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Locomotor performance and cost of transport in the northern flying squirrel *Glaucomys sabrinus*

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We assess locomotor performance by northern flying squirrels *Glaucomys sabrinus* Shaw, 1801 and test the hypothesis that gliding locomotion is energetically cheaper than quadrupedal locomotion. We measured 168 glides by 82 northern flying squirrels in Alaska. Mean glide distances varied from 12.46 m to 14.39 m, with a maximum observed glide distance of 65 m. Mean glide angles varied from 41.31° to 36.31°, and mean air speed ranged from 6.26 m/s to 8.11 m/s. There were no differences in the performance of male and female flying squirrels. We used models of transport cost to provide an initial assessment of the hypothesis that gliding locomotion is energetically less expensive than quadrupedal locomotion. For glides of average length, cost of gliding was less than cost of quadrupedal locomotion except when the animals climbed to the launch point very slowly or ran quickly. Thus the hypothesis that gliding is less expensive than quadrupedal locomotion is supported.

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Introduction

Gliding locomotion is common in vertebrates (Norberg 1985, 1990, Essner and Scheibe 2000), and may have been an important step in the evolution of powered flight (Smith 1977, Scholey 1986a, Alexander 1992, Feduccia 1996). This argument assumes that gliding locomotion is less expensive than quadrupedal locomotion, and therefore animals with the ability to glide have greater inclusive fitness. We refer to this idea as the cost of transport hypothesis. While other hypotheses have been proposed to explain the evolution of gliding (Caple 1983, Scheibe and Robins 1998), the hypothesis that gliding locomotion is energetically less expensive than quadrupedal locomotion over the same distance appears to have support (Feduccia 1996).

There have been few attempts to assess the veracity of the cost of transport hypothesis. Amongst studies of gliding performance in mammals (Hampson 1965, Polyokova and Sokolov 1965, Nachtigall *et al.* 1974, Nachtigal 1979, Scholey 1986b, Scheibe and Robins 1998, Addington *et al.* 2000, Jackson 2000, Keith *et al.* 2000, Wright 2000, Vernes 2001, Flaherty 2002, Stafford *et al.* 2002), only Scholey (1986b), Scheibe and Robins (1998), Keith *et al.* (2000), Wright (2000), and Flaherty (2002) attempted to

estimate cost of gliding transport, and only Dial (2003) explored the relationship between body mass and transport cost across taxa. Model-based estimates of gliding cost have been determined for only 4 species: *Petaurista petaurista* (giant flying squirrel), *Glaucomys volans* (southern flying squirrel), *Petaurus norfolcensis* (squirrel glider), and *Petaurus breviceps* (sugar glider). These estimates of transport cost lack the precision of direct measures of metabolic rate or excess post-exercise oxygen consumption. However, the models provide an initial assessment, and permit comparisons across species that would otherwise not be possible.

Evaluation of the cost of transport hypothesis requires estimation of both gliding cost and cost of quadrupedal transport. Because gliding requires an initial climb to a launch point, gliding cost is a monotonically decreasing function of distance while cost of quadrupedal locomotion is constant relative to distance. The distance at which the cost of gliding is less than the cost of quadrupedal locomotion over the same distance is the cost effective glide distance D_e. When D_e is greater than the glide distance typically exhibited by the animals, the cost of transport hypothesis is falsified. If quadrupedal movement across the ground or through the canopy requires climbing, the true cost of quadrupedal locomotion will be underestimated, D_e will be overestimated, and the Type I error rate increased.

Using these models, *Glaucomys volans* Shaw, 1801 (mass = 70 g) appears to realize an energetic benefit from gliding after only 3 m (Scheibe and Robins 1998), and Scholey (1986b) has reported a cost effective glide distance for *P. petaurista* (mass = 1295 g) of about 45 m. Reanalysis of Scholey's work by Scheibe and Robins (1998) suggests that distance may be an underestimate. In any case, Ando and Shiraishi (1993) reported a mean glide distance in another large glider (Japanese giant flying squirrel; *P. leucogenys*) of less than 20 m (verified by Stafford *et al.* 2002), so it may be that large flying squirrels do not realize an energetic benefit from gliding.

In this paper we use glide data collected in the field to describe the gliding performance of *G. sabrinus* (northern flying squirrel, mass = 125 g), and estimate cost of gliding transport and cost effective glide distance. We compare these data to those published for *G. volans* and *P. petaurista*, and with unpublished data for *Petaurus breviceps* and *P. norfolcensis*.

