RESEARCH ARTICLE

Gliding saves time but not energy in Malayan colugos

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SUMMARY

Gliding is thought to be an economical form of locomotion. However, few data on the climbing and gliding of free-ranging gliding mammals are available. This study employed an animal-borne three-dimensional acceleration data-logging system to collect continuous data on the climbing and gliding of free-ranging Malayan colugos, *Galeopterus variegatus*. We combined these movement data with empirical estimates of the metabolic costs to move horizontally or vertically to test this long-standing hypothesis by determining whether the metabolic cost to climb to sufficient height to glide a given distance was less than the cost to move an equivalent distance horizontally through the canopy. On average, colugos climb a short distance to initiate glides. However, due to the high energetic cost of climbing, gliding is more energetically costly to move a given horizontal distance than would be predicted for an animal travelling the same distance through the canopy. Furthermore, because colugos spend a small fraction of their time engaged in locomotor activity, the high costs have little effect on their overall energy budget. As a result, the energetic economy hypothesis for the origins of gliding is not supported. It is likely that other ecologically relevant factors have played a greater role in the origins of gliding in colugos and other mammals.

Key words: cost of transport, energetics, accelerometer, Dermoptera, locomotor ecology, flying lemur.

INTRODUCTION

Gliding mammals are a diverse and geographically widespread group, comprising more than 60 extant species inhabiting forested regions on five continents (Dudley et al., 2007). In addition, at least three extinct lineages of mammals (Mein and Romaggi, 1991; Storch et al., 1996; Meng et al., 2006) have evolved gliding flight, with the oldest group dated at 130 million years ago (Meng et al., 2006). Several hypotheses have been proposed to explain the selective pressures that resulted in gliding. These hypotheses include the reduction of predation pressure (Emmons and Gentry, 1983; Archer, 1984), movement in open or tall arboreal habitat without descending to the forest floor (Emmons and Gentry, 1983; Dudley and Devries, 1990; Dial et al., 2004), energetic economy (Norberg, 1983; Scheibe and Robins, 1998; Dial, 2003) and foraging efficiency (Wischusen, 1990; Goldingay, 2000). These hypotheses are not mutually exclusive – each may have contributed to the evolution of gliding – but none are easy to test. Here we test the hypothesis that gliding reduces the energetic costs of movement in an arboreal habitat.

This hypothesis has received the greatest attention, but measuring the potential costs of gliding locomotion and thus its benefits over other forms of locomotion is logistically demanding. As a result, mathematical models have primarily been used in the previous investigations of the potential costs of gliding locomotion (Scholey, 1986; Scheibe and Robins, 1998; Dial, 2003). These models compare the cost of climbing to a height necessary to glide a given horizontal distance with the cost of using quadrupedal locomotion to travel the same distance. These models give insight into the comparative costs of gliding in large and small animals, but rely on generalized estimates of locomotor

behavior and glide performance rather than on data collected from free-ranging individuals.

Two important predictions have emerged from the models. First, large gliders must glide a much longer distance compared with small gliders before gliding is energetically cheaper than running. For example, Scheibe and Robins (Scheibe and Robins, 1998) calculated that a small glider, the North American flying squirrel *Glaucomys volans*, must glide only 3 m compared with between 50 and 100 m for the red giant flying squirrel, *Petaurista petaurista* (Scholey, 1986; Scheibe and Robins, 1998), before gliding is a cheaper mode of transport. Second, because of differential scaling relationships for running and climbing, the energetic benefit of gliding may be greatest at intermediate body sizes (Dial, 2003). In fact, it has been predicted that the cost of climbing is independent of body size (Schmidt-Neilson, 1984). However, few studies have been conducted on the energetic cost of vertical or incline climbing (e.g. Taylor et al., 1972; Wunder and Morrison, 1974) and there has been no predictable relationship between cost, incline angle and body size (Full and Tullis, 1990). However, in primates, the sister group to colugos, the cost of climbing is independent of body mass (Hanna et al., 2008). Further work into the metabolic cost of climbing across diverse taxa is required to fully understand this relationship.

