

GLIDING BEHAVIOR OF JAPANESE GIANT FLYING SQUIRRELS (*PETAURISTA LEUCOGENYS*)

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Gliding behavior of Japanese giant flying squirrels, *Petaurista leucogenys*, was studied at Nara Park, Japan. We observed 150 glides. We were able to calculate glide ratios on 57 glides and airspeeds on 29 glides. Glide ratios (distance/[altitude lost]) averaged 1.87, and a glide ratio of 3–3.5 seems to represent an upper performance limit for *P. leucogenys*. Airspeeds (4.39–9.47 m/s) were substantially lower than reported in other studies, and glide angles were higher (17.74–34.99°). Aspect ratios of the animals in mid-glide averaged 1.42.

Key words: aerodynamics, flying squirrels, gliding, locomotion, musasabi, *Petaurista*, Pteromyinae

Gliding is a common adaptation in mammals. It has evolved independently in at least 6 extant taxa: Volitantia (the dermopterans and bats), Pteromyinae (true gliding squirrels), Anomaluridae (scaly-tail “flying squirrels”), *Acrobates* (feather-tail gliders), *Petaurus* (lesser gliding possums), and *Petauroides* (greater glider). Additional gliding mammals have been recognized in the fossil record in the dormice (Mein and Romaggi 1991) and in the eomyids (Storch et al. 1996). Dormice represent a 7th lineage that developed gliding independently. Whether the eomyids represent an 8th independent acquisition of gliding is problematical and should be reevaluated. The presence of an olecranon cartilage supporting the patagium in *Eomys quercyi* (Storch et al. 1996) suggests a phylogenetic link between eomyids and anomalurids, as suggested by Stehlin and Schaub (1951).

There have been numerous studies of vertebrate gliding (Emmerson and Koehl

1990; Jackson 2000; Russell and Dijkstra 2001; Scholey 1986; Stafford 1999; Thorington et al. 1996 and references therein). Morphological studies of flying squirrels include examinations of skeletal proportions (Stafford 1999; Thorington and Heaney 1981), myology (Endo et al. 1998; Gupta 1966; Johnson-Murray 1977, 1987; Peterka 1936), and wingtip anatomy (Thorington 1984; Thorington et al. 1996). Studies of gliding performance in the wild are provided by Ando and Imaizumi (1982), Ando and Shiraishi (1993), Jackson (2000), and Scholey (1986). Some data exist for *Glaucomys volans* (Scheibe and Robins 1998) and *G. sabrinus* (Vernes 2001) in limited contexts. The most detailed study of the aerodynamics of any gliding mammal is provided for the marsupial sugar glider (Nachtigal 1979a, 1979b, 1986; Nachtigal et al. 1974). More detailed information on gliding behavior of flying squirrels in the wild is required for a comparable analysis and to understand the aerodynamics of their adaptations.

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MATERIALS AND METHODS

Petaurista leucogenys was studied at Nara Park, Nara Prefecture, Japan (34°41'N, 135°50'E) from 12 May 1999 to 15 June 1999. Animals were observed visually, using binoculars and a headlamp, with a Sony Hi8 video camera equipped with infrared (i.e., nightshot) technology. The squirrels had previously been habituated to humans by the studies of Kawamichi (1997). Animals were not marked for identification, but at least 7 adult animals are represented in the data set. The forest in the study area consisted of straight trees such as pine and cedar and others with more complex structures such as maple and oak. Details of the study area and its ecology are given in Kawamichi (1997).

