

# LOCOMOTOR PERFORMANCE IN THE SQUIRREL GLIDER, *PETAURUS NORFOLCENSIS*, AND THE SUGAR GLIDER, *PETAURUS BREVICEPS*

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We evaluated gliding, climbing, and running performance by *Petaurus norfolcensis* in southern Queensland, Australia and by a laboratory colony of *P. breviceps*. The data were used to test the hypothesis that gliding locomotion is energetically less expensive than quadrupedal transport, and is thus a reasonable explanation for the evolution of gliding. Gliding locomotion is less expensive than quadrupedal transport only when *P. norfolcensis* is able to climb to a launch point rapidly. We found no conditions in which gliding was less expensive than quadrupedal transport for *P. breviceps*. We compare these results with published data on North American flying squirrels, and argue that gliding locomotion in mammals may be a solution to foraging optimisation problems such as decreasing travel time between patchy food resources and increasing foraging velocity.

Key words: Cost of transport, gliding, *Petaurus breviceps*, *Petaurus norfolcensis*.

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Gliding locomotion evolved in mammals as early as the Mesozoic in the extinct Order Volaticotheria, (Meng et al. 2006) and later in Eomyidae (Storch et al. 1996), and Myoxidae (Mein and Romaggi 1991). Amongst extant species, gliding evolved independently in the marsupial Order of Diprotodontia (Acrobatidae, Petauridae, and Pseudocheiridae), and the eutherian Orders of Dermoptera (Cynocephalidae) and Rodentia (Anomaluridae and Sciuridae). The evolution of gliding is often explained on the basis of foraging optimisation, cost of transport, or predator avoidance. The cost of transport hypothesis has broad general support, especially in arguments concerning the origin of powered flight (Feduccia 1996) although there are few tests in the literature (Scholey 1986; Scheibe and Robins 1998; Scheibe et al. 2006). This hypothesis argues that gliding is energetically less expensive than quadrupedal locomotion in that climbing to a launch point and gliding to another tree requires less energy than moving quadrupedally through the canopy or on the ground (Emmons and Gentry 1983; Norberg 1985). However, studies of mammalian gliding performance (Hampson 1965; Polyokova and Sokolov 1965; Scholey 1986; Ando and Shiraiishi 1993; Scheibe and Robins 1998; Jackson 2000a; Addington et al. 2000; Wright 2000; Vernes 2001; Zahler 2001; Stafford et al. 2002; Keith et al. 2000; Scheibe et al. 2006) seldom assess

cost of transport. Information on the gliding behaviour and performance of marsupials is even more limited (Nactigall et al. 1974; Johnson-Murray 1977; Nactigall 1979a, 1979b; Jackson 2000a). Of these studies, only a few estimated cost of transport (Scholey 1986; Scheibe and Robins 1998; Keith et al. 2000; Wright 2000; Scheibe et al. 2006). Consequently, the list of species for which we have estimates of gliding cost is short: *Glaucomys volans*, *G. sabrinus*, *Petaurista petaurista*, and *Petaurus breviceps*. *Glaucomys sabrinus* appears to realize an energetic benefit from gliding after distances of less than 14 m (Scheibe et al. 2006) while *G. volans* appears to realize a benefit after only 7 m (Scheibe and Robins 1998). Although there is some evidence to suggest important differences in performance and locomotor costs between small and large gliders (Scheibe and Robins 1998), there are too few data to make generalisations about the different groups of mammalian gliders.

Jackson (2000a) found patagial surface area and log body mass to be highly correlated across species of gliding possums, and predicted gliding efficiency would be very similar for all marsupial species. However, he noted that small species are more strongly affected by turbulence than large species. There are morphological differences between flying squirrels and possums, and

consequently there is no expectation that locomotor performance will be identical. Flying squirrels have a styliform cartilage that extends the wing tip of the patagium (Thorington et al. 1998) and may reduce the cost of gliding (Scheibe and Robins 1998) by reducing wing tip turbulence. In *Petaurus* and *Acrobates*, the patagium attaches to the fifth digit of the manus, and the styliform cartilage is absent. While *Glaucomys* has a distichous tail that may add 20 to 30% to the planar surface area (Thorington and Heaney 1981; Wells-Gosling and Heaney 1984) and acts like a flow rudder, *Petaurus* has a cylindrical tail that acts as a drag rudder (Scheibe and Robins 1998). *Petaurus* and all other possums have opposable digits that are lacking in *Glaucomys* and the other pteromyines.

In this paper, we use field glide data from *Petaurus norfolcensis* (squirrel glider) in southern Queensland, Australia, and laboratory glide data from *P. breviceps* (sugar glider) to estimate the cost of gliding transport, and the cost effective glide distance. Using these data, we evaluate the cost of transport hypothesis for the evolution of gliding, and compare our results with those of Scheibe and Robins (1998) and Scheibe et al. (2006).