More recently, empirical data have been added to these energetic models with varying results. In a field study of another small North American flying squirrel, it was estimated that *Glaucomys sabrinus* must glide approximately 10 m before gliding is cheaper than running the same horizontal distance (Scheibe et al., 2006). However, the comparably sized marsupial glider *Petaurus norfolcensis* must glide approximately 30 m before gliding is less

costly (Flaherty, 2002). It is possible that these large differences in cost-effective glide distance are due to substantial differences in the locomotor ecology of the two species. However, because both of these studies used empirical data only from the initial glides after release at a trap site, it is possible that the results could also reflect differences in the escape response of the two species. Further, because these studies focus on single glides, it is difficult to apply the costs to an animal's overall energy budget.

To overcome this issue, we used a novel method employing animal-borne data loggers in this study. Data loggers are becoming an increasingly important tool in both ecological and biomechanical studies of animal movement, particularly in systems where potential contact with the animal is limited (e.g. Sato et al., 2007; Byrnes et al., 2008). The major benefits of this method are that all locomotor behaviors during the sampling period are included, and that the animals go about their activities without the observer present and possibly influencing their behavior. Further, data can be continuously collected over longer periods of time than is possible for traditional focal observation. The goals of this study were thus to: (1) quantify all climbing and gliding behavior of colugos during the sampling period, and (2) use these locomotor data to estimate the energetic cost of gliding in a large gliding mammal, the Malayan colugo, testing the hypothesis that gliding is an energetically inexpensive form of locomotion relative to quadrupedal locomotion. To do this, we compared the energetic cost to climb to a given height to initiate a glide with the energy required to move horizontally through the canopy a distance equivalent to the glide distance (Fig. 1). We make this comparison, as opposed to climbing down, moving horizontally across the ground and climbing up, because colugos rarely venture to the ground, thus making this comparison less ecologically relevant for this species. In addition, the metabolic cost per unit time associated with gliding itself has been shown to be only twice basal metabolic rate (BMR) in other vertebrates (Baudinette and Schmidt-Nielsen, 1974; Sapir et al., 2010). Given the low metabolic cost per unit time and the very short time intervals over which gliding occurs, this cost should be negligible and is not included in our analysis. From the study of the locomotor energetics of this extant gliding mammal, it might also be possible to make inferences about why gliding evolved.

MATERIALS AND METHODS
Animal protocol
We wild caught 13 colugos, *Galeopterus variegatus* (Audebert 1799), in Singapore during the course of the study. Individuals of mass less than 700 g (i.e. logger mass >4% body mass), pregnant females or those carrying young were released immediately upon capture and were not used in the study. Six animals were fitted with data loggers and of these, data were retrieved from four individuals (three male, one female). Data were obtained from individuals with body masses between 0.75 and 1.3 kg (mean 1.1 kg) and head–body lengths varying between 31 and 40 cm. Details of the capture and handling of animals are given in Byrnes et al. (Byrnes et al., 2008).

Upon release, we observed each individual's initial glides until the animal could no longer be followed. We measured the horizontal distance of these glides using a laser range finder (Nikon ProStaff Laser 440, Nikon Inc., Melville, NY, USA). Using the data on glide lengths and durations of the observed glides (*n*=16, range=1.5–65 m, 6.2% of all glides) recorded from the accelerometer, we calculated the mean horizontal velocity of the observed glide(s) for each animal. To determine the relationship between glide velocity and glide duration, we fit the sigmoidal curve given in Eqn 1 (r^2=0.99) to the
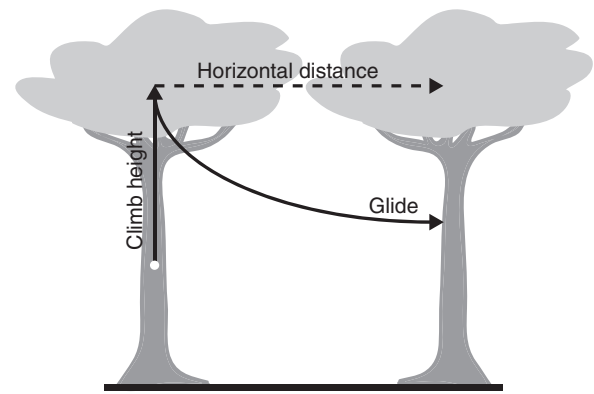