Data were collected on 25 days during 91.5 h of observation. We observed 150 glides. Glide ratios were calculated for 60 glides. Three were excluded from the analysis because they did not meet our definition of gliding. Of the remaining 57 glides, 30 were captured well enough on videotape for us to calculate velocity. Launching and landing points were noted and their heights measured with a military M2 compass. Distances to launch and landing trees and between launch and landing trees were paced off and calculated to the nearest meter. Where there was an appreciable slope ($>15^\circ$) between launch and landing trees, the distance between the trees was corrected to give the true horizontal distance between them. This distance represents the horizontal glide distance. A closer approximation of the actual glide distance was obtained by calculating the straight-line distance between the launch and landing points as the hypotenuse of a right triangle with sides equal to the drop and horizontal distance, the direct glide distance. Glide ratio was calculated as horizontal distance divided by drop. This direct glide distance was used to calculate airspeed. Glide duration was measured from videotapes by counting frames for glides in which both launch and landing were captured ($n = 3$). When landing could not be seen on the videotapes but could be heard, duration was measured with a stopwatch ($n = 27$). Other glides were observed directly, not on videotape. Glide duration calculated from video frames was also checked with the stopwatch. Pearson's product moment correlation (r) was used to evaluate correlation between airspeed and glide distance and between altitude lost and

glide distance. Reduced major axis regression was used to assess the relationship between glide distance and glide duration and between altitude lost and glide distance (Scholey 1986). The slope of the reduced major axis regression line between direct glide distance and glide duration estimates airspeed. The inverse tangent of slope of the reduced major axis regression line of altitude lost versus horizontal distance provides an estimate of glide angle during the gliding phase.

Distances were measured by pacing, and paces were converted to meters. In Japan, 1 of us repeatedly paced a measured distance (1 pace = 0.95 m, $n = 6$, $SD = 0.01$). He also repeatedly paced some gliding distances ($n = 13$) and found that variability was minor (coefficient of variation [CV] = 2.75%). Time was measured in 3 ways, all of which agreed: with the clock in the camera, by counting video frames, and with an independent stopwatch. Each videotape had time encoded on it. We counted the number of frames per second to verify calibration of the internal camcorder clock, and we checked the camcorder's clock with a stopwatch. We found no meaningful sources of measurement error.

We define 5 separate glide phases, launch, glide, transition, braking, and landing. During launch the animal leaves the support and deploys the patagium. Until the patagium is deployed and begins generating aerodynamic forces, the animal is subject largely to ballistic forces. Patagium deployment signals the start of the gliding phase, where aerodynamic forces determine the glide path. In glide phase, angle of attack (α = the angle between relative wind and chordline of the airfoil, not the angle of the airfoil with respect to horizontal, see Anderson 1985; Pamadi 1998) is relatively low (between ~ 10 and 45°). In transition phase, α is higher (30 – 60°), and during braking phase α increases to almost 90° . During landing phase, the animal begins to adduct the limbs ventrally, furls the patagium, and is again in the realm of ballistic forces. Occasionally, the transition and braking phases of the glide are eliminated, but this seems to occur only during glides with high α and low glide ratio. Measurements of wingspan and chord were taken from the videotapes when the wing planform was visible. Wingspan (b) was taken to be the average of span of the wing at the leading and trailing edges. Chordline is a straight line between leading and trailing edges

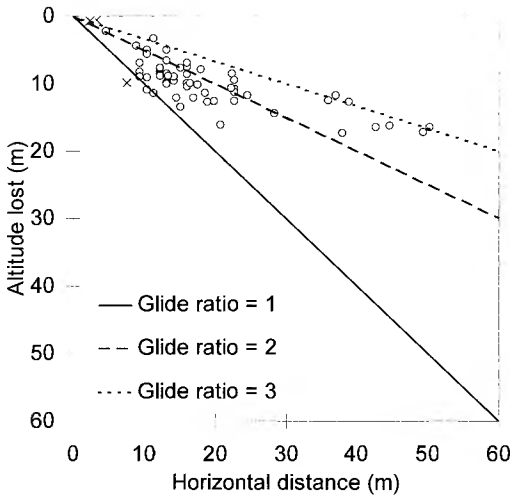


FIG. 1.—Altitude lost as a function of glide distance of *Petaurista leucogenys* at Nara Park, Japan. Glide ratios are illustrated by lines passing through the origin. The data points marked X did not meet our definition of gliding and were excluded from the analysis because they were parachutes (i.e., glide ratio <1), not glides.

of the airfoil. The length of the chordline is the chord. Wing area (S) was obtained by multiplying wingspan by chord of the wing at midline. Aspect ratios (AR) were calculated as b^2/S .

