LOCOMOTOR PERFORMANCE AND COST OF TRANSPORT IN THE
SQUIRREL GLIDER, *PETAURUS NORFOLCENSIS* (PETAURIDAE)

by

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CONTENTS

ACKNOWLEDGEMENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Data collected from field glides in southern Queensland, Australia were used to estimate the cost of gliding transport for *Petaurus norfolcensis*. The cost of running and climbing transport was also computed and compared to the cost of gliding to estimate the cost effective glide distance, and determine if gliding is cost effective in this species. Results indicate that gliding is not less expensive than quadrupedal locomotion. These findings do not support the hypothesis that gliding evolved as a means of energy conservation. Selective pressures that may have influenced the evolution of gliding in marsupials are discussed.

INTRODUCTION

Gliding locomotion evolved independently in six extant taxa including the Cynocephalidae, Anomaluridae, Sciuridae, Petauridae, Pseudocheiridae, and Acrobatidae. By definition, gliders descend at angles < 45° while species descending at angles > 45° are parachuters (Rayner 1981). A glide is initiated when an animal leaps from a launch site, extends the limbs and patagium, and achieves some thrust and lift. After the launch, some gliders use gravity to accelerate until sufficient velocity is attained to break into a glide (Moffett 2000). Movements of limbs correct for roll, yaw, and pitch (Caple et al. 1983; Essner 2002). The animal then glides toward a sometimes pre-selected landing site large enough to allow for some vertical variation in landing (Caple et al. 1983). Toward the end of the glide, the animal pitches its body to induce drag while maintaining forward momentum (Caple et al. 1983). In general, the forelimbs make initial contact with the landing site while the body and hindlimbs swing forward to come in contact with the launch site.

There are three main hypotheses for the evolution of mammalian gliding: foraging optimization, cost of transport, and predator avoidance. The foraging optimization hypothesis argues that gliding reduces travel time between foraging patches. By the marginal value theorem, reduced travel time should enable the animal to leave a foraging patch when the rate of return is still high. Changes in the structure of the forest canopy in which animals must travel and forage may provide selective pressure for species to develop a new mode of locomotion (Emmons and Gentry 1983). For example, possums may have evolved this trait to move between trees as Australian forests became increasingly open (Archer and Clayton 1984) and quadrupedal movement between trees

1

became more difficult. Researchers have found the optimum forest for petaurids is open forest with *Petaurus breviceps*, *P. australis*, *Petauroides volans*, and *Acrobates pygmaeus* preferring tall, open forest (Tyndale-Biscoe and Calaby 1975) because gliding may be impeded by dense vegetation (Suckling 1982). Additionally, Emmons and Gentry (1983) noted the paucity of gliding species in Africa where lianas tend to cross canopy gaps, allowing animals to crawl across gaps, and a much higher number of gliding species in America, Australia, and Asia where there is a lower density of lianas.

Some life history characteristics favor the ability of marsupial gliders to move long distances. Most species practice serial den use, moving between multiple dens each month (Kehl and Borsboom 1984; pers. obs.). Also, gliding species are important pollinators and move long distances in a night. Carthew (1994) recorded *P. breviceps* moving more than 265 m in an hour, and up to 59 m between flowering plants. Nightly movements of 320 and 500 m have been recorded for *P. norfolcensis* (Quin 1995). The distribution of some habitat components may limit the distribution of petaurids. The availability of tree hollows and snags (Lindenmayer et al. 1993; Lindenmayer et al. 1999a, 1999b; Meredith 1984; Pausas et al. 1995), food availability (Braithwaite 1984; Lindenmayer et al. 1999a; Pausas et al. 1995), leaf quality (Pausas et al. 1995), and slope (Pausas et al. 1995) may affect home range size. Large home ranges are expected to compensate for the low density of necessary habitat components. Relative to nongliding species, gliders maintain larger home ranges (Table 1).

The cost of transport hypothesis argues that gliding is less expensive than quadrupedal locomotion. Presumably, gliding between trees requires less energy and time than running (Emmons and Gentry 1983; Norberg 1985). Because an animal uses

Table 1. Body mass, home range size, and method of measuring home range size (HM = harmonic mean, MCP = minimum convex polygon, and MMAM = modified minimum area method) for four species of marsupial gliders.