## METHODS

Squirrel gliders were live-trapped on the western portion of Minnippi Parklands, owned and managed by Brisbane Council, Queensland, Australia, in June 2002. The habitat was open eucalypt forest composed primarily of ironbark (*Eucalyptus sideroploia*, *E. drapanophylla*), bloodwood (*E. intermedia*), red gum (*E. tereticornis*), grey gum (*E. propinqua*), and melaleuca (*Melaleuca quinquenervia*). *Lantana camera* had invaded portions of the site. Trap grids were maintained and operated by faculty and students of Southern Cross University, as part of ongoing studies of *P. norfolcensis*.

Approximately ten traps were open each night for 13 nights, then closed for five nights, and reopened for three nights. Trap grids were composed of ten traps spaced roughly 10 m apart. Traps were moved throughout the area approximately every three nights to increase trap success. Trap platforms were approximately 5 m from the ground and attached to various eucalypt species. Large Elliot traps (45 x 15 x 15 cm) were secured to the platforms with two rubber straps and baited with a mixture of honey, muesli (rolled oats), and peanut butter. Dead leaves were added to each trap to minimize cold exposure during the night. A plastic bag was secured around the trap to keep captured animals dry.

Captured animals were ear-tagged on first capture, weighed, sexed, aged, and reproductive status was determined for females by examining the pouch. Captured animals were released on the ground at the

base of a tree near the point of capture. Usually, animals climbed to a launch point on the tree and glided to another tree. When possible, both the climb up the tree and the subsequent glide were timed using a digital stopwatch. The heights of the launch and landing points were estimated using a clinometer and a fiberglass tape. The horizontal distance between the launch point and the landing point was measured using a fiberglass tape. Generally, the terrain was flat but occasionally it was necessary to measure slope of the ground between launch and landing sites, and to estimate horizontal glide distance trigonometrically. In several instances, it was possible to estimate running speed. This was done by releasing the glider several metres from the base of a tree, timing the animal with a digital stopwatch, and then measuring the distance with the fiberglass tape. Thus, it was possible to estimate glide distance, glide angle, gliding speed, running speed, and climbing speed. The 95% confidence intervals for running and climbing speed were computed.

Gliding performance was also recorded at night using spotlights with red filters, clinometers, and a fiberglass tape. The methods noted above were used to measure height of launch and landing, and horizontal ground distance between the two points. Glide angle was then estimated trigonometrically.

A colony of 12 *P. breviceps* was established and maintained at Southeast Missouri State University in 1998. The diet included fruits, vegetables, meat, pinkies, nuts, yoghurt, and high protein baby food with water provided ad lib. Animals were housed in cages 0.61 x 0.61 x 0.92 m in male/female pairs and maintained on a 12 h L/D cycle.

Gliding performance was measured in a laboratory measuring 7 x 7 x 14 m. A small wooden launch platform was attached to a section of 10 cm PVC pipe covered in AstroTurf (providing traction for the animals climbing) imbedded in a 20 L bucket filled with concrete. The height of the platform was adjusted by adding sections of pipe to the structure to increase the height of the launch platform up to 6.2 m.

Animals climbed to the launch platform and then leaped from the platform to the lab floor, or to one of two 3 m tall snags (section of dead tree collected in Missouri) in the lab. Two or three observers timed each glide using digital stopwatches. The resulting times were then averaged. Vertical drop and horizontal glide distance was measured using fiberglass measuring tapes.

Climbing performance was measured by releasing an animal at the base of a 3 m tall snag and encouraging the animal to climb as quickly as possible while two or three observers timed the climb. The times then were

averaged. Running performance was measured by encouraging an animal to run along one of the snags lying on the floor. Two or three observers timed the event and the times were averaged.

Keith et al. (2000) developed models of cost effective glide distance (distance at which the cost of gliding transport is less than the cost of quadrupedal transport). The same methods for estimating cost effective glide distance were used by Scheibe et al. (2006) for *Glaucomys sabrinus*. These models were used in this study to estimate cost effective glide distance for *Petaurus norfolcensis* and *P. breviceps*.

The cost of quadrupedal transport was estimated using:

$$(1) \quad C_r = \frac{P_r T_r}{mgD}$$

Where  $P_r$  is the power of quadrupedal transport (Taylor 1977) estimated using known body mass and speed of locomotion,  $T_r$  is the time spent moving quadrupedally,  $m$  is the mass of the animal,  $g$  is gravitational acceleration (9.81 m/s/s), and  $D$  is horizontal or ground distance. The cost of quadrupedal transport is independent of distance for any given  $V_r$  (velocity of running) because  $T_r = D/V_r$ .

The cost of gliding was estimated using:

$$(2) \quad C_g = \frac{P_c T_c + P_g T_g}{mgD}$$

Here,  $P$  and  $T$  refer to power and time respectively, with  $c$  and  $g$  subscripts representing climbing and gliding. Thus, the cost of gliding incorporates the cost of climbing to a launch point. The cost of gliding increases monotonically with distance, and gliding is cost effective at the distance at which  $C_g = C_r$ . Note that while most direct measurements of cost of transport often are reported in terms of  $J m^{-1}$  or comparable units, although cost of transport is acknowledged as a dimensionless term (Fish and Baudinette 1999), the units in our models cancel and the resulting cost estimates are unit less (Taylor 1977, Alexander 2003, Scheibe et al. 2006).

