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Quadrupedal locomotor performance in two species of arboreal squirrels: predicting energy savings of gliding

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Abstract Gliding allows mammals to exploit canopy habitats of old-growth forests possibly as a means to save energy. To assess costs of quadrupedal locomotion for a gliding arboreal mammal, we used open-flow respirometry and a variable-speed treadmill to measure oxygen consumption and to calculate cost of transport, excess exercise oxygen consumption, and excess post-exercise oxygen consumption for nine northern flying squirrels *(Glaucomys sabrinus)* and four fox squirrels *(Sciurus niger)*. Our results indicate that oxygen consumption during exercise by flying squirrels was 1.26-1.65 times higher than predicted based on body mass, and exponentially increased with velocity (from 0.84 ± 0.03 ml O_2 kg^{-1} s^{-1} at 0.40 m s^{-1} to 1.55 ± 0.03 ml O_2 kg^{-1} s^{-1} at 0.67 m s^{-1}). Also, cost of transport in flying squirrels increased with velocity, although excess exercise oxygen consumption and excess post-exercise oxygen consumption did not. In contrast, oxygen consumption during exercise for fox squirrels was similar to predicted, varying from 0.51 (±0.02) ml O_2 kg^{-1} s^{-1} at 0.63 m s^{-1} to 0.54 (±0.03) ml O_2 kg^{-1} s^{-1} at 1.25 m s^{-1}. In addition, the cost of transport for fox squirrels decreased with velocity, while excess exercise oxygen consumption and excess post-exercise oxygen consumption did not. Collectively, these observations suggest that unlike fox squirrels, flying squirrels are poorly adapted to prolonged bouts of quadrupedal locomotion. The evolution of skeletal adaptations to climbing, leaping, and landing and the development of a gliding membrane likely has increased the cost of quadrupedal locomotion by >50% while resulting in energy savings during gliding and reduction in travel time between foraging patches.

Keywords Cost of transport . Dispersal . Energetics . *Glaucomys sabrinus* . Respirometry . *Sciurus niger*

Abbreviations

COT	Cost of transport
EEOC	Excess exercise oxygen consumption
EPOC	Excess post-exercise oxygen consumption
M_b	Body mass
RMR	Resting metabolic rate
v_g	Speed
Vo_2	Rate of oxygen consumption

Introduction

Ancestors of North American flying squirrels *(Glaucomys* spp.) may have evolved gliding to exploit canopy habitats of forests as an efficient mode of locomotion between trees (Dudley et al. 2007). Evolutionary ecologists have proposed that mammalian gliding evolved as a mechanism to minimize the cost of transport, to optimize foraging by reducing

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travel time between patches, to control landings, or to avoid predation (Norberg 1985; Paskins et al. 2007; Scheibe and Robbins 1998). Previous theoretical research on *Glaucomys* and other species indicate that gliding is more energetically efficient than quadrupedal locomotion (Scholey 1986; Scheibe et al. 2006; Scheibe and Robbins 1998) but efficiency may be determined by body mass (Dial 2003). Gliding mammals use potential energy gained from climbing to a launch point, to power a glide. Little energy is used during the launch or initiation of the glide (Scheibe et al. 2007) and less to maintain gliding posture (Dial 2003; Norberg 1985). Also, because of the 2:1 glide ratio (Thorington and Heaney 1981; Vemes 2001), a flying squirrel can glide twice as far as the distance climbed. Therefore, gliding requires less energy than traveling the same distance quadrupedally through the canopy or on the ground (Emmons and Gentry 1983; Norberg 1985) for gliding mammals <400 g (Dial 2003). Investigators using gliding performance measurements and cost of transport models in North American flying squirrels reported that *Glaucomys sabrinus* appeared to realize this energetic benefit from gliding distances greater than 14 m (Scheibe et al. 2006), whereas, the smaller G. *volans* appears to realize a benefit after only 7 m glides (Scheibe and Robbins 1998).

Costs of foraging, including energetic costs involved with traveling between foraging patches, are hypothesized to be high for all gliding mammals, ostensibly comprising most of their daily energy expenditures (Geiser and Stapp 2000). According to the Marginal Value Theorem, increased travel time between foraging patches should result in increased residency time within patches (Chamov 1976), whereas reduced travel time between patches enables an animal to leave a patch while the rate of return is still relatively high (Charnov 1976; Norberg 1977). Animals that expend more time and energy searching for foraging patches continue to pay energetically for this activity even after settling in a new patch because of the metabolic costs of recovery from the oxygen debt of locomotor activity (i.e., excess post-exercise oxygen consumption - EPOC; Gaesser and Brooks 1984). Added to the costs associated with patch-occupancy and travel between patches are those associated with thermoregulation (Kilpatrick 2003). These costs will likely be higher for animals traveling through open habitats with little cover and insulation during cool weather or rain. In addition, foragers that are exposed to predation may modify patch-occupancy to minimize risk (Abrams 1984). Therefore, gliders traveling in open, unforested habitats (i.e., large gaps in the canopy that may be crossed during dispersal) will likely spend more time foraging than those traveling through closed-canopy habitats (Adler and Kotar 1999), with significant increases in risk of predation and overall energy expenditure.

Forests with tall canopies and open understories, which allow for higher launch points and unobstructed gliding, facilitate longer glide distances and increased energetic savings (Dial 2003; Mowrey and Zasada 1982). In contrast, in clearcuts and developing young-growth stands following broad-scale timber harvest that are pervasive in managed forests, the lack of tall (>6 m) launch and landing points and presence of dense mid-story canopy may impede gliding, forcing flying squirrels to rely primarily on quadrupedal locomotion for dispersal. Although flying squirrels have been sighted in regenerating forest stands (Carey 1995; 2000), the energetic costs associated with quadrupedal locomotion will likely increase the foraging time of flying squirrels by increasing travel time between patches, ultimately influencing the overall energy budget (Flaherty et al. 2010) and increasing risk of predation for these gliders. Indeed, flying squirrels in Oregon actively avoided managed forest habitats (Volz 1986).

