GLIDING PERFORMANCE OF THE NORTHERN FLYING SQUIRREL (*GLAUCOMYS SABRINUS*) IN MATURE MIXED FOREST OF EASTERN CANADA

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There is a paucity of empirical data on gliding abilities of most gliding mammals, including flying squirrels in the genus *Glaucomys*. I assessed gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) by calculating glide parameters for 100 glides observed between July 1999 and July 2000 in southern New Brunswick, Canada. *G. sabrinus* had a glide angle of 26.8° and a glide ratio of 1.98. The difference between the vertical drop at the start of a glide and the vertical rise at the end of a glide was about 1.91 m. Males tended to glide farther than females ($\bar{X}$ = 19.0 m versus 14.2 m), although sexes did not differ in heights of launch ($\bar{X}$ = 9.8 m) or landing ($\bar{X}$ = 2.0 m). Red spruce (*Picea rubens*) trees were favored as landing sites over hardwood species. Most glides (59%) were with the slope of terrain, allowing a greater net height loss ($\bar{X}$ = 10.2 m) than initial height of launch. Horizontal glide distance ranged from 3.2 to 45 m, with most glides being 5–25 m.

Key words: aerodynamic performance, flying squirrel, *Glaucomys,* glide angle, glide ratio

Gliding is defined by Vogel (1981:218) as "a situation in which an airfoil moves through the air, losing altitude just rapidly enough to maintain both a steady speed and a vertical force the same as its weight." Therefore, gliding differs from the powered flight used by birds, bats, and insects and parachuting or ballooning typically employed by small spiders, some insect larvae, and many wind-dispersed seeds (Vogel 1981). The former can achieve thrust and lift, whereas the latter has an angle of descent usually >45° (Rayner 1981).

Gliding has evolved independently in at least 6 groups of mammals. Eight species of marsupial possums in 3 families (Diprotodontia: Petauridae, Pseudocheiridae, and Acrobatidae) glide. Among eutherians, gliding occurs in the colugos (Dermoptera), African scaly-tailed squirrels (Rodentia: Anomaluridae), and flying squirrels (Rodentia: Sciuridae—Nowak 1999). The most diverse and widespread of those groups are the flying squirrels (15 genera, 44 species), including 2 North American species, the southern flying squirrel (*Glaucomys volans*) and the northern flying squirrel (*G. sabrinus*). This group also is considered to be the most aerodynamically sophisticated (Thorington et al. 1998), with patagia variously designed to direct movement patterns of airflow over the airfoil (propatagium), provide a surface for lift (plagiopatagium), and modify lift and drag (uropatagium—Thorington et al. 1998). Upturned wing tips under the control of the styliform cartilage associated with the wrist also serve to reduce drag by diffusing vortices and directing them away from edges of the patagium (Thorington et al. 1998). Several authors have noted the acrobatic nature of flying squirrels in flight, with long glides often punctuated by banking and turning to avoid objects in the flight path (Dolan and Carter 1977; Nowak 1999).

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Gliding is considered to be energetically cheap (Norberg 1985a), allowing small mammals to cover large distances quickly and efficiently. Foraging optimization may have been the most important selection force in early glider evolution (Norberg 1985a; Stapp 1994). Jackson (2000) noted that many gliding marsupials exploit patchily distributed sap and nectar, although he conceded that exploitation of patchy food is not common to all gliding mammals. Northern flying squirrels are mycophagous, consuming a diversity of hypogeous fungi that may constitute up to 80% of the diet (Blois 2000). Hypogeous fruiting bodies are typically patchily distributed throughout the forest (Fogel 1976, 1981). Therefore, the ability to cover long distances quickly and efficiently would bestow a considerable advantage on a small mycophagous mammal such as the northern flying squirrel.