The distance at which  $C_g = C_r$  can be estimated using:

$$(3) \quad D_e = \frac{(P_c T_c + P_g T_g) V_r}{P_r}$$

where  $D_e$  is the cost effective glide distance. Because velocity is  $D/T$ , and because  $P$  and  $T$  are the kinetic energy associated with either climbing or gliding, all units except distance cancel. Time to climb is dependent on distance climbed, and because launch height determines glide distance, time to glide is a function of glide distance.

The parameters of a reduced major axis regression of vertical drop (corresponds to required climbing distance) against horizontal glide distance were substituted into equation (3) for  $T_c$ . With simplification, this results in:

$$(4) \quad D_e = \beta_0 \frac{V_c}{V_r} \left( \frac{P_r}{V_r} - \frac{P_g}{V_g} \right) - \beta_1$$

In this model,  $\beta_0$  is the initial vertical drop of the glide (Scholey 1986) and  $\beta_1$  is the inverse glide ratio.  $V_c$ ,  $V_r$ , and  $V_g$  are velocity of climbing, running, and gliding, respectively. This model assumes that velocity of gliding is constant throughout the glide, which is incorrect, especially for longer gliders. Thus, velocity of gliding will be underestimated for long glides resulting in an overestimation of the cost effective glide distance.

Variation in performance among individuals was incorporated into the analysis in two ways. For *P. norfolcensis*, we constructed 95 % confidence intervals for running and climbing speeds, and these were used in the cost of transport plots to reflect the range of costs possible for the animals. For *P. breviceps* there were a sufficient number of observations to construct the RMA regressions of vertical drop against horizontal distance for each individual. The underlying distribution of the regression parameters is not  $N(\mu, \sigma^2)$ , and construction of the confidence intervals is not straightforward. Instead, we computed the quartiles for initial vertical drop ( $\beta_0$ ) and inverse glide angle ( $\beta_1$ ) and used these to explore graphically the effects of variation in performance on cost effective glide distance.

## RESULTS

Twenty-eight *P. norfolcensis* (mean weight = 190.14 g  $\pm$  3.57 SE) were trapped at Minnippi Parklands. Of these animals, it was possible to observe 25 glides, four running events, and three climbing events. Seven additional animals were observed gliding at night when illuminated with a spotlight. Based on 32 glides, *P. norfolcensis* exhibited a mean glide distance (Table 1) of 11.76 m (SE = 1.09 m) and a mean vertical drop of 9.38 m (SE = 0.98 m) resulting in a mean glide angle of 37.17° ( $\pm$  2.41 SE) with variation from 76.99° to 12.85°. The longest observed glide was 29.14 m and the shortest

		Mean	Standard Error	Min.	Max.	n
Animal Mass (g)	Pb	77.878	6.007	51.0	100.5	9
	Pn	190.143	3.568	156.0	222.0	28
Glide Distance (m)	Pb	2.779	0.109	0.430	5.870	166
	Pn	10.320	1.270	2.800	29.140	28
Glide Angle	Pb	50.777	1.050	0.000	84.034	166
	Pn	37.169	2.409	12.848	76.986	32
Running Speed (m/s)	Pb	1.323	0.029	0.483	2.056	147
	Pn	2.992	0.383	2.204	3.922	4
Climbing Speed (m/s)	Pb	0.716	0.021	0.243	1.460	145
	Pn	0.836	0.238	0.488	1.292	3
Horizontal Ground Velocity (m/s)	Pb	2.159	0.091	0.277	5.549	166
	Pn	4.992	0.377	1.000	9.251	21

Table 1. Summary of performance measurements. Pb signifies *Petaurus breviceps*. Pn signifies *Petaurus norfolcensis*

was 2.8 m. Mean running speed for four animals was 2.99 m/s ( $\pm 0.38$  SE) and mean climbing speed for three animals was 0.84 m/s ( $\pm 0.24$  SE).

We measured 168 glides by *P. breviceps* in 2000 and 2001. Mean weight for males was 90.59 g while females averaged 66.03 g compared to wild weights of 140 g for males and 115 g for females reported by Henry and Suckling (1984) and 60 to >80 g reported by Jackson (2000b). Glide distance and vertical drop were restricted by laboratory size, and maximum observed glide distance was 5.87 m with a mean glide

distance of 2.77 m ( $\pm 0.109$  SE). Averaged across individuals to avoid pseudo-replication, male and female glide distances were not significantly different ( $2.38 \text{ m} \pm 0.58 \text{ SE}$  vs.  $2.92 \text{ m} \pm 0.27 \text{ SE}$  respectively,  $t = 0.95$ ,  $P > .05$ ). However, females were more likely to launch from a greater height than males. Average glide angles exhibited by males were considerably shallower than those of females:  $43.22^\circ (\pm 5.34 \text{ SE})$  vs.  $56.27^\circ (\pm 2.28 \text{ SE})$  respectively. These differences approached significance (2-sided Watson-Williams Test;  $F = 5.79$ ,  $P < .10$ ). Averaged across individuals,

