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Source: Journal of Mammalogy, 88(4) : 850-861

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/06-MAMM-S-331R1.1

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Journal of Mammalogy, 88(4):850–861, 2007

KINEMATICS AND FUNCTIONAL MORPHOLOGY OF LEAPING, LANDING, AND BRANCH USE IN *GLAUCOMYS SABRINUS*

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We assessed the locomotor performance of captive northern flying squirrels (*Glaucomys sabrinus*) over short glide distances and on small branches. We used stroboscopic photography, digital video, and an instrumented force pole to estimate takeoff and landing forces, angle of attack, and velocity profiles over short glides. We determined stride phases and duty factors of the animals as they moved across small branches, and compared these results with those for a small marsupial glider. Launch velocity, initial acceleration, and glide angle were not related significantly to animal mass. Initial velocity, terminal velocity, and landing force increased with increasing glide distance. Angle of attack at launch was not related to glide distance, but at landing it increased with increasing distance, suggesting active stalling. Simultaneous observations of takeoff and landing forces suggest that at distances greater than 2 m, landing forces are smaller than takeoff forces. The flying squirrels did not demonstrate a high level of agility as they traversed small branches. As branch diameter decreased below 2.5 cm, duty factors were greater than 0.5, indicating use of a walking gait. In comparison, small marsupial gliders (*Petaurus breviceps*) used running gaits with duty factors less than 0.5 for the same branches. We used relative warp analysis to explore pelvic and femoral shape variation in flying squirrels, and relate these to differences in locomotor performance. Small squirrels such as *Glaucomys* appear to have a pelvic and femoral architecture that has greater mechanical advantage for leaping than large squirrels such as *Petaurista*. We interpret these differences in the context of predator avoidance and foraging strategies.

Key words: force, *Glaucomys sabrinus*, kinematics, landing, leaping, relative warps

The ecology of bats and birds is influenced by how they move through the environment, and it is not surprising to discover functional relationships between the morphology of the flight engine and foraging mode, behavior, or both (Norberg 1994). Similarly, gliding mammals are capable of exploiting resources in ways that are not readily available to nongliding mammals. For example, gliders are able to cover large distances relative to similar-sized nongliding mammals (Goldingay 2000; Hanski et al. 2000) and can thus exploit patchily distributed resources, in essence, treating a coarse-grained habitat in a fine-grained fashion. Habitat structure also is related to the distribution of gliders (Dudley and DeVries 1990; Emmons and Gentry 1983) and may influence the evolution of glider design (Dial 2003). It is possible that the density of lianas (woody vines) has influenced the distribution of gliding mammals (Emmons and Gentry 1983), or perhaps canopy structure (Dudley and DeVries 1990), particularly the height of the canopy and distance between trees, has had a direct effect on the diversity of gliders in Asia and Australia. Yet, the level of understanding that relates bird or bat morphology to habitat use does not yet exist for gliding mammals. An understanding of the link between glider morphology and glider ecology will help elucidate the evolution of this novel locomotor mode.

The link between morphology and fitness (Koehl 1996; Wainwright 1994) is difficult to establish empirically for gliding mammals, although parts of the puzzle have been described. It is necessary to 1st establish the relationship between morphology and locomotor performance, and 2nd, relate locomotor performance to resource use. The 3rd and final step involves studies exploring the effects of resource use on fitness. Our current level of understanding is, to a large

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extent, limited to descriptions of morphology and some aspects of locomotor performance, but synthesis of these details is lacking. We know that pteromyine gliders possess morphological attributes that may represent adaptations to gliding locomotion (Thorington and Heaney 1981; Thorington et al. 2005). Furthermore, at least with respect to the skull, there is significant geographic variation in some species (*Glaucomys*—Robins 2006), suggesting adaptation to a variety of habitats. Also, Robins at al. (2000) and Fokidis et al. (2007) explored sexual size dimorphism in the southern flying squirrel (*G. volans*), and noted the possible consequences and selective pressures of increased wing loading during pregnancy. The connection between phenotype and locomotor performance was explored by Essner (2002), who compared launch kinematics in ground-dwelling squirrels (chipmunks [*Tamias striatus*]), tree squirrels (*Tamiasciurus hudsonicus*), and flying squirrels (*G. volans*). Thus, morphological variation related to gliding locomotion is present, and in a general sense there are performance consequences associated with that variation.

The next step in understanding the functional morphology of the glider ''bauplan'' or architecture is to explore the relationship between locomotor performance and resource use (Wainwright 1994). There are some descriptions of gliding performance in the field (Ando and Shiraishi 1993; Corbin and Cordeiro 2006; Flaherty 2002; Hampson 1965; Polyokova and Sokolov 1965; Scheibe and Robins 1998; Scheibe et al. 2006; Scholey 1986; Stafford et al. 2002; Vernes 2001; Zahler 2001), and numerous studies exploring habitat relations of flying squirrels (Carey 2000; Menzel et al. 2006; Smith et al. 2004; Timossi et al. 1995; Wheatley et al. 2005). However, we are familiar with no studies directly relating locomotion to habitat use or investigating how patterns of locomotion might change in response to habitat structure.

Thus, we have a basic understanding of the functional morphology of gliding, but we do not yet understand how this relates to resource use and ultimately fitness. Furthermore, it is not clear whether glider morphologies represent optimal solutions to the problems presented by gliding locomotion, nor is it clear what constraints govern the evolution of glider design, although Fokidis et al. (2007) and Robins et al. (2000) make cogent arguments that reverse size dimorphism in *G. volans* is related to reproduction. Furthermore, Thorington and Heaney (1981) and Thorington et al. (1998) provide convincing evidence that body proportions in gliders are related to problems of wing loading, and that wing tips in pteromyines are related to the control of wing-tip turbulence.

In this paper we analyze locomotor performance in northern flying squirrels (*G. sabrinus*), specifically looking at the launch and landing components of gliding, as well as branch use. We compare performance in *G. sabrinus* with that in other small gliders, and then explore morphological variation within the pelvis and femur as a possible means of understanding differences in locomotion across mammalian gliders. This is a preliminary effort to explore the relationship between morphology and locomotor performance, and between locomotor performance and habitat use.

Materials and Methods

Animal colony.—We used animals from a laboratory colony of 17 *Glaucomys sabrinus*. Twelve squirrels were live-trapped in Idaho (*G. sabrinus bangsi*) and these produced progeny in the laboratory. Two squirrels were live-trapped in Wisconsin (*G. sabrinus sabrinus*). Animals were maintained on a diet of pecans, hickory nuts, acorns, sunflower seeds, apples, yams, corn, mushrooms, lichens, and commercial hamster food (Kaytee Products, Chilton, Wisconsin). Water was provided ad libitum, and bird vitamins were added to the drinking water 3 times each week. Calcium tablets were crushed and sprinkled over the moist foods each week. Body weights were recorded weekly, and across all individuals varied from 125 g to 305 g. All animal care was monitored by the Institutional Animal Care and Use Committee of Southeast Missouri State University, and followed the guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998). The colony was inspected on a regular basis by the United States Department of Agriculture.

