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Launch Dynamics in *Glaucomy's volans*

Abstract

We used high speed strobes to photograph launches by *Glaucomy's volans* in a laboratory setting. The photographic images were digitized, and launch trajectories determined via quadratic regression. We used a model of transport cost to estimate the overall effect of launch cost on cost effective glide distances. Launching added little to the overall cost of gliding in *G. volans*, and gliding was still less expensive than quadrupedal transport. Maximum ballistic range did not change with body mass, but there was a weak trend for launch acceleration to decrease with mass. We interpret these data in light of hypotheses for the evolution of mammalian gliding.

Keywords

Glaucomy's, leaping, cost of transport

1 Introduction

Even though gliding is common among vertebrates, there have been few attempts to explore performance, energetic, or behavioral components of gliding locomotion. Notable exceptions include work by Scholey [29] on *Petaurista petaurista*, Polyakova and Sokolov [25] on *Pteromys volans*, Scheibe and Robins [27] on *Glaucomy's volans*, Nachtigall et al. [22] and Nachtigall [21] on *Petaurus breviceps*, Ando and Shiraishi [4] on *Petaurista leucogenys*, Hendershott and Scheibe [18] on *Ptychozoon kuhli* (Reptilia: Gekkonidae), and

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Emerson and Koehl [13] and Emerson [12] on Rhacophorid frogs. Furthermore, relatively little is known about the gliding capabilities of most mammals. Scholey [29], Scheibe and Robins [27], Ando and Shiraishi [4], Polykolov and Sokolov [25], and Nachtigall [21] have published some performance data for *Petaurista*, *Glaucomys*, *Pteromys*, and *Petaurus*. These studies report glide angles, glide distances, and glide speeds, but lack information on many aspects of gliding. For example, we know little about how glides are initiated, the energetic cost of launching, or how launch performance relates to glide performance.

Understanding performance and energetic aspects of launching is important because of what it may tell us about the natural history and evolution of gliders. That is, if gliding represents a strategy for predator avoidance, rapid acceleration during launch would be expected [11]. However, the cost of rapid acceleration may be high if gliding locomotion represents a mechanism designed to minimize transport costs. Thus, under normal circumstances launches may involve lower velocities. In either event, there are no data in the literature enabling us to evaluate this aspect of gliding. We know little about how gliding mammals initiate their glides, or how launches influence overall glide performance and cost. This paper represents an effort to explore the energetic and performance attributes of launching in *Glaucomys volans*, and provides some speculation about *Petaurista*.

We used still photography with high speed strobes to capture images of launching *Glaucomys volans*. Others have used cinematography and/or force plates to explore the mechanics of jumping [1, 2, 6, 17]. We relied on large sample sizes to provide a reasonable index of launch parameters. Images were analyzed in an effort to estimate launch velocity and acceleration, launch angle, launch energetics, and parametric equations describing the initial phase of the glide. These data are then used to evaluate performance and overall energetics of launching and gliding in *G. volans*. We then consider several hypotheses for the evolution of gliding, and make inferences about launching in larger gliders like *Petaurista*.

2 Methods

Launches were photographed in a converted handball court. The court measured 7 m by 14 m and had a 7 m ceiling. The walls were solid concrete, and a single door and three ventilation windows were at one end of the court. Two walls were painted flat black, and a third was painted color separation overlay blue. Two 3.5 m snags were erected in the court and served as launching and landing sites. The snag used for launching had a short section of 3.8 cm by 8.9 cm pine board attached to the top. This served as a launching platform. Attached to the side of the pine board was a 16 cm long ruler. The ruler was used to calibrate distances within the images.

Two 35 mm cameras were used to photograph launches and glides. The first camera captured only the launch phase of the glide, and the second cap-

tured a larger portion of the glide. Individually numbered animals were released on the launch snag and coaxed onto the launch platform. The lab lights were extinguished and camera shutters opened. When the animals initiated a launch, two Canon 540 ez high-speed strobes were fired at 15 hz for 0.7 s. Approximately 15 % of the resultant images were useful, in that they contained the complete launch sequence. Each of these images contained multiple images of a launching or gliding squirrel, spaced 0.067 s apart in time. The images gathered from the second camera were not used in this portion of the study.