RESULTS

Mean glide ratio (Fig. 1) was $1.87 \text{ m} \pm 0.60 \text{ SD}$ (range 0.96–3.41, $n = 57$). Mean horizontal glide distance was $19.46 \pm 10.75 \text{ m}$ (range 4.75–50.35, $n = 57$). Mean airspeed ([direct glide distance]/time) was $6.23 \text{ m/s} \pm 1.36 \text{ SD}$ (range 4.39–9.47, $n = 30$). Mean ground speed ([horizontal distance]/time) was $5.28 \pm 1.42 \text{ m/s}$ (range 3.03–8.89, $n = 29$). These variables are strongly correlated, airspeed with horizontal distance ($r = 0.74$, $n = 29$, $P < 0.0005$), airspeed with direct glide distance ($r = 0.74$, $n = 29$, $P < 0.0005$), airspeed with glide ratio ($r = 0.44$, $n = 29$, $P = 0.016$), glide ratio with horizontal distance ($r = 0.65$, $n = 57$, $P < 0.0005$), and glide ratio with direct distance ($r = 0.58$, $n = 57$, $P < 0.0005$). Reduced major axis regressions of direct glide distance on glide duration

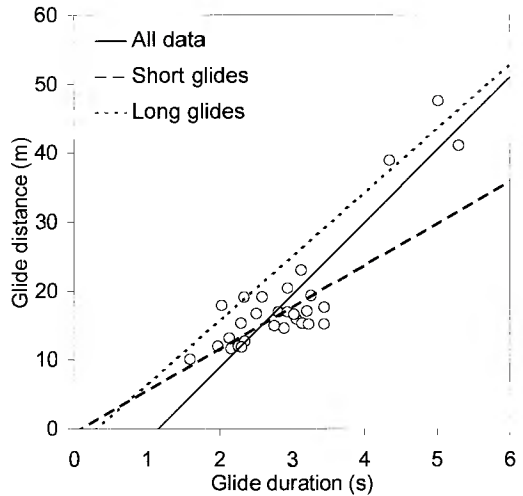


FIG. 2.—Airspeed of *Petaurista leucogenys* at Nara Park with reduced major axis regression lines partitioned by glide distance. All data, $y = 10.53x - 12.19$, $r = 0.87$, $n = 29$, $P < 0.0005$; short glides $< 25 \text{ m}$, $y = 6.09x - 0.65$, $r = 0.57$, $n = 27$, $P = 0.003$; long glides $\geq 25 \text{ m}$, $y = 9.28x - 2.93$, $r = 0.45$, $n = 3$, $P = 0.70$. The regression lines for short ($< 25 \text{ m}$) and long ($\geq 25 \text{ m}$) glides have intercepts within 1 SD of the origin.

(Figs. 2 and 3) give similar estimates of airspeed for shorter glides with low glide ratios, but they give higher estimates of airspeed for longer glides with high glide ratios.

Glide angles were higher than those reported by Scholey (1986). Short glides had higher glide angles than long glides (Fig. 4), and there was an inverse relationship between glide ratio and glide angle (Fig. 5). Three types of glide path were observed. “S-shaped” glide paths were most often used. The squirrel leaps from the tree, gaining a bit of elevation before it assumes a downward glide path. The least common glide path is “J-shaped,” in which the animal dives from the perch, losing elevation quickly, and then pulls out of the glide to a more horizontal glide angle. An intermediate or “straight” glide occurred with intermediate frequency, in which the animal leaps from its perch at approximately the