Methods

Flying squirrels were live-trapped on Prince of Wales and Mitkof Islands in the Tongass National Forest of Southeast Alaska in the fall of 2000 and 2001. Six grids were established on the islands in either an 8-by-12 or 10-by-10 station configuration. Between trap spacing was 40 m on all grids. Both grids on Mitkof Island were in old-growth habitat composed primarily of western hemlock (*Tsuga heterophylla*), mountain hemlock (*Tsuga*), red alder (*Almus rubra*), Sitka alder (*Almus crispa sinuata*), and Sitka spruce (*Picea sitchensis*). Height to the bottom of the canopy was about 45 m. On Prince of Wales Island there were 2 old-growth grids and two muskeg grids. The muskeg habitats were comprised primarily of shore pine (*Pinus contorta*), western hemlock, mountain hemlock (*Tsuga mertensiana*), yellow cedar (*Chamaecyparis nootkatenis*) and red cedar (*Tsuga plicata*). Here, height to the canopy was about 20 m.

Two Tomahawk traps (www.livetrap.com) baited with a mixture of peanut butter, rolled oats, and molasses, were used at each trap station. One trap was placed on the ground within 5 m of a tree, and the 2nd trap was mounted on the tree at breast height. Each trap was covered with moss, bark, and/or a water resistant cardboard box to keep trapped squirrels dry. Wooden boxes or bottoms of milk cartons filled with dry polyfil batting were placed behind the treadle of each trap for insulation. Traps were operated for 12 nights during each trapping cycle.

Captured squirrels were ear-tagged, weighed, sexed, and released about 1.5 m above the ground on a tree trunk near the point of capture. Typically, squirrels climbed to a launch point on a tree and glided to another tree. The time (s) required to climb the tree was determined with a digital stopwatch. The heights (m) of the launch and landing points were estimated using a clinometer and either a laser rangefinder or a fiberglass tape. The horizontal distance (m) between base of the launch tree and the base of the landing tree was estimated with a laser rangefinder or a clinometer and a fiberglass tape. Because the terrain was not flat, we measured the slope of the ground between the launch and landing tree and estimated the horizontal glide distance trigonometrically. Glides were timed (s) using a digital stopwatch. Sometimes, the squirrels did not climb the trees but leapt to the ground and ran to a nearby tree. In these cases, squirrels were timed (s) as they ran along the ground, and the distance (m) covered was measured with a fiberglass tape to the nearest cm. These measures were used to estimate running speed. All times were recorded to the nearest 0.01 s. Distances estimated with clinometers and rangefinders were measured to the nearest dm.

Running and climbing speed data were supplemented with laboratory data for 4 animals from a captive colony of *G. sabrinus bangsi* (captured in Idaho, USA) and *G. sabrinus sabrinus* (captured in Wisconsin, USA). These animals were induced to climb a 3-m tall snag (diameter = 0.27 m) erected in the lab. A 2-m section of the snag was marked, and the time to climb this distance was averaged from measurements by 3 observers with digital stopwatches. To estimate running speed, the snag was placed in an elevated horizontal position, and squirrels were induced to run along the snag. Three observers timed each event. In running and climbing trials in the lab, squirrels were induced to move as rapidly as possible by tapping the snag directly behind the animal. In the field, the animals selected their own pace. Because cost-effective glide distance and cost of transport are dependent on velocity (eqns 1-3), use of a range of running and climbing speeds enabled us to assess the precision of our results.

Cost of transport was estimated using the model of Scholey (1986b) and Scheibe and Robins (1998). The model compares the cost of gliding with that of quadrupedal transport. Gliding locomotion requires an animal to climb to a launch point, thus the cost of gliding includes the cost of climbing. Cost of gliding was estimated using:

$$C_g = \frac{P_c T_c + P_g T_g}{MgD} \tag{1}$$

where P_c and P_g denote the metabolic power of climbing and gliding respectively (see Appendix 1), and T_c and T_g the time spent climbing and gliding. Thus, PT represents the total work associated with either climbing or gliding, M – body mass, g – gravitational acceleration, and D – horizontal or ground distance. The resultant cost estimate is unit free (Taylor 1977, Alexander 2003). Similarly, the cost of quadrupedal transport (C_r) can be estimated using:

$$C_r = \frac{P_r T_r}{MgD}, \tag{2}$$

where P_r – power of quadrupedal locomotion (see Appendix 1), and T_r – time spent moving quadrupedally.