In contrast to flying squirrels, fox squirrels *(Sciurus niger,* Linnaeus), are a non-gliding sciurid, native to the eastern and central United States (Koprowski 1994). These arboreal squirrels likely evolved in relatively open forest habitats, are highly mobile, and do not appear to be as sensitive to fragmentation (Nupp and Swihart 2000; Zollner 2000). While loss of vertical structure could increase the risk of predation, mainly from aerial predators, it is less likely to affect the energy budget of these non-gliding sciurids. Therefore, for non-gliding arboreal animals, quadrupedal locomotion and the energetic costs involved with this mode of transport are expected to be lower than those of flying squirrels and more similar to predictions based on body size (Fournier and Weber 1994; Taylor et al. 1982).

To compare quadrupedal locomotor performance between a gliding and a non-gliding arboreal sciurid, we: (1) measured the energetic cost of quadrupedal locomotion for a glider, *Glaucomys sabrinus,* and a non-glider, *Sciurus niger,* (2) evaluated and compared costs of locomotion including excess oxygen consumed during and after exercise and recovery time between the two species, because recovery costs can add significantly to the total energetic costs of locomotion (up to 90% during a 60 s bout in *Mus musculus* (Baker and Gleeson 1999), and, (3) compared the energetic costs of quadrupedal locomotion between the two species in the context of the adaptations of gliding.

Materials and methods

Animals

Ten northern flying squirrels were trapped in early October of 2005 using Tomahawk No. 201 (41 x 13 x 13 cm) live

traps (Tomahawk Live Trap, Tomahawk, WI, USA). Nine squirrels, (four females and five males) were captured at Eagle's Nest Campground on Balls Lake, Prince of Wales Island, Alaska (55°42'13" N, *132°50'45"* W). One squirrel (adult female) was captured near the community of Naukati *(55°52'12"* N, l33°12'16" W). Traps were placed approximately 1.5 m above the forest floor on the bole of a tree and baited with a mixture of rolled oats, peanut butter, and molasses (Smith and Nichols 2003). Traps were checked at sunrise and captured animals were transferred to holding cages. Upon capture, all squirrels were marked with a unique PIT tag (Biomark, Boise, ID, USA) for identification. Within 7 days, and after a health assessment by a veterinarian, these northern flying squirrels were flown to the University of Wyoming via a commercial airline (Alaska Department of Fish and Game Permit #05-123).

Fox squirrels were captured in April 2006 on the University of Wyoming campus in Laramie, Wyoming, (41°l8'46"N 105°35'0l" W). Four juvenile males were removed from nest boxes approximately 1 week before they were completely weaned. We also live-trapped two adult males using Tomahawk No. 201 traps baited with peanut butter and black oil sunflower seeds. The four juveniles were initially fed Ebsilac© kitten milk replacement (PetAg Inc., Hampshire, IL, USA) every 4 h until they began eating solid food, after approximately 1 week in captivity.

All squirrels were housed in the University of Wyoming Animal Care Facility in the Biological Sciences Building (Wyoming Game and Fish Chapter 10 Permit #1247 and Chapter 33 Permit #386). The ten flying squirrels were housed together in a 2.5 x 2.5 x 3.0 m room with access to five nest boxes. Those fox squirrels that were captured individually were housed in separate cages; the rest were housed in cages with their nest mate. Fox squirrel cages were 1.0 x 2.0 x 3.0 m in size. A window in the flying squirrel room, covered with hardware cloth, remained open throughout the year to expose the squirrels to outside temperatures and natural light regimes. The window in the fox squirrel room remained closed but allowed squirrels to adjust to ambient light fluctuations. Water was provided to all animals ad libitum. Hartz® Hampster and Gerbil Nutrition Bonanza Gourmet Blend chow (Hartz Mountain Corporation, Secaucus, NJ, USA), nuts, apple, yam, mushrooms, and fresh com were fed to maintain body masses similar to those of wild animals (130-145 g for the flying squirrels; 500-700 g for the fox squirrels). Powdered calcium supplements were added to the food twice weekly. Animals were weighed every week to monitor body mass and health. All squirrels were allowed approximately 3 months to acclimate to captivity prior to the initiation of experiments and all squirrels were housed in enclosures with sufficient space for free movement and daily exercise.

We measured rate of oxygen consumption $(\dot{V}O_2)$ for four male and five female flying squirrels and four male fox squirrels. One male flying squirrel and two male fox squirrels were removed from the trials after consistently failing to adjust to the conditions of the experiment. At the end of the trials, the fox squirrels were released at the site of capture on the campus of the University of Wyoming; flying squirrels were transferred to Southeast Missouri State University to supplement a captive breeding colony.

Respirometry

We used open-flow respirometry methods, modified from Ben-David et al. (2000) and Williams et al. (2002), to evaluate resting and running energetics in both species of squirrels. A Plexiglas chamber (35.0 cm long x 15.0 cm wide x 16.5 cm high for flying squirrels, and 61.0 cm long x 15.0 cm wide x 16.5 cm high for fox squirrels) was mounted on a variable speed treadmill. Both chambers were large enough to allow each species of squirrel to run with legs and tail fully extended. Ambient air was drawn into and through the chamber from around the lower edges of the chamber using a vacuum pump (Gast DOA-l0l-AA; Gast Manufacturing, Inc., Benton Harbor, MI, USA) at flow rates averaging 3.7 L min^{-1} at standard temperature and pressure (STP) for the flying squirrels, and 6.2 L min^{-1} STP for fox squirrels. Flow rates were monitored continuously using a mass flow controller valve (Tylan FC-261V; Entegris Inc., Chaska, MN, USA), calibrated by Coastal Instruments (Coastal Instruments, Burgaw, NC, USA), and flow rates were tested regularly against a rotameter (FL-3439ST; Omega Engineering, Inc., Stamford, CT, USA). Air samples from the chamber were removed through a finely perforated hose running the length of the chamber and exited through a port in the front. Samples were pulled through a Drierite (W.A. Hammond Drierite Co. LTD., Xenia, OH, USA) column to remove water vapor prior to entering the mass flow controller valve. A subsample of air, collected following the sealed pump, was again scrubbed of water and CO_2 using Ascarite (Thomas Scientific, Swedesboro, NJ, USA). Percent oxygen was continuously monitored and recorded (% O_2 value collected every 0.5 s) using an oxygen analyzer (Sable Systems FX 0501-20 or "FOXBOX"; Sable Systems International, Las Vegas, NV, USA) connected to a personal computer running Expedata software (Sable Systems International, Las Vegas, NV, USA). The oxygen analyzer was calibrated before every run using atmospheric air, and several times a week, the entire system was tested for leaks by infusion of nitrogen gas (Fedak et al. 1981). Values generated by the oxygen analyzer were then converted to $\dot{V}O_2$ STP, dry using the program Expedata and modified equations from Fedak et al. (1981) and Withers

(1977) with an assumed standard respiratory quotient of 0.85 (Withers 1977).