Although morphological adaptations to gliding in flying squirrels is reasonably well understood (Johnson-Murray 1977; Oshida et al. 2000a, 2000b; Thorington and Heaney 1981; Thorington et al. 1998), considerably less detail is known about gliding ability in this group. In a recent review of gliding in mammals, Jackson (2000) identified a lack of reliable data on gliding abilities of most mammalian gliders, including both species of *Glaucomys* found in North America. Most field accounts of gliding angle and associated glide ratio are based on approximations of parameters necessary to calculate these values, including height of launch, height of landing, distance of the glide, and weight of the gliding animal. Accurate field data of this nature only really exist for the giant red flying squirrel (*Petaurista petaurista*—Scholey 1986), the Japanese giant flying squirrel (*Petaurista leucogenys*—Ando and Shiraishi 1993), and 2 species of gliding marsupial, the sugar glider (*Petaurus breviceps*—Jackson 2000) and the mahogany glider (*Petaurus gracilis*—Jackson 2000). Glide performance also was assessed by Scheibe and Robins (1998) for *G. volans* with a com-

bination of field and laboratory observations.

Knowledge of gliding ability and limitations provides insight into theoretical rates of home-range traversal, foraging efficiency, dispersal ability, and in some respects, ability to withstand pressures associated with forest fragmentation and linear barriers to movement, such as roads and powerline corridors. This study presents empirical data on gliding performance of the northern flying squirrel. It is the 1st study of its kind on the North American genus *Glaucomys* and 1 of the few accounts of aerodynamic performance by a gliding mammal.

Materials and Methods

The study was undertaken from July 1999 to July 2000 at Fundy National Park (45°37′N, 65°02′E) in southern New Brunswick, Canada. The study area in the southern region of the park comprised a mature 2nd growth (50- to 70-year-old) stand of mixed hardwood–coniferous forest dominated by white birch (*Betula papyrifera*), yellow birch (*B. alleghaniensis*), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*). Less common trees were beech (*Fagus grandifolia*), red maple (*Acer rubra*), and striped maple (*A. pennsylvanicum*). Average canopy height was 12–17 m, with emergent trees reaching 20–22 m. Tree density was about 760 trees/ha, and canopy cover was about 70%. The landscape of the park was characterized by an elevated plateau with rolling hills and steep river valleys. Northern flying squirrels were livetrapped at 4 sites in the study area with treadle-activated wire cages tied to trees at a height of about 2 m and baited at dusk with a combination of apple and peanut butter. Traps were insulated with cotton batting and encased in cardboard and plastic to protect trapped animals from exposure to weather. Traps were checked the following morning, at which time trapped animals were weighed, sexed, measured, marked, and released at the base of a nearby tree.

Released animals typically climbed rapidly toward the top of the release tree, but gliding often took several minutes to occur or was not observed. After a glide was observed the following data were collected: height of launch tree
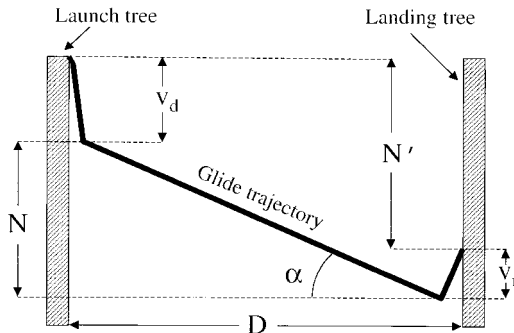
FIG. 1.—Model of a theoretical glide trajectory and glide parameters of flying squirrels measured or derived to yield glide-performance parameters of vertical drop − vertical rise ($v_d − v_r$) and glide angle (α).

from base to point of launch, to the nearest 0.1 m (with a clinometer); height of landing tree from base to point of landing, to the nearest 0.1 m (with a clinometer or tape measure); horizontal distance between base of launch tree and base of landing tree, to the nearest 0.1 m (with a tape measure); and slope of terrain between launch tree and landing tree, to the nearest 0.5° (with a clinometer).

