

Morphological Attributes of Gliding Rodents: A Preliminary Analysis

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Abstract: In this paper we use multivariate statistical techniques to explore some morphological attributes associated with ground dwelling, arboreal, and gliding sciurids and anomalurids. The data were obtained from the literature and included three external and three internal measurements. A principal components analysis revealed a general size axis and an axis associated with tail length. A canonical discriminant function analysis showed significant morphological differences between the three groups of mammals. Ground dwelling forms had short tails and narrow interorbital breadths while the arboreal and gliding forms did not. The gliding forms had shorter hind feet and longer maxillary tooth rows than the other mammals. The data are interpreted in light of the evolution of ground dwelling, arboreal and gliding life histories.

Key words: Gliding, Sciuridae, Anomaluridae.

Introduction

The evolution of vertebrate flight has received considerable attention (Caple *et al.*, 1983; Nopsca, 1907; Norberg, 1985; Ostrom, 1974). However, most of this research has been focused on flight in birds or on the transition from gliding to powered flight. The evolution of gliding in amphibians, reptiles, and mammals has not been extensively studied (Savile, 1962). The fact that fish, frogs, lizards, snakes, phalangers, anomalurids, sciurids, dermopterans, and chiropterans are all capable of some form of flight indicates that the invasion of the aerial habitat is not a rare event. At the same time, the transition from an arboreal life style to a glissant one has been largely overlooked. It is not clear precisely how the morphologies of gliding mammals are related to habitat use, diet, or ecology.

Thorington and Heaney (1981) studied the flight characteristics and external morphology of flying squirrels and identified some morphological differences with tree squirrels. Others, (McKenna, 1962; Black, 1963; Mein, 1970) have studied the phylogenetic evolution of gliding sciurids, but few attempts have been made to study the selective forces that have led to the evolution of volant locomotion in non-chiropteran mammals.

One hypothesis that has been suggested for the evolution of gliding is foraging optimization (Norberg, 1985). This hypothesis states that gliding from one tree to another and then climbing upwards can maximize energy gain (Norberg, 1981; 1983). However, the presence of patagia reduces maneuverability and speed of locomotion on the ground (Sollberger, 1940). While glissant rodents may be optimizing foraging efficiency within the canopy, they are probably minimizing their ability to forage on the ground.

Predator avoidance is an alternative or concomitant hypothesis for the evolution of glissant locomotion. The importance of predation to sciurids is

obvious. Arboreal squirrels respond to noises in the forest by moving to the opposite sides of trees. Flying squirrels respond to disturbances in the forest by evacuating their tree holes, climbing upwards and gliding to the next tree. While gliding may provide an escape from mammalian and reptilian predators, it is not clear that it provides an escape from their most likely predators, owls. Thus, the flying squirrels may actually suffer increased levels of predation rather than decreased predation.

Finally, patagia may simply allow the squirrels to reduce or control landing speeds. *Tamiasciurus* and *Sciurus* will "parachute" when jumping from tree to tree, and will assume the position of a landing *Glaucomys*. Patagia would add some degree of control to a landing (Thorington and Heaney, 1981).

This study is an attempt to characterize a few morphological attributes associated with gliding mammals. When the morphologies of ground dwelling, arboreal, and glissant mammals are well understood, it may be possible to develop and carefully evaluate hypotheses for the selective regimes that have led to gliding.

Methods

In order to gain some insight into the morphologies associated with different modes of squirrel locomotion, we used principal components analysis and canonical discriminant analysis to study the morphological attributes of ground dwelling, arboreal, and volant sciurids and anomalurids. Morphological measurements were obtained for 85 species representing 315 subspecies and races of ground-dwelling, arboreal, and flying sciurids and anomalurids. The measurements for the animals were obtained from taxonomic treatises on European (Miller 1912), African (Rosevear 1969), Eurasian (Ognev 1940, 1947), and North American mammals (Hall and Kelson 1959), and included head and body length, tail length, hind foot length, total skull length, interorbital breadth, and length of the upper tooth row.

For the principal components analysis, the data were averaged across subspecies, localities, and gender to produce mean values for each species. The factor scores for each species were then derived, and plotted with respect to the first two principal axes. The factor scores for the three groups of squirrels were compared using nonparametric schematic plots (Tukey, 1977). For the canonical discriminant analysis, the data were not averaged in an effort to maximize the degrees of freedom associated with the test. The centroids of the three groups (ground dwelling, arboreal, and gliding) were then plotted with respect to the first two canonical discriminant axes.