Experimental protocol

Animals were trained to run inside the Plexiglas chamber by placing them in the chamber and slowly increasing the speed of the treadmill over the course of approximately 10 min until the animal was running. Prior to running, squirrels were fasted for approximately 12 h to ensure that measurements were collected in post-absorptive animals. Each individual was weighed before and after each trial, and the mean mass was used in all calculations related to that experiment. At the beginning of each trial, individuals were placed inside the chamber on a perforated aluminum tray that was placed over the moving tread inside the chamber to measure resting metabolic rate. This tray allowed mixing of the air in the chamber through movement of the tread. During all resting measurements, the overhead lights in the room were turned off to minimize visual disturbance; fox squirrels were less active (scratching the bottom of the tray) when the lights were off and the flying squirrels placed their tail over their heads and remained still during most ofthe resting metabolic rate measurements. After the animals had rested for approximately 15 *min* or when a steady rate of oxygen consumption had been reached, the tray was gently removed and the squirrel dropped onto the moving tread. The squirrels then ran for 5-8 min or until oxygen use varied by approximately <5% over a 1 *min* period. Following the end of the run, the aluminum tray was slowly replaced so that the squirrel could jump back on top to rest. We continued to collect air samples from the chamber for at least 15 *min* after the completion of the run to measure EPOC. A dim red light allowed the observer to record behavior following running. Immediately following trials, squirrels were returned to their enclosure and food was provided. Each squirrel was allowed to rest 24 h between successive experiments.

Running energetics data were collected for each squirrel at four different speeds that facilitated walking, trotting, trot/bound, and bounding gaits. We likely were conservative in choosing the fastest speed as we were interested in minimizing stress and preventing overheating from maintaining higher speeds for the time required to obtain a steady rate of oxygen consumption. For the flying squirrels, those speeds were 0.40, 0.49, 0.58, and 0.67 m s^{-1} for fox squirrels, the speeds were 0.63, 0.81, 1.03, and 1.25 m s^{-1}. To assess the cost of vertical transport, we also ran the squirrels at different inclines using the trotting speed. The flying squirrels ran at 1.5, 5, and 10% incline while the fox squirrels were run at 1.5 and 10%. Fox squirrels were not included in trials with a 5% incline to minimize their time in captivity and to facilitate an early fall release, thereby providing animals with sufficient foraging time to cache for winter. Each individual squirrel ran at each speed and incline three times, for a total of 18 runs per flying squirrel and 12 runs per fox squirrel. We randomly chose the order in which the runs were performed for each individual to avoid a training effect.

Because of the constant movement of the tread in the chamber and because we were using an open flow-through system, small amounts of air were lost through the back edge of the chamber. To correct this air loss, we used methods modified from Ward et al. (2002). A known amount of N_2 gas was introduced into the chamber as a single bolus of known volume at all experimental speeds with and without the presence of the aluminum tray for both chambers. Then, using the procedures described above for calculating oxygen content in air samples drawn from the chamber, we recorded the volume of oxygen after the N_2 gas was introduced. We repeated this procedure three times per speed per chamber. We then used non-linear curve-fitting procedures (Neter et al. 1996) with oxygen volume as the dependent variable and speed as the independent one to calculate a correction factor that was equivalent to the amount of sample lost at each speed ($R^2 = 0.954$ for correction factors with the tray in the chamber and 0.955 with the tray removed). Finally, we multiplied the observed values from our squirrel trials by this correction factor to obtain estimates of oxygen consumption for each individual squirrel.

All field and laboratory methods involving the squirrels were approved by the University of Wyoming Institutional Animal Care and Use Committee and followed guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Data analysis and statistics

For each species, we measured the mass-specific rate of oxygen consumption (V_{O_2}, ml O_2 kg^{-1} s^{-1}; Alexander 1968; Fournier and Weber 1994), both during resting and at various speeds and inclines during experimental trials on the treadmill. We used V_{O_2} measures and bout times, as well as individual body mass data to calculate the cost of transport (COT, J N^{-1} m^{-1}), excess exercise oxygen consumption (EEOC, ml s^{-1}) and excess post-exercise oxygen consumption (EPOC, ml s^{-1}). We calculated predicted net oxygen consumption using established allometric equations for resting and running metabolic rate. Predicted resting metabolism was calculated using (Fournier and Weber 1994; Kleiber 1932):

$$\dot{V}_{O_2}/M_b \ (\text{ml}\, O_2\, \text{kg}^{-1}\, \text{sec}^{-1}) = 0.188 M_b^{-0.250}, \quad (1)$$

where M_b is body mass in kg and Vo_2/M_b is in ml O_2 kg^{-1} s^{-1}. For each trial, we used the mass of the individual recorded as an average from measurements

made immediately before and after the experiment. Predicted metabolic rate during quadrupedal locomotion was calculated using (Taylor et al. 1982):

$$\dot{V}_{O_2}/M_b = 0.53M_b^{-0.319}v_g + 0.303M_b^{-0.311}, \quad (2)$$

where V_g is speed or velocity in m s^{-1} and V_{o2}/M_b ml O_2 kg^{-1} s^{-1}.

Because fox squirrels were continuously agitated in the chamber and did not appear to habituate prior to running, we used the predicted value of resting metabolic rate in the calculations for net oxygen consumption during locomotion [mean measured RMR = 0.37 ml O_2 kg^{-1} s^{-1} (22.19 ml O_2 kg^{-1} min^{-1}) and predicted RMR = 0.23 ml O_2 kg^{-1} s^{-1} (13.51 ml O_2 kg^{-1} min^{-1}), $n = 60$]. In contrast, the flying squirrels appeared to rest and had near predicted resting rates (predicted mass-specific resting rates calculated using Eq. 1; mean measured RMR = 0.36 ml O_2 kg^{-1} s^{-1} and predicted RMR = 0.31 m1 O_2 kg^{-1} s^{-1}, $n = 165$); therefore for flying squirrels, we used measured resting V_{O2} in our calculations of cost of transport.