The following model was assumed for data analysis. I observed that flying squirrels, upon launching, dropped a vertical distance (v_d) before beginning to glide, and often rose a smaller vertical distance (v_r) just before landing (Fig. 1). If the vertical distance dropped during the actual gliding phase was denoted N, my measurement of height loss between launch and landing was $N' = N + v_d − v_r$ (Fig. 1). For an individual gliding event, the glide angle α was calculated as tan α = N/D, which implied α = arctan(N/D), where D was the horizontal distance (m) between the launch tree and landing tree (Fig. 1). That equation could be rearranged to read N = D tan α, which was the equation of a straight line of slope tan α and of zero y-intercept. I did not measure N but rather measured N'. Thus, a plot of N' versus D gave the following result: N = N' − v_d + v_r, which implied N' = D tan α + (v_d − v_r). That also was the equation of a straight line, with a slope of tan α and a y-intercept of (v_d − v_r). Thus, the glide angle could be calculated from the slope of a plot of N' versus D, and the difference between vertical drop and vertical rise (v_d − v_r) could be assessed from

the y-intercept. The model assumed that (v_d − v_r) was constant, regardless of glide distance.

The mean weight of flying squirrel in the study and the calculated glide angle (α) were used to calculate glide-performance parameters of lift (L) and drag (DR) according to the equations L = Mg cos α and DR = Mg sin α from Norberg (1985b), where Mg was force in newtons (based upon the weight of the animal in kilograms).

The type of tree (or other substrate) used as a landing point was noted and compared with the frequency of tree stems (including snags) in the study area. Stem density was estimated from three 10- by 20-m vegetation plots surveyed in August 2000 at each of the 4 trapping sites. Trees and snags with a diameter at breast height <10 cm were not included because the trunks of small saplings were not selected as landing points by flying squirrels.

Comparisons between males and females were made with independent *t*-tests. To reduce risk of type II errors arising from multiple tests, significance for each test was adjusted with Bonferroni correction (Bärlocher 1999).

RESULTS

Glide parameters.—I recorded 100 glides (44 by males, 56 by females) for 53 animals (27 males, 26 females; Table 1). Males tended to glide greater distances ($\bar{X}$ = 19.0 m) during each glide than females ($\bar{X}$ = 14.2 m; t = 2.84, *d.f.* = 98, P = 0.01; Table 1; Fig. 2), despite no significant difference in the height of launch ($\bar{X}$ = 9.8 m) or landing ($\bar{X}$ = 2.0 m) between sexes (Table 1). Horizontal glide distance varied between 3.2 and 45.0 m (Table 1; Fig. 3), but the majority (78%) of glides ranged from 5 to 25 m (Figs. 2 and 3).

Horizontal glide distance and net height loss were correlated (r = 0.88, P < 0.0001; Fig. 3). The equation derived from that plot suggested that the difference between the vertical drop at the start of the glide and a vertical rise at the end of the glide (y-intercept) was about 1.91 m ± 0.50 *SE* (Fig. 3; Table 2) and that glide trajectories had a mean angle of descent of 26.8° and a mean glide ratio of 1.98 (Table 2). Little difference was found in estimated glide angle and

TABLE 1.—Summary of parameters for 100 glides by *Glaucomys sabrinus* (53 individuals) at Fundy National Park, southern New Brunswick, Canada, July 1999–July 2000.

Glide parameter	Males ($n = 44$)			Females ($n = 56$)			Statistic		All glides ($n = 100$)	
	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	t	P	$\bar{X}$	SD
Weight (g)	89.5	12.3	36–113[a]	95.3	14.0	42–128[b]			92.7	13.5
Height of launch (m)	9.8	3.3	4.2–17.1	9.9	4.1	3.5–19.2	0.14	0.9	9.8	3.7
Height of landing (m)	2.0	1.6	0.0–6.9	1.9	1.4	0.0–6.4	0.35	0.7	2.0	1.5
Net height loss (m)	11.2	5.9	2.5–27.9	9.3	4.3	3.5–21.7	1.86	0.07	10.2	5.1
Horizontal distance (m)	19.0	10.3	3.2–45.0	14.2	7.1	3.9–31.3	2.84	0.01[c]	16.4	9.0

[a] Lower limit of range includes juvenile animals.
[b] Upper limit of range includes pregnant females.
[c] Significant value after Bonferroni correction.

glide ratio between males and females (Table 2). The difference between vertical drop and vertical rise was somewhat smaller for males, but based on associated error values, it probably was not significantly different (Table 2).