We used 135 images from 14 squirrels captured on Kodak Plus X Pan or Tmax 100 film. Negatives were developed in D76 or Tmax developer, and digitized using a Minolta Snappy frame grabber. The digitized images were analyzed using SigmaScan (SPSS Inc., 444 N. Michigan Ave., Chicago, IL 60611). Each image was calibrated using the 16 cm ruler attached to the side of the launch platform. Coordinates of each squirrel image were determined using a clearly recognizable landmark on the squirrel (tip of rostrum or eye). Coordinates were also determined for the end of the launch platform. All coordinates were then transported to QuatroPro (Borland International, Inc., 1800 Green Hills Road, P.O. Box 660001, Scotts Valley, CA 95067-0001, USA) and SAS (SAS Institute Inc., Cary, NC, USA) for analysis.

Quadratic regressions of horizontal and vertical positions against time were computed for each launch sequence. These regressions were used to produce vectors in space and time, and a complete description of the animals' position. First and second derivatives of the quadratic regressions provided horizontal, vertical, and total velocity and acceleration. Also, for each negative the first image of a squirrel no longer in contact with the launch platform (or nearly so) was used to compute the launch angle and initial velocity.

We estimated glide angles using the trajectories determined above. The predicted spatial position at 0.7 s was computed relative to the starting platform. The arctangent of this value provided an index of glide angle. We used 0.7 s because the regression was strictly valid to 0.7 s (total time through which the strobes fired), and because lesser values would have incorporated too much of the launch. The estimated values serve only as an index, but are representative of the initial glide angle. Postural changes during the glide, changes in velocity, lift, and drag may influence dramatically the final glide angle. We explored the effect of launch angle on initial glide angle using linear regression.

The energetic cost (C_L) and kinetic energy (E_k) of launching was computed from ballistics equations as:

$$E_k = \frac{mV_L^2}{2} \quad (1)$$

where E_k is the kinetic energy of the launch, m = mass, and V_L is the initial launch velocity. Cost of transport has been defined by Taylor [31], and is used here to characterize launching. The cost of launching is

$$C_L = \frac{P_L}{mgV_L}$$

where P_L is the power of the launch and $g =$ gravitational acceleration. Launch velocity is D/T and $P_L T$ is the kinetic energy of the launch. Therefore, the cost of launching can be estimated as:

$$C_L = \frac{E_k}{mgD_L} \quad (3)$$

where D_L is the distance through which the force of acceleration is applied. Based on a review of our images and the work of Caple et al. [7], it seems reasonable to estimate D_L as the animal's body length. The cost and kinetic energy of launching was estimated for each of the 135 images.

The effect of launch cost on the overall cost of gliding was estimated using the model of Scheibe et al. [28]. This model computes the cost effective glide distance, based on the work of Taylor [31] and Scholey [29]. Basically, the cost of gliding is modeled as

$$C_g = \frac{E_c + E_g}{mgD} \quad (4)$$

where E_c and E_g represent the energy of climbing and gliding respectively, and D is the distance of the glide. Similarly, the cost of quadrupedal transport, for comparison, is

$$C_r = \frac{P_r}{mgV_r} \quad (5)$$

where P_r and V_r are the power and velocity of quadrupedal transport. The cost of gliding, including launch costs, can then be computed as

$$C_g = \frac{P_c T_c + P_g T_g}{mgD} + \frac{P_L}{mgV_L} \quad (6)$$

and the cost effective glide distance becomes

$$D_e = \frac{\beta_0}{\frac{V_c}{P_c} \left(\frac{P_r}{V_r} - \frac{P_g}{V_g} - \frac{P_L}{V_L} \right) - \beta_1} \quad (7)$$

Here, β_0 is the initial vertical drop experienced during the glide (computed via regression of launch height against glide distance in Scholey [29]) and β_1 is the inverse of the glide ratio, also determined via regression. We used parameter estimates for the gliding and quadrupedal components of the model derived from the work of Scheibe and Robins [27].

Our photographs did not contain the landing portion of the glide, which varied greatly from glide to glide. Some glides ended on the landing snag, while others ended at various points on the lab floor. Thus, landings were not recorded and no overall glide distances computed. However, we estimated glide range using ballistics. This provided a distance at which the launching animal returned to its initial launch height. Although postures and behavior employed during the glide modify the actual glide range, our estimate provides a reasonable index of range. We defined range (R) as

$$R = V_0 \sqrt{\frac{2h}{g}} \quad (8)$$

where h = maximum height of the launch, g = acceleration due to gravity, and V_0 = initial launch velocity.