The colony was housed in a room measuring 4.6 × 4.4 m with a 2.6-m-high ceiling. The walls were constructed of painted cinder block, and the floor was concrete. A floor drain in the center of the room made it possible to rinse the floor every other day. Three standing dead oak trees (snags) with a diameter at breast height of about 20 cm and a height of about 2.3 m were erected in the room, together with tree branches angled against walls and small oak and hickory logs laying on the floor. Each snag held two 14 × 17.5 × 39.5-cm nest boxes at a height of 2 m, for a total of 6 boxes. The room had a single west-facing window providing natural light, and fluorescent lighting was maintained on a cycle of 8L:16D during the autumn and winter, and a 12L:12D cycle during spring and summer. Temperature in the room varied from 18.9°C to 23.3°C.

Marsupial sugar gliders (*Petaurus breviceps*) from a captive-bred colony of more than 50 animals were used in studies of branch use. The original colony of 12 animals was purchased from a veterinarian, and several animals were added to the colony as donations from private individuals. Body weights varied from 75 to 105 g. The animals were housed in a room similar to that used for the flying squirrels, but were kept in 12 wire-mesh cages varying in size from 0.6 × 0.6 × 0.6 m to 1.2 × 0.6 × 1.5 m. Each cage had 1 or more wooden nest boxes measuring 14 × 17.5 × 30.5 cm, and the floor of each cage was covered with pine shavings. Temperature and light conditions for the sugar gliders were identical to those used for the flying squirrels.

Petaurus breviceps was maintained on a diet of yogurt, chopped yams, raisins, fresh corn, and 2nd-stage baby food containing pureed vegetables and meats (Gerber Products Co., Parsippany, New Jersey). Fresh food and water were provided daily. The maintenance regime for these animals conformed to guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998). Animals were inspected regularly by the United States Department of Agriculture.

Performance trials were conducted in the room where the animals were housed, and in a pole barn measuring 7 × 14 m

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with a 7-m-high ceiling. The pole barn was built using wood posts and trusses. The roof and siding were steel; the barn was not insulated, heated, or cooled; and it was illuminated by four 0.9 × 2.8-m translucent panels on the west wall. The floor in the barn was of soil. During performance trials the east wall of the barn was covered with a black canvas tarp to produce a high-contrast background for stroboscopic photographs of the gliding squirrels, and the translucent panels were covered with black plastic to reduce ambient light. Two snags were erected in the barn, and served as launch and landing sites. They were oriented parallel to the canvas tarp on the east wall and were 2 m apart and 2.7 m tall with a diameter at breast height of about 30 cm. The launch snag had a wooden platform mounted at the top measuring 3.8 × 8.9 cm with a length of 61 cm. This platform provided a consistent launch point for the animals.

Launch trials.—Launching squirrels were photographed in the pole barn using strobes. An infrared triggering device (Woods Shutterbeam; Woods Electronics Inc., Poway, California) was used to direct an infrared beam across the launch platform. This device was connected to a Canon A2E 35-mm camera and 3 Canon 540EZ high-speed strobes (Canon U.S.A. Inc., Lake Success, New York), so that when the infrared beam was broken by a launching animal, the strobes and camera were triggered. The strobes fired synchronously at 15 Hz, and the camera shutter remained open for 0.7 s, sufficiently long to capture 2-m glides in their entirety Thus, each frame of film contained multiple images of a single launching squirrel, with images spaced 0.067 s apart in time.

All images were captured on Kodak Tmax 400 film and developed in Kodak Tmax developer (Kodak Graphic Communication Group, Rochester, New York). The film was then digitized using a Nikon Super Coolscan 8000 ED film scanner (Nikon, Melville, New York) at a resolution of 1,000 dots per inch (dpi). The images were then imported to program tpsDIG (http://life.bio.sunysb.edu/morph/) to extract (x, y) coordinates of each animal (either the tip of the rostrum or the eye; but consistent within each launch–glide event) during each component of each launch–glide event. Size of each image was calibrated using a metal strip of known size affixed to the launch platform. We used only those launch events where the 1st image of the squirrel showed it to be still in contact with the launch platform or where it had just lost contact with the launch platform.

For each launch event, we computed 2nd-order polynomial regressions of horizontal position against time, and vertical position against time. The 1st and 2nd derivatives of these equations were used to estimate horizontal and vertical velocity and acceleration, and these vectors were then solved to estimate total instantaneous velocity and acceleration. We estimated glide angles by computing the animal's spatial position relative to the horizontal surface of the launch platform at 0.7 s. The kinetic energy (E_k) of launch was estimated using the ballistic equation:

$$E_k = \frac{mV_0^2}{2}.$$

Here, E_k is the kinetic energy of launch (J), m is animal mass (kg) measured with a Pesola scale (Kapuskasing, Ontario, Canada), and V_0 is the initial launch velocity (m/s). The maximum height (h) for each launch was estimated by computing the 1st derivative of the 2nd-order polynomial regression of vertical versus horizontal position, and setting the derivative equal to 0. This was then used in the equation to estimate predicted range (R) of the glide:

$$R = V_0\sqrt{\frac{2h}{g}}.$$

Here, g is gravitational acceleration (9.81 m/s^2) and V_0 is initial launch velocity.

We explored the relationship between animal mass and performance parameters by regressing initial velocity, initial acceleration, glide angle, launch energy, and launch cost (Keith et al. 2000) against mass. Because individual animals were used multiple times, we computed weighted means for each animal and used these in the analysis. Four animals were used only at the beginning and end of this portion of the study (and not during the middle), and experienced sufficient weight change to warrant treatment of these performance trials as independent events.

Launch and landing trials.—We constructed a force pole following the general design of Demes et al. (1999). Four model FLA-2-11-3L strain gauges (Tokyo Sokki Kenyujo Co., Ltd., Tokyo, Japan) were affixed vertically to a 2-m section of galvanized mild steel conduit with a 2.34-cm diameter. The conduit was secured in a steel base measuring 36 × 41 cm, with a thickness of 30 mm. A 41-cm-long steel tube with an internal diameter of 2.5 cm was welded to the base and supported by 30-mm-thick gussets. The tube served as a receptacle for the instrumented galvanized conduit, and was drilled and tapped to accept 2 locking bolts for the conduit. The steel base was bolted to a slab of concrete measuring 61 × 61 × 9 cm (Fig. 1). Attached to the top of the conduit was a 1.5-m section of schedule 40 polyvinyl chloride (PVC) pipe with a diameter of 10.4 cm. At each end of the PVC pipe we used PVC adaptors to mate the PVC pipe to the conduit. The strain gauges were located halfway between the top of the steel pipe from the base plate and the bottom of the PVC pipe. A layer of dense, short-pile carpeting was glued to the PVC pipe to provide a nonslip surface for squirrels to land on.

A metal collar was attached to the galvanized conduit just above the strain gauges. This collar was then attached to a BIOPAC Systems model SS12LA force transducer, which was connected to a BIOPAC Systems model MP30A computer interface (BIOPAC Systems Inc., Goleta, California). The force pole was calibrated by applying known forces (to 2,500 × g) to the length of the pole, at 10-cm intervals. A calibration curve was then computed using a 2nd-order polynomial regression, and this was used to estimate a force constant. The force constant was then used to convert voltages to units of body weight. The force transducer was used in trials measuring only landing forces, whereas the strain gauges were used in trials measuring simultaneous takeoff and landing forces.