Net cost of transport (COT, J N^{-1} m^{-1} which is a dimensionless value), the metabolic cost of moving a unit of mass a specific distance (Tucker 1970), was calculated by converting net V_{o_2} during locomotion (ml O_2) to energy units (1 ml O_2 = 20.1 J; B1axter 1989; Fournier and Weber 1994). We then divided this value by gravitational acceleration (9.8 m s^{-2} multiplied by running velocity in m s^{-1}; Fish and Baudinette 1999).

Because each squirrel ran at each speed and incline three times and had slightly different estimates of body mass before each trial, we accounted for the repeated measures by calculating linear least-squares regressions using each squirrel's identification number as a random effect to ensure that no squirrel was significantly unique in their energetic expenditures. We calculated linear least-squares regressions for net cost of locomotion (running metabolic rate minus resting) and cost of transport for both the measured and predicted values for each species of squirrel. We employed a 2-way ANOVA to determine if measured and predicted values of V_{o_2} and COT were significantly different for both species and again included squirrel ID as a random effect (Zar 1999).

We evaluated excess exercise oxygen consumption (EEOC, ml O_2 kg^{-1} s^{-1}), the volume of oxygen consumed in during exercise in excess of resting metabolic rate, and excess post exercise oxygen consumption (EPOC, ml O_2 kg^{-1} s^{-1}), the excess post-exercise oxygen consumed during recovery, by calculating the volume of oxygen consumed during and following exercise and subtracted the volume of oxygen during resting behavior that would be consumed during those time periods (Fig.1). We calculated EPOC at two stages of recovery: when the rate of oxygen consumption returned to 1.5 x RMR value as measured before the trial (Baker and Gleeson 1999) and when it returned to the full RMR observed before the trial. We used ANOVA to evaluate the effects of speed and incline on EEOC, and EPOC, and recovery time and again included squirrel ID as a random effect (Zar 1999). We accepted $p < 0.05$ as indicating statistical significance.

Results

When resting above the moving tread, mean measured resting rate of oxygen consumption for flying squirrels was 0.36 (SE = 0.01, $n = 162$) ml O_2 kg^{-1} s^{-1} and 0.43 (SE = 0.01, n = 60) ml O_2 kg^{-1} s^{-1} for fox squirrels. Corresponding predicted mean rates were 0.31 (SE = 0.0003, $n = 162$) ml O_2 kg^{-1} s^{-1} and 0.23 (SE = 0.0005, $n = 60$) ml O_2 kg^{-1} s^{-1}. Mean measured resting metabolic rate was significantly different than predicted for both species ($F_{1,161} = 107.87$, $P < 0.001$ for flying squirrels and $F_{l,59} = 388.21$, $p < 0.001$ for fox squirrels), but less so for flying squirrels.

Mean measured metabolic rate while running was 1.6-2.8 times greater for flying squirrels than fox squirrels (Table l). The relationship between measured V_{o2} for flying squirrels and velocity (m s^{-1}) was best described by

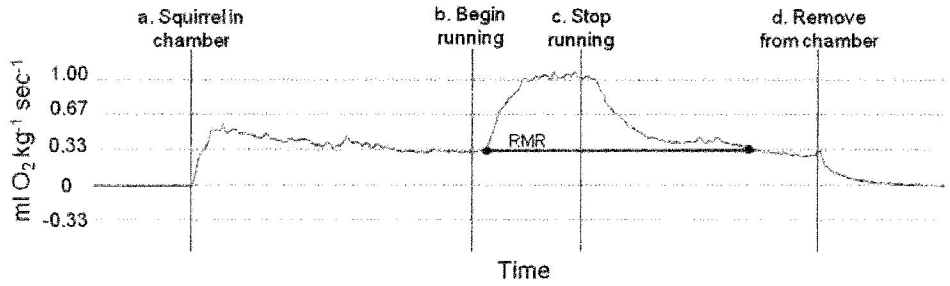

Fig. 1 Measured oxygen consumption (ml O_2 kg^{-1} s^{-1}) over time for one *G. sabrinus*. **a** Squirrel introduced into the respirometry chamber. **b** Squirrel begins quadrupedal locomotion. **c** Quadrupedal locomotion ends. **d** Squirrel removed from chamber. During running bout and recovery time, volume above the bold line indicating resting metabolic rate (RMR) is considered "excess oxygen consumption"

Table 1 Mean net cost of locomotion ($\dot{V}_{O_2}$ during locomotion − $\dot{V}_{O_2}$during resting) and cost of transport (±SE) for *Glaucomys sabrinus* and *Sciurus niger* as measured at room temperature using open-flow respirometry. Cost of transport (COT); the metabolic cost of moving mass over a specific distance, calculated by converting $\dot{V}_{O_2}$to energy units and dividing by the gravitational acceleration (9.8 m s^{-1}) multiplied by running velocity (m s^{-1}) for both species. The resulting units, J N^{-1} m^{-1}, are dimensionless. Nine *G. sabrinus* captured on Prince of Wales Island, southeast Alaska in 2005, and four *S. niger* captured on the campus of the University of Wyoming, in Laramie, Wyoming in 2006, were held at the small animal facility at the University of Wyoming for 3 months before the start of the experiment. Each individual was tested three times at each of the experimental running speeds

Velocity m s^{-1}	Net $\dot{V}_{O_2}$ for locomotion (ml O_2 kg^{-1} s^{-1})	Cost of transport (J N^{-1} m^{-1})
G. sabrinus		
0.40	0.84 ± 0.03	4.28 ± 0.14
0.49	1.02 ± 0.02	4.27 ± 0.08
0.58	1.23 ± 0.02	4.33 ± 0.07
0.67	1.55 ± 0.03	4.75 ± 0.10
S. niger		
0.63	0.51 ± 0.02	2.28 ± 0.06
0.81	0.51 ± 0.03	1.80 ± 0.09
1.03	0.51 ± 0.03	1.45 ± 0.07
1.25	0.54 ± 0.03	1.25 ± 0.05

the exponential equation ($F_{0.05(1),1,105} = 410$, $p < 0.001$, $r^2 = 0.801$; Fig. 2):

$$\dot{V}_{O_2} = 0.3279e^{2.292(\text{velocity})}. \quad (3)$$

In contrast, V_{O2} for fox squirrels was not significantly related to velocity-em s-1; $F_{O.05(1)'1.44} = 0.059, p = 0.809$, $r^2 = 0.001$; Fig. 2) although there was a general increase in V_{O2} as treadmill speed increased.

