, petaurids, and pseudocheirids, shows that across gliders in general, their results are not supported. In fact, small gliders have shorter tails than small arboreal mammals, but gliders with head and body lengths greater than 17 cm have longer tails. The slope of the regression for gliders is significantly larger than that for tree squirrels. So although tail length scales with size in both forms, it increases faster in gliding forms. This result supports the initial hypothesis of Thorington and Heaney (1981).

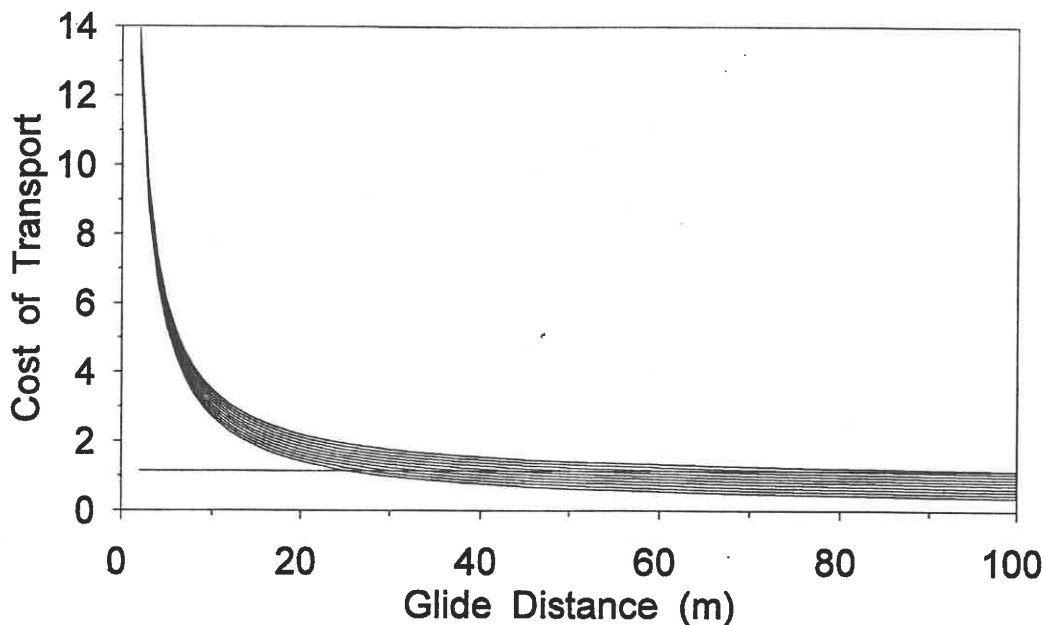


Fig. 8.—The cost of gliding in *Petaurista petaurista* as a function of reducing the slope of the vertical drop/horizontal distance regression. This is the same as increasing the glide ratio. Each lower line represents a percentage increase in the glide ratio. The cost of quadrupedal locomotion is indicated by the horizontal line.

The steering problems of large gliding squirrels are partially a consequence of their increased wing loading. Thorington and Heaney (1981) found wing loadings of the largest forms to be about 3.6 times as large as the smaller forms. They suggested that this would necessitate faster glide speeds for the larger forms. This appears to be the case. Glide speeds reported by Scholey for *P. petaurista* were ca. 15.1 m/s; and Ando (1993) reported glide speeds of 7 to 13.3 m/s for *P. leucogenys*. Our analysis of glides for *G. volans* revealed a mean glide speed of 6 m/s.

Tail shape appears to be related to body size in gliders. Schaller (1984) identified two tail morphologies relevant to gliders: cylindrical tails which act as drag rudders, and flat caudal wings (tails) which act as flow rudders. Small gliders such as *Glaucomys*, *Pteromys*, *Hylopetes*, *Petinomys*, *Acrobates*, and *Iomys* tend to have flow rudders, while large animals like *Petaurista*, *Eupetaurus*, *Petauroides*, and *Anomalurus* have drag rudders. There is some overlap, for example *Petaurus breviceps* has a cylindrical tail. This pattern may be related to the glide characteristics of large and small animals. Flow rudders in small gliders certainly add to the surface area of the wing, but perhaps more importantly may be ideally suited for the control of speed and pitch (Norberg, 1990). This would improve maneuverability in slow flying species. The drag rudders of large gliders may serve to 'orient the body-axis towards the aerial pathway-axis' (Schaller, 1984), perhaps minimizing drag and maximizing speed and lift.