A launch pole made of 10.4-cm-diameter PVC pipe (schedule 40; wall thickness = 6.1 mm) was imbedded in a

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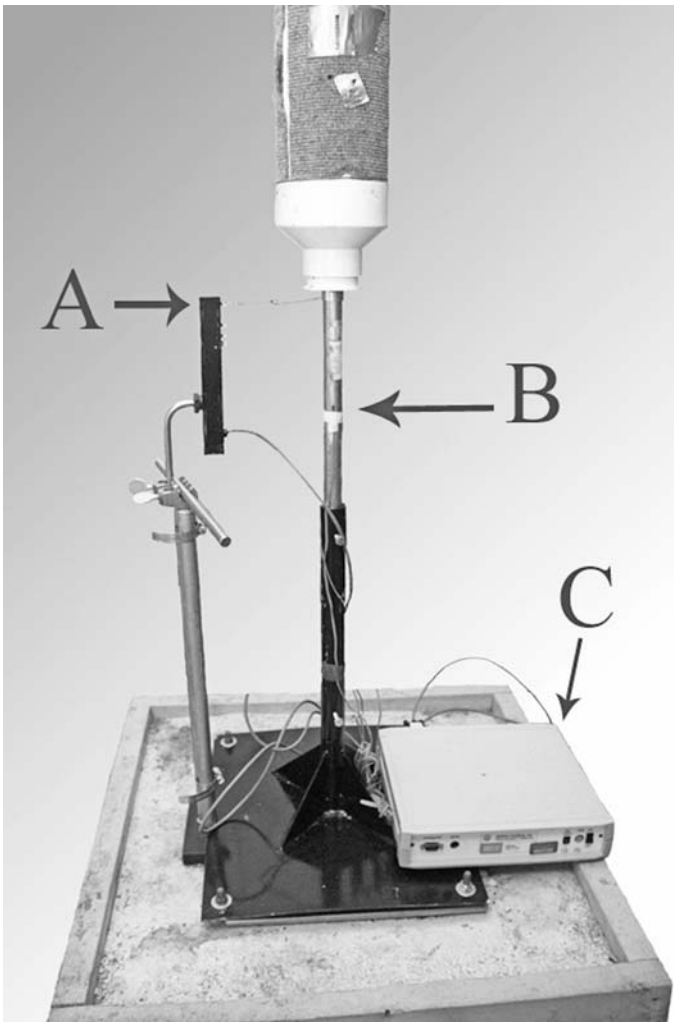


Fig. 1.—Base of force pole illustrating A) the force transducer, B) strain gauges mounted on steel conduit, and C) the BIOPAC interface module resting on the steel base and concrete slab.

20-liter plastic bucket filled with concrete. A board made of oak, measuring 61 × 2.9 × 1.9 cm, was attached to the top of the pole and served as a launch point. The launch pole was placed at distances varying from 0.5 m to 1.5 m from the force pole. A Canon GL2 digital video camera was mounted on a tripod to provide a lateral view of the launch and landing sequences.

Flying squirrels (*G. sabrinus*) were released on the launch platform and allowed to leap to the force pole (video 1, available online at http://dx.doi.org/10.1644/06-MAMM-S-331.s1). The sequence was captured by the video camera (30 frames/s) and the force transducer (200 Hz). The video sequences were edited in Adobe Premiere 6.5 (Adobe Systems Inc., San Jose, California) to remove extraneous frames, and then opened in Irfanview (www.Irfanview.com) to extract individual frames. Each frame was then opened in tpsDIG, where we estimated the squirrel's angle of attack (angle between the chord line formed by the vertebral column, and the horizontal) and determined the (x, y) coordinates of the animal's eye. We then computed horizontal and vertical distances and velocities at one-thirtieth-second intervals.

Initial velocity, terminal velocity, launch angle, landing angle, and landing force were regressed against glide distance. Again, because individual animals were used multiple times, we used weighted means for each animal at each distance.

Simultaneous launch and landing forces.—Launch forces were measured using an instrumented branch (Paskins et al. 2007). The branch was constructed of aluminum bar (10 × 10 mm in cross section), fixed at one end to a base plate. The terminal end of the bar was covered with tightly wound rope to provide a secure launch point. Four strain gauges (CEA-13-240UZ-120; Vishay, Basingstoke, United Kingdom) were mounted 50 mm from the base of the aluminum bar. The instrumented branch was bolted to a vertical pine board measuring 8.9 cm × 3.8 cm × 2.4 m, and was adjustable so that its vertical position could be modified for varying glide distances. The strain gauges in the instrumented branch and the force pole (described above) were connected to 2 amplifier boards, each with 2 channels using AD524 chips (Analog Devices Inc., Norwood, Massachusetts) or equivalent.

Performance trials were conducted both in the colony room and in the metal pole barn described above. Each event was recorded using digital video cameras with frame rates of 30 and 25 frames/s. The 1st camera was positioned to capture a lateral view of the takeoff, and the 2nd to capture a lateral view of the landing. Because it was not possible to mount the takeoff camera perpendicular to the instrumented branch in the pole barn, it was necessary to correct these derived takeoff angles and distances trigonometrically. Also, because temperatures in the pole barn varied dramatically, it was necessary to record ambient temperatures at hourly intervals using Thermochron iButtons (Maxim Integrated Products Inc., Sunnyvale, California) mounted on the vertical pine board about 1 m above and 1 m below the instrumented branch, and at ground level so that thermal effects on calibration curves could be estimated.

Both the force pole and instrumented branch were calibrated statically by applying known forces at intervals along each device. Calibration curves were used to estimate a force constant k, where $F = kx$. Here, force (F) is measured in Newtons and x is the strain signal measured in volts. We used edge-detection software (LabView, National Instruments, Austin, Texas) for the body of the squirrel and principal component analysis to define a best-fit ellipse characterizing the posture of the animal, the takeoff angle based on the major axis of the ellipse, and the animal's approximate center of mass.

Because takeoff angles were shallow, the output force derived from the strain gauges on the instrumented branch were integrated with respect to time, and compared to takeoff velocities derived from the cameras to derive takeoff force (Paskins et al. 2007).

Branch use.—Both *G. sabrinus* and *P. breviceps* were used to assess locomotion across a branch. We used *P. breviceps* for comparative purposes because they represent an alternative solution to locomotor and foraging problems. We constructed a wooden frame with a 1-m horizontal dowel rod, in front of

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TABLE 1.—Regression results for effect of mass on glide parameters. A total of 123 glides by 12 *Glaucomys sabrinus* were used in the analysis. Four animals were used at the beginning and end of the study, and experienced sufficient weight change to warrant use of these trials as independent events; *d.f.* = 1, 15.