The measured and predicted net cost of locomotion (resting V_{O2} subtracted from V_{O2} during locomotion) for fox squirrels were not significantly different (two-way ANOVA $F_{2,95} = 3.071$, $P = 0.178$; Fig. 2), but those values were significantly different for flying squirrels (two-way ANOVA $F_{2,215} = 338.179$, $P < 0.0001$; Fig. 3). Individual ID did not significantly influence results for either model (two-way ANOVA $F_{2,95} = 1.622$, $p = 0.360$; $F_{2,215} = 1.812$, $P = 0.208$, for fox and flying squirrels, respectively).

Net cost of transport (COT) varied in a statistically significant linear manner in response to velocity for both species (Fig. 2), but in opposite directions. For flying squirrels, COT was positively related to velocity whereas it was a negative relationship in fox squirrels.

Net cost of transport (COT) varied with velocity for flying squirrels and was best described by the equation ($F_{0.05(l),1,105} = 10.300$, $P = 0.002$, $r^2 = 0.089$; Fig. 3):

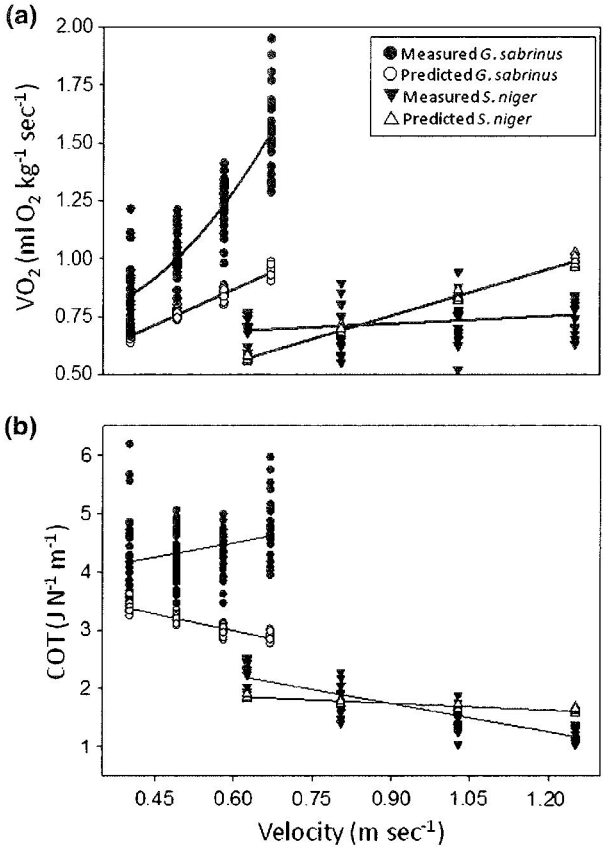

Fig. 2 **a** Measured and predicted $\dot{V}_{O_2}$(ml O2 kg^{-1} s^{-1}) for nine *G. sabrinus* and four *S. niger* held in captivity at the University of Wyoming. Measured and predicted values for *S. niger* were not significantly different ($p = 0.178$) but significantly differed for *G. sabrinus* ($p = 0.002$). **b** Cost of transport (COT); the metabolic cost of moving mass over a specific distance, calculated by converting $\dot{V}_{O_2}$to energy units and dividing by the gravitational acceleration (9.8 m s^{-1}) multiplied by running velocity (m s^{-1}) for both species. The resulting units, J N^{-1} m^{-1}, are dimensionless. Net cost of transport (COT) varied with velocity for flying squirrels and was best described by the equation ($F_{0.05(1),1,105} = 10.300$, $p = 0.002$, $r^2 = 0.089$): COT = 3.515 + 1.645(velocity). The relationship for COT of fox squirrels and speed was best described by ($F_{0.05(1),1,45} = 117.291$, $p < 0.001$, $r^2 = 0.718$; Fig. 3): COT = 3.198 − 1.618(velocity)

$$\text{COT} = 3.515 + 1.645(\text{velocity}) \quad (4)$$

whereas the COT relationship for fox squirrels and speed was best described by ($F_{0.05(1),1,45} = 117.291$, $p < 0.001$, $r^2 = 0{,}718$; Fig. 3):

$$\text{COT} = 3.198 - 1.618(\text{velocity}). \quad (5)$$

The measured and predicted COT were significantly different for flying squirrels (two-way ANOVA $F_{2,216} = 264.466$, $p < 0.001$; Table 1; Fig. 2) but not for fox squirrels (two-way ANOVA $F_{2,96} = 0.294$, $p = 0.625$; Table 1; Fig. 2).