We define the cost effective glide distance (D_e) as that distance at which $C_g \leq C_r$. As noted by Keith *et al.* (2000), if we ignore the cost of launching this occurs when

$$D_e = \beta_0 \Big/ \frac{V_c}{P_c}\left(\frac{P_r}{V_r} - \frac{P_g}{V_g}\right) - \beta_1. \tag{3}$$

To estimate this distance, we first fitted a RMA (reduced major axis) regression (Sokal and Rohlf 1995) to the data for vertical drop and horizontal glide distance. The parameters of the regression model represent the initial vertical drop (β_0) of the glide (Scholey 1986b) and inverse glide ratio (β_1: Δ altitude / Δ distance). Second, estimates of power (P_c, P_r *and* P_g) were obtained using the models of Scholey (1986b). Third, the velocity of running (V_r) and climbing (V_c) were obtained as described above, and velocity of gliding (V_g) was derived form a log linear regression of air speed on glide distance. Finally, we plotted D_e as a function of climbing and running speed, and as a function of changes in gliding performance. That is, we used RMA regression parameters (β_0 and β_1) as well as these parameter estimates ± 1 SE.

Robins *et al.* (2000) identified reverse sexual size dimorphism in *Glaucomys volans*. Because body size has possible aerodynamic consequences, we measured glide parameters and performed all regressions separately for males and females. Data for horizontal glide distance and air speed were trimmed by removing the largest and smallest observation for each sex. The remaining data were log transformed, and normality evaluated using the Kolmogorov-Smirnov test and box plots (Tukey 1977). Glide angles for males and females were compared using the Watson-Williams test (Zar 1999). This test assumes the data follow the von Mises, or circular normal distribution (Gumbel *et al.* 1953; cited in Zar 1999), but is robust to deviations from the distribution except when sample distributions are not unimodal or have unequal dispersion. We evaluated stem and leaf plots and box plots (Tukey 1977) to assess possible deviations from these assumptions.

Results

We measured 168 glides by 35 individual females and 47 males. Components of some glides were not measured. Weighted mean glide distance varied from 12.5 (± SD = 16.1) m for females in 2001, to 14.4 (± SD = 8.5) m for males in 2000. Comparison of glide parameters using t-tests for trimmed and log transformed data revealed no significant differences between glide distances of males and females ($t_{0.05,76} = 0.580$, $p = 0.58$). Similarly, air speed did not differ between sexes ($t_{0.05,64} = 1.395$, $p = 0.17$). Air speed varied from 6.3 (± SD = 1.8) m/s for males in 2000, to 8.1 (± SD = 3.8) m/s for females in 2001. Weighted mean glide angles varied from 36.3 (± SD = 9.4)° for males in 2000 to 44.0 (± SD = 17.1)° for females in 2001. The distributions of angles for males and females were unimodal. Glide angles did not differ between sexes (Watson-Williams test, $F_{0.05,1,80} = 2.599$, $p > 0.1$).

Results of the RMA regressions of vertical drop against horizontal glide distance are presented in Fig. 1. The intercept is equivalent to the initial vertical drop of the glide (Scholey 1986b), or alternatively, the initial vertical drop minus the climb to stall during landing (Vernes 2000). Initial vertical drop varied from 1.5 m for males in 2000, to 3.9 m for males in 2001. Vertical drop of females varied from 2.5 m (2001) to 3.9 m (2000). RMA regression slopes are equiva-