Fig. 1. Schematic representation of the movement of a colugo between two trees. We compare the cost to climb to a given height to initiate a glide (E_{climb}) with the estimated cost of moving a distance equivalent to the glide distance horizontally through the canopy (E_{hor}).

observed data using the mean (±s.d.) take-off velocity of gliding colugos (3.7±1.49 m s^{-1}) (Byrnes et al., 2008) as the initial velocity. We chose *a priori* to use a sigmoidal curve because at short glide durations, we expect horizontal velocity to be dominated by the take-off velocity, and at high velocities reached in the longest glides, equilibrium will be approached as drag forces increase, resulting in a sigmoidal velocity profile. Using this equation, we estimated the mean velocity (*U*) of subsequent glides from the glide duration (*t*) recorded from the accelerometer (Byrnes et al., 2011). The mean velocity of each glide was multiplied by its duration recorded from the accelerometers to estimate glide distance:

$$U = 3.7 + \frac{6.41}{1 + e^{-\left(\frac{t-1.75}{-0.165}\right)}} \ . \tag{1}$$

Accelerometry data loggers
The custom-designed data loggers used in this study are described in detail elsewhere (Byrnes et al., 2008). The loggers used include two accelerometers (ADXL210, 2.5 m*g* resolution at 100 Hz bandwidth, Analog Devices, Norwood, MA, USA) measuring acceleration along the three body axes of the animal, and were capable of logging to NAND flash memory at 100 Hz for up to 304 h. Data-logger dimensions including the battery were 45×32×11 mm and devices weighed 29 g. Data loggers were placed on the animal's dorsal surface over their estimated center of mass. A small patch of fur was shaved, and loggers were affixed to the skin using cyanoacrylate glue. Females carrying young weighing 400 g or more have been observed gliding (G.B., personal observation); thus, it is unlikely that the weight of the data logger had a large influence on the animals' aerodynamic performance. A radio frequency telemetry tag was included in the design to track the animal during the sampling period and facilitate recovery once the logger dropped naturally from the animal.