Morphological overlap is greatest between gliders and arboreal mammals, and least between gliders and ground dwelling mammals. Yet, definite differences exist between gliders and arboreal forms. Generally, gliders have shorter tooth rows and shorter skulls than arboreal forms. Analyzing sciurids and anomalurids, Scheibe et al. (1990) found tooth rows in gliding squirrels to be longer than those in nongliding squirrels. They speculated that foraging constraints may have selected for greater efficiency in food processing. Based on our data set, that hypothesis appears to be incorrect. However, marsupial gliders have different dental formulas than sciurids and anomalurids. Additionally, many marsupial gliders are exudivorous, obviating the need for large dental surface areas.

Body size may have a great deal to do with the transition from tree squirrel to glider. The energetic advantages of gliding accrue to a smaller glider much more rapidly than to a large one. Our analysis of Scholey's (1986) model using glide data

for *G. volans* reveals that it is energetically cheaper for small gliders to glide than to use quadrupedal locomotion. For large gliders like *P. petaurista*, Scholey (1986) found a glide distance of about 45 m to be necessary before an energetic advantage was realized. In fact, our reanalysis of his model demonstrates that more than 100 m are required for large gliders. Ando and Shiraishi (1993) found the glide distances of *P. leucogenys* to be determined primarily by forest structure and 'learned' glide routes. They reported mean glide distances in five shrine groves to range from 17.5 m to 33.1 m. Using Scholey's (1986) analysis, it would be cheaper for *P. leucogenys* to use quadrupedal locomotion as well. In fact, Ando and Shiraishi (1993) reported the use of quadrupedal locomotion predominated for movements over short distances.

A number of factors can reduce the cost of gliding. These include decreasing the glide angle, increasing the efficiency of climbing, and reducing the initial vertical drop. Increasing the glide angle can be achieved by decreasing wing loading. The fact that styliiform and unciform cartilages exist among many forms, and limb lengths of gliders tend to be longer than those of tree squirrels suggests that evolution has resulted in greater patagial surface area. The efficiency of climbing is probably also improved by lengthening of the distal elements of the front appendage. Thorington and Thorington (1991) showed that a wider grasp on a tree trunk increases the normal force of the claws into the trunk, and reduces the tangential force. However, climbing efficiency has a relatively small effect on the cost effectiveness of gliding. Increasing the glide ratio by 10% results in considerably cheaper glides. Increasing the glide ratio through reduced wing loadings is probably difficult for large gliders, and may explain the positive allometry of tail length with head and body length for large gliders. Reducing the extent of the initial vertical drop reduces the glide cost during the initial stages of the glide. However, this results in a slower glide, which may not be possible for large gliders because of the greater wing loadings. Also, slower glides may subject smaller gliders to greater predation risks.

The transition to a gliding morphology is not trivial. Gliders tend to have modifications of the limbs, wrists, and shoulder girdle (Peterka, 1936; Oxnard, 1968; Thorington and Heaney, 1981; Bou et al., 1987) in addition to patagia. If gliding morphologies evolved with the accumulation of modifications, the earliest gliders probably had lower glide ratios and perhaps lower climbing efficien-

cies than extant forms. This would reduce the hypothesized energetic advantage of gliding. The hypothesis that energetics has driven the evolution of gliding locomotion requires scrutiny.

The hypothesis that gliding conveys some measure of predator avoidance seems suspect for smaller gliders. *Glaucomys* are prey items for many avian, reptilian, and mammalian species (Dolan and Carter, 1977), and form a large portion of the diets of northern spotted owls (Forsman et al., 1984). Smaller gliders may be subject to greater predation pressures because of their slower glide speeds. Also, predation has clearly played a role in the behavior of *G. volans*. Scheibe (in litt) used infrared sensors to study the activity patterns of *G. volans* and determined that the animals exhibit surveillance behavior before emerging from their nest boxes each evening, and follow each evening's activity with surveillance behavior as well. Austad and Fischer (1991) and Holmes and Austad (1994) have argued that gliding mammals live longer than nongliding forms, presumably because of reduced environmental vulnerability (due to arboreal, nocturnal, and nesting habits). However, Stapp (1994) has noted statistical difficulties with the analysis of Austad and Fischer (1991) and Holmes and Austad (1994), and suggests that the data are insufficient to conclude that gliders live longer than tree squirrels.