Species	Weight (g)	mean Home range (ha)	Method	Citation
Petaurus norfolcensis	192-213	3.08	HM	Quin 1995
P. norfolcensis	170-300	5.07	HM	Sharpe 1996
P. norfolcensis		6.07	MCP	Sharpe 1996
P .breviceps	104-119	3.82	HM	Quin 1995
P. breviceps		5.3775	MCP	Quin et al. 1992
P. breviceps		3.5333	HM	Quin et al.1992
P. australis	529-635	34	MCP	Goldingay 1992
P. australis	435-710	53	MMAM	Henry and Craig 1984
P. australis		63	MCP	Goldingay and Kavanagh 1993
Petauroides volans	130	1.3-2.5	kernel	Comport et al. 1996
Petauroides volans		2.6	min. home range	Kehl and Borsboom 1984

potential energy gained while climbing to a launch point, and little energy during the glide, gliding should be an energetically inexpensive means of locomotion (Norberg 1985).

The overall energy budget of gliders is more complicated than just the energetics of locomotion. For example, petaurids are able to conserve energy even though they are highly active and territorial (which is energetically expensive; Smith and Lee 1984). Smith and Lee (1984) hypothesized that the high dietary ratio of energy to protein allows petaurids to defend territories. The diets of marsupial gliders consist mainly of plant exudates such as gums, saps, manna, honeydew, and nectar, while protein sources of insects and pollen generally comprise only about 20% of the diet (Quin 1995; Sharpe 1996; Smith 1982; Smith and Lee 1984).

While energy is conserved through huddling in *Glaucomys volans* (Stapp et al. 1991), energy conservation is an unlikely explanation for huddling in marsupials. Generally, *A. pygmaeus*, *P. breviceps*, and *P. norfolcensis* nest in groups of two to nine animals, but many nest individually (Frey and Fleming 1984; Quin 1995). It is unlikely that this conserves energy and is more likely to be a result of highly social behavior (Frey and Fleming 1984). *A. pygmaeus* and *P. breviceps* will enter daily torpor to minimize heat loss and energy expenditure (Frey and Fleming1984; Kortner and Gieser 2000).

Predator avoidance is the third hypothesis for the evolution of gliding. The hypothesis argues that animals can avoid predation by plunging from the canopy without injury, although some species accomplish this without a patagium or other gliding membranes (Emmons and Gentry 1983). Additionally, gliding allows animals to avoid leaving a continuous scent trail (Jackson 1999). Holmes and Austad (1994) suggested

that gliding mammals experience increased longevity as a result of decreased predation compared to similar non-volant mammals. They attributed this to behaviors including hole-nesting and nocturnality. However, Stapp (1994) found statistical errors in their work and no real difference between gliding and non-gliding species. Thus, the predation hypothesis seems unlikely, at least for some species of gliders. For example, *Glaucomys sabrinus* is the main food for Northern Spotted Owls (*Strix occidentalis*; Carey et al. 1992) with a single pair of owls consuming as many as 500 flying squirrels in a year. Black rat snakes (*Elaphe obsoleta obsoleta*) were found in *Glaucomys volans* nest boxes indicating they are capable of capturing nesting squirrels (Keith et al. 2000). Moreover, when disturbed, *Glaucomys* spp. leave their hole, climb the tree, and glide to another tree, exposing the animal to avian predators (Scheibe et al. 1990).

Few studies have measured gliding performance in mammals (Addington et al. 2000; Ando and Shiraishi 1993; Hampson 1965; Jackson 1999; Keith et al. 2000; Polyokova and Sokolov 1965; Scheibe and Robins 1998; Scheibe et al. in review; Scholey 1986; Stafford et al. 2002; Vernes 2001; Wright 2000; Zahler 2001). Information on the gliding behavior and performance of marsupials is even more limited with papers by Jackson (1999), Johnson-Murray (1977), Nactigall (1979a, b), and Nactigall et al. (1974). Of these studies on mammalian gliding, only a few estimated cost of transport (Keith et al 2000; Scheibe and Robins 1998; Scheibe et al. in review; Scholey 1986; Wright 2000) providing information about cost of gliding in *Glaucomys volans*, *G. sabrinus*, *Petaurista petaurista*, and *P. breviceps*. *Glaucomys sabrinus* appears to realize an energetic benefit from gliding after distances of less than 14 m (Scheibe et al. in review), while *P. breviceps* may not realize any energetic benefit from gliding (Wright

2000). Thus, gliding performance and the cost of gliding relative to quadrupedal locomotion may vary considerably between *Glaucomys* spp. and *Petaurus* spp. There is some evidence to suggest important differences in performance and locomotor costs between small and large gliders (Schiebe and Robbins 1998).