Data processing and analysis
Upon recovery of the data loggers, data were downloaded to a computer using custom software written in MATLAB v. 7.3 (The MathWorks Inc., Natick, MA, USA). We calibrated each device by rotating it through 360 deg about each axis and comparing the voltage output with the known magnitude and direction of gravitational acceleration. The calibration was then applied to the recorded voltage output of the accelerometers to transform the data to units of gravitational acceleration.
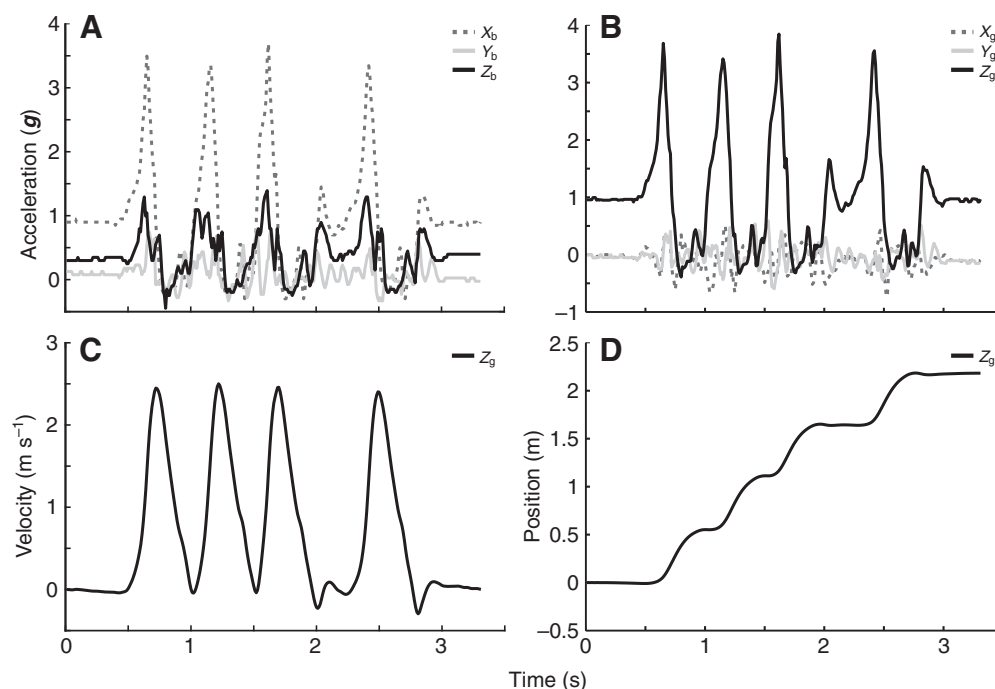
Fig. 2. Rotation and integration of acceleration signal of four climbing strides to calculate climb height. Acceleration in a body-fixed coordinate system (A) is rotated using a quaternion rotation to obtain acceleration in a global, gravity-defined coordinate system (B). X_b, Y_b and Z_b are the axes of a body-fixed coordinate system, and X_g, Y_g and Z_g are the axes of a global, gravity-based coordinate system. This vertical component of acceleration is then integrated resulting in vertical velocity (C) and integrated a second time resulting in vertical displacement (D). The final displacement of each bout of climbing is summed to result in the total vertical height climbed for each individual glide.

To climb trees, colugos use bounding locomotion, moving the hindlimbs and forelimbs together as pairs. Each bound of locomotion is readily identifiable in the acceleration record (Fig. 2). To estimate the vertical distance travelled, we first transformed the data from climbing animals from an animal-based coordinate system to global coordinates, using a quaternion rotation described in detail in Haslwanter (Haslwanter, 1995), and then double-integrated the transformed data to find the change in vertical position (Fig. 2). For each trial, we first measured the resting acceleration before and after the climbing bout. The direction of the gravity vector gives the animal's orientation with respect to real-world coordinates. If the orientation changed significantly over the course of the bout, it was omitted. Visual inspection of the change in the z-axis baseline between the start and end of each trial was used to determine which trials were omitted. The average change for included trials was $0.04\,g$ compared with $0.14\,g$ for omitted trials. We then rotated the acceleration data into real-world coordinates to obtain the animal's vertical acceleration (Fig. 2B). The baseline acceleration due to gravity was removed from the trial, and the data were numerically integrated to yield velocity (Fig. 2C). If velocity was not zero at the end of the integrated section, which could also be the result of body rotation during the bout of climbing, the trial was omitted. The remaining trials were integrated again to find vertical displacement (Fig. 2D). In all cases, the number of strides was measured by counting the individual bounds in each bout of locomotion. We found the mean stride length by dividing bout displacement by the number of strides. Displacement for the bouts of climbing that were thrown out because they did not meet the above criteria was estimated using the mean stride length and number of strides for that sequence. Statistical analyses were conducted using SPSS v. 14 (SPSS Inc., Chicago, IL, USA).

Validation and error estimation of vertical displacement

A number of problems could arise when using an accelerometer to estimate position as a function of time. Most importantly, a single accelerometer cannot resolve rotations, meaning the method can only be used when motions are strictly translational. Further, errors can accumulate because the numerical integration process does not perfectly capture the actual continuous signal being measured. Finally, integration of the random noise in the signal yields a root-mean-squared output that increases with integration time (similar to a random walk) (Thong et al., 2004).

However, the use of the integration method can be used contingent on the following conditions: (1) animals do not rotate significantly about the pitch or yaw axes during strides, (2) animals climb with roughly the same body orientation that they hold prior to and after a climbing bout, (3) bouts of climbing are short enough to avoid accumulation of random-walk integration error, and (4) the chosen accelerometer is accurate enough to capture the animal's natural accelerations with significant fidelity for double integration.