Parameter	$\bar{X} \pm$ SE	R^2	F	P
Initial velocity (m/s)	3.07 ± 0.11	0.002	0.03	0.86
Initial acceleration (m/s^2)	8.80 ± 0.25	0.088	1.44	0.25
Glide angle (°)	−31.19 ± 1.90	0.177	3.23	0.09
Kinetic energy of launch E_k (J)	1.04 ± 0.07	0.036	0.56	0.47
Launch cost	3.11 ± 0.20	0.010	0.15	0.71

a mirror mounted at a 45° angle to the floor. This enabled us to view both sides of the animal as it traversed the dowel rod. We used dowel rods with diameters of 0.65 cm, 0.96 cm, 1.30 cm, 1.91 cm, and 2.54 cm. A digital video camera (Canon GL2) was used to film each event at 30 frames/s. The video footage was edited in Adobe Premiere, and individual frames were extracted using Irfanview. Video frames were then viewed sequentially to estimate velocity, stride phase, and mean duty factor (fraction of the stride cycle a foot is on the substrate averaged across all feet) for each event.

Morphometrics.—We photographed femora and pelvic girdles of prepared skeletons of the flying squirrels *Aeromys tephromelas*, *A. thomasi*, *Belomys pearsonii*, *Eoglaucomys fimbriatus*, *G. sabrinus*, *G. volans*, *Iomys horsfieldii*, *Petaurista alborufus*, *P. elegans*, *P. leucogenys*, *P. petaurista*, *P. philippensis*, *Pteromys volans*, and *Trogopterus xanthipes* from the collections of the Field Museum of Natural History in Chicago, Carnegie Museum of Natural History, the National Museum of Natural History, the American Museum of Natural History, and the Regional Natural History Collection at Southeast Missouri State University. A digital Canon D10, a Canon A2E 35-mm film camera, or both, with a Canon 100-mm macro lens, was used to photograph the long axis (posterior aspect) of femora mounted parallel to the plane of the camera. Similarly, pelvic girdles were oriented so that the lateral aspect of the girdle was parallel to the plane of the camera. Film images were digitized using a Nikon Super Coolscan 8000 scanner at 4,000 dpi and then resized to 1,000 dpi for easier processing within tpsDIG.

Femoral landmarks included medial epicondyle, point of maximum curvature on the medial edge of the medial condyle, center of the articular capsule, point of maximum curvature on the lateral edge of the lateral condyle, lateral epicondyle, margin of the 3rd trochanter, proximal margin of the greater trochanter, point of greatest inflection between the greater trochanter and the neck of the femur, margin between the dorsal aspect of the neck and the head of the femur, fovea capitis, margin between the ventral aspect of the neck and the head of the femur, dorsal margin of the lesser trochanter, and ventral margin of the lesser trochanter. Pelvic landmarks were ventral margin of the ischial tuberosity, dorsal margin of the ischial tuberosity, spine of the ischium, posterior inferior spine, posterior superior spine, anteriormost tip of the ilium, anterior superior spine, iliopectineal eminence, pubic symphysis, point of maximum curvature on the posterior margin of the obturator foramen, and point of maximum curvature on the anterior margin of the obturator foramen.

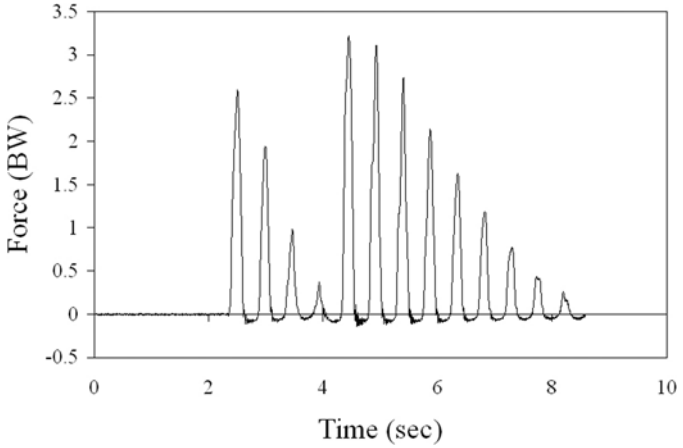


FIG. 2.—Typical raw signal from the force transducer after a landing by *Glaucomys sabrinus*. The 1st peak corresponds to the landing, followed by force pole oscillations that dampen with time. The 5th peak corresponds to the animal launching from the force pole to a snag erected in the laboratory. Force is given in units of body weight (BW).

Relative warp analysis (Zelditch et al. 2004) was used to explore patterns of shape variation in both the pelvic girdles and femora. In both cases we used $\alpha = 0$ so that neither localized nor global shape variation would be emphasized.

RESULTS

Launch and landing.—When *G. sabrinus* launched from a platform to a snag more than 2 m away or to the ground, mean initial launch velocity was 3.07 m/s ($SE = 0.011$ m/s) and mean launch acceleration was 8.80 m/s^2 ($SE = 0.25$ m/s^2). Glide angle was −31.19° ($SE = 1.90$°), indicating the animals were gliding rather than parachuting (glide angle < -45°). The average launch required 1.04 J ($SE = 0.07$ J) and the relative unit free cost of launch was 3.11 ($SE = 0.20$). There was no significant relationship between body mass of the flying squirrels and initial velocity, launch acceleration, glide angle, the kinetic energy of launch, or launch cost (Table 1). All R^2 values except for glide angle were <0.10.

Glaucomys sabrinus landing on the force pole produced signals with a strong initial peak corresponding to the force of landing, followed by oscillations that dampened with time (Fig. 2). Mean initial takeoff velocity was 2.43 m/s, somewhat lower than the 3.07 m/s calculated for animals launching from a launch platform to a snag somewhat farther away (or to the ground; Table 1). Initial takeoff velocity was positively related to distance ($F = 22.33$, *d.f.* = 1, 31, $P < 0.0001$, $R^2 = 0.41$; Table 2) so that animals gliding longer distances had higher takeoff velocities than animals going shorter distances. Similarly, velocity just before landing on the force pole was significantly positively related ($F = 30.68$, *d.f.* = 1, 31, $P < 0.0001$, $R^2 = 0.49$) to distance, but was about 0.36 m/s slower than the takeoff velocity, although terminal velocity increased faster with increasing distance than did initial velocity. Launch

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TABLE 2.—Regression results for study of *Glaucomys sabrinus* launching to and landing on force pole. The response variable listed in the 1st column was regressed against distance. Landing force is measured in units of body weight (BW) to enable direct comparison with other studies.

Response variable	*n*	Weighted mean	Slope	R^2	*F*	*P*
Initial velocity (m/s)	33	2.428	0.0095	0.411	22.33	0.01
Terminal velocity (m/s)	33	2.064	0.0111	0.489	30.68	0.01
Launch angle (°)	33	23.480	−0.0406	0.082	2.88	0.10
Landing angle (°)	33	44.627	0.2682	0.219	8.98	0.01
Landing force (BW)	32	2.886	0.0162	0.515	32.86	0.01

angle was not related to glide distance ($F = 2.88$, $d.f. = 1, 31$, $P > 0.05$, $R^2 = 0.08$), but angle of attack just before landing was related to glide distance ($F = 8.98$, $d.f. = 1, 31$, $P < 0.01$, $R^2 = 0.22$). Landing angle increased with distance, with a mean angle of about 45°. Finally, the force of landing increased with glide distance ($F = 32.86$, $d.f. = 1, 30$, $P < 0.01$, $R^2 = 0.52$), and varied from 1.01 to 6.13 body weights (BW), with a mean observed landing force of about 2.9 BW ($SE = 0.09$ BW). Landing force increased by about 0.02 g for each additional centimeter of glide distance (Fig. 3).