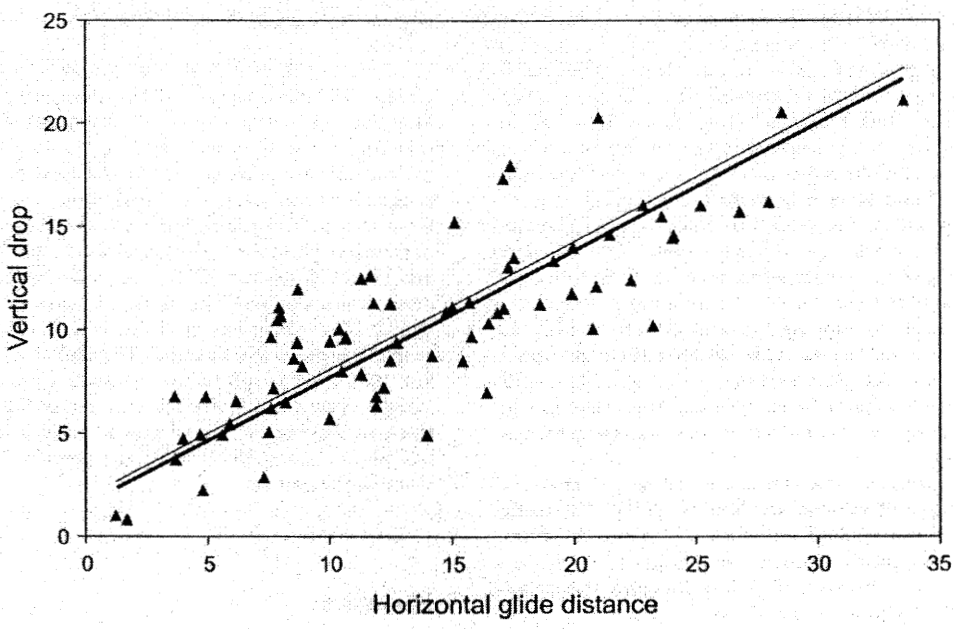

Fig. 1. Vertical drop (m) versus horizontal glide distance (m) for 168 glides recorded for *Glaucomys sabrinus* in the field. Heavy line (males: Drop = 1.53 + 0.61Distance, SE of slope = 0.61) and fine line (females: Drop = 1.87 + 0.62Distance, SE of slope = 0.62) represent reduced major axis regressions.

lent to the inverse glide ratio (Scholey 1986b), and varied from 0.38 (glide ratio = 2.65) for males in 2001 to 0.61 (glide ratio = 1.64) for females in 2001. The dispersion of points about the regression lines (Fig. 1) indicates extensive variation in performance. Weighted mean glide ratios varied from 1.36 to 1.54 (Table 1).

Weighted mean air speed varied from 6.3 m/s to 8.1 m/s, and increased with ground distance (Fig. 2) in a logarithmic fashion. Terminal velocity appears to be close to 15 m/s. Because the animals accelerated through the early portions of the glides, the mean glide speeds reported here (and in other papers) underestimate terminal velocity. Our longest glide of about 65 m had a mean air speed of about 10 m/s. Clearly, terminal velocity is dependent on wind condition, direction of the animal relative to the wind, body mass, and the posture assumed by the animal during the glide.

Table 1. Parameter estimates for male and female *Glaucomys sabrinus* during the 2000 (00) and 2001 (01) field seasons. Total sample size is indicated by N, and number of individuals by *n*. $\bar{x}$ – mean, SD – standard deviation, M – males, F – females.

Parameter	M/00				M/01				F/00				F/01			
	N	*n*	$\bar{x}$	SD	N	*n*	$\bar{x}$	SD	N	*n*	$\bar{x}$	SD	N	*n*	$\bar{x}$	SD
Weight (g)	72	33	125.9	12.63	30	14	120.7	21.07	50	27	125.4	11.68	13	7	115.9	19.29
Glide Distance (m)	72	33	14.4	8.49	30	15	13.3	10.46	50	27	14.1	9.24	13	8	12.5	16.13
Vertical Drop (m)	72	33	10.2	5.16	30	15	8.8	5.04	50	27	10.5	4.52	13	8	10.1	6.48
Glide Angle (°)	72	33	36.3	9.39	30	15	39.8	17.57	50	27	41.3	11.43	13	8	44.0	17.05
Glide Ratio	72	33	1.5	0.57	30	15	1.5	1.20	50	27	1.4	0.68	13	8	1.5	1.01
Ground Speed (m/s)	63	26	5.0	1.56	29	14	5.2	2.42	46	23	5.0	2.38	13	8	5.6	2.85
Air Speed (m/s)	63	26	6.3	1.84	29	14	7.5	4.98	46	23	6.4	2.32	13	8	8.1	3.80