Jackson (1999) found patagial surface area and log body mass to be highly correlated among all species of gliding possums, and predicted that gliding efficiency of all species would be very similar, although he noted that small species are more strongly affected by turbulence than large species (Jackson 1999). There are morphological differences among flying squirrels and possums, and consequently there is no expectation that their locomotor performance will be identical. Flying squirrels have a styliform cartilage that extends the wing tip of the gliding membrane (Thorington et al. 1998) and may help reduce the cost of gliding (Scheibe and Robins 1998) by reducing wing tip turbulence. In petuarids 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 Robbins 1998). *Petaurus* and all other possums have opposable digits that are lacking in *Glaucomys* and the other pteromyines.

This thesis relies on field glide data for the squirrel glider, *Petaurus norfolcensis*, from southern Queensland, Australia, to estimate the cost of gliding transport and to estimate cost-effective glide distance. The data are compared to previously collected data for northern flying squirrels, sugar gliders, and southern flying squirrels. Conveniently, the southern flying squirrel and sugar glider are similar in size and mass, and the northern

flying squirrel and squirrel glider are of similar size and mass (Table 2). This permits a

comparison of eutherian and metatherian gliders, as well as an evaluation of size effects

on small mammalian gliders.

Table 2. Summary of gliding performance from previous studies. Table includes means from four studies on three difference species. The weights in bold are from Goldingay 2000.

Species	Weight (g)	Horizontal Distance (m)	Glide Angle (°)	Glide Ratio	Reference Study
Glaucomys sabrinus	89.5 (males) 95.3 (females) **120**	19.0(males) 14.2 (females)	26.8	1.98	Vernes (2001)
G.sabrinus	125.9 males (2000)	14.31 ± 0.99 (SD)	35.81 ± 1.20		Scheibe et al. (in review)
	125.2 males (2001)	13.31 ± 2.21	31.90 ± 3.83		
	125.4 females (2000)	14.09 ± 1.30	40.20 ± 1.61		
	125.6 females (2001)	15.19 ± 3.76	31.94 ± 4.95		
G. volans	**70**			1.53	Scheibe and Robins (1998)
Petaurus breviceps	69-150 **120**	20.42 ± 1.33 (SE)	29.69 ± 1.10 (SE)	1.82 ± 0.07	Jackson (2000)

MATERIALS AND 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. tereticorphis*), 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 squirrel gliders.

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. Elliot traps 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 meters 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.

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. (in

review) for northern flying squirrels. These models were used in this study to estimate

cost effective glide distance for squirrel gliders and to determine if distance was less than

or greater than the mean glide distance observed for this species.

The cost of quadrupedal transport was estimated using:

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

Where P_r is the power of quadrupedal transport, 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) since $T_r = D_r/V_r$.

The cost of gliding was estimated using

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

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 $C_g \leq C_r$.

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

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

where D_e is the cost effective glide distance. Because velocity is distance/time, and

because PT is the kinetic energy associated with either climbing or gliding, all units

except distance cancel. Time to climb is dependent upon distance climbed, and then in

turn is dependent on 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)
$$D_e = \beta_0 \bigg/ \frac{V_c}{P_c}\left(\frac{P_r}{V_r} - \frac{P_g}{V_g}\right) - \beta_1.$$

In this model, β_0 is the initial vertical drop of the glide (Scholey 1986) and β_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.

RESULTS

Twenty-eight *Petaurus norfolcensis* were trapped at Minnippi Parklands and mean weight was determined to be 190.14 g (± 3.57 SE). Of these animals, it was possible to observe 25 glides, four running events, and three climbing events. A total of seven additional animals were observed gliding at night, when illuminated with a spotlight. Maximum observed glide distance was 29.14 m with a mean glide distance of 10.32 m (± 1.27 SE). Mean glide angle was 37.17° (± 2.41 SE). Mean running speed was 2.99 m/s (± 0.38 SE) while mean climbing speed was 0.84 m/s (± 0.24 SE). These data are summarized in Table 3.