The fact that gliding has evolved so many times in vertebrates suggests that evolutionarily, it is not difficult to do. The biogeographic distribution and abundance of gliders suggests some relationship between forest structure and gliding. Studies published to date have not provided convincing evidence that gliding provides an energetic advantage over quadrupedal locomotion, nor has any conclusive evidence been published that gliding minimizes predation risks. The scaling of tail lengths and shapes, and limb proportions (Thorington and Heaney, 1981) with glider size, as well as the energetic differences of large and small gliders, suggests a variety of selection regimes. Foraging optimization, predator avoidance, or locomotor efficiency may drive the evolution of gliding, but detailed ecological studies of most gliders are lacking. It seems that a great deal of work is needed before we can understand fully the evolution of gliding locomotion.

ACKNOWLEDGMENTS

We thank J. Dunlap, C. Newhouse, W. Suchland, and D. Dowling for assistance in the field and lab, and D. Figgs and J. Heiland for work during the early stages of the project. We are par-

ticularly indebted to T. Flannery, L. Godwin, and the entire curatorial staff of the Australian Museum for their efforts on our behalf. Luba Turchyn graciously provided a translation of the Polyakova and Sokolov (1965) paper. Richard Thorington, R. Goldingay, S. Van Dyke, M. Ando, and S. Ward provided thoughtful comments, ideas, and speculation that encouraged us to pursue this project. Without their insight and experience with gliders, we would have learned much less.

LITERATURE CITED

- ALLEN, J. A. 1915. Review of the south American Sciuridae. *Bulletin of the American Museum of Natural History*, 34:147-309.
- ANDO, M., AND S. SHIRAISHI. 1991. Arboreal quadrupedalism and gliding adaptations in the Japanese giant flying squirrel, *Petaurista leucogenys*. *Honyurui Kagaku (Mammalian Science)*, 30:167-181.
- . 1993. Gliding flight in the Japanese giant flying squirrel, *Petaurista leucogenys*. *Journal of the Mammalogical Society of Japan*, 18:19-32.
- AUSTAD, S. N., AND K. E. FISCHER. 1991. Mammalian aging, metabolism, and ecology: evidence from the bats and marsupials. *Journal of Gerontology: Biological Sciences*, 46:B47-53.
- BAUDINETTE, R. V., AND K. SCHMIDT-NIELSEN. 1974. Energy cost of gliding flight in the herring gull. *Nature*, 248:83-84.
- BOU, J., A. CASINOS, AND J. OCANA. 1987. Allometry of the limb long bones of insectivores and rodents. *Journal of Morphology*, 192:113-123.
- DOLAN, P. G., AND D. C. CARTER. 1977. *Glaucomys volans*. *Mammalian Species*, 78:1-6.
- DUDLEY, R., AND P. DEVRIES. 1990. Tropical rain forest structure and the geographical distribution of gliding vertebrates. *Biotropica*, 22:432-434.
- EMERSON, S. B. 1991. The ecomorphology of Bornean tree frogs (family Rhacophoridae). *Zoological Journal of the Linnean Society*, 101:337-357.
- EMERSON, S. B., AND M. A. R. KOEHL. 1990. The interaction of behavioral and morphological change in the evolution of a novel locomotor type: "flying" frogs. *Evolution*, 44:1931-1946.
- EMMONS, L. H., AND A. H. GENTRY. 1983. Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *The*