Results

The results of the principal components analysis are presented in Table 1. The first two principal components explained almost 92 percent of the variation in the data set. Principal component 1 explained 77.5 percent of the variation in the data set, and was loaded relatively evenly by all variables except the tail length variable. Since all of the loadings were positive, the first principal component is considered a general size axis. The second principal component explained 14.2 percent of the variation in the data set, and was loaded most heavily by the tail length variable. The second principal component is interpreted as a tail length axis.

Table 1. Eigenvectors for the principal components analysis. PC 1 represents the first principal component while PC 2 represents the second principal component.

Variable	PC 1	PC 2
Head & Body Length	.408	-.222
Tail Length	.251	.896
Hind Foot Length	.456	.008
Skull Length	.453	-.119
Interorbital Breadth	.421	.139
Maxillary Tooth Row Length	.423	-.338
Variance	.775	.142
Cumulative Variance	.775	.917

The distribution of the 85 species of mammals with respect to the first two principal components is presented in Figure 1. Overall, ground dwelling forms tend to have negative values for principal component two while arboreal and

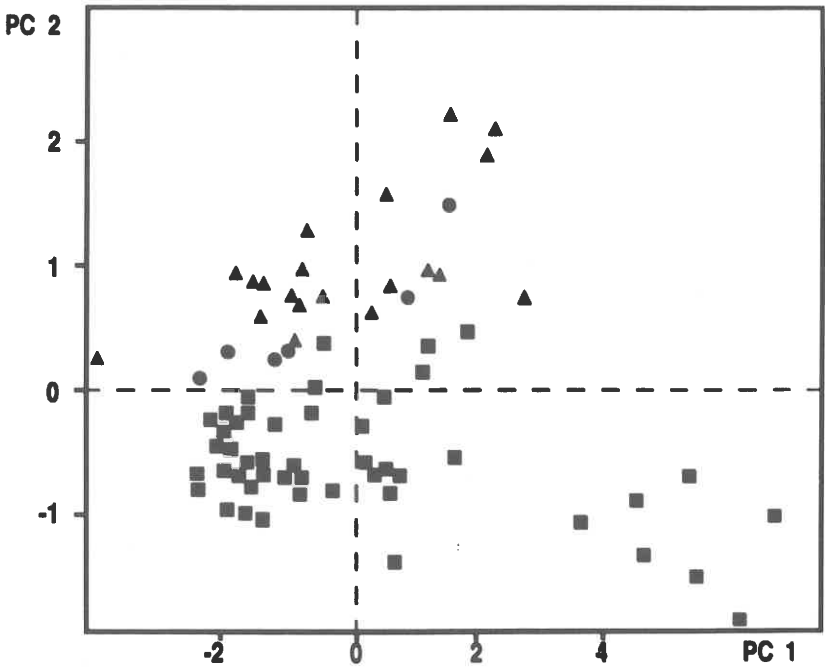


Fig. 1. The distribution of the 85 species of ground-dwelling (plus signs), arboreal (open squares) and flying (closed squares) sciurids and anomalurids with respect to the first two principal axes. Some observations are hidden.

gliding forms tend to have positive values. Thus, ground squirrels have shorter tails than do the other animals. However, it is interesting to note that gliding forms tend to be intermediate in terms of tail length. The arboreal forms tend to have the longest tails. These results are also indicated by the nonparametric schematic plots (Tukey 1977) presented in Figure 2. These plots present the medians, quartiles, and pseudo-standard deviations of each group (arboreal, flying and ground dwelling) with respect to the first and second principal components. From this figure it is clear that there are no significant differences with respect to the first size axis. The distributions are completely overlapping. However, with respect to the second "tail length" axis, ground forms have much shorter tails than do the arboreal and flying forms, and arboreal forms tend to have longer tails than the flying forms.