Results of the reduced major axis regression of vertical drop against glide distance are presented in Figure 1. Points located above the line of isometry are considered parachuting events. Just as in data reported by Scheibe et al. (in review), the variability about the regression line indicates considerable control by the animals over the flight paths of their glides.

Results of the least squares regression of glide time against horizontal glide distance are given in Figure 2 and Table 4. The regression was significant at the 0.05 level, with glide time increasing significantly with glide distance. The coefficient of determination (R^2) was 0.544, indicating that 54% of the variance in glide time was explained by glide distance. Although the linear regression was significant, Figure 2 shows clearly that the relationship was not linear. 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.

Table 3. Summary of performance measurements.

	Mean	Standard Error	Standard Deviation	Min.	Max.	n
Animal Mass (g)	190.143	3.568	19.544	156.000	222.000	28
Glide Distance (m)	10.320	1.270	6.721	2.800	29.140	28
Glide Angle	37.169	2.409	13.627	12.848	76.986	32
Running speed (m/s)	2.992	0.383	0.766	2.204	3.922	4
Climbing speed (m/s)	0.836	0.238	0.413	0.488	1.292	3
Horizontal Ground Velocity (m/s)	4.992	0.3770	1.728	1.000	9.251	21

Figure 1. – Reduced major axis regression for vertical drop against horizontal glide distance for 32 field glides by *Petaurus norfolcensis*. The heavy line represents the reduced major axis regression line and the fine line represents the line of isometry. Regression equation: y = -0.322659 + 0.8885439x, where y = vertical drop and x = glide distance.
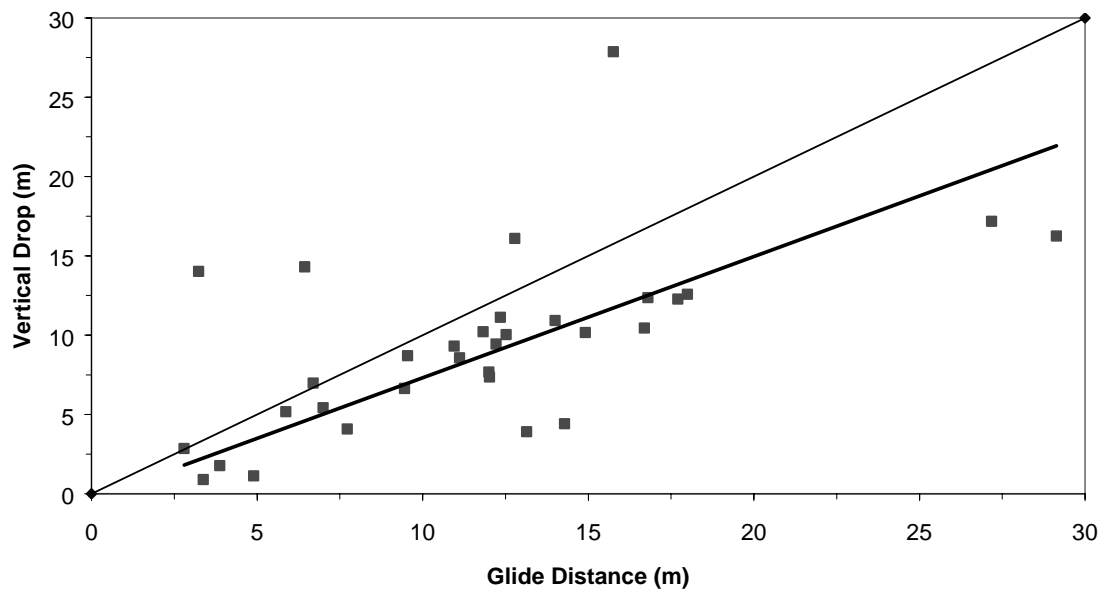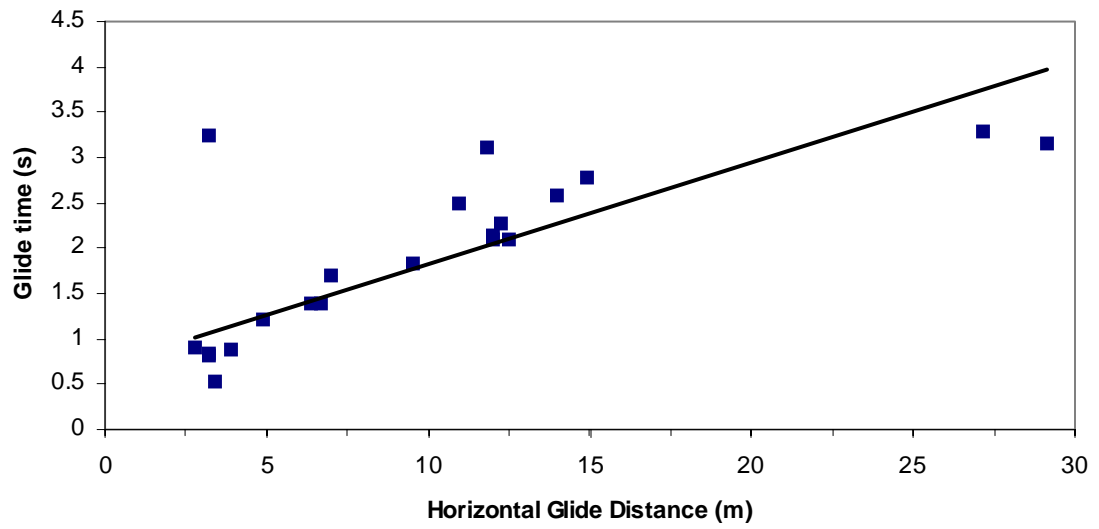
Figure 2. – Reduced major axis regression for glide time against horizontal glide distance for 21 field glides by *Petaurus norfolcensis*.