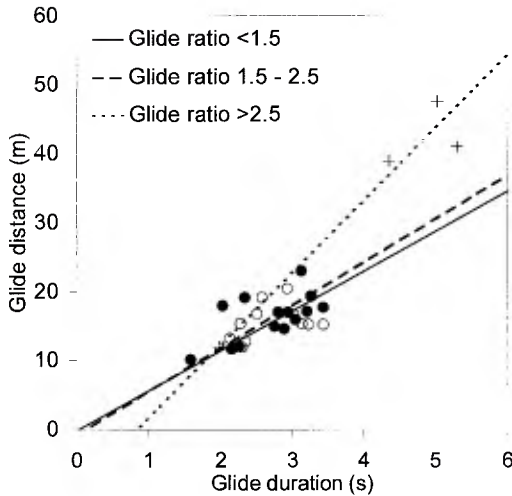


FIG. 3.—Airspeed of *Petaurista leucogenys* at Nara Park with reduced major axis regression lines partitioned by glide ratio. Glide ratio <1.5, open circles; glide ratio 1.5–2.5, closed circles; glide ratio >2.5, crosses. Glide ratio <1.5, $y = 5.78x - 0.23$, $r = 0.35$, $n = 11$, $P = 0.29$; glide ratio 1.5–2.5, $y = 6.28x - 0.85$, $r = 0.62$, $n = 14$, $P = 0.017$; glide ratio >2.5, $y = 10.4x - 8.60$, $r = 0.97$, $n = 4$, $P = 0.034$. The regression lines for low (<1.5) and moderate (1.5–2.5) glide ratios have intercepts within 1 *SD* of the origin. The intercept for the high glide ratio (>2.5) regression line is within 2 *SD* of the origin.

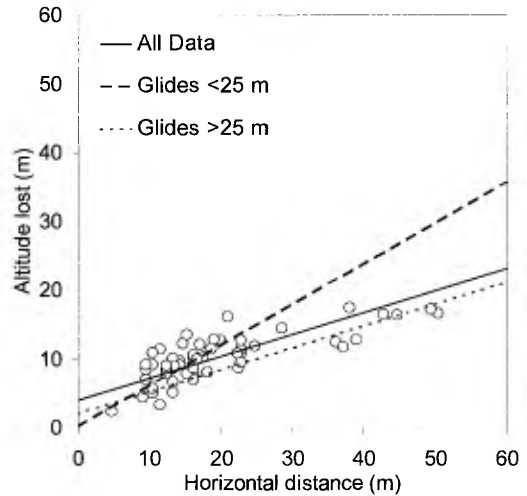


FIG. 4.—Glide angles (θ) in *Petaurista leucogenys* at Nara Park with reduced major axis regression lines partitioned by glide distance. All data, $y = 0.32x + 4.06$, $r = 0.78$, $n = 57$, $P < 0.0005$; short glides <25 m, $y = 0.59x + 0.27$, $r = 0.62$, $n = 48$, $P < 0.0005$; long glides >25 m, $y = 0.32x + 2.05$, $r = 0.57$, $n = 9$, $P = 0.11$. Regression lines for short and long glides have intercepts within 1 *SD* of the origin. Glide angle statistics (mean glide angle, 95% *CI*) for these lines, all data, 17.74, 14.96–20.45; glides <25 m, 30.54, 24.52–35.90; glides >25 m, 17.74, 8.24–26.35; Scholley (1986), 11.86, 10.09–13.60.

glide angle of most of the glide. It is our impression that S-shaped glide paths are preferred, but environmental geometry may determine the particular glide path used.

Tail movements are common during the glide but are not always associated with maneuvering. They also do not appear to produce movement of the uropatagium. The hind limbs produced marked uropatagial deviations. Adduction and ventral flexion of the forelimb induced yawing and rolling in the opposite direction of the limb that moved (Fig. 6). It is unclear how pitching moments associated with flaring and braking phases of the glide are produced. In all cases where wingtip position could be observed, the styliiform cartilage was markedly dorsiflexed, confirming the observations of Thorington et al. (1998). In all cas-

es where propatagial position could be observed, the surface of the propatagium and the portion of the plagiopatagium between the forelimb and styliiform cartilage were held roughly parallel to the relative wind. The mean aspect ratio of *P. leucogenys* while gliding was 1.42 ± 0.21 (range = 1.10–1.73, $n = 8$). This value is similar to aspect ratios calculated from museum specimens (Table 1).