Overall glide trajectories were explored via quadratic regression of vertical position against the corresponding horizontal position for each launch by each animal. Samples of these regressions representing the range of launches from most negative to most positive launch angle were plotted to illustrate the capabilities of the animals. The relationship between launch angle and launch acceleration, and animal mass and launch acceleration was explored via linear regression.

3 Results

Launches at positive angles from the platform were stereotypical (Fig. 1). The animals used a bounding gait to the end of the platform with the tail upright. Both fore and hind feet were at the end of the platform at the moment before launch, with the head down over the end of the platform. The pectoral appendages appeared to provide some thrust, elevating the anterior portion of the body. The tail was elevated and flipped over the dorsal aspect of the animal, and the pelvic appendages pushed the animal forward. Within the first 0.067 s after leaving the launch platform, the pelvic appendages were extended posteriorly, there was plantar flexion of the feet, and forward rotation of the pectoral appendages with forward flexion of the forefeet and subsequent extension of the styliform cartilage. Within the next 0.067 s, there was complete extension of the pectoral appendages, and especially the styliform cartilage. The pelvic appendages moved laterally with complete plantar flexion. The tail moved back, forming a posterior airfoil that often moved laterally from side to side.

The mean launch angle for 135 images was 4.267° (SE = 1.197) and varied from 40.752° to -31.304°. Initial launch velocities varied from 0.721 m/s to 4.083 m/s with a mean of 2.295 m/s (SE = 0.063). Clearly, launch performance varied considerably within and between animals. This is illustrated in Fig. 2a and 2b, showing results of quadratic regressions of horizontal and vertical positions against time for 6 launches ranging from a launch angle of -30° to 40°. The regressions are strictly valid only to 0.7 s, but illustrate likely trajectories under the ballistics model.

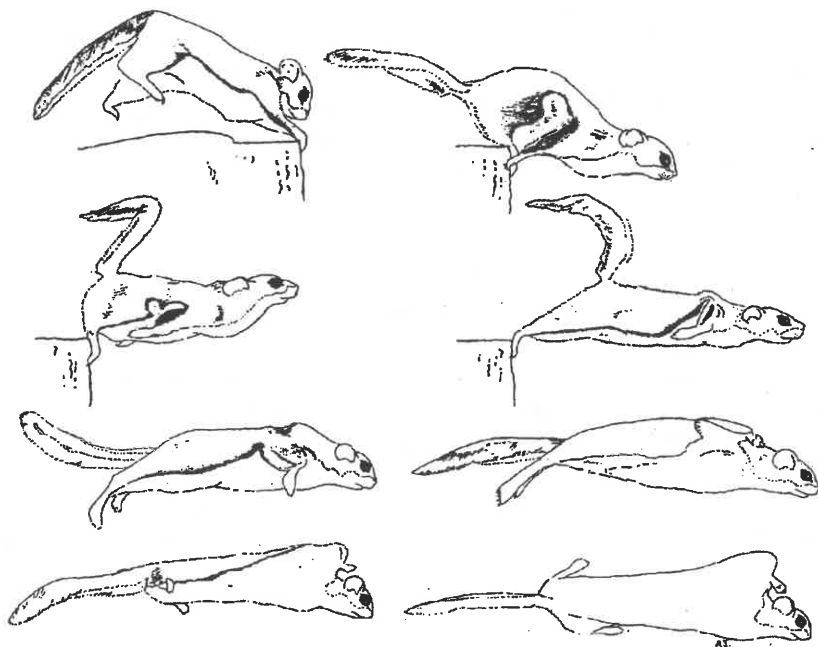


Fig. 1. Illustration of a typical launch by *Glaucomys volans* from the launch platform.

Second derivatives of the quadratic regressions of horizontal and vertical positions against time provided horizontal and vertical acceleration values at each moment. Resolution of the initial vectors provided overall initial acceleration for each launch. These values were negatively regressed with launch angle ($p = 0.0001$; Table 1). Thus, launch acceleration decreased with increasing launch angle. Animals that launched horizontally or downward had greater acceleration than those launching at 40° . Similarly, the regression of launch acceleration against mass was negative and nearly significant ($p = 0.079$; Table 1).