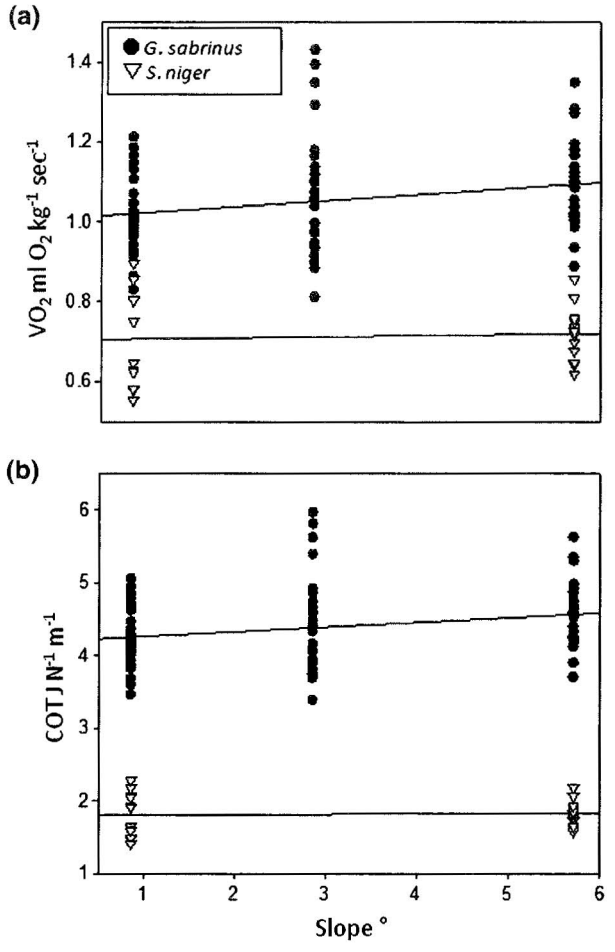

Fig. 3 **a** Measured $\dot{V}_{O_2}$ (ml O_2 kg^{-1} min^{-1}) in response to running on an incline for nine individual *G. sabrinus* and four individual *S. niger* held in captivity at the University of Wyoming. Although these relations were not significant ($p = 0.106$ for *G. sabrinus* and $p = 0.083$ for *S. niger*), the slopes were positive in both. **b** Cost of Transport (COT; J N^{-1} m^{-1}) in response to running incline. The relationship was significant for *G. sabrinus* ($p = 0.044$) but not for *S. niger* ($p = 0.083$), yet the slope of the regression for both was positive

The relationship between measured V_{O_2} for flying squirrels and incline was marginally significant ($F_{0.05(1),1,79} = 2.31$, $P = 0.106$, $r^2 = 0.006$; Fig. 3). Similarly, for fox squirrels V_{O_2} was not significantly related to velocity ($F_{0.05(1,1,22} = 0.11$, $P = 0.7443$, $r^2 = 0.005$; Fig. 3). Likewise, COT varied slightly with slope for flying squirrels ($F_{O,05(l),1,79} = 3.33$, $p = 0.044$, $r^2 = 0.072$; Fig. 3) but did not vary significantly for fox squirrels ($F_{0.05(1),1,22} = 2.81$, $p = 0.083$, $r^2 = 0.211$; Fig. 3).

The excess oxygen consumed (EEOC) above resting for flying squirrels was significantly different among velocities ($F_{005(1).1,l06} = 158$, $P < 0.001$, $r^2 = 0.644$; Table 2), but only marginally so among inclines ($F_{0,05(1),1.88} = 3.09$, $p = 0.082$, $r^2 = 0.034$; Table 2). EEOC was not significantly different among velocities ($F_{0,05(l),1,58} = 0.957$, $p = 0.332$, $r^2 = 0.016$; Table 2) or between inclines ($F_{0.05(l),1.22} = 2.31$, $P = 0.142$, $r^2 = 0.095$; Table 2) for fox squirrels. The average volume of EPOC consumed until the metabolic rate returned to 1.5 x RMR was 79.77 ± 1.97 ml O_2 kg^{-1} for flying squirrels and 69.94 ± 3.79 ml O_2 kg^{-1} for fox squirrels. There was no effect of velocity ($F_{2,159} = 0.650$, $P = 0.591$; $F_{2,57} = 2.24$, $P = 0.152$) or incline ($F_{2,l60} = 0.246$, $P = 0.246$; $F_{2.58} = 0.161$, $P = 0.715$) on EPOC at 1.5 times resting metabolism for flying squirrels or fox squirrels, respectively (Table 2). The average volume of EPOC consumed until the metabolic rate returned to resting was 93.66 ± 2.28 ml O_2 kg^{-1} for flying squirrels and 80.21 ± 4.20 ml O_2 kg^{-1} for fox squirrels. Finally, there was no significant effect of velocity ($F_{2.139} = 0.203$, $p = 0.893$; $F_{2.54} = 0,217$, $P = 0.882$) or slope ($F_{2,140} = 1.39$, $P = 0.276$; $F_{2,55} = 0.286$, $p = 0.629$) on EPOC while returning to full resting metabolic rate for either flying squirrels or fox squirrels (Table 2).

Mean recovery time for flying squirrels returning to 1.5 x RMR following exercise was 2.98 min; it took 6.32 min for flying squirrels to return to full RMR. Mean recovery time for fox squirrels was 3.14 min to return to 1.5 x RMR and a mean of 5.92 min to return to full RMR. The relationship between recovery time and velocity was not significant for EPOC at 1.5 times resting metabolism ($F_{2,158} = 0.711$, $p = 0.555$; $F_{2,57} = 1.58$, $p = 0.260$) or with incline ($F_{2,159} = 0.763$, $P = 0.482$; $F_{2.58} = 1.65$, $P = 0.290$) for flying squirrels and fox squirrels, respectively. Recovery time for EPOC when returning to full resting metabolism also did not differ significantly among velocities ($F_{2,139} = 0.426$, $P = 0,736$; $F_{2,54} = 0.050$, $p = 0.984$) or incline ($F_{2,140} = 0.012$, $p = 0.988$; $F_{2,55} = 0.117$, $P = 0.754$; Table 2).

Discussion

Net cost of quadrupedal locomotion for flying squirrels in our study was significantly greater than values predicted from the allometric equations for a mammal of that body size. Furthermore, their metabolic rate increased exponentially with velocity (Fig. 2). These findings indicate that long bouts of quadrupedal locomotion in this species may be energetically inefficient. In contrast, net cost of quadrupedal locomotion for fox squirrels in our study was similar to that predicted by the mass-based allometric equations, suggesting that this species is an energetically efficient runner as observed by Nupp and Swihart (2000) and Zollner (2000). Fox squirrels have larger bodies than flying squirrels, which may raise questions about the suitability of our comparison. Because of the limitations of identifying adaptive differences in a two-species

Table 2 Measurements of Excess Oxygen Consumed (±SE) during locomotion for *Glaucomys sabrinus* and *Sciurus niger* and Post-Exercise recovery times (±SE). EEOC is the amount of oxygen consumed during exercise in excess of resting metabolism. One and a half times resting metabolic rate (RMR) EPOC was the excess post-exercise oxygen consumed until recovery is equal to 1.5 times resting metabolic rate. Full recovery EPOC is the excess post-exercise oxygen consumed until metabolic rate returned to resting rate measured before run. During bouts of exercise, *G. sabrinus* ran on average approximately 300 s (5 min), while *S. niger* ran 390 s (6.5 min)