DISCUSSION

Our glide ratios (Fig. 1) agree with those of Ando and Imaizumi (1982), based on a single individual in a small, isolated, and restricted habitat, and with those of Ando and Shiraishi (1993), measured on glides of numerous animals at sites specifically selected for their heterogeneous structure. In

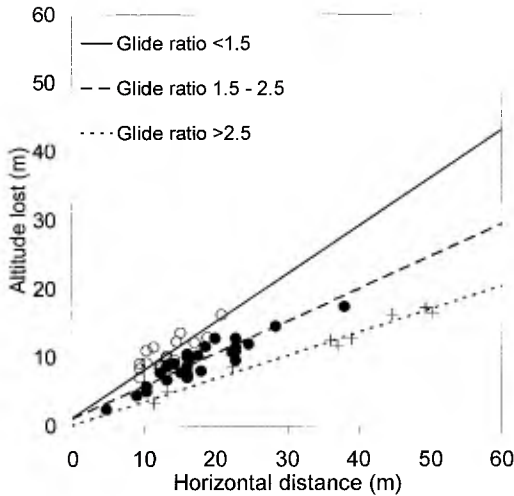


FIG. 5.—Glide angles (θ) in *Petaurista leucogenys* at Nara Park with reduced major axis regression lines partitioned by glide ratio. Glide ratio <1.5 , open circles; glide ratio $1.5\text{--}2.5$, closed circles; glide ratio >2.5 , crosses. Glide ratio <1.5 , $y = 0.70x - 1.13$, $r = 0.83$, $n = 18$, $P < 0.0005$; glide ratio $1.5\text{--}2.5$, $y = 0.47x - 1.03$, $r = 0.92$, $n = 29$, $P < 0.0005$; glide ratio >2.5 , $y = 0.34x - 0.09$, $r = 0.98$, $n = 10$, $P < 0.0005$. Regression lines for low (<1.5) and high (>2.5) glide ratio glides have intercepts within 1 SD of the origin. The intercept for the moderate ($1.5\text{--}2.5$) glide ratio regression line is within 2 SD of the origin. Glide angle statistics (mean glide angle, 95% CI) for these lines, glide ratio <1.5 , 34.99, 27.36–41.43; glide ratio $1.5\text{--}2.5$, 25.17, 21.80–28.37; glide ratios >2.5 , 18.78, 17.07–20.46; Scholey (1986), 11.86, 10.09–13.60.

all of these environments, as at Nara Park, glide ratios of 3.0–3.5 appear to represent an upper performance limit for *P. leucogenys*. There were no environmental obstacles preventing animals from using higher glide ratio glides had they chosen to do so. In many cases, animals used a series of 2 or 3 glides to reach a feeding tree that, it appeared to us, they could have glided to directly.

The gliding velocities observed at Nara Park are lower than those reported by others. On the basis of horizontal glide distance, we calculated ground speeds of 3.03–

8.89 m/s. Ando and Shiraishi (1993) reported ground speeds of 7.0–13.3 m/s. Scholey (1986) reported airspeeds of 15.1 ± 3.2 m/s. The differences are partly because of methods. Our ground speeds and those reported by Ando and Shiraishi (1993) are averages, using horizontal distance and total duration of the glide. Scholey (1986) estimated the average speed in the middle of the glide by regression analysis. Using Scholey's (1986) method (Fig. 2), we obtained airspeeds of 10.53 ± 0.96 m/s for our data. This analysis is based on the assumptions that launch and landing phases of the glide are of equal duration on short and long glides and that there is no consistent difference in mid-glide speeds between short and long glides. We question these assumptions. Ando and Shiraishi (1993) found long glides to have higher velocities, as did we, whether measuring glide distance as horizontal distance or as direct distance (Fig. 2). Therefore, longer glides would require a longer braking phase to reach landing speeds. This last point assumes some maximum safe landing velocity or that animals seek to minimize landing velocity and therefore landing force.