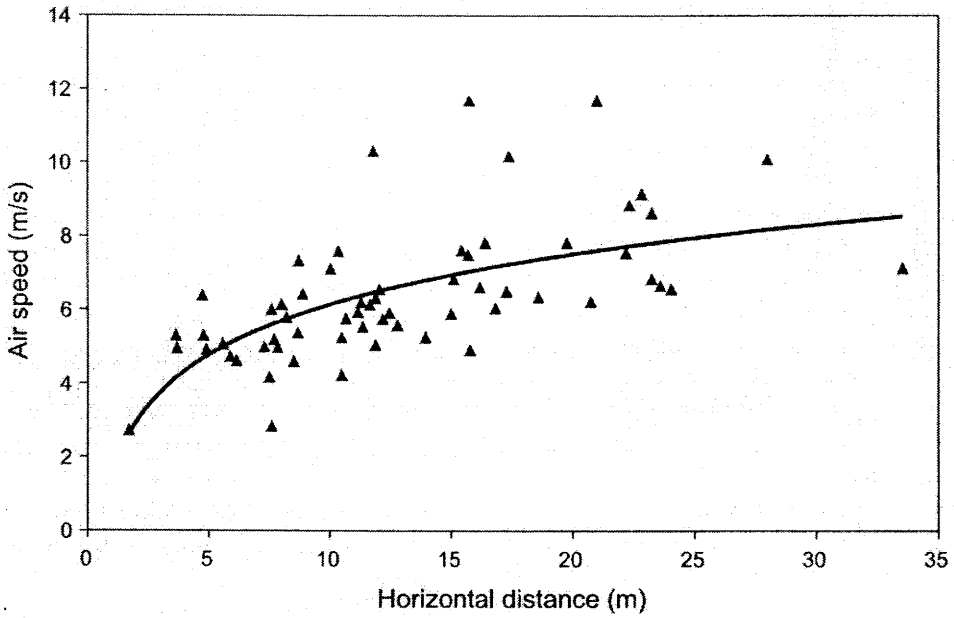

Fig. 2. Estimated direct glide speed (m/s) relative to horizontal ground distance (m) for *Glaucomys sabrinus*. The direct glide speed is an estimate of air speed. The curved line represents a log linear regression of estimated air speed against distance: $V = 1.57 + 1.98 \ln D$; $R^2 = 0.38$.

Running and climbing speeds measured in the lab and field differed dramatically (Table 2). In each case, the animals were able to run faster than they were able to climb. Running speeds varied from 0.8 m/s for males in the field, to 3.7 m/s for a female *G. sabrinus sabrinus* in the lab. The running speeds for the *G. sabrinus sabrinus* female and male were different. The female in this case was a 160 g adult, while the male was a 90 g young adult. Climbing speeds varied from 0.3 m/s for females in the field, to 1.5 m/s for the adult female *G. sabrinus sabrinus*.

Table 2. Estimates of running and climbing speeds for a pair of *Glaucomys sabrinus sabrinus* (Wisconsin, USA), a pair of *G. sabrinus bangsi* (Idaho, USA), and field caught *G. sabrinus griseifons* (Alaska, USA). $\bar{x}$ – mean, SD – standard deviation, n – sample size, F – females, M – males.

	Running			Climbing		
	$\bar{x}$	n	SD	$\bar{x}$	n	SD
Wis F	3.7	18	0.52	1.5	21	0.21
Wis M	1.8	25	0.73	0.9	13	0.26
Idaho F	2.4	10	0.31	1.2	10	0.24
Idaho M	2.5	10	0.25	1.3	10	0.30
Ak F	1.0	4	0.43	0.3	19	0.24
Ak M	0.8	4	0.33	0.3	34	0.23

The cost of gliding transport (Fig. 3) decreased rapidly with increasing glide distance, while cost of quadrupedal transport is necessarily constant (eq. 2). Both males and females exhibited cost effective glide distances that were shorter than 14 m when climbing speed was high (1.5 m/s). Cost effective glide distance was dependent on climbing and running speed (Fig. 4) as well as air speed, glide angle, and initial vertical drop. D_e decreased with increasing climbing speed, but increased dramatically with increasing running speed. Similarly, steep descents with large initial vertical drops (β_0 + 1 SE and β_1 + 1 SE) resulted in longer cost effective glide distances than glides with shallow descents and small initial vertical drops (β_0 – 1 SE and β_1 – 1 SE). Flying squirrels with glide parameters that fall within 1 SE of the mean values have cost effective distances that are shorter than mean glide distances.