The initial launch velocity estimated from each image and animal mass, measured during the performance trial, were used to calculate kinetic energy associated with each launch. The mean kinetic energy for a *G. volans* launch was 0.2327 Joules (SE = 0.0109) and varied from 0.0236 Joules to 0.748 Joules. Linear regression (Table 1) of kinetic energy of launch against launch angle revealed a significant positive relationship ($p = 0.0001$). Thus, launches at positive angles required more kinetic energy than those at negative angles.

The overall cost of launching was calculated using a mean mass of 78.002 g. The average length through which *Glaucomys* accelerated during launch was estimated as one body length of 0.1322 m. Using equation (2), this becomes

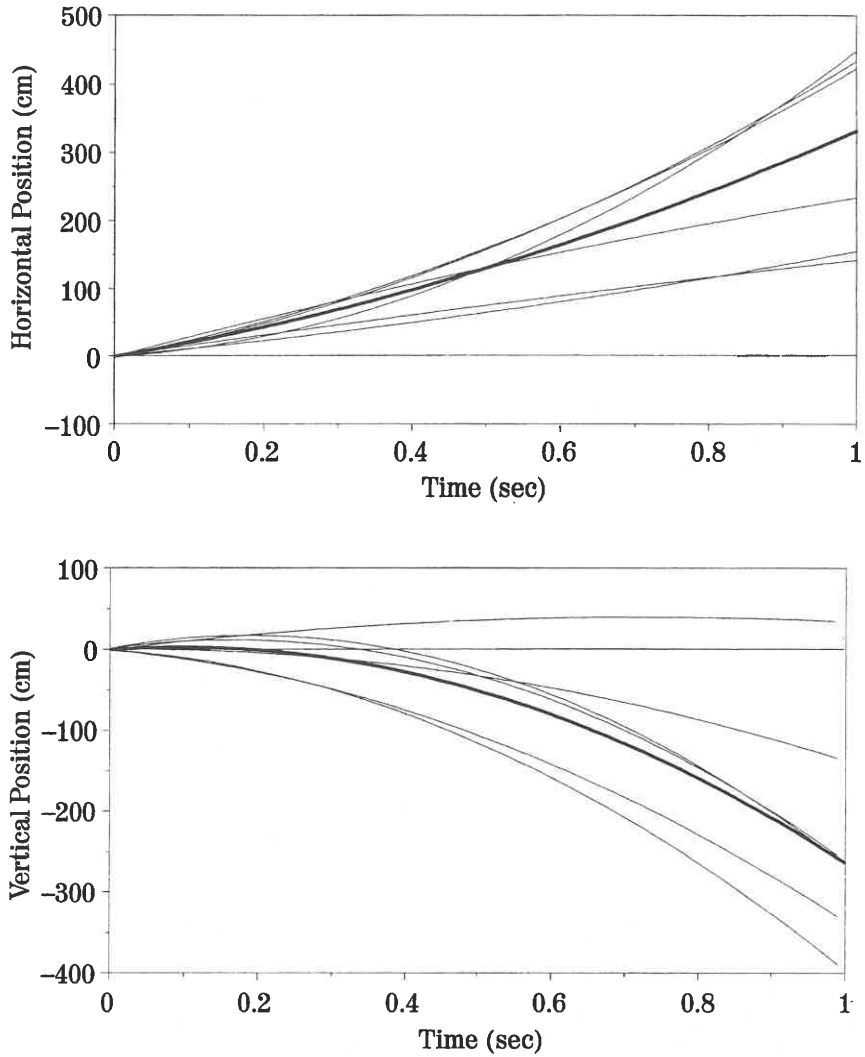


Fig. 2. Horizontal (A) and vertical (B) flight trajectory during launch for *Glaucomys volans*. The heavy line represents the mean trajectory for 135 launches. Other lines are for launch angles of -30° , 15° , 0° , 15° , 30° , and 40° .

$2.609 \text{ Jkg}^{-1}\text{m}^{-1}$. Scheibe and Robins [27] and Scheibe et al. [28] estimated the cost effective glide distance for *G. volans* as 5.18 m. This is based on parameter estimates from more than 100 lab and field glides ($V_r = 2.237 \text{ m/s}$, $P_r = 79.375 \text{ W/kg}$, $V_c = 1.655 \text{ m/s}$, $P_c = 64.597 \text{ W/kg}$, $V_g = 8.092 \text{ m/s}$, $P_g = 13.159 \text{ W/kg}$, initial vertical drop $b_0 = 1.848$, inverse glide ratio $b_1 = 0.511$). Using these estimates together with those for the cost of launching and equation (7), the

Table 1

Regression results for *Glaucomys* launch data. E_L = launch energy, Acceleration = total initial launch acceleration, and angle = launch angle. The range-launch angle and range mass regressions had 1,83 degrees of freedom, all others have 1 numerator and 134 denominator degrees of freedom.