Using Scholey's (1986) method to determine airspeeds, we still find that shorter glides have lower airspeeds than longer glides (Fig. 2) and that airspeed increases as glide ratio increases (Fig. 3). Higher airspeed on longer glides is not surprising, even assuming constant launch speed and constant acceleration in mid-glide. Low airspeeds at low glide ratios are also expected, because low glide ratios are characterized by high angles of attack, α , resulting in an increase in drag and a reduction in velocity.

There is an interesting discordance between our data and Scholey's (1986). When we partition our data into long and short glides, our reduced major axis regression lines pass within 1 SD of the origin of the graph (Fig. 2). Therefore, our data provide no evidence that the intercept is different from 0. In Scholey's analysis, there is a non-zero intercept on the time axis that he

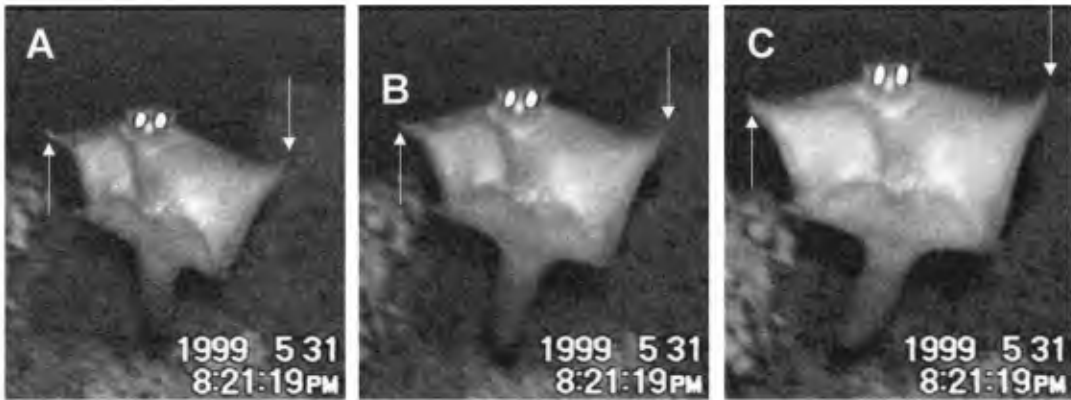


FIG. 6.—Digitized video frames of *Petaurista leucogenys* in a right turn. A) In the beginning of the turn, the right forelimb is adducted and ventrally flexed. B) As the animal comes out of the turn, the right forelimb is returning to typical gliding position. C) At the completion of the turn, the right forelimb is returned to typical gliding position. Note that the tail moves little during the turn and that the wingtips (arrows) remain dorsally flexed throughout the turn. Images digitized from videotape of *Petaurista leucogenys* gliding at Nara Park.

interprets as “. . . time required for acceleration and deceleration to and from glide speed. . .” When we partition our data according to glide ratio (Fig. 3), regression lines for low and intermediate glide ratios pass through the origin. The regression line

for high glide ratios does not, but if it were not for 1 anomalous short glide with a high glide ratio, all of these regression lines would pass within 1 *SD* of the origin. Accordingly, we do not accept the idea that intercepts of these analyses are meaningful.

TABLE 1.—Aspect ratios and wing loadings of gliding mammals. *Petaurista elegans*, *P. petaurista albiventer*, *P. p. grandis* from Thorington and Heaney (1981); *P. petaurista* from Scholey (1986); *P. leucogenys* from this study; all other taxa from Stafford (1999).