Table 4. Regression statistics for glide time against horizontal glide distance.

Regression Statistics: Glide time against Distance

Multiple R	0.737456472
R Square	0.543842048
Adjusted R Square	0.519833735
Standard Error	0.616988945
Observations	21

Analysis of Variance

	df	Sum of Squares	Mean Square	F	Significance F
Regression	1	8.6231492	8.6231492	22.65223892	0.0001364
Residual	19	7.2328318	0.3806754		
Total	20	15.855981			

	Coefficients	Standard Error	t Statistic	P-value	Lower 95.00%	Upper 95.00%
Intercept	1.029745055	0.2334821	4.4103818	0.000269607	0.5410615	1.5184286
x1	0.090369976	0.0189875	4.7594368	0.000119737	0.0506286	0.1301113

Horizontal glide velocity (velocity relative to the ground, and not air speed) was significantly related to glide angle (Table 5). The coeffient of determination was 0.316, indicating that about 32% of the variance in glide velocity was explained by glide angle. The relationship was negative (Table 5, Figure 3), so that as glide angles became shallower, glide velocities increased. This makes sense in that within the context of a shallow glide, a greater portion of the total glide is along the horizontal axis. When glide angles are large, the animals are parachuting to the ground and most of the glide velocity is along the vertical axis rather than the horizontal axis. The greatest horizontal glide velocity was 9.25 m/s, while the lowest was 1.00 m/s. Mean horizontal glide velocity was 4.99 m/s (0.377 SE).

Results of the analysis of cost of transport are given in Figure 4. Cost of gliding transport decreased rapidly during the first few meters of a glide, and approached an asymptote after distances of about 20 m. Cost of quadrupedal transport is necessarily constant. Thus, when the cost of gliding transport curves drop below the cost of quadrupedal transport lines, the animal realizes an energetic benefit from gliding.

In my analysis, the cost of gliding was influenced most strongly by distance and climbing speed, while climbing efficiency had little effect. Figure 4 illustrates cost of gliding transport for the mean climbing speed, as well as the upper and lower 95% confidence limits for climbing speed. Slower climbing speeds resulted in increased gliding cost, primarily because the animals must work against gravity longer when climbing slowly. The three lines for cost of quadrupedal locomotion shown in Figure 4 represent cost estimates based on the mean, upper, and lower 95% confidence limits for

Table 5. Regression statistics for horizontal glide velocity against glide angle.