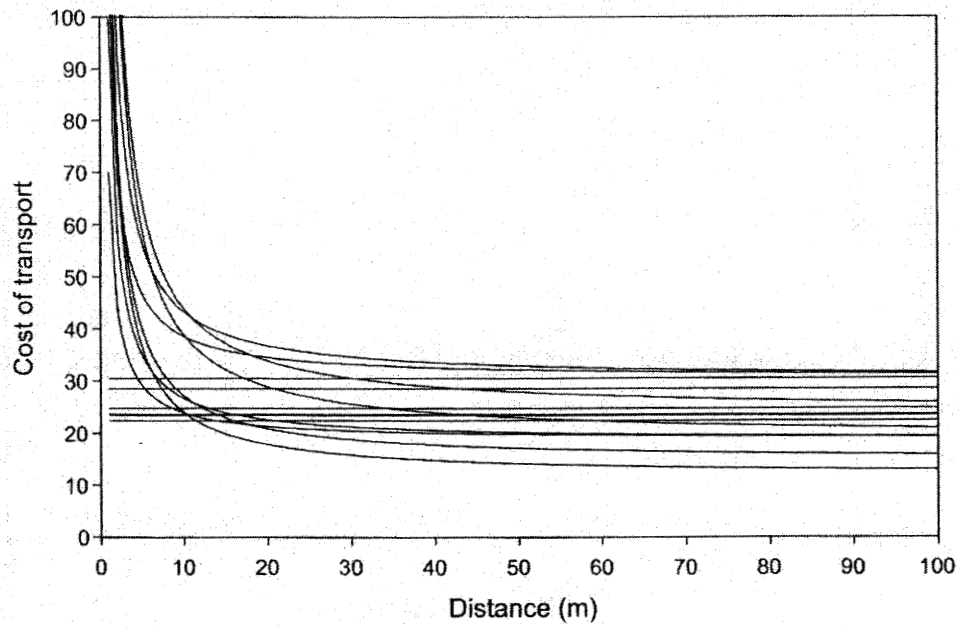

Fig. 3. Estimated cost of transport for *Glaucomys sabrinus*. Curved lines represent the cost of gliding, and horizontal lines represent cost of quadrupedal transport. The curved lines represent costs for males and females during 2 field seasons using the fastest observed climbing speeds (4 lower curves) and the slowest observed climbing speeds (4 upper curves). The horizontal lines represent the range of costs derived from lab animals induced to run fast, and field animals allowed to chose their own pace. Note that cost of transport is unit free.

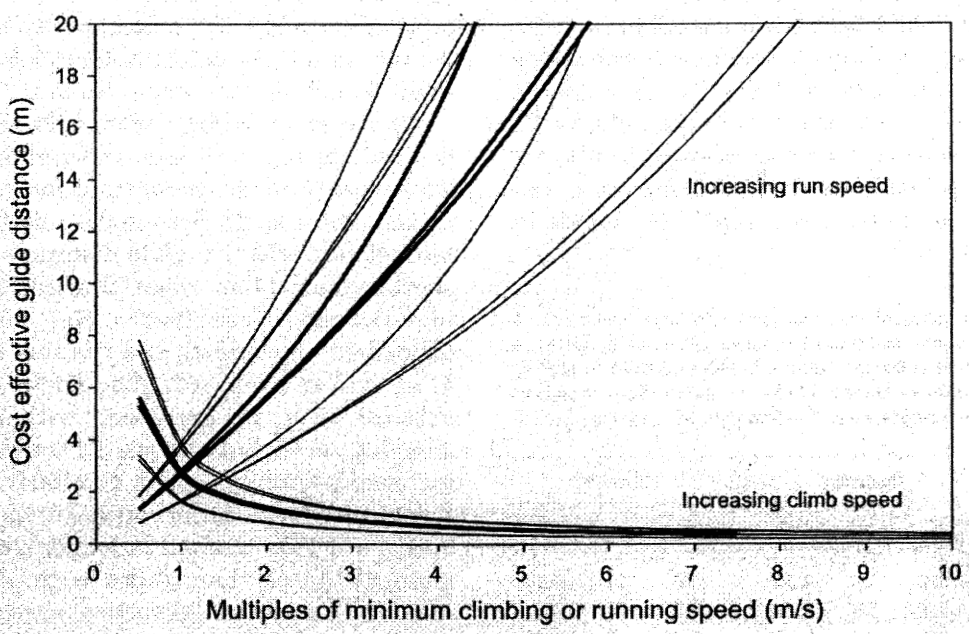

Fig. 4. Cost effective glide distance as a function of performance. Curves with positive slope depict D_e with respect to increasing running speed, while those with negative slope depict D_e with respect to increasing climbing speed. Heavy lines illustrate glides with mean glide ratios and mean initial vertical drops; light lines illustrate glides with 1 SE of initial vertical drop and glide ratio. Because glide speed increases with distance, each scenario is modeled for glide speeds corresponding to 5, 50, and 100 m glides.

Discussion

There have been few determinations of the cost of gliding transport (Scholey 1986b, Hendershott 1996, Scheibe and Robins 1998, Wright 2000, Flaherty 2002), even though gliding is often assumed to be a consequence of selection for reduced cost of transport (Alexander 1992, Feduccia 1996). Scholey (1986b) reported a cost effective glide distance of about 45 m for *Petaurista petaurista*, and his work has been cited as an example of the energetic advantage of gliding. Scheibe and Robins (1998) noted several errors in Scholey's paper, and estimated the cost effective glide distance for *Petaurista* to be closer to 100 m. Work by Ando and Shiraishi (1993) and Stafford *et al.* (2002) revealed a mean glide distance for *Petaurista leucogenys* of about 20 m, certainly less than the 100 m (or even 45 m) needed for a cost effective glide. Unfortunately, Stafford *et al.* (2002) did not collect data necessary to evaluate directly the cost of transport in *P. leucogenys*, and consequently our knowledge of cost of transport for large pteromyines is limited.

Cost of transport decreases with increasing body mass (Taylor 1977), but the relationship between cost effective glide distance and body mass (Table 3) is not certain. An important component of the cost of gliding is the cost of climbing to the launch point, and climbing is proportionately more expensive for larger animals (Dial 2003).