A combination of behavioral and environmental factors enabled the use of this method. Most climbing strides occur on the trunk of the tree, constraining horizontal displacement and generally orienting the animal along a linear path. The animals favor short, intermittent bursts of locomotion, allowing for measurement of body orientation immediately before and after movement and avoiding long integration times, which increase the likelihood of drift. Finally, their stereotyped bounding locomotion lends well to estimation of distance traveled using mean stride length and number of strides when integration is not possible.

Observations of animals climbing in their natural habitat indicate that assumptions of conditions one and two are generally valid. Near the canopy, branches become less vertical and animals may change pitch during locomotion. These climbing sections are clearly identifiable in the acceleration record by a large change in the gravity vector over the course of the run.

Conditions three and four were evaluated directly in the field and the laboratory. To quantify position drift due to random walk, we recorded data from the data loggers during the animals' rest phase. Using segments of data in which the animal was motionless for greater than 2h, we used a sliding window to select 1000 non-overlapping segments. We then double integrated each of these sections of the logged data to measure the mean absolute drift as a function of time (Fig. 3A). The median duration of climbing
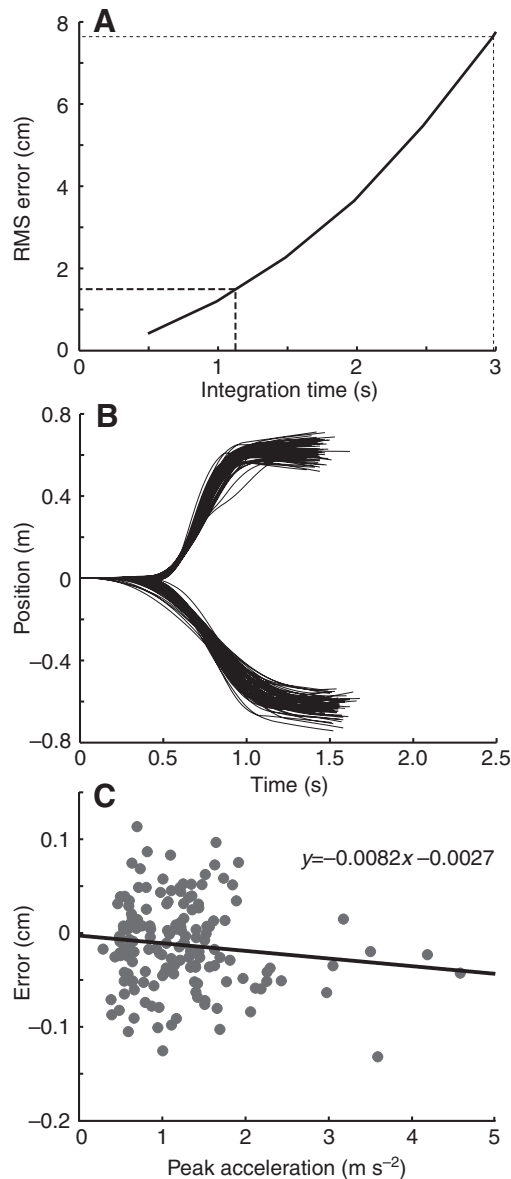
Fig. 3. Validation of the method for determining height climbed from accelerometers. (A) Root mean square error due to signal drift *versus* integration time. Heavy dashed line indicates median duration (1.15 s) of climbing bouts and corresponding error. Light dashed line indicates 95th percentile of climbing bout durations (2.98 s) and associated error. (B) Positions *versus* time for accelerometer moved up and down a vertical linear track a known distance of 0.658 m. Mean (±s.e.m.) error was 1.6±4.7 cm) moving upwards and −1.0±4.7 cm moving downwards. (C) Magnitude of integration error *versus* peak acceleration. The integration error was uncorrelated with the peak acceleration of a trial ($F=2.3$, $P=0.13$).

bouts was 1.15 s. The duration of the 95th percentile of climbing bouts was 2.98 s. The accumulated errors at the median duration and duration at the 95th percentile were 1.5 and 7.7 cm, respectively.