- American Naturalist, 121:513-524.
- FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildlife Monographs*, 87:1-64.
- GUPTA, B. B. 1966. Notes on the gliding mechanism in the flying squirrel. *Occasional Papers of the Museum of Zoology, University of Michigan*, 645:1-7.
- HALL, E. R., AND K. R. KELSON. 1959. *The mammals of North America*. Ronald Press Co., New York, 1083 pp.
- HARNER, J. E., AND R. C. WHITMORE. 1977. Multivariate measures of niche overlap using discriminant analysis. *Theoretical Population Biology*, 12:21-36.
- HOFFMEISTER, D. F. 1986. *Mammals of Arizona*. University of Arizona Press and the Arizona Game and Fish Department, Tucson, 602 pp.
- . 1989. *Mammals of Illinois*. University of Illinois Press, Urbana, 348 pp.
- HOLMES, D. J., AND S. N. AUSTAD. 1994. Fly now, die later: life history correlates of gliding and flying in mammals. *Journal of Mammalogy*, 75:224-226.
- JOHNSON-MURRAY, J. L. 1987. The comparative myology of the gliding membranes of *Acrobates*, *Petauroides* and *Petaurus* contrasted with the cutaneous myology of *Hemibelideus* and *Pseudocheirus* (Marsupialia: Phalangeridae) and with selected gliding rodentia (Sciuridae and Anomaluridae). *Australian Journal of Zoology*, 35:101-113.
- LEKAGUL, B., AND J. A. MCNEELY. 1977. *Mammals of Thailand*. Association for the Conservation of Wildlife. Sahakarnbhat Co., Bangrak, Bangkok 5, Thailand, 746pp.
- MILES, D. B., AND A. E. DUNHAM. 1992. Comparative analyses of phylogenetic effects in the life-history patterns of iguanid reptiles. *The American Naturalist*, 139:848-869.
- MILLER, G. S. 1912. *Catalogue of the mammals of western Europe (Europe exclusive of Russia) in the collection of the British Museum*. The British Museum, London, 1019 pp.
- NACHTIGALL, W. 1979. Gleitflug des flugbeutlers *Petaurus breviceps papuanus*. II Filmanalysen zur einstellung von gleitbahn und rumpf sowie zur steuerung des gleitflug. *Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology*, 133:89-95.
- NACHTIGALL, W., R. GROSCH, AND T. SCHULTZE-WESTRUM. 1974. Gleitflug des flugbeutlers *Petaurus breviceps papuanus* (Thomas): flugverhalten und flugsteuerung. *Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology*, 92:105-115.
- NETER, J., AND W. WASSERMAN. 1974. *Applied linear statistical models*. Richard D. Irwin, Homewood, Illinois, 842 pp.
- NORBERG, U. M. 1985. Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. *The American Naturalist*, 126:303-327.
- . 1990. Gliding flight. Pp. 65-75, in *Zoophysiology 27, Vertebrate flight: mechanics, physiology, morphology, ecology and evolution* (S. D. Bradshaw, et al., eds.). Springer-Verlag, New York, 291 pp.
- NOWAK, R. M. 1991. *Walker's mammals of the world*. The Johns Hopkins University Press, Baltimore, Maryland, 1629 pp.
- OGNEV, S. I. 1940. *Mammals of the U.S.S.R. and adjacent countries*. Vol. IV. Rodents. Israel Program for Scientific Translations Ltd., 1966. IPST Cat. No. 1254. S. Monson Binding: Wiener Bindery Ltd., Jerusalem, Israel, 491 pp.
- . 1947. *Mammals of the U.S.S.R. and adjacent countries*. Vol. V. Rodents. Israel Program for Scientific Translations Ltd., 1963. IPST Cat. No. 745. S. Monson Binding: Wiener Bindery Ltd., Jerusalem, Israel, 662 pp.
- OXNARD, C. E. 1968. The architecture of the shoulder in some mammals. *Journal of Morphology*, 126: 249-290.
- PETERKA, H. E. 1936. A study of the myology and osteology of tree sciurids with regard to adaptation to arboreal, glissant and fossorial habits. *Transactions of the Kansas Academy of Science*, 39:313-332.
- POLYAKOVA, R. S., AND A. S. SOKOLOV. 1965. Structure of the locomotor organs in the volant squirrel, *Pteromys volans* L. in relation to its plane flight. *Zoological Journal*, 44: 902-916.
- ROSEVEAR, D. R. 1969. *The rodents of west Africa*. Trustees of the British Museum (Natural History), London, 604 pp.
- SCHALLER, D. 1984. Wing evolution. Pp. 333-348, in *The beginnings of birds: Proceedings of the International Archaeopteryx Conference*, Eichstatt (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, eds.). Freunde des Jura-Museums Eichstatt, Willibaldsburg, Germany, 382 pp.
- SCHNEIBE, J. S., D. FIGGS, AND J. HEILAND. 1990. Morphological attributes of gliding rodents. *Transactions of the Missouri Academy of Science*, 24:49-55.