Gliding behavior.—Many flying squirrel captures did not result in a glide being recorded (46%), either because vegetation or terrain obstructed the beginning or end points of a glide, or because the animal remained high in the canopy after release. Animals that did glide usually took several minutes to begin gliding but were often reluctant to do so until investigators moved a short distance from the point of release. Several of those hesitant animals glided to daytime nesting cavities. Gliding almost always began from a horizontal crouched position, with the tail curved slightly downward. Flying squirrels appeared to observe the intended flight path before gliding and were occasionally seen to sway from side to side before launch.

In plan view, most glides had a linear trajectory; however, some ($n = 11$) incorporated changes in direction (banking and turning) during gliding to avoid trees or other obstacles. Against the assumption that slope of the terrain beneath the glide path was chosen randomly, significantly more glides were directed downslope ($n = 55$)
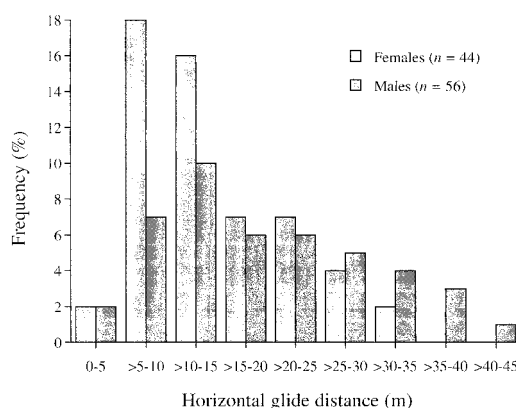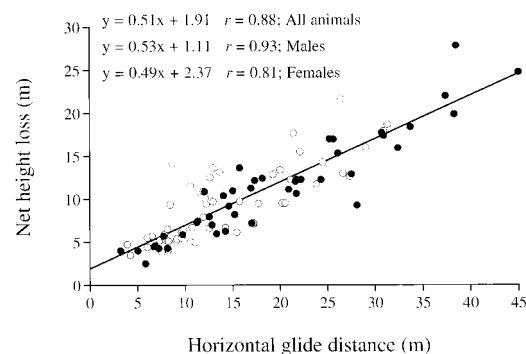

FIG. 2.—Frequency distribution of glides of northern flying squirrels (*Glaucomys sabrinus*) at Fundy National Park, July 1999–July 2000.

FIG. 3.—Horizontal distance of glides of male (closed circles) and female (open circles) northern flying squirrels (*Glaucomys sabrinus*) as a function of net height loss at Fundy National Park, July 1999–July 2000. Line represents simple correlation with all data; $P < 0.001$ for all correlation coefficients.

TABLE 2.—Glide-performance parameters derived from 100 glides by *Glaucomys sabrinus* at Fundy National Park, southern New Brunswick, Canada, July 1999–July 2000.

Glide-performance parameter	Males		Females		All animals	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Slope (=tan α)	0.529	0.032[a]	0.491	0.049	0.505	0.027
Vertical drop − vertical rise ($v_d - v_r$, m)	1.11	0.69	2.37	0.78	1.91	0.50
Glide angle (α, °)	27.9	1.4[b]	26.2	2.3	26.8	1.2
Lift to drag ratio (L:DR)	1.89	0.11	2.03	0.20	1.98	0.11

[a] Standard deviations were obtained from linear regression analysis.

[b] Uncertainties were propagated from standard deviation of slope according to Taylor (1982).

versus upslope ($n = 23$) or those at right angles ($n = 16$) to the slope of the terrain ($\chi^2 = 26.5$, *d.f.* $= 2$, $P < 0.001$). An additional 6 glides were made in an area where the slope of the terrain was effectively 0°. Two glides were not included in analyses because squirrels, upon launching into the glide, struck outer foliage of the launch tree, which halted their forward momentum and resulted in a compensatory downward-parachute maneuver.