A velocity profile (Fig. 4) with superimposed angle of attack (relative to the ground) for a 1.5-m trial illustrates a reduction in velocity as the squirrel approached the force pole. Importantly, there was a corresponding increase in angle of attack as the animal slowed. Even over a relatively short distance of 1.5 m, *G. sabrinus* exhibited typical gliding postures (video 1).

Gait analysis.—There was a marked difference in locomotor performance by *G. sabrinus* (video 2, available online at http://dx.doi.org/10.1644/06-MAMM-S-331.s2) and *P. breviceps* (video 3, available online at http://dx.doi.org/10.1644/06-MAMM-S-331.s3) on the dowel rods. Average duty factors across all 4 limbs varied from 0.60 to 0.80 for *G. sabrinus*, with a mean of 0.70, and from 0.33 to 0.58 with a mean of 0.48 for *P. breviceps*. Thus, *P. breviceps* used running gaits (duty factors < 0.5) most of the time whereas *G. sabrinus* used walking gaits (duty factors > 0.5). The relationship between

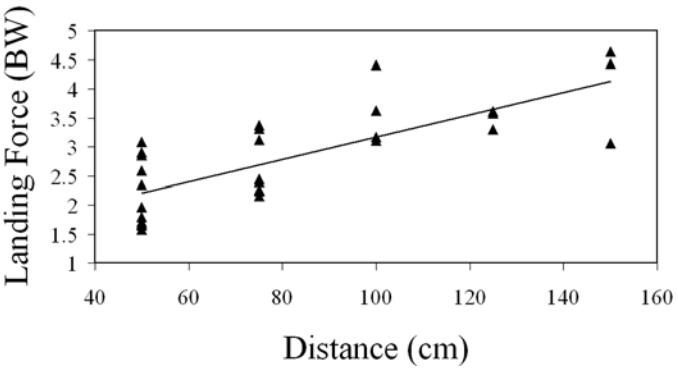


FIG. 3.—Relative force of landing (in units of body weight [BW]) for *Glaucomys sabrinus* regressed against horizontal leap distance. The regression equation (y = 1.238 + 0.019x) was significant at the level of $P = 0.01$.

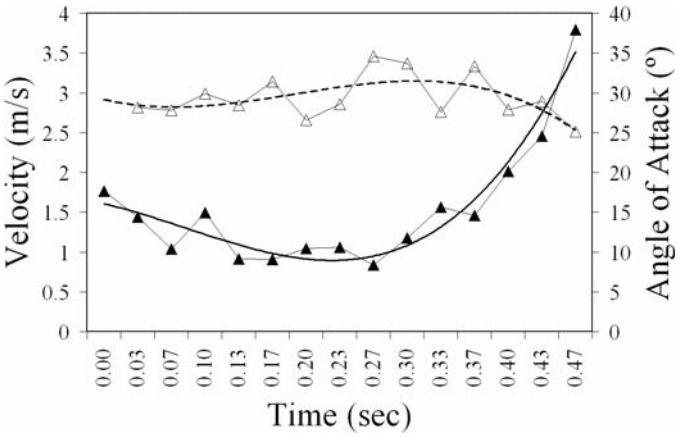


FIG. 4.—Velocity profile and angle of attack relative to the horizontal for a single *Glaucomys sabrinus* covering a horizontal distance of 150 cm. Velocity of the squirrel (open triangles, upper curve) decreases as the angle of attack increases (solid triangles, lower curve), indicating the squirrel stalls as it lands. Each curve was computed as a 3rd-order polynomial regression.

speed and duty factor (Fig. 5) was negative for both species (*P. breviceps*: duty factor = 1.179 − 1.2022 × distance; *G. sabrinus*: duty factor = 0.5055 − 0.3309 × distance) but more strongly so in *P. breviceps*. For each 10% increase in duty factor there was a 12-cm/s decrease in speed for *P. breviceps*, and a 3.3-cm/s decrease in speed for *G. sabrinus*. Gaits used by *P. breviceps* varied from gallops on large-diameter dowel rods to trots and walks on the smallest dowel rod. *G. sabrinus* never used any gait other than a walk (Fig. 5).

Morphometrics.—Results of the relative warp analysis for pteromyine femora are presented in Table 3 and Fig. 6. The first 2 relative warps accounted for more than two-thirds of the variance in shape space. The 1st relative warp describes shape change associated with the epicondyles and trochanters. At the negative end of the warp, the epicondyles exhibit widening

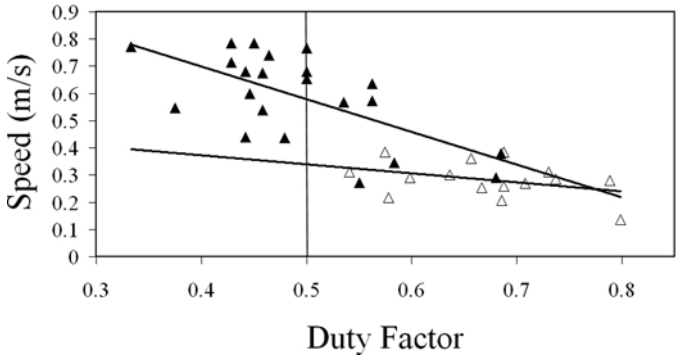


FIG. 5.—Linear regression of speed on duty factor for *Glaucomys sabrinus* (open triangles, lower line) and *Petaurus breviceps* (closed triangles, upper line). For *G. sabrinus*, speed = 0.51 − 0.33 × duty factor, whereas for *P. breviceps*, speed = 1.18 − 1.20 × duty factor. Speeds for *G. sabrinus* are lower, and their duty factors higher than those of *P. breviceps*. Observations with duty factors < 0.5 represent runs, whereas those with duty factors > 0.5 are walks. *P. breviceps* tends to use runs, whereas *G. sabrinus* always used a walking gait.

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TABLE 3.—Variance associated with the singular values for relative warp analyses of pteromyine femora and pelvic girdles. In this case, the singular values are equivalent to principal components and can be interpreted accordingly.

	Variance	
Singular value	Femur	Pelvis
1	58.37	31.74
2	10.51	13.59
3	7.07	12.00
4	5.52	10.99
5	3.63	7.57
6	3.20	4.80
7	2.40	3.81
8	2.00	3.29
9	1.55	2.17
10	1.16	2.15

and proximal movement, whereas the greater and lesser trochanters exhibit widening and distal movement. At positive regions of the 1st warp, the epicondyles and trochanters exhibit narrowing, whereas the epicondyles move distally and the trochanters move proximally. Along the 2nd warp, shape change is associated primarily with the proximal portion of the femur. Here there is a change in the angle formed between the shaft of the femur and an axis drawn between the head and greater trochanter. At negative regions of the warp this angle is larger on the medial side of the femur, and at positive regions of the warp the angle is smaller.