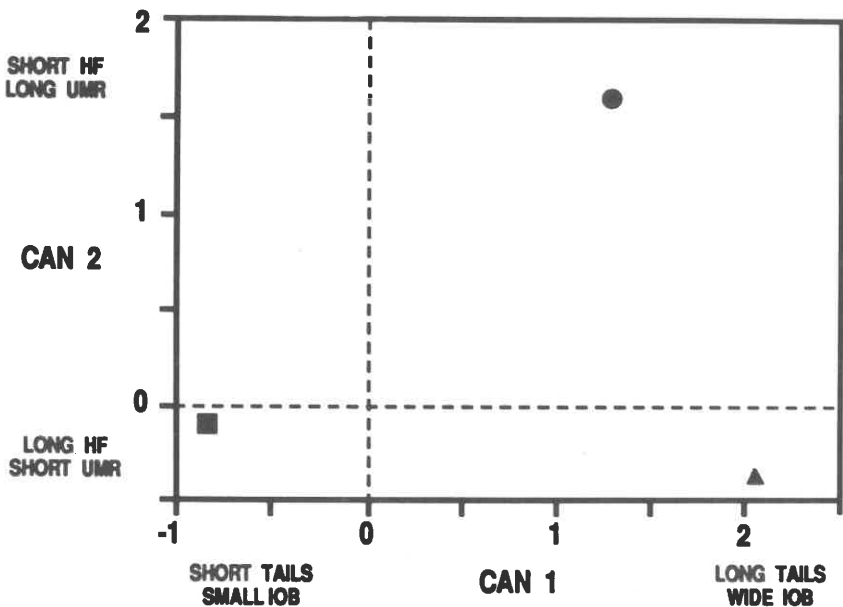


Fig. 2. The distribution of the principal component scores along the first two principal axes (PC 1 = a general size axis, PC 2 = a tail length axis) for ground-dwelling (G), arboreal (A) and flying (F) sciurids and anomalurids. The vertical line associated with each box represents a pseudo-standard deviation. The upper, middle, and lower horizontal lines represent the upper quartile, median, and lower quartiles respectively.

The results of the canonical discriminant analysis are presented in Table 2. Here, the first canonical discriminant function is loaded most heavily by tail length and interorbital breadth, while the second canonical discriminant function is loaded most heavily by hind foot length and upper tooth row length. Thus, the variables that provide the best discrimination between the gliding, arboreal, and

Table 2. Canonical coefficients for discrimination of squirrel habitats based on squirrel morphology. Can 1 = the first canonical discriminant axis, Can 2 = the second canonical discriminant axis.

Variable	Can 1	Can 2
Head & Body Length	-.790	.970
Tail Length	1.249	1.419
Hind Foot Length	-.073	-2.693
Skull Length	-.598	-1.436
Interorbital Breadth	1.129	-.241
Maxillary Tooth Row Length	-.460	2.906

ground dwelling forms are tail length and interorbital breadth, followed by hind foot length and upper tooth row length.

The distribution of the group means with respect to the canonical discriminant space is presented in Figure 3. From this figure it is clear that ground

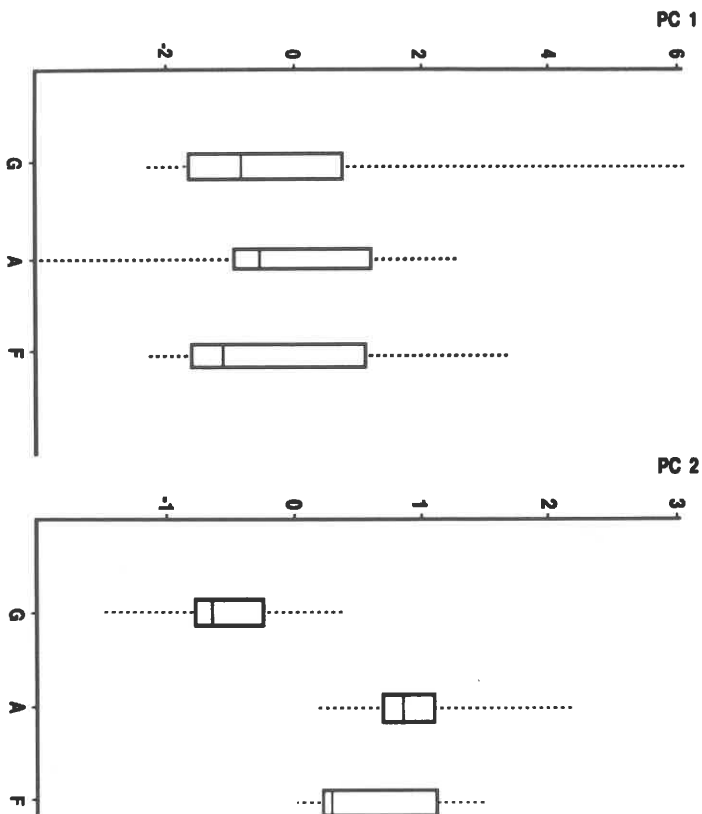


Fig. 3. The distribution of the group centroids for ground-dwelling (plus), arboreal (open square) and flying (closed square) sciurids and anomalurids in the canonical discriminant space.