Landing typically was on a tree trunk near its base (<3 m height; 75% of glides). The most common landing tree was red spruce (46%) and red spruce snags (13%; Fig. 4), whereas hardwood species were used less often (12%; Fig. 4). Trees were
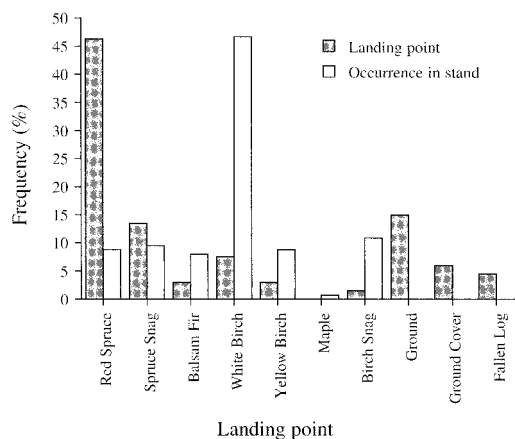

FIG. 4.—Frequency distribution of landing points selected by the northern flying squirrel (*Glaucomys sabrinus*) compared with estimated frequency of tree species at Fundy National Park, July 1999–July 2000.

used as landing sites disproportionate to their occurrence in the study area; white birch dominated the stand (47% of stems > 10-cm diameter at breast height), whereas red spruce was considerably less common (9% of stems > 10-cm diameter at breast height; Fig. 4). Twenty-one percent of glides were to ground or dense ground cover such as regrowth of spruce or fern thickets (Fig. 4).

DISCUSSION

Thorington and Heaney (1981) predicted that on the basis of limited anecdotal observations gleaned from the literature, few flying squirrels have glide ratios >3.0. For *Glaucomys,* field observations have returned estimates ranging from about 2.0 (Sumner and Dixon 1953) to 2.8 (Nowak 1999) and ". . . between 2 and 3" (Thorington and Heaney 1981:112). Those estimates are similar to the gliding ratio of 1.98 that I calculated in the current study for the northern flying squirrel (Table 1). Ando and Shiraishi (1993) recorded similar glide ratios between 1 and 3 for the Japanese giant flying squirrel (*P. leucogenys*). Under laboratory conditions, Scheibe and Robins (1998) estimated that the mean glide ratio of *G. volans* was 1.53, but they noted that this value would be higher if actual rather than direct glide angles were used. For comparative purposes, use of direct glide angles from data I collected on *G. sabrinus* yielded a mean glide ratio of 1.62. Thus, *G. volans* and *G. sabrinus* probably exhibit very similar glide performances.

Similarly, the difference between the vertical drop made by *G. sabrinus* to gather speed at the start of a glide and the vertical rise achieved during the landing phase was 1.91 ± 0.5 m, comparable to the 1.85-m vertical drop reported by Scheibe and Robins (1998) for *G. volans.* Although I was unable to separate vertical drop from vertical rise in my gliding model, I estimate the vertical rise component to be minor in most instances, based upon field observations. A necessary shortcoming of my model is the assumption that vertical drop and vertical rise do not change with glide distance, a situation that probably does not hold true in reality. Several factors could influence those parameters. For example, Scholey (1986) recorded a considerably greater vertical drop (7.45 m) for *P. petaurista* before gliding. Members of the genus *Petaurista* weigh 1–2.5 kg (Nowak 1999) and thus require a greater vertical drop at the start of a glide than the smaller *Glaucomys* (about 45–120 g); increased wing loading (Thorington and Heaney 1981) would necessitate greater glide speeds of *Petaurista* (Scheibe and Robins 1998). Within a species, vertical drop could be influenced by desired glide speed, intended glide distance or individual variations in body mass, or patagium area.

Jackson (2000) calculated glide ratios of 1.1–2.5 for 2 Australian marsupial gliders, the mahogany glider (*P. gracilis*), and sugar glider (*P. breviceps*). The smaller of those species, the sugar glider, attains an adult weight (69–150 g) similar to that of the northern flying squirrel (70–128 g). Despite their considerably different evolutionary histories, patagia morphology, and differing ecological pressures relating to habitat structure, diet, and predation pressure, sugar gliders and flying squirrels show a great deal of convergence in gliding abilities. Jackson (2000) calculated a mean glide ratio of 1.82 (cf. 1.98 for *G. sabrinus*), glide angle of 29.7° (cf. 26.8° for *G. sabrinus*), and a mean glide distance of 20.6 m (cf. 16.4 m for *G. sabrinus*) for the sugar glider.