To quantify error for individual bounds, we fixed the accelerometer to a linear track at an arbitrary angle and slid the device up and down the track 150 times from a lower stop to an upper stop in smooth motions at a velocity similar to that of climbing animals. We then rotated and double integrated the acceleration data as described above and compared the position with the actual

displacement on the track (Fig. 3B). The error at the end of each 'stride' was determined based on the displacement of a known distance of 0.658 m. Errors were calculated while moving the device both upwards and downwards. Mean (±s.e.m.) error was 1.6±4.7 cm moving upwards and −1.0±4.7 cm moving downwards. The magnitude of this integration error was uncorrelated with the peak acceleration of a trial ($F=2.3$, $P=0.13$; Fig. 3C).

Energetic models

No data are available on the metabolic rates of colugos during rest or exercise. To determine whether the metabolic cost of climbing to a given height to glide is less energetically expensive than it would be to run a distance equivalent to the glide distance, estimates of locomotor costs were calculated from scaling relationships. To estimate the rate of energy consumption during horizontal movement ($\dot{E}/m_b$, W kg^{-1}), we used the empirical scaling relationship determined by Taylor et al. [eqn 10 (Taylor et al., 1982)] for mammals and birds ranging in body mass from 15 g to over 250 kg:

$$\dot{E}/m_b = 10.7 m_b^{-0.316} \times v + 6.03 m_b^{-0.303}, \tag{2}$$

where m_b is body mass and v is velocity. Because reliable estimates of the velocity of horizontal quadrupedal locomotion for colugos are not available, we estimated these costs over a range of velocities (0.25–2 m s^{-1}) spanning the mean climbing velocity and similar to those of other arboreal mammals (Delciellos and Vieira, 2007; Stevens, 2008). To convert $\dot{E}/m_b$ to units of distance from units of time, we divided the estimate of $\dot{E}/m_b$ by v to obtain the mass-specific metabolic energy (cost) required to move 1 m ($C_{\text{Tot–hor}}$, J kg^{-1} m^{-1}). We calculated the total cost of quadrupedal locomotion over a distance equivalent to the glide distance (E_{hor}) in kJ for each night of sampling ($n=18$) by multiplying by m_b and total horizontal distance travelled.

To estimate the mass-specific metabolic cost to climb 1 m ($C_{\text{Tot–climb}}$), we used the scaling relationship for climbing primates, the sister group to colugos, determined by Hanna et al. (Hanna et al., 2008):

$$C_{\text{Tot–climb}} = 109.8 m_b^{-0.134}. \tag{3}$$

We calculated the total cost of climbing to initiate glides (E_{climb}) by multiplying the value obtained from Eqn 3 by m_b and the summed climb distance each night for each animal. Because the scaling equation given by Hanna et al. (Hanna et al., 2008) was calculated based on a single preferred speed for each species, we also calculated E_{climb} using a second method to corroborate the results. To do this, we calculated the total mechanical work done against gravity on a nightly basis using the equation $W_{\text{mech}} = m_b g \times h_{\text{climb}}$, where h_{climb} is the climb height and g is the acceleration due to gravity. We divided the total mechanical work by the climbing efficiency for primates based on the scaling equation $9.50 m_b^{-0.109}$ (%) given in Hanna et al. (Hanna et al., 2008). Paired *t*-tests were used to compare differences in E_{climb} using both methods and E_{hor} for each individual each night. We accounted for the uncertainty in these relationships by calculating both $C_{\text{Tot–climb}}$ and $C_{\text{Tot–hor}}$ using the published 95% confidence intervals for the slopes and intercepts of these relationships (Taylor et al., 1982; Hanna et al., 2008). We also used paired *t*-tests to compare the costs of climbing and horizontal movement at these bounding parameters to confirm the generality of our results.