	N	Vertical Drop	Glide Distance	$\beta_0$	$\beta_1$
<i>Petaurus norfolcensis</i>	28	9.713	10.642	0.683	0.849
<i>Petaurus breviceps</i>	168	3.775	2.765	-0.001	1.366
<i>P. breviceps</i> M1	13	1.176	1.285	-0.789	1.529
<i>P. breviceps</i> M2	21	4.219	3.541	0.810	0.963
<i>P. breviceps</i> M3	15	2.117	1.865	-0.201	1.243
<i>P. breviceps</i> M4	12	1.203	1.294	-1.822	2.332
<i>P. breviceps</i> M6	10	6.100	3.944		
<i>P. breviceps</i> F1	35	4.451	3.593	0.074	1.219
<i>P. breviceps</i> F2	10	4.624	3.373	0.347	1.268
<i>P. breviceps</i> F3	16	3.296	1.810	0.623	2.332
<i>P. breviceps</i> F4	5	2.763	2.471	0.039	1.104
<i>P. breviceps</i> F5	19	4.552	2.374	1.531	1.273
<i>P. breviceps</i> F6	12	5.667	3.724	1.930	1.003
<i>P. breviceps</i> $Q_1$				-0.201	1.529
<i>P. breviceps</i> $Q_1$				0.810	1.104

Table 2. Glide parameters for both species of marsupial gliders, *Petaurus breviceps* and *P. norfolcensis*. The data for *P. breviceps* are also reported by individual, with M1 referring to male 1, F1 = female 2 etc.

females exhibited a mean running speed of 1.26 m/s ( $\pm 0.060$  SE), and males were somewhat faster (1.38 m/s  $\pm 0.045$  SE), although the difference was not significant ( $t = 0.394$ ,  $P = 0.20$ ). Males were able to climb at 0.75 m/s ( $\pm 0.032$  SE) while females climbed at 0.59 m/s ( $0.025 \pm$  SE). This difference was not significant ( $t = 2.005$ ,  $P = .07$ ).

The reduced major axis regressions of vertical drop against glide distance differed between the species (Fig. 1, Table 2). The slope of the line for *P. norfolcensis* was shallower than for *P. breviceps*. The inverse of the slope is the glide ratio, and the arctangent is the glide angle (Scholey 1986). Thus, *P. norfolcensis* was able to glide at a shallower angle than *P. breviceps*, and most glides by *P. breviceps* had angles greater than  $45^\circ$ , indicating parachuting events rather than glides. There was considerable variation about the regression lines, suggesting the animals were able to exert control over their glide trajectories.

Results of the least squares regressions of glide time against log glide distance are given in Fig. 2. The regression for *P. norfolcensis* was significant ( $F_{1,19} = 26.07$ ,  $P < 0.0001$ ) with glide time increasing significantly with glide distance. The coefficient of

determination ( $R^2$ ) was 0.578, indicating that 58% of the variance in glide time was explained by glide distance. Because animals with low mass reach terminal velocity relatively quickly, it is not surprising that glide times, and by extension glide velocities, appear to approach an asymptote within the range of distances observed in this study. The regressions of glide time against horizontal glide distance for *P. breviceps* were also significant at the 0.05 level. For both sexes (females:  $F_{1,96} = 131.93$ ,  $P < 0.0001$ ,  $R^2 = 0.579$ ; males:  $F_{1,66} = 49.66$ ,  $P < 0.0001$ ,  $R^2 = 0.429$ ) the regressions were significant and in both, the animals required more time to glide a given distance than *P. norfolcensis* with female *P. breviceps* being the slowest.

Cost of gliding transport decreased monotonically for both species, but gliding cost was less than the cost of quadrupedal transport only in *P. norfolcensis* (Fig. 3). The cost of gliding reached an asymptote at about 20 m, and only animals that climbed with speeds approaching the upper 95 % confidence limit realized an energetic benefit from gliding. This occurred at about 10 m when the upper 95% confidence interval for cost of gliding dropped below the cost of quadrupedal locomotion. As in the study of Scheibe and Robins (1998), climbing efficiency had little effect on the results. In *P. breviceps*