Regression Statistics: Horizontal
ground velocity against glide angle

Multiple R	0.561870423
R Square	0.315698372
Adjusted R Square	0.27292952
Standard Error	1.558619851
Observations	18

Analysis of Variance

	df	Sum of Squares	Mean Square	F	Significance F
Regression	1	17.93185251	17.93185251	7.381502174	0.015235337
Residual	16	38.86873342	2.429295839		
Total	17	56.80058593			

	Coefficients	Standard Error	t Statistic	P-value	Lower 95.00%	Upper 95.00%
Intercept	7.870828241	1.071919225	7.3427438	1.14917E-06	5.598460998	10.14319548
x1	-0.075065849	0.027629309	-2.716892006	0.014648895	-0.133637367	-0.01649433
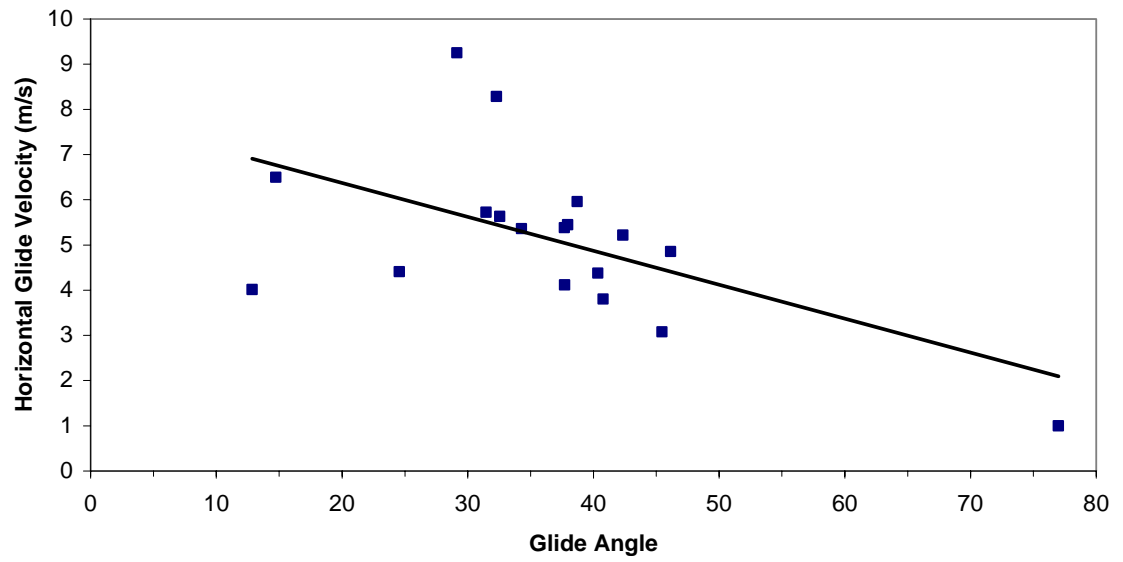
Figure 3. - Least squares regression for horizontal glide velocity against glide angle.
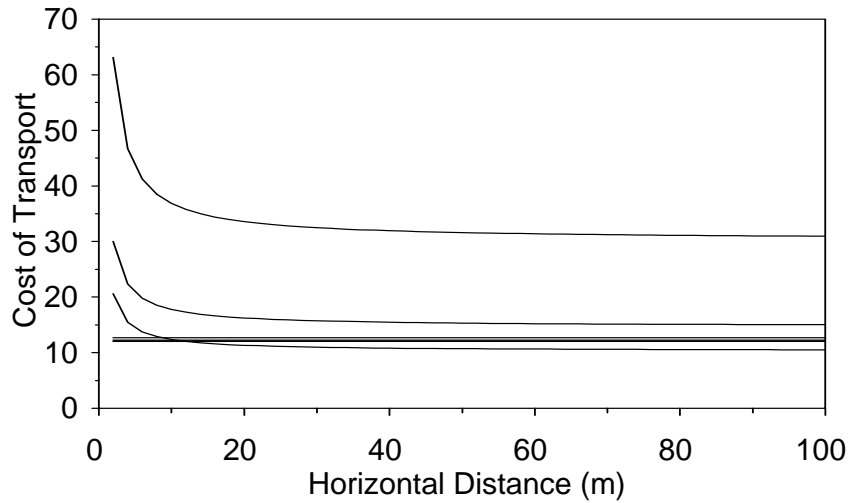
Figure 4. - Cost of transport for quadrupedal locomotion by *Petaurus norfolcensis*. The horizontal lines indicate the cost of quadrupedal locomotion while the curves indicate the cost of gliding. The three horizontal lines indicate the lower 95% interval, mean, and upper 95% interval running speeds (beginning with the uppermost line). The three curves indicate the lower 95% interval, mean, and upper 95% interval climbing speeds (beginning with the uppermost line). A cost effective glide occurs when the curve for the cost of gliding drops below the line for cost of quadrupedal locomotion.

running speed. Again, running slowly has a greater cost than running quickly, because the animal must work against gravity longer when running slowly.