Within warp space, *G. volans*, *G. sabrinus*, and *Eoglaucomys fimbriatus* occupied the negative portion of warp 1, whereas *P. alborufus*, *P. leucogenys*, *P. petaurista*, and *P. philippensis* varied from quadrant 3 (negative regions of warps 1 and 2) to the positive end of warp 1. Thus, femora of *Glaucomys* and *E. fimbriatus* were characterized by having broader epicondyles and wider distally displaced trochanters. *Petaurista*, on the other hand, tended to have trochanters that were proximally displaced and narrower than those of *Glaucomys*.

Relative warp analysis of pelvic shape (Table 3; Fig. 7) required 4 warps before two-thirds of the variance in shape could be explained, because the first 2 warps accounted for only about 45% of the variance. At negative portions of the warp there was rotation of the posterior portion of the girdle, involving anterior movement of the pubic symphysis and posterior movements of the acetabulum and spine of the ischium. At positive portions of this warp, there was posterior movement of the pubic symphysis and anterior movement of the acetabulum, spine of the ischium, and iliopectineal eminence. Along the 2nd warp, there was anterior rotation of the ischial tuberosity at the negative end of the warp, whereas at the positive end of the warp there was posterior rotation of the ischial tuberosity as well as a slight broadening of the iliac crest.

Glaucomys and *Hylopetes* occupied the positive portion of warp 1, exhibiting posterior deflection of the pubic symphysis and anterior deflection of the iliopectineal eminence and

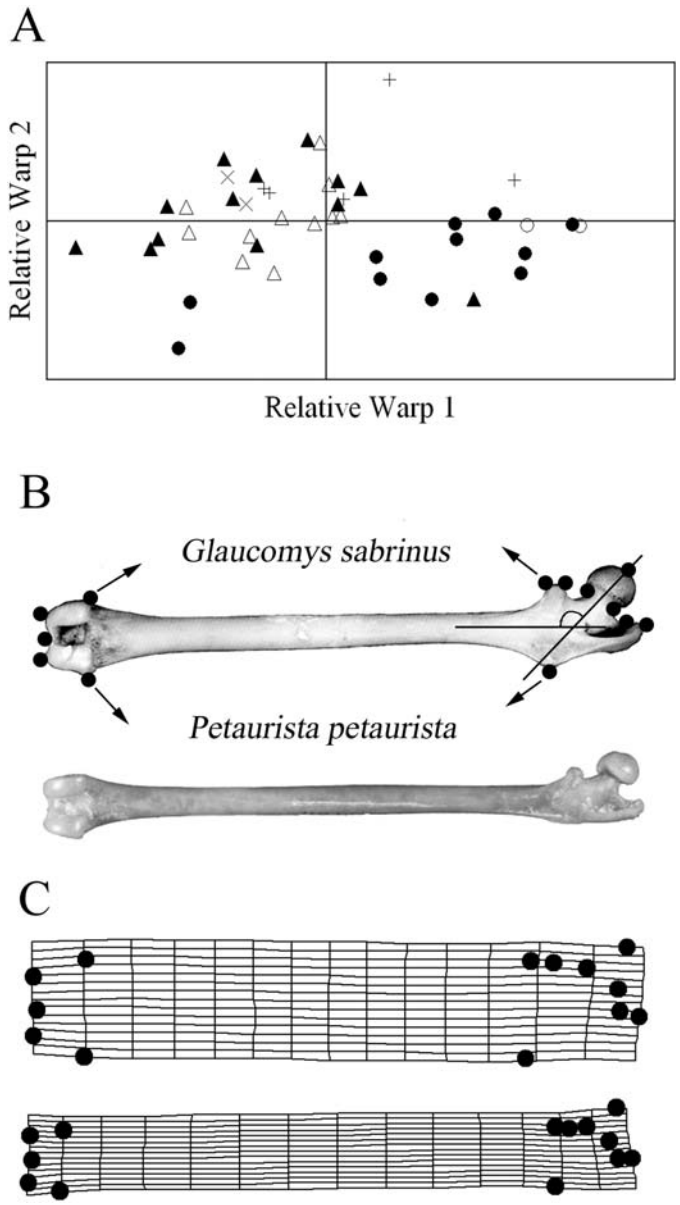


FIG. 6.—A) Plot of first 2 relative warps for the femora of pteromyine squirrels. Solid triangles = *Glaucomys volans*; open triangles = *G. sabrinus*; X = *Eoglaucomys fimbriatus*; closed circles = *Petaurista alborufus*, *P. elegans*, *P. leucogenys*, *P. petaurista*, and *P. philippensis*; open circles = *Aeromys tephromelas and A. thomasi*; and + = other species including *Trogopterus xanthipes*, *Iomys horsfieldii*, *Belomys pearsonii*, and *Pteromys volans*. B) Femurs of *G. sabrinus* (above, with landmarks) and *P. petaurista* (below). Vectors illustrate shape changes along the 1st relative warp for *G. sabrinus* relative to *P. petaurista*. C) Deformation grids for the 1st relative warp illustrating *G. sabrinus* (above) and *P. petaurista* (below).

acetabulum. Also, these animals displayed a dorsal deflection of the tip of the ilium and the anterior superior spine. *Petaurista* spp. and *Aeromys* spp. occupied negative regions of the 1st warp, with a posterior deflection of the iliopectineal eminence, acetabulum, and spine of the ischium, and anterior deflection of the pubic symphysis. Surprisingly, *E. fimbriatus* occupied a space within the cluster of *Petaurista* rather than within the

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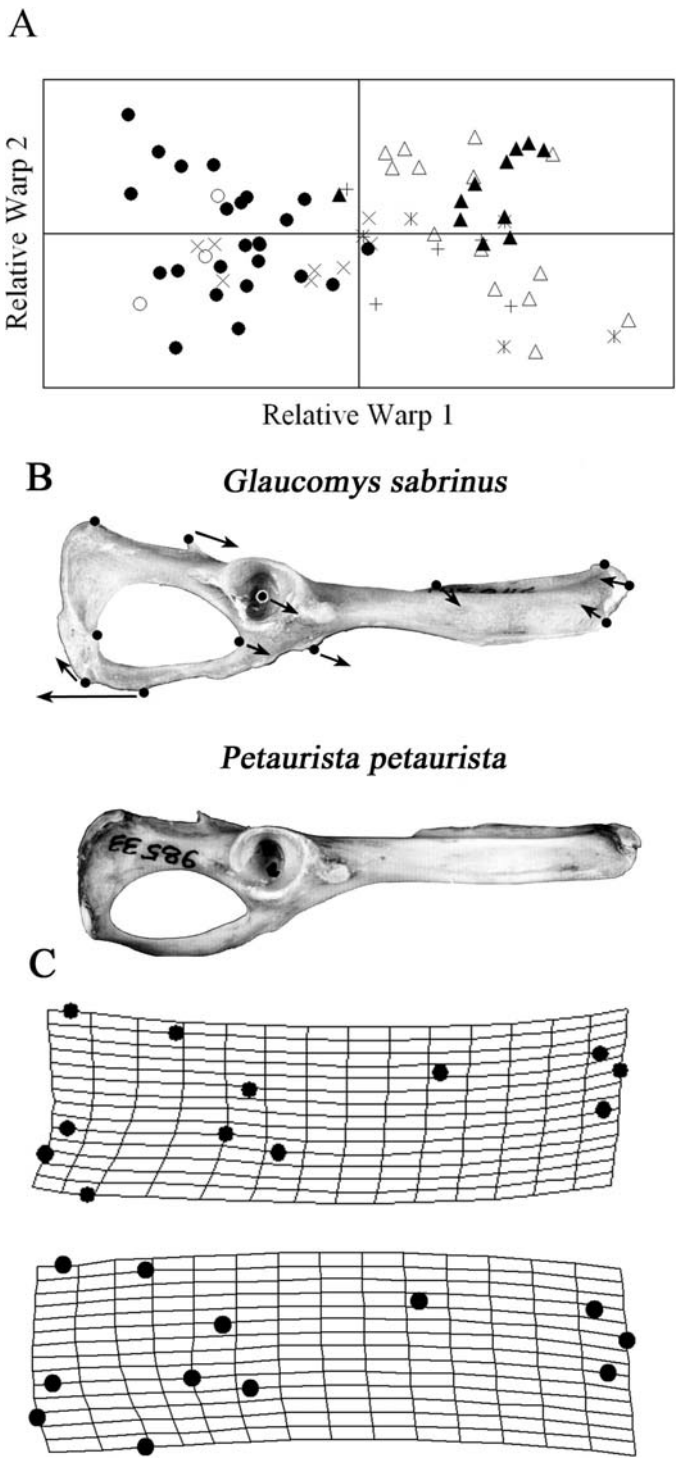