Velocity	EEOC	1.5 RMR EPOC		Full Recovery EPOC	
m s^{-1}	ml O_2 kg^{-1}	ml O_2 kg^{-1}	Time (s)	ml O_2 kg^{-1}	Time (s)
G. sabrinus					
0.40	212.09 ± 11.18	73.66 ± 3.95	174.9 ± 11.3	87.87 ± 4.99	379.9 ± 27.8
0.49	254.83 ± 8.47	79.97 ± 6.08	185.9 ± 16.1	93.67 ± 6.67	400.9 ± 36.5
0.58	321.29 ± 10.37	76.59 ± 2.60	170.7 ± 7.5	90.05 ± 3.53	382.7 ± 26.8
0.67	410.34 ± 15.44	75.24 ± 3.39	167.0 ± 8.5	90.29 ± 4.32	359.8 ± 27.0
	$p = 0.001$	$p = 0.591$	$p = 0.555$	$p = 0.893$	$p = 0.736$
S. niger					
0.63	164.28 ± 6.35	69.28 ± 5.84	175.6 ± 14.6	83.99 ± 5.54	352.3 ± 3.2
0.81	172.20 ± 14.66	78.51 ± 9.69	214.0 ± 29.8	79.61 ± 7.93	352.4 ± 37.7
1.03	158.51 ± 11.73	66.70 ± 7.84	189.3 ± 21.3	73.91 ± 8.67	330.1 ± 32.1
1.25	157.52 ± 6.79	61.15 ± 7.07	180.4 ± 20.6	75.04 ± 9.22	364.2 ± 46.8
	$p = 0.792$	$p = 0.152$	$p = 0.260$	$p = 0.882$	$p = 0.984$

comparative study (Garland and Adolph 1994), we compared our results to those of Wunder and Morrison (1974). These researchers estimated net horizontal running costs of red squirrels *(Tamiasciurus hudsonicus),* another arboreal sciurid with a mass similar to flying squirrels (200-250 g; Steele 1998), at approximately 0.3 ml O_2 kg^{-1} s^{-1} at 0.42 m s^{-1} and 0.52 ml O_2 kg^{-1} s^{-1} at 0.58 m s^{-1} (Wunder and Morrison 1974). Both of these estimates are lower than our estimates for flying squirrels at similar speeds. Thus, it appears that the energetic costs of quadrupedal locomotion for flying squirrels are greater than expected for an arboreal squirrel (Table 1). Nevertheless, we do not suggest that flying squirrels avoid quadrupedal locomotion completely; indeed, they can spend considerable time on the ground searching for hypogeous fungi (e.g., truffles; Pyare and Longland 2001). Rather, our data indicate that flying squirrels expend less of their daily energy budget by employing gliding locomotion when traveling long distances though forest canopies (Scheibe et al. 2006; Vemes 2001).

Our COT results provide additional support for the conclusion that flying squirrels are poorly adapted to a running mode of locomotion. Generally, as we observed with fox squirrels, the relationship between COT and speed is negative (Fish and Baudinette 1999; Fournier and Weber 1994); but for flying squirrels in our experiments, COT increased with speed. This finding is unusual because in other species that appear poorly adapted for long bouts of quadrupedal locomotion, such as the Virginia opossum *(Didelphis virginiana),* COT decreases with speed (Fournier and Weber 1994). Although northern flying squirrels do spend time on the forest floor, speed may not be an important attribute in their life-history given that they use quadrupedal locomotion while slowly searching for truffles, which they detect underground using olfaction (Pyare and Longland 2001).

Recovery time was approximately equal to the amount of time each species spent running; and whereas it was shorter than that recorded for other species during brief amounts of intense exercise (up to 20 min following <60 s of intense running in *Mus musculus;* Baker and Gleeson 1998), it is still a significant added cost to locomotion in laboratory experiments. Oxygen consumption during recovery added 22-41% and 48-51 % to the total energetic costs of flying squirrels and fox squirrels, respectively. This similarity in EPOC and recovery time for these two species in view of their differences in EEOC further supports the notion that they differ in adaptation to quadrupedal locomotion. Flying squirrels seem to consume more oxygen during exercise and less so during recovery, and are therefore likely incapable of prolonged bouts of constant quadrupedal locomotion. In contrast, fox squirrels were able to consume less oxygen during exercise possibly by tolerating higher blood lactate concentrations (Gleeson 1996) and then decrease those levels during recovery. This likely renders fox squirrels better adapted for prolonged bouts of running.

Many squirrel species use intermittent locomotion probably because increased vigilance during motionless periods may reduce predation risks (McAdam and Kramer

(1998). Some investigators suggested that this form of locomotion is more energetically expensive than constant movement because acceleration and deceleration are more costly (Kramer and McLaughlin 2001). However, other researchers hypothesized that alternating bouts of movement with periods of inactivity is less costly because an animal can rest and allow blood lactate levels to decrease between bouts of exercise (Gleeson and Hancock 2002). Given the differences in EEOC and EPOC for flying squirrels and fox squirrels, it appears that for the former, intermittent locomotion will be more costly, whereas for the latter it will be more beneficial. How such differences translate to behavior during quadrupedal locomotion in open habitats is unclear and merits further investigation. Nonetheless, this difference in energetic costs associated with intermittent locomotion further supports the conclusion that fox squirrels are better suited for moving through open habitats with little cover and increased aerial predation risks.

Although not statistically significant, our data suggest that running on an incline may be more energetically expensive than horizontal locomotion (Fig. 3). Similarly, Wunder and Morrison (1974) found incline running to be considerably more energetically expensive than horizontal running in red squirrels. Whereas red squirrels running at 6° consumed slightly less energy than those running on a horizontal surface, they consumed 7% more energy when running along a *37*° incline (Wunder and Morrison 1974). Taylor et al. (1972), however, suggested that running uphill costs slightly more than horizontal nmning for small mammals, and Dial (2003) proposed that small gliding mammals, those considerably less than 400 g, should use approximately the same energy climbing to glide as their non-gliding relatives use walking. Unfortunately, because of the limitation imposed by the structure of the treadmill, we were only able to measure energy expenditure at a slope of less than *6*°. It would have been preferable to test oxygen consumption by squirrels running at steeper inclines.