Taxon	Aspect ratio	Wing loading (N/m ²)
<i>Petaurista elegans</i>		110
<i>Petaurista petaurista albiventer</i>	1.14	93
<i>Petaurista petaurista albiventer</i>	1.34	80
<i>Petaurista petaurista grandis</i>	1.42	104
<i>Petaurista petaurista</i>	1.52 ± 0.15	120
<i>Petaurista</i> sp.	1.28–2.02	86–109
<i>Petaurista leucogenys</i>	1.10–1.73	
<i>Trogopterus edithae</i>	0.97–1.54	
<i>Eoglaucomys fimbriatus</i>	0.98–1.69	88–95
<i>Glaucomys sabrinus</i>	1.04–1.83	56–61
<i>Anomalurus derbianus</i>	0.86–1.86	69–93
<i>Anomalurus peli</i>	0.85–1.80	103–139
<i>Petaurus australis</i>	1.04–2.11	63–81
<i>Petaurus breviceps</i>	1.05–2.15	45–59
<i>Petauroides volans</i>	0.76–1.36	134–143
<i>Acrobates pygmaeus</i>	0.73–1.23	84–92
<i>Cynocephalus volans</i>	1.08–1.35	38–48
<i>Galeopterus variegatus</i>	1.36–1.94	49–71

The gap between the origin and the reduced major axis intercept with the ordinate may be an artifact of running a regression line between sets of longer and shorter glides with different performance parameters.

Scholey may also have underestimated glide duration under field conditions. We simulated this problem while collecting data on glide duration from videotapes. We collected an initial glide duration and 3 subsequent duration times. The 1st time was collected on the 1st pass through the videotape, replicating field conditions, when there is often little warning before a glide is initiated. The 3 subsequent times were collected by rewinding the videotape and determining as accurately as possible exactly when the animal left its support. Our 1st times averaged 92% of the average of the 3 subsequent times. The range was from 74% to 100% of the average of the subsequent times for any glide because there often is a delay between the squirrel launching its glide and the observer hitting the start button on the stopwatch. Underestimating glide duration leads to overestimating velocity. This may partly explain the differences between Scholey's (1986) data and the velocities estimated by Ando and Shiraishi (1993) and by us.

The "J-shaped" glide path described by other workers (Scheibe and Robins 1998; Scholey 1986) is not commonly used at Nara Park. This may be largely because of environmental geometry. Much of Nara Park is not covered by a continuous canopy. Rather than dropping out of the canopy to glide through the subcanopy, squirrels at Nara Park commonly launch from, or near, the apex of trees. This often requires an initial strong horizontal or altitude-gaining leap over branches below the launch point to reach clear gliding space. Gliding in the subcanopy requires an initial drop to reach clear gliding space. Environmental geometry may, therefore, affect initial glide path and probably subsequent velocity, glide ratio, glide angle, and glide distance.

Aspect ratios have important aerodynam-

ic implications and have been calculated for most gliding mammals (Stafford 1999; Thorington and Heaney 1981; Table 1). High aspect ratio wings incur less drag for lift being produced and can glide further, but a broad wing may better maintain lift at high angles of attack (Anderson 1985; Pamadi 1998). As calculated from museum specimens, aspect ratios may change by up to 58% in *Petaurista* (Stafford 1999) depending on limb position, suggesting that animals are able to significantly alter performance characteristics of the wing during glide. However, there is close correspondence between values calculated from museum specimens (Table 1) and those observed in the wild, both by us and by Scholey (1986).

Wing loading is another important parameter affecting the performance of gliding mammals (Table 1). For example, wing loading is correlated with maneuverability. Maneuverability is defined as the minimum turning radius at a given velocity. Animals with high wing loading should be less maneuverable than animals with low wing loading, all other factors being equal. This is largely because low wing loading indicates a relatively large lift-producing surface per unit of mass. We would hypothesize that dermopterans are more maneuverable than *Petauroides* (Table 1). *Petaurista* should be intermediate between these 2 extremes. However, whether there are significant differences in maneuverability among species of *Petaurista* is difficult to say. Mass can vary with season or reproductive condition, and such variations could be as important as the variability seen among *Petaurista* in Table 1.