Fig. 7.—A) Plot of first 2 relative warps for the pelvic girdles of pteromyine squirrels. Solid triangles = *Glaucomys volans*; open triangles = *G. sabrinus*; X = *Eoglaucomys fimbriatus*; closed circles = *Petaurista alborufus*, *P. elegans*, *P. leucogenys*, *P. petaurista*, and *P. philippensis*; open circles = *Aeromys tephromelas and A. thomasi*; asterisks = *Hylopetes nigripes* and *H. phayrei*; and + = other species including *Trogopterus xanthipes*, *Iomys horsfieldii*, *Belomys pearsonii*, and *Pteromys volans*. B) Pelvic girdles and landmarks for *G. sabrinus* and *P. petaurista*. Vectors illustrate shape change for *G. sabrinus* relative to *P. petaurista* along the 1st relative warp. C) Deformation grids for the 1st relative warp illustrating the shapes of pelvic girdles for *G. sabrinus* (upper) and *P. petaurista* (lower).

cluster of *Glaucomys*, to which it is more closely related (Arbogast 2007:figure 1).

Discussion

Gliding locomotion by *G. sabrinus* in the field has been described by Scheibe et al. (2006) and Vernes (2001). In these studies, mean glide distances were shorter than 20 m but longer than the estimated cost-effective glide distance (Scheibe et al. 2006). The maximum glide distance observed by Scheibe et al. (2006) was about 65 m. Neither study investigated takeoffs or landings, although Vernes (2001) noted stalling behavior at the terminus of the glides and considered this in his assessment of gliding performance.

The results presented here illustrate that takeoff and landing components of glides are not trivial in terms of energetic cost. Launches, glides, and landings by *G. volans* are complex events (videos 4 and 5, available online at http://dx.doi.org/10.1644/06-MAMM-S-331.s4 and http://dx.doi.org/10.1644/06-MAMM-S-331.s5), and this is certainly true for *G. sabrinus* as well (video 1). It is unknown how these components affect glide performance. Compared to *G. volans* (Keith et al. 2000), *G. sabrinus* launched at a steeper angle (23.5° versus 4.3°), launched with greater initial velocity from a launch platform to an object more than 2 m away (3.1 m/s compared to 2.3 m/s), and launched with considerably more energy (1.04 J compared to 0.23 J). When *G. sabrinus* leapt to a force pole less than 2 m from the launch point, the initial velocity was somewhat lower than that of *G. volans*. The unit-free cost of launching was greater for *G. sabrinus* than for the smaller *G. volans* (3.1 compared to 2.6). Previous studies by some of us (JSS and SF) show that in the laboratory under identical circumstances, both *Glaucomys* species launched with greater velocities than *P. breviceps*. The higher launch velocities of *G. sabrinus* make sense from an aerodynamic perspective, in that larger flying squirrels must glide faster to achieve the same glide angle as smaller gliders (Norberg 1990; Thorington and Heaney 1981). In the present study, male *P breviceps* had mean initial launch velocities of 1.53 m/s and females launched at 1.79 m/s.

If the unit-free cost of launching is added to the cost of gliding to a tree and then climbing to the next launch point as estimated in Scheibe et al. (2006), the cost of gliding locomotion is increased by about 10% with a concomitant increase in the cost effective glide distance. Although this increase is insufficient to falsify the cost of transport hypothesis (namely, that the energetic cost of climbing to a launch point and gliding a given distance is less than the cost of moving over the same distance quadrupedally), veracity of the cost of transport hypothesis does not falsify other hypotheses for the evolution of gliding locomotion. Furthermore, neither the cost of launching in similar-sized nongliders nor the strength of selection for reduced cost of transport is known. Garland (1983) evaluated ecological cost of transport rather than energetic cost of transport by exploring the portion of an animal's daily energy expenditure used for transport costs. This is a function of daily movement distance and metabolic rate. We should expect strong selection for reduced cost of transport

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when the ecological cost of transport is high. At present, this cost has not been estimated for flying squirrels.

The cost of transport hypothesis may be too simplistic in terms of selection for gliding locomotion. Gill (1985) demonstrated that hummingbirds did not use flight speeds that minimized the overall cost of transport. Instead, the birds increased flower visitation rates and thus compensated for the increased cost of locomotion. Shipley et al. (1996) studied the dynamics of foraging velocity and noted that small herbivores achieved foraging velocities similar to those of large herbivores. Using their model based on distance, acceleration, and maximum velocity, we expect *G. sabrinus* to have a foraging velocity significantly higher than that of nongliding mammals. Of course, this is dependent on the extent to which *G. sabrinus* comes to the ground to exploit hypogeous fungi. But, it is reasonable to argue that gliding in flying squirrels maximizes the encounter rate with potential food items, allows squirrels to forage more efficiently by reducing travel time between patches, or both (Charnov 1976; Lendrem 1986).

It is possible that gliding enables flying squirrels to avoid predation (Holmes and Austad 1994; but see Stapp 1994). Gliding locomotion can reduce the chance of predation either by placing as much distance as possible between the squirrel and the predator or by enabling the squirrel to escape the immediate reach of the predator as quickly as possible. One way to maximize distance between squirrel and predator is to maximize the ballistic range of the glide. This occurs when the angle of launch is near 45°, a value not achieved by *G. sabrinus* in the laboratory, even though the animals behave in a way that suggests they are attempting to escape from the handler. Clearly, launching to a specific landing point (e.g., when leaping to the force pole less than 2 m away) may not require maximizing ballistic range, but the squirrels performed no better when gliding to the ground. If the squirrels maximize the speed with which they escape the reach of the predator, we would expect the animals to maximize launch velocity. Any jump upward will result in deceleration due to gravity, so the animals should launch with a flatter trajectory to increase flight speed, which to some extent, they appear to do (launching at 23.5° from the horizontal). However, Essner (2002) showed that *G. volans* does not maximize extension of the pelvic appendage when launching, suggesting this species does not maximize initial launch velocity. Although we do not have data on extension of limb elements, the animals did launch faster when gliding to a more distant object (or the ground) than when gliding to the nearby force pole. Either the nearby landing point (force pole) constrained launch velocity, or the animals did not maximize launch velocity.