Regression	b_0	b_1	F	P	R^2
E_L -angle	0.029513	0.001553	88.753	0.0001	0.400
Acceleration - angle	3.799521	0.047916	25.563	0.0001	0.161
Acceleration - mass	5.616156	-0.02014	3.140	0.0786	0.023
Range - Launch angle	17.77886	0.945275	53.137	0.0001	0.390
Range - mass	29.44968	0.004913	0.003	0.9598	0.000
Glide angle - Launch angle	36.07336	-0.70206	60.169	0.0001	0.311
Glide angle - Initial velocity	57.98388	-10.8523	34.052	0.0001	0.204
Glide angle - mass	41.33475	-0.10313	0.728	0.3950	0.005

cost effective glide distance is increased from 5.18 m to 5.94 m. Consequently, a leaping launch adds little to the overall cost of gliding for *G. volans*.

The mean range for 85 launches with positive launch angles was 0.298 m (SE = 0.013). Range was positively related to launch angle ($p = 0.0001$), but showed no linear relationship with mass ($p = 0.583$, Table 1). Thus, animal mass does not appear to influence the ability of the animals to employ a ballistic launch.

4 Discussion

A variety of hypotheses have been proposed to explain the evolutionary transition from gliding to active flight [7, 23, 24], and the distribution of gliding mammals [10, 14]. Typical hypotheses for the evolution of gliding locomotion include the low cost of gliding transport, predator avoidance, and foraging optimization. Although it is difficult to evaluate the veracity of these hypotheses, it is possible to gain some insight to critical components of each. In this paper we are concerned with how leaping launches influence the cost of gliding transport, and if leaping launches may enhance predator avoidance. The few studies that have explored cost of gliding transport [27, 29] have not analyzed costs associated with launching. We have observed leaping launches in *G. volans*, *Acrobates pygmaeus*, and *Petaurus breviceps*, and assume *Petaurista* employs leaping launches as well. Leaping by animals adds to the cost of transport, but if improved glide velocity or glide angle are the result, cost effective glide distances may be reduced.

We treated launches as ballistic events, even though changes in posture and subsequent lift and drag components probably result in some deviation

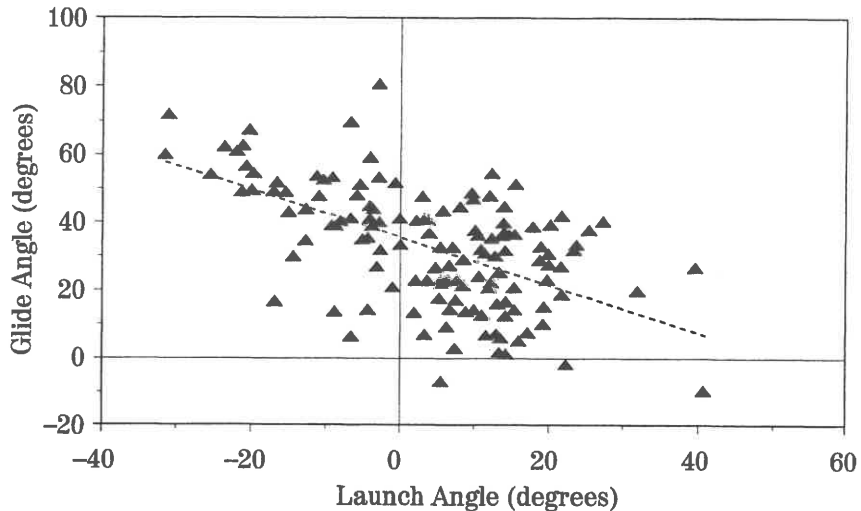


Fig. 3. Glide angle as a function of launch angle. The line represents the best fit linear regression based on 135 launches. Glide angles $> 45^\circ$ constitute parachuting, not gliding. Maximum ballistic range is achieved at a launch angle of 45° .

from this model. The discrepancies are probably not meaningful over the ranges and error margins of the study. As expected, our results show that glide performance and ballistic range increased with launch angle (Table 1, Fig. 3 and 4). The greatest angle observed was 40.75° , short of the 45° needed to provide maximum ballistic range. Mean launch angle was only 4.27° , but included many launches at negative angles. This suggests either the squirrels were not attempting to maximize ballistic range, or within the lab setting, maximum ballistic range was meaningless because of restrictions on possible glide distances. Launches at higher angles are associated with greater acceleration, and greater launch energy (Table 1). The result of this increased energy investment is an improved glide angle, with potential reductions in overall glide costs.