Table 3. Comparative performance data for gliding mammals. Sources: 1 – unpublished data for Robins 1994, 2 – Robins 1994, 3 – Scheibe and Robins 1998, 4 – Vernes 2001, 5 – this study, 6 – Jackson 2000, 7 –Wright 2000, 8 – Flaherty 2002, 9 – Scholey 1986b, 10 – Ando and Shiraishi 1993, 11 – Stafford *et al.* 2002

Species	Mass	Mean glide distance (m)	Estimated cost effective glide distance (m)	Source
Glaucomys volans	70	14.2	3	1, 2, 3
Glaucomys sabrinus	125	14–19	< 10	4, 5
Petaurus breviceps	70–100	20.4	> 100	6, 7
Petaurus norfolcensis	190	10.3	> 100	8
Petaurista petaurista	1295	60	45–100	9, 3
Petaurista leucogenys	1300	20		10, 11

Thus, we expect the cost effective glide distance to increase with increasing body mass (see Dial 2003). Using both lab and field glides, Scheibe and Robins (1998) estimated a cost effective glide distance of about 3 m for *G. volans*. Our results for *G. sabrinus* suggest that this larger pteromyine has a correspondingly longer cost effective glide distance (ca 10 m). This finding is consistent with the much longer cost effective glide distance for *P. petaurista*. Wright (2000) found the marsupial *Petaurus breviceps* (males 100 g, females 70 g) did not realize a consistent energetic benefit from gliding in a laboratory setting. His result for this small marsupial does not fit our pattern, but can be explained in 2 ways. First, the maximum vertical drop possible for his animals was 6.2 m, and Jackson (2000) indicated that *P. breviceps* requires an initial vertical drop of 10 m before assuming a normal glide trajectory. Second, *P. breviceps* climbs very differently than *Glaucomys*, using a relatively slow contralateral gait. The most expensive component of gliding locomotion is the climb to the launch point, and the slow gait by *Petaurus* means these animals are working against gravity for an extended period. In a field study of the marsupial squirrel glider (*Petaurus norfolcensis*: mass = 190 g) Flaherty (2002) estimated that the cost effective glide distance was significantly greater than the mean glide distance. Thus, phylogenetic history may be important in the evolution of gliding locomotion.

Robins *et al.* (2000) found significant reverse sexual size dimorphism (RSD) in a sample of *G. volans*, particularly with respect to distal limb elements and the tail. While mass did not differ, the longer limbs and tails of females resulted in reduced wing loading. They estimated that pregnant females would have wing loadings equivalent to those of males. It is possible that the reduced wing loading of females results in higher glide ratios, although Scheibe and Robins (1998) noted no differences. Vernes (2001) found Canadian *G. sabrinus* males glided on average 19.0 m while females glided 14.2 m, and there was a slight corresponding difference between glide angles and glide ratios. His results are inconsistent with expectations of reverse size dimorphism (RSD), although no careful morphological

work has been done to identify RSD in *G. sabrinus*. In our study there was little difference between the distances glided by males and females. It is possible that the differences in our results are a consequence of season: our observations occurred during the fall, after reproduction had ceased, while Vernes' study occurred in July when females may have been pregnant or transporting litters. Increased mass associated with pregnancy may have resulted in faster, shorter glides by females in Vernes' study. The veracity of this idea is dependent on the identification of RSD in *G. sabrinus*. The effect of forest structure on gliding performance is unknown, and in light of the diversity of habitats used by *G. sabrinus*, potentially important.

Other than anecdotal information for *Eupetaurus* (Zahler 2000), *Colugo* (B. Wischusen, pers. comm.), and *Anomalurus* (L. Robbins and T. Macyntire, pers. comm.), we know little about gliding in larger mammals, or gliding in nonpteromyid mammals. We know that *Colugo* may glide as fast as 25 m/s (B. Wischusen, pers. comm.), and that the very large woolly flying squirrel of Kashmir is capable of executing 180° turns (Zahler 2000). Although Scholey (1986b), Ando and Shiraishi (1993) and Stafford *et al.* (2002) have published some information about gliding in *Petaurista*, the data necessary to evaluate comprehensively the cost of transport in this genus is lacking.

Our assessment of cost effective glide distance relies on a comparison of climbing and gliding, with quadrupedal movement either through the canopy or across the ground. Clearly, this simple comparison ignores the complexity of canopy structure and/or obstacles to direct movement on the ground or in the canopy. If an arboreal quadruped moves from tree to tree by climbing down to the ground, moving to the next tree, and climbing up the next tree, our estimate of cost of quadrupedal transport is a significant underestimate. In this scenario, the cost effective gliding distance would be less than we have estimated. This would not change our result with respect to the veracity of the cost of transport hypothesis.