- SCHOLEY, K. 1986. The climbing and gliding locomotion of the giant red flying squirrel *Petaurista petaurista* (Sciuridae). Biona-report, 5:187-204.
- STAPP, P. 1992. Energetic influences on the life history of *Glaucomys volans*. Journal of Mammalogy, 73:914-920.
- . 1994. Can predation explain life-history strategies in mammalian gliders? Journal of Mammalogy, 75:227-228.
- TAYLOR, C. R. 1977. The energetics of terrestrial locomotion and body size in vertebrates. Pp. 127-141, in Scale effects in animal locomotion (T. J. Pedley, ed.). Academic Press, New York, 545 pp.
- THORINGTON, R. W., JR., AND L. R. HEANEY. 1981. Body proportion and gliding adaptations of flying squirrels (Petauristinae). Journal of Mammalogy, 62:101-114.
- THORINGTON, R. W., JR., AND E. M. THORINGTON. 1989. Postcranial proportions of *Microsciurus* and *Sciurillus*, the American pygmy tree squirrels. Pp. 125-136, in Advances in Neotropical mammalogy (K. H. Redford and J. F. Eisenberg, eds.). The Sandhill Crane Press, Inc., Gainesville, Florida, 614 pp.
- WHITMORE, R. C., AND J. E. HARNER. 1980. Analysis of multivariately determined community matrices using cluster analysis and multidimensional scaling. Biometrical Journal, 22:715-723.
- (C, R), *Pseudocheirus forbesi* (C, R), *Pseudocheirus herbertensis* (C, R), *Pseudocheirus mayeri* (C, R), *Pseudocheirus peregrinus* (C, R), *Pseudochirops albertisii* (C, R), *Pseudochirops archeri* (C, R), *Pseudochirops corinnae* (C, R), *Pseudochirops cupreus* (C, R). Vombatidae: *Vombatus ursinus* (R). Phascolarctidae: *Phascolarctos cinereus* (R). Sciuridae (Petauristinae): *Aeromys tephromelas* (R), *Belomys pearsonii* (C, R), *Eupetaurus cinereus* (R), *Glaucomys sabrinus* (C, R), *Glaucomys volans* (C, R(2)), *Hylopetes alboniger* (C(2), R(2)), *Hylopetes lepidus* (C, R(2)), *Hylopetes phayrei* (C, R), *Iomys horsfieldi* (R), *Petaurista elegans* (R), *Petaurista petaurista* (C, R), *Petinomys genibarbis* (R), *Petinomys setosus* (C, R), *Pteromys volans* (C, R(2)), *Pteromyscus pulverulentus* (R). Sciuridae (Sciurinae): *Ammospermophilus harrisii* (C, R), *Ammospermophilus insularis* (C, R), *Ammospermophilus interpres* (C, R), *Ammospermophilus leucurus* (C, R), *Ammospermophilus nelsoni* (C, R), *Callosciurus caniceps* (C, R), *Callosciurus erythraeus* (C, R), *Callosciurus finlaysonii* (C, R), *Callosciurus nigrovittatus* (C, R), *Callosciurus notatus* (C, R), *Callosciurus prevostii* (C, R), *Cynomys gunnisoni* (C, R), *Cynomys ludovicianus* (C, R), *Dremomys rufigenis* (C, R), *Epixerus ebii* (R), *Funisciurus anerythrus* (R), *Funisciurus isabella* (R), *Funisciurus leucogenys* (R), *Funisciurus pyrropus* (R), *Funisciurus substriatus* (R), *Heliosciurus gambianus* (R), *Heliosciurus rufobrachium* (R), *Lariscus insignis* (C, R), *Marmota baibacina* (C, R), *Marmota bobak* (C, R), *Marmota camtschatica* (C, R), *Marmota caudata* (C, R), *Marmota marmota* (R), *Marmota monax* (C, R), *Marmota sibirica* (C, R), *Menetes berdmorei* (C, R), *Myosciurus pumilio* (R), *Paraxerus cooperi* (R), *Protoxerus aubinnii* (R), *Protoxerus stangeri* (R), *Ratufa affinis* (C, R), *Ratufa bicolor* (C, R), *Rhinosciurus laticaudatus* (C, R), *Sciurus aberti* (C, R), *Sciurus arizonensis* (C, R), *Sciurus carolinensis* (C, R), *Sciurus nayaritensis* (C, R), *Sciurus niger* (C, R), *Sciurus vulgaris* (C, R), *Spermophilopsis leptodactylus* (C, R), *Spermophilus adocetus* (C(2), R(2)), *Spermophilus alaschanicus* (C, R), *Spermophilus armatus* (C, R), *Spermophilus atricapillus* (C, R), *Spermophilus beecheyi* (C, R), *Spermophilus beldingi* (C, R), *Spermophilus brunneus* (C, R), *Spermophilus citellus* (C, R), *Spermophilus columbianus* (C, R), *Spermophilus dauricus* (C, R), *Spermophilus erythrogegens* (C(2), R(2)), *Spermophilus franklinii* (C, R), *Spermophilus lateralis* (C, R), *Spermophilus madrensis* (C, R), *Spermophilus major* (C, R), *Spermophilus mexicanus* (C, R), *Spermophilus mohavensis* (C, R), *Spermophilus mollis* (C, R), *Spermophilus parryi* (C(3), R(3)), *Spermophilus perotensis* (C, R),