Data obtained in this study show that cost of launching adds only 4 to 10 %, depending on glide distance, to the overall cost of gliding determined by Scheibe and Robins [27] for *G. volans*. Using the model of Scheibe et al. [28], cost effective glide distance changes from approximately 5 m to 6 m. Thus, use of a leaping launch adds little to the overall cost of gliding for this species. Also, this small glider appears to be free of potential energetic constraints imposed by gliding locomotion.

Although launch costs have not been determined for other species, it is possible to estimate launch cost for *Petaurista* using data provided by Scholey [29]. Since running velocity approximates launch velocity ([7]; this study), E_k for *P. petaurista* should be about 1.5 Joules. If *Petaurista* launches through one body length of 412 mm [32], then C_L should be roughly $0.28 \text{ Jkg}^{-1}\text{m}^{-1}$. How-

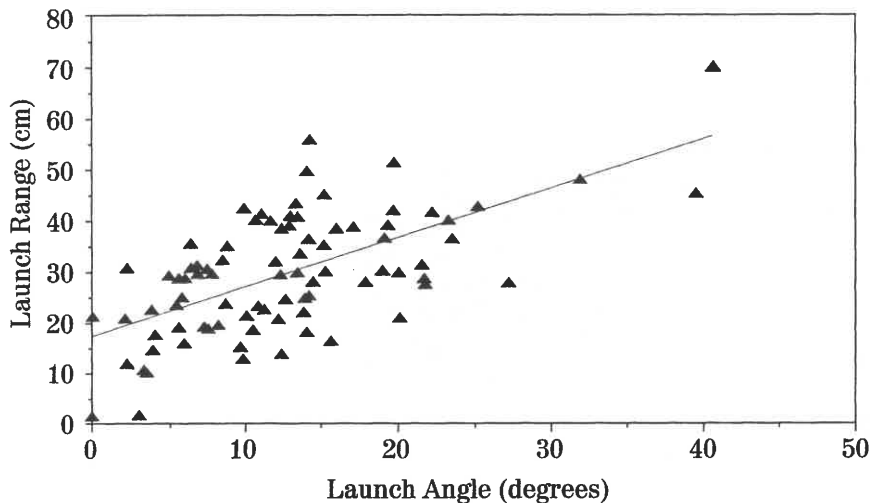


Fig. 4. Range (determined as distance at which animal returns to height of launch) as a function launch angle. Only positive launch angles are included in the analysis.

ever, using the model and results of Scheibe and Robins [27], the cost effective glide distance for *Petaurista* is increased from about 100 m to > 200 m. Thus, the situation for *Petaurista* appears to be very different from that for *Glaucomys*. This large glider, if it employs a leaping launch, may experience a significant energetic cost. Observations and photos by Takeo Kawamichi (personal communication) reveal a leaping launch in *P. leucogenys*, but descriptions of launches by Scholey suggest a 'dropping' launch in *P. petaurista*. At the same time, Ando and Shiraishi's [3, 4] observations of *P. leucogenys* reveal that this large glider usually glides over relatively short distances. Consequently, gliding in this species is expensive, and the launch does not facilitate the situation.

We conclude from this that small pteromyine gliders may well enjoy an energetic benefit from gliding, while larger pteromyines may not. The cost of gliding and launching varies with size and across groups. Preliminary analyses of gliding in *Petaurus breviceps* suggest that this species, in spite of its low glide angle [21, 22] and low mass, experiences cost effective glide distances of about 100 m, primarily because of its slow climbing speeds and slow running speeds. Although Scholey [29] determined a cost effective glide distance of about 45 m for *Petaurista petaurista*, Scheibe and Robins [27] showed this result to be incorrect. *Petaurista petaurista* must glide about 100 m before realizing an energetic benefit from gliding, and if *Petaurista* employs a leaping launch similar to that of *Glaucomys* or *Petaurus*, the cost effective glide distance is increased significantly. This suggests that gliding locomotion is not a universal consequence of selection for reduced transport costs.