Our measurements of the cost of running at an incline may translate into inflated estimates of climbing costs. However, they provide conservative estimates of energy savings for flying squirrels when gliding. To estimate the cost of gliding, we calculated the energetic cost of gaining vertical elevation during 1 min of travel when running on the treadmill at a slope of 5.8 (or 10%), which was 4.51 ml O_2 kg^{-1} (calculated by subtracting mean V_{O_2} at 0.49 s^{-1} with no slope from the mean V_{O_2} at the same speed with slope of *5.8°;* 1.09-1.02 ml O_2 kg^{-1} s^{-1}). We then calculated the length of horizontal distance gained during that 1 min of travel by multiplying the speed (i.e., 0.49 m s^{-1}) by 60 s yielding 29.4 m, and estimated vertical gain with the equation:

$$\text{Height} = \text{Distance} \times \tan(5.8). \quad (6)$$

Using the resulting gain in elevation of 2.99 m in 1 min of travel, we calculated that while gaining 20 m in vertical elevation, a flying squirrel will consume 30.17 ml O_2 kg^{-1}. Because of the 2:1 glide ratio (i.e., the horizontal distance covered by a glide is approximately twice the distance climbed; Vernes 2001), this would also be the estimated cost of a 40 m glide. However, when running 40 m horizontal distance at the same speed, flying squirrels would consume 82.93 ml O_2 kg^{-1}. Thus, flying squirrels should experience at least a 64% energetic savings by gliding. Moreover, the relative benefit of gliding will likely be substantially higher if flying squirrels running on the ground must use higher speeds. Recall, oxygen consumption in our trials increased exponentially with velocity during horizontal running.

Furthermore, this estimate of energy savings from gliding is highly conservative. Morphological adaptations not investigated here, such as leg musculature or other possible skeletal or muscular adaptations, may actually make climbing at steeper angles less expensive for arboreal mammals compared with running on relatively shallow slopes (Essner 2008; Scheibe et al. 2007). Flying squirrels have considerably longer limbs than other tree squirrels (Essner 2008; Peterka 1936) possibly resulting in a more crouched nmning posture, which has fewer mechanical advantages compared with more upright postures (Biewener 2003). Scheibe and Essner (2000) also noted morphological adaptations of the pelvic girdle related to improved leaping in the Pteromyine and Anomalurid rodents and Essner and Scheibe (2000) recognized adaptations in the scapulae of gliders that likely facilitate climbing and landing. Such morphological adaptation for leaping, climbing and landing may reduce the efficiency of running locomotion. Similarly, Thorington and Heaney (1981) suggested that the higher forelimb-to-hindlimb ratio in flying squirrels compared with other arboreal squirrels may impose high energetic costs during quadrupedal locomotion while traversing small diameter trees. Morphological adaptations to swimming have been previously implicated in the higher than predicted energetic costs of running in American mink *(Mustela vison;* Williams 1983) and North American river otters *(Lontra canadensis;* Williams et al. 2002). It is possible that the higher than predicted energetic costs of running in flying squirrels result from specific adaptations to climbing such as skeletal adaptations, the higher forelimb to hind limb ratio and the development of a gliding membrane which attaches the legs along each side of the body and impedes running movements. Indeed, it is likely that the development of a gliding membrane and the associated increased costs of quadrupedal locomotion imposed a selective disadvantage in early gliders and led to directional evolution towards

gliding. This is supported by the observation that mammals with vestigial gliding membranes are rare and occupy restricted ranges [e.g., Leadbeater's possum *(Gymnobelideus leadbeateri)* in Southeast Australia; Strahan 1998].

Our data and calculations support the cost of transport hypothesis to explain the evolution of gliding locomotion in the ancestors of flying squirrels. Tucker (1970) reported that cost of transport for flying animals was 27 times lower than that of a walking animal. Furthermore, the costs incorporated into calculations by Tucker (1970), including drag and body mass, do not necessarily apply to gliders. Because gliding mammals do not actively fight drag while gliding (although it is a force involved in gliding) and are not actively working to support their body mass in the air, both of which would require energy, the gliding portion of locomotion should be relatively cheap in energy use (Tucker 1970). This is further supported by our observation that for northern flying squirrels the cost of transport during quadrupedallocomotion increases with speed. No such increase would be expected to occur during gliding. Nonetheless, we are reluctant to dismiss other plausible hypotheses. Because northern flying squirrels consume a resource (truffles) that has a patchy distribution (Flaherty et al. 2010; Pyare and Longland 2001), gliding may reduce travel time between food patches (Charnov 1976; Scheibe et al. 2007), providing support for the foraging efficiency hypothesis. Home range size of mammalian gliders <600 g, including the northern flying squirrel, is larger than their expected home range based on body mass (Swihart et al. 1988; Goldingay 2000) possibly as a result of these patchy resources and their energetic needs. Mace and Harvey (1983) noted that diet influences home range size in G. *sabrinus* and Flaherty et al. (2010) suggested gliding as a means of increasing encounter rates with key resources. Therefore, gliding both saves energy during locomotion and reduces travel time between foraging patches suggesting that this adaptation may have evolved in response to more than one selective pressure in *Glaucomys* spp.

Finally, our results corroborate the findings of previous studies that arboreal, gliding species respond negatively to fragmentation and loss of old-growth forest habitats. Selonen and Hanski (2003; 2004) found that Siberian flying squirrels *(Pteromys volans)* avoided open areas that could not be crossed in a single glide and animals changed direction to avoid running on the ground. Southern flying squirrels are often undetected in the smallest of forest fragments even when other species of sciurids are present (Nupp and Swihart 2000; Rosenblatt et al. 1999; Woodworth et al. 2000), suggesting that dispersal and recolonization of these patches across open habitat is low or nonexistent. Similarly, with the loss of launching and landing structures for gliding, increased reliance on expensive quadrupedal locomotion at high movement speeds with multiple pauses to avoid predation (Flaherty et al. 2008), northern flying squirrels are likely to exhibit lower dispersal through the modified matrix of intensively managed landscapes.

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