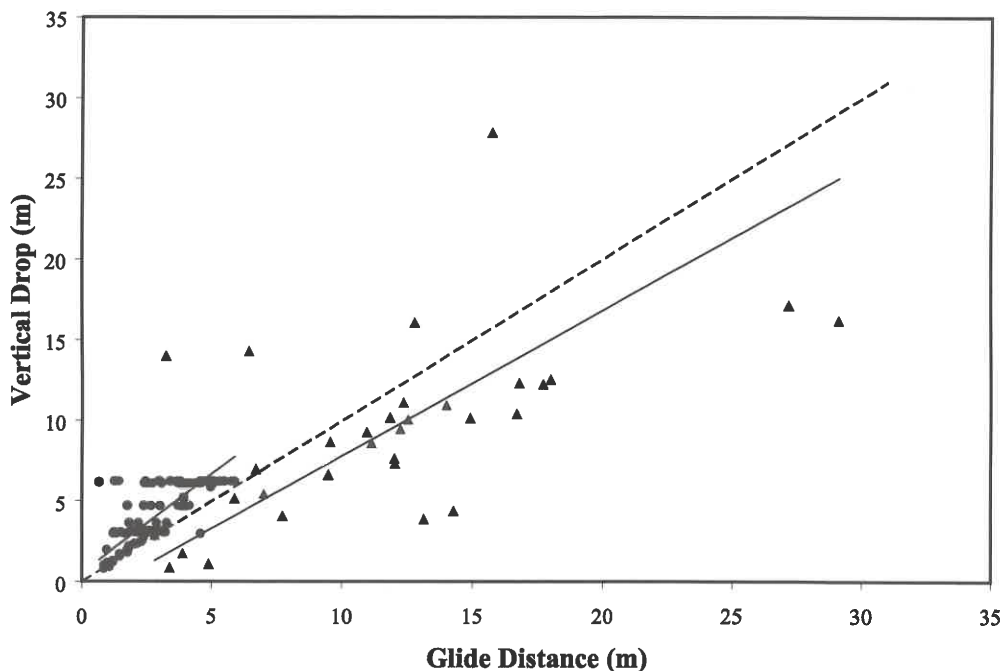


Fig. 1. Reduced major axis regressions for vertical drop against horizontal glide distance for 32 field glides by *Petaurus norfolcensis* (closed triangles:  $Y = -1.22 + 0.90 X$ ) and 168 laboratory glides by *P. breviceps* (closed circles:  $Y = 0.54 + 1.23 X$ ). The dashed line represent the line of isometry. Points below the line indicate glides, those above the line represent parachuting.

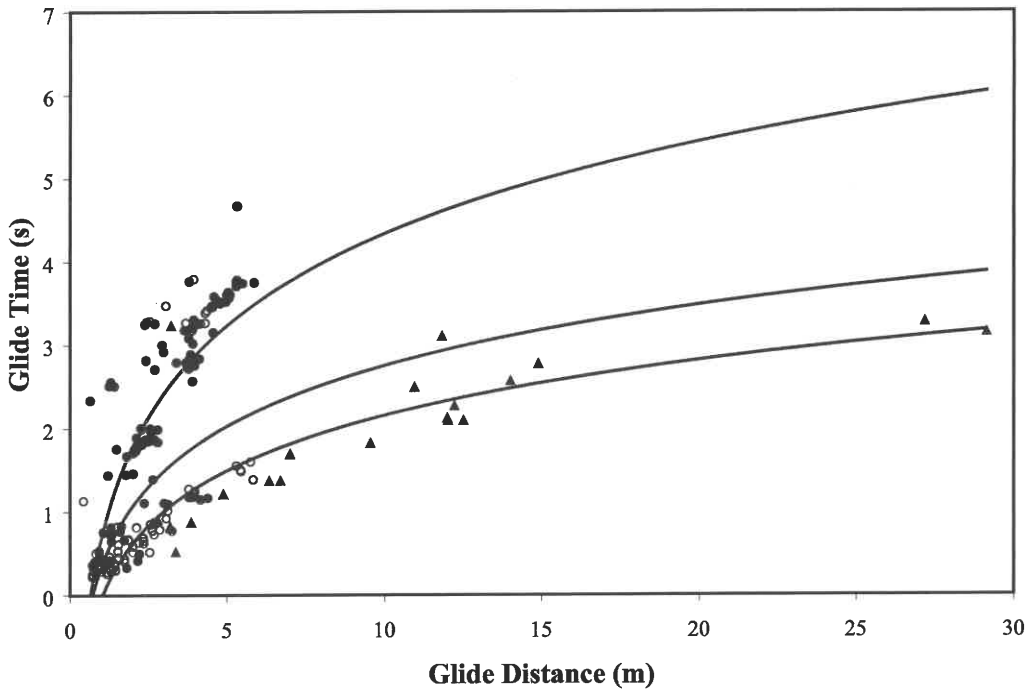


Fig. 2 Least squares regressions of glide time against the natural log of horizontal glide distance for 21 field glides by *Petaurus norfolcensis* (closed triangles:  $\text{Time} = -0.041 + 0.954 \ln \text{Dist.}$ ) and 168 laboratory glides by *P. breviceps* (females = open circles:  $\text{Time} = 0.674 + 1.591 \ln \text{Dist.}$ ; males = closed circles:  $\text{Time} = 0.338 + 1.050 \ln \text{Dist.}$ ).

the cost of gliding was always greater than the cost of quadrupedal transport suggesting that in this species, the animals realized no direct energetic benefit from gliding. When solving directly for the cost effective glide distance ( $D_e$ , equation 4) it is clear that cost of gliding was influenced strongly by climbing speed (Fig. 4). As climbing speed increased,  $D_e$  decreased markedly, presumably because the animals spend less time working against gravity. Similarly,  $D_e$  increased with increasing running speed. That is, moving across the ground rapidly (which increases the power of transport) essentially decreases the energetic advantage of gliding by increasing the cost of gliding. Because cost of gliding transport was never less than cost of quadrupedal transport for *P. breviceps*,  $D_e$  was undefined for this species.