Some insight to the veracity of the predator avoidance hypothesis can be gained from morphological and performance data. Hill [19] argued that animals which are geometrically similar should jump the same absolute distances independent of size, since smaller animals must accelerate less mass, but accelerate through shorter distances than larger animals. Emerson [11] tested this hypothesis with frogs, and proposed alternative functions for jumping: quickness of movement that facilitates predator avoidance, and consistent absolute jump distances. We can explore these ideas and determine if *G. volans* 1) maximizes quickness of movement and/or 2) ballistic range and consequently glide performance.

If leaping launches facilitate predator escape in gliders, body shape changes are expected with increasing size, and acceleration would be constant. Larger gliders moving more mass should be architecturally different from small gliders in order to improve acceleration. That is, a regression of launch acceleration against mass should produce a regression slope that is not different from 0, and morphological data should reveal shape changes associated with leaping performance. Alternatively, if launches provide maximal ballistic range, a decrease in acceleration would be expected with increasing body size, and body shape changes are not expected. A regression of ballistic range against mass should produce a regression slope that does not differ from 0.

Our performance data show that launch acceleration does not decrease significantly with increasing mass ($p = 0.0786$), although the data are suggestive of a trend towards decreased acceleration. At the same time, data reported by Robins and Scheibe [26] demonstrate shape changes in the hind limbs of *G. volans*. They determined that tibia length in *G. volans* is positively allometric with body mass. Since the tibia is an important element of the propulsive machinery, and has been hypothesized to scale positively with size in leaping animals [11], *Glaucomys* appears to change shape with size in a way that improves launch acceleration. This provides weak supporting evidence for the predator avoidance hypothesis. Some have noted greater life expectancies in gliding mammals than in non-gliders [5, 20], but a critical evaluation of these claims noted significant statistical flaws [30]. Clearly, *Glaucomys sabrinus* [9, 15] is exposed to significant levels of predation, and *G. volans* in Missouri is often found in owl pellets. We have observed black rat snakes (*Elaphe obsoleta obsoleta*) in *G. volans* nest boxes, and assume they are capable of capturing the squirrels. This suggests selection pressure for leaping, and detailed studies of predator avoidance behavior are warranted.

Our data do not provide consistent support for the hypothesis that leaping launches provide maximal ballistic range. The shape changes within the hind limbs of *G. volans* were not predicted under this hypothesis, and launch acceleration did not decrease significantly ($p = 0.0786$) with mass (Table 1). At the same time, when the data were restricted to those observations with positive launch angles, ballistic range did not change with mass ($p = 0.58$) as predicted. Thus, we are not able to reject the hypothesis that *G. volans* employs leaping launches which maximize range. Within the context of the laboratory

setting, the animals may have responded to a variety of factors, including the inability to initiate long glides, and the perceived predatory threat of the animal handlers.

It is important to note that our data may reflect two patterns. First, across individuals, larger animals may possess shapes or propulsive architectures that improve leaping and/or launch acceleration. The positive allometry of the hind limbs suggests acceleration through a greater distance, and consequently higher launch velocities than would otherwise be expected. Second, within individuals increasing mass may reduce launch acceleration, but not ballistic range. Although within individuals, mass may be expected to change over relatively short periods, it is unlikely that there is a corresponding change in shape. The fact that our results show a weak trend of decreasing acceleration, and no change in ballistic range with increasing mass, suggests the launch is designed to maximize initial range and not necessarily predator avoidance.

Additional detailed studies of launching may reveal a consistent maximization of launch acceleration, which would suggest predator avoidance. Interspecific comparisons across a broad size range may provide greater insight to the importance of leaping launches for predator avoidance and/or ballistic range. Alternatively, gliding locomotion may represent an effective strategy for moving from one foraging patch to another. Goldingay [16] has noted the unique nature of gliding mammal diets, and it is reasonable to expect their food resources to be patchily distributed. This is certainly true for *Glaucomys*, *Petaurus*, and *Colugos*. In the context of optimal foraging theory [8], reduced travel time between patches enables animals to leave patches earlier, while rates of return are still very high. If gliding represents a tool for effective foraging, the energetic cost of gliding and launching, and use of leaping launches for predator avoidance may be of secondary importance.

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