Further, height of launch (12.0 m), height of landing (2.0 m), and net height loss (10.0 m—Jackson 2000) are all very similar to values I recorded for the northern flying squirrel (Table 1), although those parameters obviously have much to do with local canopy height and general forest structure. Size of a gliding mammal is related directly to drag, and therefore to the best (i.e., minimum) glide angle that it can achieve (Vogel 1981). Therefore, it is perhaps not surprising that the similar-sized *P. breviceps* and *G. sabrinus,* despite other differences, have achieved similar gliding ability over evolutionary time. Whether or not comparisons drawn here have general relevance to other gliding mammals is unknown.

Only slight differences were detected between gliding parameters for male and female northern flying squirrels, except for glide distance. Males on average glided further (19.0 m) than females (14.2 m), with the 6 longest glides attributable to males. I believe that this result may be an artifact of the methods I used to record glides rather than a preponderance by males toward greater glide distances. Glides made by most animals were probably in the direction of the den site, given that trapped animals were released during morning daylight and several glides terminated at dens. Male flying squirrels were reported by Gerrow (1996) in the study area to have larger home ranges than females (12.5 ha versus 2.8 ha) and thus by chance, were likely to be further from the den tree at the point of capture. That fact alone probably accounts for the greater glide distances reported for males.

Gliding mammals are believed to select a landing point before takeoff (Caple et al. 1983). Aerial maneuvers such as banking and turning result in losses in altitude, so the landing point must be large enough to allow vertical variation in the point of contact (Caple et al. 1983). Thus, for longer glides, gliding mammals usually select vertical tree trunks (Caple et al. 1983). More than one-half of the glides I observed ter-

minated with the flying squirrel landing on a vertical red spruce trunk or a spruce snag near its base, although occasionally animals appeared to misjudge the landing point and glide to the ground just short of the tree stem. Despite their dominance in the stand, nonconiferous trees were used infrequently as landing points, probably because flying squirrels have difficulty maintaining traction on the smooth, flaky bark characteristic of common hardwoods such as white and yellow birch (K. Vernes, in litt.). Attempts to release flying squirrels on birch trees usually resulted in the animal leaping to the ground and seeking a nearby spruce.

This study has several limitations that are difficult to overcome when studying glide parameters of free-ranging animals. Flying squirrels are nocturnal, yet all the glides I measured were during daylight hours after release of trapped animals. As such, I cannot assume that squirrels behaved as they would do during normal activity. More glide paths were directed downslope than upslope or at right angles to the slope of the terrain, and I assume this to be a flight response, whereby animals are attempting to put as much distance as possible between themselves and the release point. Alternatively, some glides were quite short when squirrels were seeking a nearby den tree, and these are probably not representative of true gliding ability. Furthermore, to effect a more rapid escape, flying squirrels may have increased glide speed by increasing their glide angle, which in turn would reduce glide ratio. Localized variation in wind speed and direction also might affect the optimal speed (and glide angle) at which a glider chooses to operate (Vogel 1981). Scheibe and Robins (1998) measured glide speeds of *G. volans* in the laboratory and field and found them to vary between 4.12 and 8.85 m/s. Ando and Shiraishi (1993) recorded variations in glide speeds of *P. leucogenys* in the field between 7.0 and 15.1 m/s. Measurement of glide speeds would be a useful addition to the data I gathered but requires >1 observer to simultaneously time each glide if precision of the estimate is to be calculated.

Finally, gliding mammals do not move at a constant speed and glide angle throughout a glide, so each glide I measured should be considered as the mean of a more complex event. Work on the sugar glider by Nachtigall (1979) showed that glides typically began with a high glide angle, which was reduced as speed was gained. At the end of a glide, sugar gliders underwent aerodynamic braking, where angle of attack was increased to very high values to limit speed of impact just before landing (Nachtigall 1979; Vogel 1981). I observed similar changes in glide paths of northern flying squirrels; however, without use of high speed cinematography under controlled conditions (as was done by Nachtigall 1979), such changes are impossible to quantify. Therefore, further work in this area is desirable.

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