It is clear from Fig. 3 that only under some conditions (running slowly and climbing quickly), do the squirrel gliders realize an energetic benefit from gliding after a distance of about 10 to 20 m. Because the mean glide distance is only 10.32 m, it does not appear that *P. norfolcensis* typically approach the cost effective glide distance. The situation is worse

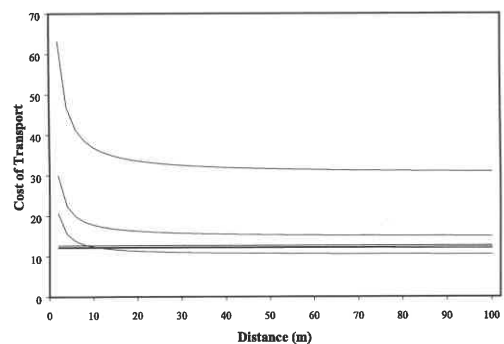


Fig. 3. Cost of gliding transport (curves) and quadrupedal locomotion (lines) by *Petaurus norfolcensis*. The horizontal lines represent cost of quadrupedal transport derived with the mean and 95% confidence intervals for running speed, and the curves represent the cost of gliding transport derived with the mean and 95% confidence intervals for climbing speeds. A cost effective glide occurs when the curve for the cost of gliding drops below the line for cost of quadrupedal locomotion.



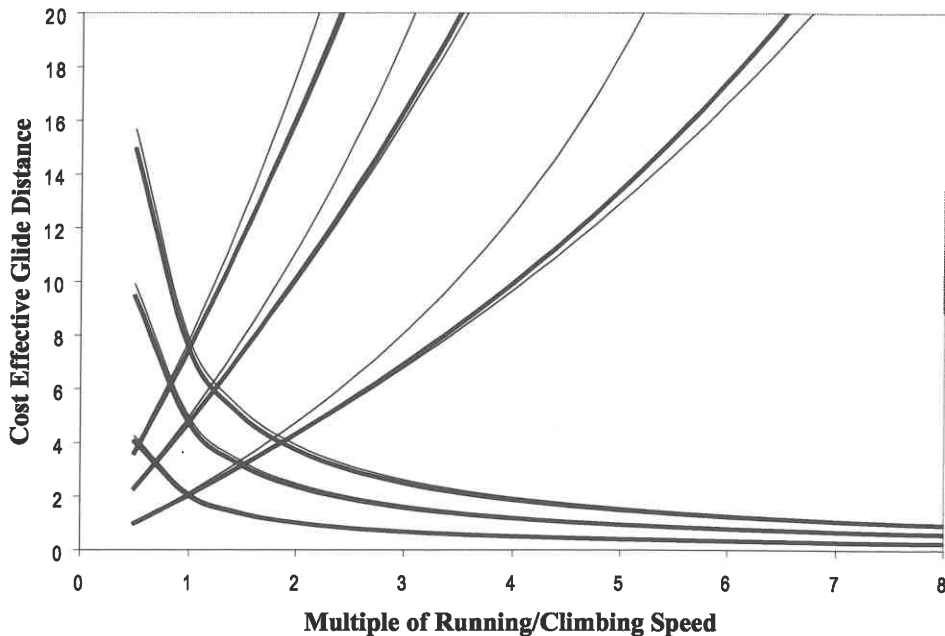


Fig. 4. Cost effective glide distance as a function of multiples of average running and climbing speeds for *Petaurus norfolcensis*. Each group of lines represents a solution for a gliding speed at 5, 50 or 100 m. The monotonically decreasing curves are for climbing speeds (mean  $\pm$  SE), and the increasing curves are for running speeds (mean  $\pm$  SE).

for *P. breviceps*. Here, regardless of mass, running speed, or climbing speed values used in the model, the animals did not realize an energetic benefit from gliding within a distance of less than 100 m. Even under ideal circumstances, when the sugar gliders moved slowly quadrupedally, climbed quickly and efficiently using a contralateral gait and not pausing, the range of glide parameters were not sufficient to include a cost effective glide distance within a 100 m range. This was true even when the mean glide ratio of 1.82 reported by Jackson (2000a) was used in the model.

## DISCUSSION

The hypothesis that gliding locomotion is energetically less expensive than quadrupedal transport, and thus conveys a selective advantage is tenuous. While data for *G. volans* and *G. sabrinus* (Sciuridae) provide strong evidence that the cost effective glide distance is shorter than the mean glide distance (Scheibe and Robins 1998, Scheibe et al. 2006), data for *Petaurista petaurista* (Scholey 1986) is less convincing. While Scholey (1986) reported a cost effective glide distance of about 45 m, that distance is much greater than the mean glide distance of 20 m for *P. leucogenys* (Ando and Shirashi 1998), and when mathematical errors in Scholey's (1986) work are

corrected (Scheibe and Robins 1998), the cost effective glide distance is closer to 100 m. The data presented here seem to add to the confusion in that *P. norfolcensis* may realize an energetic benefit from gliding while the smaller *P. breviceps* may not.

Although the sample sizes for *P. norfolcensis* are relatively small (but see Scholey 1986) the observed glides cover reasonable distances and the model behaves as expected. Using the approach of Scholey (1986) the squirrel glider realizes an energetic benefit at about the mean observed glide distance if the animal climbs quickly to its launch point. Using a direct estimate of  $D_0$  and average running and climbing performance, the cost effective glide distance is shorter than the mean glide distance. Because the ground is rarely level and under storey structure may impede direct travel, running locomotion is likely to require extra travel time which if considered, may increase the costs involved in quadrupedal locomotion and decrease the overall cost of gliding especially in smaller species such as *P. breviceps* and *Acrobates pygmaeus*.