dwelling forms have short tails, small interorbital breadths, long hind feet, and short maxillary tooth rows. The arboreal forms have long tails, wide interorbital breadths, long hind feet, and short maxillary tooth rows. The gliding forms are similar to the arboreal forms with respect to tail length and interorbital breadth, but differ from them in that they have short hind feet and long maxillary tooth rows.

Discussion

Relative to powered flight, the evolution of gliding has received little attention. This is curious since the selective pressures involved in the transition are unclear. Even though the development of patagia may be relatively simple, they impose both foraging and predation costs that may be significant.

The canonical discriminant analysis revealed the importance of the tail in discriminating between ground-dwelling and volant/arboreal animals, but also identified interorbital breadth as an important discriminatory variable. Interorbital breadth may in some way be a measure of binocularity. The plot of arboreal, volant, and ground-dwelling animals relative to the canonical space shows that both arboreal and volant forms tend to have wide interorbital breadths, while ground-dwelling forms tend to have narrow interorbital breadths. Binocular vision would have a selective advantage for volant or arboreal animals that jump or glide from one tree to the next.

Along the second canonical discriminant axis, the volant animals were separated from the arboreal and ground-dwelling animals. This axis shows that the gliding animals have shorter hind feet and longer maxillary tooth rows than do the other two groups. Running speed depends on stride length, and increased stride length can be achieved in part by increasing the length of the foot. The advantages of short feet to a gliding animal are not clear.

Perhaps of greater importance, gliding animals possess longer maxillary tooth rows than do nonvolant animals. Longer tooth rows provide greater surface area for food mastication and may increase the efficiency with which an animal uses a particular food item. It appears that the volant animals may possess greater foraging efficiency than do nonvolant animals, not only by being able to move from one foraging patch to another at a lower cost, but also by being able to extract more energy from each food item taken. This supports the foraging efficiency hypothesis. However, the foraging behavior of most volant forms limits their ability to utilize food items on the ground to the same extent as nonvolant animals. Thus, these animals may be effectively restricted to foraging in the tree canopies, whereas arboreal sciurids and anomalurids can forage both in the tree canopies and on the ground. Because of their restricted foraging niches, the volant sciurids and anomalurids may be forced to utilize their limited foraging opportunities more effectively. The longer tooth rows may represent a consequence of their mode of locomotion.

Head and body length did not provide good discrimination between the three groups. This suggests that there is no real difference in the overall sizes of gliding, arboreal, and ground dwelling forms. As noted by Thorington and Heaney (1981), large flying squirrels compensate for large size through increased glide speeds rather than through an allometry that allows reduced wing loadings.

It is clear that much work needs to be done to provide a better understanding of the transition from arboreal squirrel to gliding squirrel. A more complete data set containing additional form-function variables may provide some new insights into the problem. Perhaps more important are data on the comparative life histories, foraging characteristics, and predator regimes of ground dwelling, arboreal, and flying squirrels. Obviously, the phalangers provide a unique opportunity to test any new hypotheses. Perhaps only when the comparative biology of gliders and nongliders is well understood will it be possible to truly understand the selective regimes that have led to the evolution of glissant locomotion.

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ERRATUM

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There are a number of errors associated with the figure in this publication. In Figure 1, the triangles, circles, and squares represent arboreal, flying, and ground-dwelling sciurids and anomalurids respectively. Figure 2 should be labeled Figure 3, and should have the following legend: The distribution of the group centroids for ground-dwelling (square), arboreal (triangle), and flying (circle) sciurid and anomalurids in the canonical discriminant space. Figure 3 should be labeled Figure 2, and should have the following legend: The distribution of the principal component scores along the first two principal axes (PC 1 = a general size axis, PC 2 = a tail length axis) for ground-dwelling (G), arboreal (A) and flying (F) sciurids and anomalurids. The vertical line associated with each box represents a pseudo-standard deviation. The upper, middle, and lower horizontal lines represent the upper quartile, median, and lower quartiles respectively. Finally, this figure should be rotated 90 degrees.