Wing loading is also related to the speed at which an animal must fly in order to generate enough lift to remain airborne. Stall speed is proportional to the square root of wing loading (Anderson 1985; Pamadi 1998). Theoretically, increased wing loading does not decrease gliding angle or gliding distance. However, animals with higher wing loading must glide faster at any given

angle of attack to produce the same relative lift force and remain airborne, all other factors being equal. To increase velocity, a gliding mammal with high wing loading may either have a higher launching speed or glide at a steeper angle than an animal with lower wing loading. There is little information on launch speeds in gliding mammals, and there is no anatomical evidence that more highly loaded gliders have greater leaping abilities, i.e., they do not have relatively longer hind limbs or relatively higher crural indices (Stafford 1999). Therefore, heavily loaded mammalian gliders may have to glide at steeper angles than gliders with lower wing loadings, at least at the beginning of their glide. The J-shaped glide may result in faster gliding speeds but possibly in lower glide ratios.

Jackson (2000) reports glide ratios of 1.1–2.5 for *Petaurus gracilis* and *P. breviceps* and glide angles of 21.8–42.4 for *P. gracilis* and 22.0–43.1 for *P. breviceps*. These data are similar to our data on *P. leucogenys* (Table 1; Fig. 1); however, *Petaurista* has wing loadings twice that of *Petaurus* (Table 1). Consequently, we expect that *Petaurista* must fly 1.41 times as fast as *Petaurus* or should show lower glide ratios. Jackson's (2000) data contradict this hypothesis, but Jackson provides no data on gliding velocity. Similarly, Vernes (2001) reports average glide ratios of 1.98 for *G. sabrinus*, and *G. sabrinus* is much more lightly loaded than *Petaurista* (Table 1).

On the other hand, Scheibe and Robins (1998) give a velocity of 8.27 m/s for *G. volans*, using Scholey's (1986) method. Our comparable value for *Petaurista* is a velocity of 10.53 m/s. Stafford (1999) estimated *Petaurista* to have wing loadings roughly 1.54 times that of *Glaucomys* (Table 1), predicting that *Petaurista* must fly 1.24 times as fast as *Glaucomys*. In fact, *Petaurista* glides 1.27 times as fast as *Glaucomys*.

It is unclear exactly what these comparisons reveal. Data from Jackson (2000) and from Vernes (2001) are only from glides

observed immediately upon release from capture. Scheibe and Robins (1998) combine captive and wild data. Their data from the wild are only from animals released after capture. In neither case is the total performance envelope being sampled under natural conditions, a constraint recognized by Vernes (2001). Consequently, *Petaurista* is still the only gliding taxon about which we have detailed information on gliding performance.

Statements about gliding performance inferred from such simple aerodynamic parameters as those presented in the foregoing (Table 1) must be considered provisional hypotheses to be tested against field observations of gliding behavior in its natural context.

Thorington et al. (1998) proposed that wingtips of flying squirrels act to enhance performance by reducing induced drag. Stafford (1999) proposed that these structures act in control and maneuverability. Wingtips have no role in initiating rolling maneuvers (Fig. 6) because they are flexed throughout this maneuver, which is apparently accomplished by adducting and ventrally flexing the right forelimb. This serves to increase the camber on the right wing and rolls the animal to the left. Although we can provisionally discount the role of the wingtips in maneuverability, they still may play an important role in controlling the glide. Specifically, they may enhance static stability by providing the wing with a small dihedral effect (Anderson 1985; Parnadi 1998).

CONCLUSIONS

Gliding behavior seems to be more diverse than previously recognized, and environmental geometry may have a significant role in determining glide paths. Also, glide distance, glide angle and ratio, and velocity are important interdependent variables that need to be considered when evaluating gliding behavior and performance. All glides are not alike. Still, *P. leucogenys* seems to operate within a well-defined per-

formance envelope regardless of habitat. Finally, we need more and better data on gliding. The context of the data is critical. Trap-and-release observations cannot encompass the entire gliding repertoire and likely represent only a subset of gliding performance. Most importantly, the data need to be comparable. It is doubtful that the more subtle aspects of gliding can be studied in the wild, but wild studies provide the necessary context within which to conduct more specifically focused laboratory studies. Although we now have a clearer understanding of the role of certain wing components in gliding, we are still a long way from understanding exactly how these animals control their glides and maneuver.

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