It is clear from Figure 4 that only under the best cost conditions (running slowly and climbing quickly), do the squirrel gliders realize an energetic benefit from gliding after a distance of about 20 m. Because the mean glide distance is only 10.32 m, it does not appear that *Petaurus norfolcensis* typically approach the cost effective glide distance.

DISCUSSION

The hypothesis that gliding locomotion by *Petaurus norfolcensis* is energetically less expensive than quadrupedal locomotion was not supported. Glides were cost effective only when an animal climbed as quickly as possible to the launch point. Because this is expected to occur only 2.5% of the time, and because the cost effective glide distance is much greater than the mean glide distance, gliding is not a cost effective means of locomotion in this species. My results were similar to those of Wright (2000), who analyzed locomotor performance in *Petaurus breviceps*. It is interesting that the cost effective glide distance for *P. breviceps* is about 100 m while the larger *P. norfolcensis* has an estimated cost effective glide distance of about 30 m. The theoretical explanation is that increased mass corresponds to increased cost effective glide distances, but also reduced overall cost of transport (Taylor 1977). The observed pattern for *Petaurus* may be a consequence of the restricted nature of the laboratory glides of *P. breviceps* observed by Wright (2000). His glides could not exceed 14 m in length and were restricted to a maximum vertical drop of 6.2 m.

Using a combination of laboratory and field glides, Scheibe and Robbins (1998) found the 70 g sciurid glider *Glaucomys volans* realized an energetic benefit from gliding after about 7 m. Similarly, Scheibe et al. (in review) found *G. sabrinus* (125 g) to have a cost effective glide distance of about 10 m. In both cases, the cost effective glide distances are shorter than the mean glide distances. Calculations by Scheibe and Robbins (1998) estimate the cost effective distance of gliding for the large *Petaurista petaurista* to be approximately 100 m, much longer than the distances reported by Scholey (1986), and

much longer than the mean glide distances for *Petaurista leucogenys* reported by Ando and Shirashi (1998).

The contralateral gait described by Wright (2000) for climbing and running by *P. breviceps* did not appear to be the same gait employed by *P. norfolcensis*. In fact, *P. norfolcensis* gaits more closely resembled the climbing and running gaits of *Glaucomys*. Although based on only four observations, the mean running speed for *P. norfolcensis* was faster than that of *P. breviceps*, *G. volans*, and *G. sabrinus* (Sheibe and Robbins 1998; Scheibe et al. in review; Wright 2000). Animals that are able to climb faster have a reduced cost of gliding because they work against gravity for a shorter time. Similarly, running fast reduces the cost of quadrupedal transport, but increases the cost effective glide distance. If natural selection favors short cost effective glide distances, the animals should climb quickly but run slowly. The fact that the squirrel gliders I observed climbed and ran relatively quickly suggests they were responding to a potential predation event.

Observations of launch behavior in *Glaucomys* spp., *P. breviceps*, and *P. gracilis* (Jackson 1999; Scheibe et al. 1990), reveal the animals to weave back and forth and bob the head up and down before launching as a means of assessing the potential glide. My observations of *P. norfolcensis* revealed the same behavior. It seems likely the animals are evaluating distances and potential landing spots.

Mean glide angle for *P. norfolcensis* was 37.17°, while glide angles for both *P. breviceps* and *P. gracilis* were approximately 31° (Jackson 1999). Their glide angles were similar to those measured in the field for *G. sabrinus*, which varied from 31.9° to 40.2° (Scheibe et al. in review; Vernes 2001). Work by Dial (Department of Environmental Science and Outdoor Studies, Alaska Pacific University, Anchorage, AK

99508, pers. comm.) 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 behavior of the animals as well as other factors. Observed glide angles may reveal more about habitat use than optimal performance.