RESULTS

We collected a total of 382 h of data at 100 Hz from the four animals between June and August in 2006 and 2007 (mean=96 h, 76–154 h
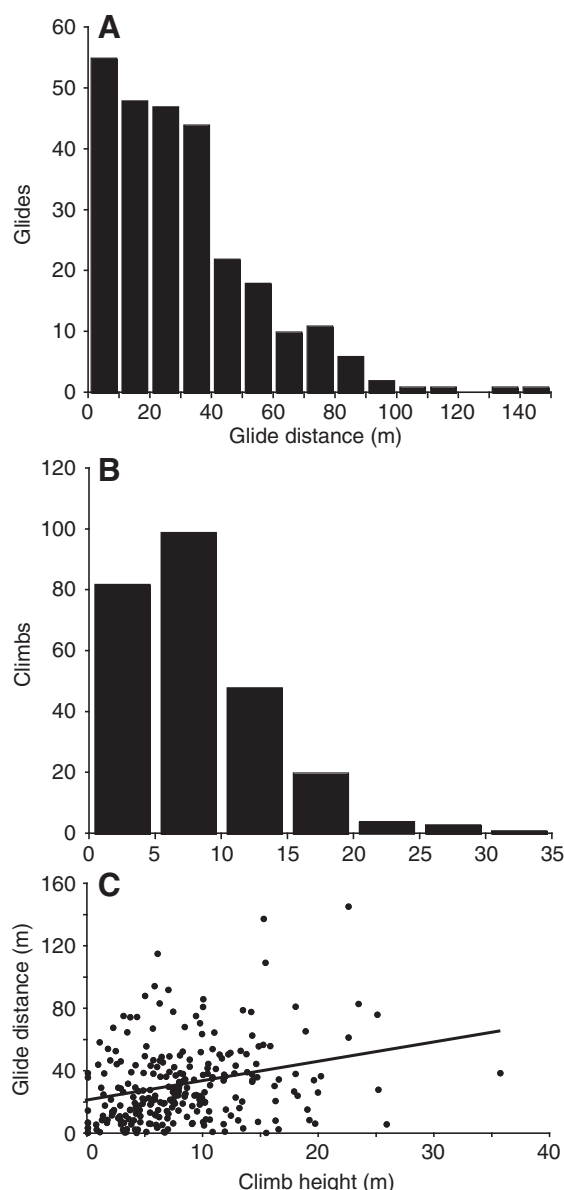
Fig. 4. Distribution of glide and climb distances. (A) Distribution of glide distances for colugos (*N*=258). Mean (±s.d.) glide distance was 31.0±24.8 m. (B) Distribution of climb heights prior to individual glides for colugos (*N*=258). Mean (±s.d.) climb height was 8.1±5.5 m. (C) Relationship between height climbed and resulting glide length. Longer glides were initiated after climbs to greater height (estimate=1.24, *P*<0.001). Note that points along the *y*-axis result from glides that were made in immediate succession without intervening bouts of climbing.

per animal). Animals were active almost exclusively between sunset and sunrise. During the sampling period, we recorded a total of 258 glides and associated bouts of climbing. Glide duration varied between 0.64 and 15.14 s (mean ± s.d.=3.48±2.10 s).

Locomotor behavior

Estimates of glide distance from glide duration ranged between 1 and 145 m for all animals (mean ± s.d.=31.0±24.8 m; Fig. 4A). Vertical climb distance, calculated by integrating the measured acceleration data twice, ranged from 0 m, meaning the animal glided twice in succession without climbing, to 36 m (mean ±

s.d.=8.1±5.5 m; Fig. 4B). Climb distance was significantly related to glide distance, with longer glides following climbs to greater heights (general linear mixed model, estimate=1.24, *P*<0.001; Fig. 4C).

For individual animals, the total vertical height climbed per night ranged between 38 and 320 m (mean ± s.d.=115±68 m). Total horizontal distance travelled per night for each individual colugo ranged from 130 to 1342 m (mean ± s.d.=436±306 m). The total horizontal distance travelled by gliding was 7960 m and the total distance animals climbed during the sampling period was 2090 m, resulting in a mean angle of descent of 15 deg.