APPENDIX I

List of species used in the morphological analyses. Species used in the canonical discriminant analysis are indicated with a C, and those used in the regression analysis are indicated with an R. Numbers indicate replication resulting from different sources, with measurements suggesting geographical or subspecific differences.

Acrobatidae: *Distoechurus pennatus* (C, R), *Acrobates pygmaeus*, (C, R). Burramyidae: *Burramys parvus* (C, R), *Cercartetus caudatus* (C, R), *Cercarterus concinnus* (C, R), *Cercartetus lepidus* (C, R), *Cercartetus nanus* (C, R). Petauridae: *Dactilopsila megalura* (R), *Dactilopsila palpator* (C, R), *Dactilopsila tatei* (R), *Dactilopsila trivergata* (C, R), *Gymnobelideus leadbeateri* (C, R), *Petaurus australis* (C, R), *Petaurus breviceps* (C, R), *Petaurus norfolcensis* (C, R). Pseudocheiridae: *Hemibelideus lemuroides* (C, R), *Petauroides volans* (C, R), *Petropseudes dahli* (C, R), *Pseudocheirus canescens*

VIRGINIA MUSEUM OF NATURAL HISTORY

Spermophilus pygmaeus (C, R), *Spermophilus relictus* (C, R), *Spermophilus richardsonii* (C, R), *Spermophilus saturatus* (C, R), *Spermophilus pilosoma* (C, R), *Spermophilus suslicus* (R), *Spermophilus tereticaudus* (C, R), *Spermophilus townsendii* (C, R), *Spermophilus tridecemlineatus* (C, R), *Spermophilus undulatus* (C, R), *Spermophilus variegatus* (C, R), *Spermophilus washingtoni* (C, R), *Sundasciurus hippurus* (C, R), *Sundasciurus lowii* (C, R), *Sundasciurus tenuis* (C, R), *Tamias cinereicollis* (C(2), R(2)), *Tamias dorsalis* (C(2), R(2)), *Tamias minimus* (C, R), *Tamias quadrivittatus* (C(2), R(2)), *Tamias sibiricus* (C, R), *Tamias striatus* (C, R), *Tamias umbrinus* (C(2), R(2)), *Tamiasciurus hudsonicus* (C, R), *Tamiops macclellandi* (C, R), *Tamiops rodolpheii* (C, R), *Xerus erythropus* (R).
Anomaluridae: *Anomalurus beecrofti* (C, R), *Anomalurus derbianus* (C, R), *Anomalurus pelii* (C, R), *Anomalurus pusillus* (C, R), *Idiurus macrotis* (C, R), *Idiurus zenkeri* (C, R).