If gliding locomotion did not evolve in this species as a means of energy conservation, it is necessary to consider other selective pressures that may have resulted in this trait. Marsupials may have evolved the ability to glide as Australian forests became increasingly open (Archer and Clayton 1984). In this scenario, quadrupdeal movement through understory vegetation is slower, resulting in increased travel time between foraging patches in the trees. By the Marginal Value Theorem of optimal foraging theory (Norberg 1977), we know that increased travel time between patches necessitates increased patch residency times. This results in the animal remaining in a foraging patch as the rate of return in the patch begins to decrease. A gliding animal has reduced travel time, and can therefore leave a foraging patch while the rate of return is still high. Most species of marsupial gliders are exudivores, and one is folivorous (*Petauroides volans*). Concentrated sources of protein are dispersed widely through the habitat (Goldingay 1989; Goldingay 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), and it seems likely that den cavities and slope of the terrain may play an important role in the foraging economics of marsupial gliders. Open forests and the patchy distribution of resources, as well as faster travel speeds between patches, should result in increased home range size.

In general, home range size is related to animal body mass and energetic needs (Lindstedt et al. 1986; Mace and Harvey 1983; McNab 1963; Swihart et al. 1988). Because glider species forage actively, they are considered "hunters" when estimating expected home range sizes from allometric equations. Swihart et al. (1988) found home range sizes (ha) of hunters related to body mass (kg) as A= $15.14M^{1.26}$. According to this equation, the expected home range size of a 200 g *P. norfolcensis* is 1.99 ha. However, Goldingay's (2000) summary reported home range size for this species to be about is 3-3.5 ha. In fact, for all gliders less than 600 g, actual home range size is much larger than home range size expected on the basis of the allometric relationship (Table 6). The ratio of measured home-range to predicted home-range is never greater than 0.61, indicating the home range for gliders is larger than expected for an animal that size. If the resources important to gliders are patchily distributed, as suggested by the open nature of Australian forests (Archer and Clayton 1984), then the larger than expected home ranges of the smaller gliders make sense in terms of foraging economics. The smaller than expected home ranges of the larger gliders (*Petauroides* and *Petaurista*) may be a consequence of the unique constraints affecting arboreal folivores (see Wischusen and Richmond 1998), and deserves further exploration.

This study of locomotor performance in squirrel gliders is not exhaustive, and perhaps raises more questions than it addresses. This study demonstrates that squirrel gliders released from traps have a cost effective glide distance that exceeds the mean glide distance, thus providing no support for the transport economics hypothesis. It is unknown if animals released at night, or animals gliding undisturbed have the same mean glide distance. Similarly, there is no information available on the energetic cost of

Table 6. A summary of the measured home-range and the home-range predicted by the allometric equation derived by Swihart et al. (1988) along with the ratio of predicted home-range over measured home-range. Weights and home-range sizes are from the summary in Goldingay (2000). The measured home-range value used in the ratio is the mean of the range given.

* Denotes non-gliding species with weight and home range values taken from summary by Swihart et al. 1988.

Species	Weight (g)	Measured Home-range Area (ha)	Predicted Home-range Area (ha)	Predicted/Measured
Acrobates pygmaeus	12	?	0.058	--
Glaucomys volans	70	0.4-9.9	0.53	0.10
Glaucomys sabrinus	120	3.4-4.9	1.05	0.25
Petaurus breviceps	120	0.5-4	1.05	0.47
Pteromys volans	130	3-123	1.16	0.02
Petaurus norfolcensis	200	3-3.5	1.99	0.61
Tamiasciurus hudsonicus*	200	0.49	1.99	4.06
Petaurus gracilis	315	20	3.53	0.18
Petaurus australis	590	25-85	7.79	0.14
Petaurista petaurista	1300	3.2	21.07	6.58
Petauroides volans	1400	1.3-2.6	23.19	11.89
Petaurista leucogenys	>1000	1.1-2.1	15.14	9.46
Petaurista alborufus	> 1000	?	15.14	--

launching or landing, nor has there been any analysis of the overall energy budgets of squirrel gliders. Thus, even with respect to the transport economics hypothesis, there is much that needs to be learned.

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