For *P. breviceps*, neither Scholey's (1986) approach nor direct estimation of  $D_0$  produced a finite distance. This may be because the sugar gliders were restricted

to relatively short laboratory glides with a maximum vertical drop of 6.2 m and a maximum glide distance of 15.5 m. Jackson (2000a) noted that *P. breviceps* net height loss is approximately 10 m during a glide, so these animals might accelerate via gravity before assuming a gliding posture. The 6.2 m vertical limit in our lab may have prevented the animals from employing typical glides. However, our laboratory data (Scheibe and Robins 1998, and unpublished data) on 2 species of sciurid gliders (*G. volans* and *G. sabrinus*), and work by Essner (2002), Paskins et al. (2007) and Scheibe et al. (2007) suggest flying squirrels glide over short distances, and Gump (2007) found captive sugar gliders to exhibit glide postures over distances shorter than 1 m. There may be a fundamental difference in the way gliders from different taxa initiate their glides (Scheibe and Essner 2000). The velocity profiles for sugar gliders may prevent them from generating sufficient lift over short distances. An alternative explanation is that these captive born animals have had insufficient experience gliding, although importantly, even our use of Jackson's (2000a) glide ratio did not improve the results dramatically.

In this study, mean glide angle for *P. norfolcensis* was 37.17° and that for *P. breviceps* was 51.18° while glide angles for *P. breviceps* and *P. gracilis* in the field were approximately 28–29° (Jackson 2000a) suggesting that the animals in the captive trials never reached terminal velocity due to low launch points. *P. norfolcensis* glide angles were similar to those measured in the field for *G. sabrinus*, which varied from 31.9° to 40.2° (Vernes 2001; Scheibe et al. 2006). Work by Dial (2003) on optimal body mass in gliding mammals suggests a typical glide angle of 25°. Clearly, glide angle is a function of habitat structure, available landing sites, and the postural behaviour of the animals as well as other factors. Observed glide angles may reveal more about habitat use than optimal performance. The *P. norfolcensis* glides observed and measured may have been from smaller trees or from lower than average heights as the animals were likely trying to move away from the observers quickly.

Among sciurid gliders the pattern appears to be that cost effective glide distance increases with body mass (70 g *G. volans* ≈ 7 m, 125 g *G. sabrinus* ≈ 10 m, 1.5 kg *P. petaurista* ≈ 45–100 m). It is unknown if a similar pattern holds for the petaurid gliders. Likewise it is unknown if gliding in marsupials is a response to the same selective forces that favoured gliding in sciurids. Clearly, there are morphological similarities amongst the gliders in terms of the basic architecture of the airfoil, but differences as well: sciurids (Thorington et al. 1998) and anomalurids support the wing-tip with the styliform and unciform cartilages while petaurids support the wing-tip with the 5<sup>th</sup> digit. The wing tip in

petauristine gliders may contribute both to the reduction of turbulence (Thorington et al. 1998) and to total planar surface area (Addington et al. 2000). *Glaucomys* has a distichous tail that may add 20 to 30% to the planar surface area (Thorington and Heaney 1981; Wells-Gosling and Heaney 1984) and acts like a flow rudder (Schaller 1984), while *Petaurus* has a cylindrical tail that acts as a drag rudder (Scheibe and Robins 1998). Sciurid gliders smaller than 500 g have a distichous tail but amongst marsupials, only the acrobatids have a distichous tail. Thus, the bauplan for marsupial and eutherian airfoils are different, and may produce different performance profiles.

An important difference between marsupial and eutherian gliders concerns gaits, digits, and diet. *Petaurus* and all other possums have opposable digits that are lacking in pteromyines. Our observations of climbing by *P. breviceps*, *G. volans*, and *G. sabrinus* suggest that the sciurids use a bounding gait when climbing with the hind limbs nearly synchronous. However, *P. breviceps* uses its digits to grasp the tree bark and employs a contralateral gait when climbing. Consequently, the climbing speeds of *P. breviceps* are slower than those of *Glaucomys* with a concomitant increase in the cost of climbing and cost effective glide distance. While climbing and running speeds in sugar gliders and squirrel gliders are slower than those of *Glaucomys* (Scheibe and Robins 1998, Scheibe et al. 2006), they are probably more agile on small branches and in structurally complex vegetation. Scheibe et al. (2007) analysed gaits and speeds in sugar gliders and northern flying squirrels as they moved across dowel rods of various sizes, and noted that the squirrels were less likely to use a running gait, and were ultimately slower on all sizes of dowel rods compared to sugar gliders. Thus, while flying squirrels are able to climb quickly, they are not able to navigate small branches as effectively as the petaurid gliders. It should be noted that petaurid gliders are exudivorous and may forage while climbing to a launch point. While this would negatively affect energy costs due to the slower speed, it would have positive effects through the replenishment of energy reserves. However, we assume the overall energy required to climb to the launch point remains the same when considering input for our models.