Our analysis is based on means of performance events that vary considerably. The animals exhibit a variety of behaviors when released from traps, and we do not know how dissimilar these are from those exhibited by undisturbed animals. However, an expected response to trap release that might differ from more typical locomotor behavior is rapid climbing to a possible launch point, and this decreases the cost effective glide distance. Differences in glide trajectory following release from a trap would affect our conclusion if they resulted in significantly shorter mean glide distances or steeper descents.

Other hypotheses may explain the selective advantage of gliding locomotion, either alone or in concert with cost of transport. Predator avoidance (Emmons and Gentry 1983, Keith *et al.* 2000) and optimal foraging (Goldingay 2000, Keith *et al.* 2000) have been offered as explanations, and each is testable to some extent. For example, if gliding represents a means of avoiding predation, we can predict gliding animals to maximize launch acceleration and/or ballistic range (Keith *et al.* 2000). That is, the animals should get away from the predator as quickly as possible, or they should maximize the distance between themselves and the predator. Tests of this hypothesis require precise measurements of leaping performance in the lab (Essner 2002) as well as careful analysis of the allometry associated with the skeletal and muscular components of leaping. Keith *et al.* (2000) explored this question, but only in a very superficial way. In accordance with the predictions of Hill (1950) they found that for *G. volans*, neither launch acceleration nor ballistic range changed with body mass (Keith *et al.* 2000). That is, both large and small animals achieved similar launch acceleration and ballistic range, and presumably are equally adept at avoiding predation. If launch performance (and predator avoidance) is similar in large and small individuals, then shape differences in the propulsive machinery are expected (Hill 1950, Scheibe and Essner 2000). Essner (2002) demonstrated that *G. volans* does not maximize extension of the pelvic appendages during launch as expected under the predation hypothesis, suggesting that other factors like control and stability during launch are important. Furthermore, whereas Holmes and Austad (1994) suggested that gliding mammals

lived longer than non-gliding forms, perhaps as a consequence of predator avoidance, that analysis has been questioned by Stapp (1994) on statistical grounds. Comparative data on the natural history, morphology, and locomotor performance of gliders and related taxa are needed to assess the predator avoidance hypothesis.

Gliding locomotion may have little to do with cost of transport, and may instead represent a means of foraging over large areas in a relatively short time. When a food source is patchily distributed, gliding may enable animals to reduce travel time between foraging patches and thus leave the patch when the rate of return is still high (Charnov 1976). In this way, they can treat a coarse-grained habitat in a fine-grained fashion. A non-gliding mammal of similar size would be less able to exploit a patchy resource.

We were unable to reject the cost of transport hypothesis. However, a comprehensive test of the hypothesis will require analysis of transport costs across the full size range of mammalian gliders, and across taxa of eutherian and metatherian gliders. Only then will it be possible to assess the relationship between size, evolutionary history, and cost effective glide distance. Even then, the alternative hypotheses are still viable and may in fact be more interesting. Evaluation of the predator avoidance hypothesis will require comparative studies of locomotor performance and morphology across many species, thereby establishing if there is size invariant maximization of potential launch performance within species. Behaviorally, it is important to know if gliders respond to perceived predation threat. Is foraging behavior and/or gliding performance different when predation threat is high? Finally, knowledge of space use by gliding mammals (Hanski *et al.* 2000, Selonen *et al.* 2001) is essential to understand how gliding facilitates foraging, and if, in spite of the cost of transport, the animals are able to forage more efficiently than non-gliding mammals.

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Appendix 1.

Power associated with climbing (joules/s) is estimated as:

$$P_c = \left(f + \frac{Mg}{\eta}\right) V_c + aP_b$$

where f is a constant defined by Taylor (1977) as $10.7M^{-0.4}$, M – mass, g – gravitational acceleration (9.81m/s/s), η – climbing efficiency, V_c – climbing velocity (m/s), a is a constant with value 1.7 (defined by Taylor 1977), and P_b is the power of metabolism (joules/s) estimated as $3.42M^{-.25}$ (Stapp 1992). Analysis by Scheibe and Robins (1998) revealed the model to be robust with respect to climbing efficiencies in the range of 0.2 and 0.4. We used a climbing efficiency of 0.4 in the analysis presented here. The power of quadrupedal locomotion was estimated similarly as:

$$P_c = fV_r + aP_b$$

where V_r is the velocity of quadrupedal locomotion. The power consumption of gliding was estimated simply as $2P_b$ (Baudinette and Schmidt-Nielsen 1974).