Hill (1950) argued that animals of different size that scale isometrically should have equivalent performance when leaping. The smaller animal will accelerate through a shorter distance, but will move less mass than the larger animal, and consequently realize similar performance. If the animals do not scale isometrically, we would expect different levels of performance. In this study, initial velocity did not regress significantly against mass, a result that is consistent with Hill's prediction. However, the range of body mass exhibited by our squirrels was limited, and we do not know if the animals scale isometrically. Furthermore, the argument does not consider air resistance, which is surely important for gliders. But, if the pelvis and pelvic appendage scale isometrically in *G. sabrinus*, we can assert that the species maximizes launch performance, perhaps minimizing the chance of predation.

In laboratory studies evaluating response to potential predator threats, Caton (2006) found that a laboratory population of *G. sabrinus* did not modify its foraging behavior significantly in the presence of recorded owl calls, but did preferentially select feeding sites that offered greater chance of escape even when no owl calls were present. The animals did not respond to direct cues of predation (owl calls), but did respond to indirect cues (potential exposure to owl attack). This suggests that in spite of the potentially heavy cost of predation on flying squirrel populations (Carey 2000; Munton et al. 2002), the evolutionary response of *G. sabrinus* to predation may not be easily measured.

The idea that the evolutionary response to predation is complex is reinforced by the fact that locomotor performance by *G. sabrinus* on branches was surprising. The animals used a walking gait with mean duty factors > 0.5 even on relatively large dowel rods, suggesting limited agility and slow movement. In comparison, *P. breviceps* was able to use a running gait on all but the smallest diameter dowel rods. In both species, speed decreased with increasing duty factor, and it decreased faster in *P. breviceps* than in *G. sabrinus*. However, *P. breviceps* was always faster moving across the dowel rods than *G. sabrinus*. One obvious explanation for this is the presence of opposable digits in *P. breviceps*, enabling the animals to gain a secure purchase on even the smallest dowel rods. *P. breviceps* is smaller than *G. sabrinus* (females about 80 g and males about 100 g), their use of the dowel rods was dramatically better, but their gliding performance in the laboratory was poorer (Wright 2000; but see Jackson 2000). There may be a trade-off in terms of locomotor performance: *G. sabrinus* is able to glide relatively long distances, and can glide even over short distances (Paskins et al. 2007), whereas *P. breviceps* parachuted over short distances (Wright 2000). On the other hand, *G. sabrinus* exhibited only walking gaits on the horizontal dowel rods, whereas *P. breviceps* was able to use running gaits. Even if speed is scaled to the cube root of body mass, or if dowel rod diameter is scaled to cube root body mass, locomotion by *P. breviceps* over the dowel rods was faster and more agile than that of *G. sabrinus*.

Differences in the abilities of *G. sabrinus* and *P. breviceps* to use small dowel rods may be reflective of how these species forage and use habitat. *G. sabrinus* feeds on lichens and hypogeous fungi (Loeb et al. 2000; Maser et al. 1985; McKeever 1960), often on the forest floor, whereas *P. breviceps* feed on tree sap (*Eucalyptus bridgesiana*), arthropods (noctuid and hepialid moths and scarabaeid beetles), manna (sap exudate resulting from arthropod damage on leaves and branches of, for example, *E. radiata* and *E. viminalis*), honey dew (excreted by insects in the families Coccoidea and Psyllidae), and acacia gum (*Acacia mearnsii*—Goldingay 2000; Smith 1982). Petaurids move extensively among flowers (Carthew 1994;

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Carthew and Goldingay 1997; Goldingay 1990; Quin et al. 1996; Sharpe and Goldingay 1998; Van Dyck 1993). Thus, selection may have favored agility in complex habitats in petaurids, and foraging velocity in *Glaucomys*.

Morphologically, small flying squirrels such as *Glaucomys* possess femora that are less gracile than those of *Petaurista* (Fig. 6). Additionally, both the minor and 3rd trochanters and the epicondyles are displaced from the axis of the femur; the epicondyles also are displaced proximally, whereas the trochanters are displaced distally. The angle defined by the head of the femur and 3rd trochanter with the axis of the femur is more obtuse in *Glaucomys* and more acute in *Petaurista*. Because the gluteal muscles insert on the 3rd trochanter, this should increase the moment arm and mechanical advantage of the gluteals during extension of the femur in *Glaucomys*. The ventral margin of the ischial tuberosity in *Glaucomys* is deflected ventrally relative to *Petaurista* (Fig. 7), suggesting perhaps that the biceps femoris has a greater mechanical advantage in the smaller species. These features suggest that *Glaucomys* uses a musculoskeletal architecture that has greater mechanical advantage for leaping than does *Petaurista*. Because *Petaurista* has greater mass and higher wing loadings than *Glaucomys* (Thorington and Heaney 1981), it probably glides very differently, and certainly faster than *Glaucomys* (Ando and Shiraishi 1993; Scholey 1986; Stafford et al. 2002). Scheibe and Essner (2000) noted that within the Pteromyini and within *Petaurista*, there was a tendency for the relative length of the ilium to increase with total pelvic girdle length, which differs from the expected pattern for a leaping design of decreased relative length of the ilium. Thus, the propulsive machinery of the pelvic girdle in *Glaucomys* exhibits a design with increased mechanical advantage for leaping, and *G. sabrinus* employs a faster launch than either *G. volans* or *P. breviceps*, suggesting that the animals initiate their glides differently. One explanation for these differences as well as the morphological differences between *Petaurista* and *Glaucomys* is that *G. sabrinus* minimizes predation. However, not only are the aerodynamics of large and small gliders different, the animals forage differently, with species of *Petaurista* being folivorous (Kawamichi 1997; Lee et al. 1986; Muul and Lim 1978), and this may have some significance for the design of mammalian gliders.

Understanding the evolution of gliding locomotion and its ecological significance is important if we wish to manage or preserve viable populations of flying squirrels. Flying squirrels differ morphologically and functionally from tree squirrels, and presumably these differences represent adaptations to gliding locomotion, although this has not been demonstrated in a comparative study. It is reasonable to ask what selective pressures led to the evolution of gliding because this helps us understand the functional ecology of the species. Because we do not know the ecological cost of transport (Garland 1983) and because hypotheses for the evolution of gliding are not mutually exclusive, the predator avoidance, cost of transport (Scheibe and Robins 1998; Scheibe et al. 2006), and optimal foraging hypotheses remain viable. A better understanding of foraging behavior, foraging velocity, and the ecological cost of transport will provide a deeper understanding of gliding and the functional ecology of flying squirrels.

Acknowledgments

We thank B. Pashai for technical assistance with the force pole and instrumented branch, E. Flaherty for extensive help with the flying squirrel colony, and J. Robins and R. Essner for many hours of fruitful discussion.

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Special Feature Editor was Barbara H. Blake.

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