Gliding locomotion may be a response to selection for transport economics, predator escape, or optimal foraging. In this paper, we have evaluated the transport economics hypothesis and the results provide tenuous support for the hypothesis, at least for *P. norfolcensis*. However, this does not falsify either the predator escape or optimal foraging hypotheses. The predator escape hypothesis received some support from Holmes and Austad (1994) who noted that sciurid gliders live longer than similar sized non-gliding mammals. Statistical



concerns with that analysis (Stapp 1994) and the large number of flying squirrels taken by owls (Carey et al. 1992) suggest that gliding may not be an effective anti-predator strategy. Potential predators of *Petaurus* spp. include avian (*Ninox* spp.), reptilian (*Morelia spilota*), and mammalian predators (*Felis sylvestris*; Jackson 2000b) that would all employ different means of prey detection and subsequent attacks on gliders. Scheibe et al. (2007) noted that launching into a glide may enable a flying squirrel to evade an arboreal predator rapidly, or place as much distance as possible between a potential predator and the squirrel. This approach requires maximization of either launch velocity or ballistic range. Sugar gliders use relatively slow launches compared to similar sized sciurids (Initial launch velocity: *P. breviceps* 1.53–1.79 m/s, *G. volans* = 2.16–2.61 m/s, *G. sabrinus* = 2.05–2.28 m/s; Scheibe unpublished data). These slow launches and their corresponding shallow launch angles (Gump 2007) do not produce maximal ballistic ranges, and seem unlikely to minimize the chance of predation. We have no similar data for squirrel gliders, but evidence favouring the role of predation in the evolution of marsupial gliding does not appear to be strong.

Gliding may be an evolutionary response to foraging economics. Marsupial gliders evolved as Australian forests became increasingly open (Archer and Clayton 1984), resulting in slower movement through understorey vegetation using quadrupedal locomotion and increased travel time between foraging patches in trees. The marginal value theorem of optimal foraging theory (Charnov 1976) predicts that increased travel time between patches necessitates increased patch residency time. Thus, the animal remains in a foraging patch as the rate of return in the patch declines. Gliding locomotion reduces travel time and thus enables early departure from a foraging patch while the rate of return is still high, while also allowing the animal to remain in the patch longer to take full advantage of the resource. Because all species of marsupial gliders are exudivores or folivorous, their sources of concentrated protein are dispersed widely through the habitat (Goldingay 1989, 2000; Kavanagh and Lambert 1990; Sharpe 1996) and may represent important foraging patches. Folivorous gliders (*Petauroides volans*) may recognize specific leaves or leaf quality as foraging patches (see Wischusen and Richmond 1998) but may only glide to a few trees in a single night to forage (Kehl and Borsboom 1984). Additionally, this species has a low field metabolic rate and low feed intake and *Eucalyptus* foliage generally has low energy value (Hume et al. 1984), thus gliding may indeed be a way to minimize energy use for this species when speed of travel is less important. Therefore, the advantage of gliding may be two-fold. First, gliding may enable mammals to increase their foraging range and thereby utilize patchily distributed resources like

den cavities or food resources. Second, gliding is more rapid than quadrupedal locomotion and may enable the animals to increase their foraging velocity (Shipley et al. 1996). In this scenario, the actual cost of transport is less important. Just as humming birds do not move from flower to flower at a speed that is most efficient, but instead at a speed that maximizes their net energy intake (Gill 1985), sugar gliders and squirrel gliders may use gliding to maximize their encounter rate with some key resources.

While there are concerns about comparisons of wild and captive animals, our data provide initial insights to gliding performance, the evolution of gliding in two species of Petaurids, and are relevant to current conservation issues. The captive *P. breviceps* were not exposed to launch sites high enough to mimic natural glides and resulted in glide distances shorter than those reported for wild animals (20.42 m; Jackson 2000a). However, our data on running and climbing provide parameter estimates for the models, and allow initial predictions about gliding performance. Furthermore, Paskins et al. (2007) and Scheibe et al. (2007) have shown that northern flying squirrels (*G. sabrinus*) assume typical glide postures even over 'glide' distances of less than 1 m, and exhibit trajectories better than those predicted for a ballistic object. Essner (2002) found similar results for southern flying squirrels (*G. volans*). Gliding performance by captive and wild flying squirrels (*G. sabrinus* and *G. volans*) are not significantly different (JSS unpublished data and Scheibe and Robins 1998), so it is reasonable to suggest performance by captive sugar gliders is similar to short or constrained glides by wild animals.

The fitness of the captive animals held in small enclosures may have affected our results. However, we used only the healthiest and seemingly most fit animals from the captive colony in the trials (most of these animals are still living 9 years after the colony was established). Additionally, the weights of our captive animals were within the published ranges of weights reported in field trials.

Although these species evolved in a landscape with some fragmentation, additional land clearing and further fragmentation may have serious consequences for their conservation. If gliding evolved in these animals to increase foraging efficiency, then a fragmented landscape that impedes gliding (trees are too far apart for launching and landing) and requires increased travel time may negatively affect their survival and persistence in a landscape.

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