Total E_{hor} for individual colugos per night would be between 2.37 and 21.50 kJ (mean ± s.d.=7.16±4.92 kJ) if the animals moved quadrupedally instead of gliding. Total E_{climb} for individual animals ranged between 3.83 and 33.75 kJ per night (mean ± s.d.=12.34±7.27 kJ) based on the scaling relationship for primates (Hanna et al., 2008). Using the total mechanical work, E_{climb} for individual animals ranged between 4.7 and 37.4 kJ per night. Climbing to glide a given distance resulted in energetic costs more than 1.5 times higher than the estimated cost of moving horizontally through the forest the same distance (t_{17}=4.76, *P*<0.01; Fig. 5). Similarly, using total mechanical work to estimate metabolic costs resulted in higher costs for climbing than for moving horizontally (t_{17}=4.68, *P*<0.01). Using the values of the parameters for Eqns 2 and 3 that bounded the variation in these relationships, we found that no combination of parameters changed our conclusions. Using the parameters that minimize E_{climb} and maximize E_{hor}, thus making it most difficult to disprove the locomotor economy hypothesis, still resulted in a cost of climbing to glide a given distance that was not less than the cost of moving horizontally the same distance (t_{17}=1.04, *P*=0.197). Similarly, using the values that maximized E_{climb} and minimized E_{hor} resulted in a higher cost to climb to glide than to move the same distance horizontally (t_{17}=6.31, *P*<0.01).

DISCUSSION

In this study, we quantified all bouts of vertical and horizontal movement through the forest by way of climbing and gliding, respectively. In doing so, we are able to make the first evaluation of a long-standing hypothesis regarding the economy of gliding locomotion based on empirical data collected over an extended period of time.

Our analysis was based on three assumptions that should be noted. First, colugos are capable of moving through the canopy without moving across the ground. Colugos initiate glides at high velocities (Byrnes et al., 2008), giving them a ballistic leaping range of greater than 5 m. Furthermore, the distance between trees in which colugos were observed and the nearest adjacent tree (nearest neighbor distance) was less than 5 m at ground level in 85% of cases (G.B., unpublished data). Therefore, colugos should be capable of crossing the majority of gaps between adjacent trees in the study area without climbing to the ground. Second, we assumed that their horizontal velocity moving through the canopy would be similar to their climbing velocity. Although we don't have systematic data on the horizontal velocities of colugos moving in the canopy, data from other similarly sized arboreal mammals moving on narrow substrates support this (Delciellos and Vieira, 2007; Stevens, 2008). However, if horizontal velocity is very slow compared with vertical movement, gliding can in fact be more economical. Finally, the cost of moving on narrow branches is similar to the cost of running across the ground. One could imagine added costs related to maintaining stability or energy damping on narrow or compliant substrates, increasing the metabolic cost of locomotion on these substrates.
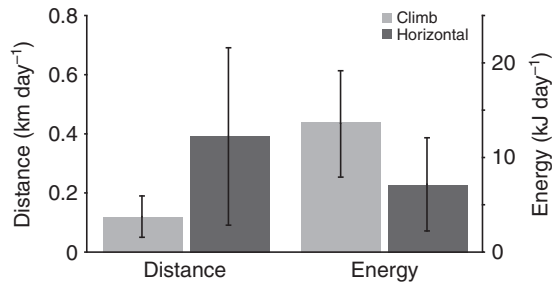
Fig. 5. Total nightly distance travelled and total energy expended (*E*) for vertical and horizontal movements of colugos. Dark bars represent horizontal movement and light bars represent vertical movement by climbing. Total energy is estimated from Eqns 2 and 3 for horizontal and vertical locomotion, respectively. E_{climb} is significantly greater than E_{hor} (t_{17}=4.76, P<0.01).

Table 1. Descent angle (glide angle) for gliding mammals

Species	Descent angle (deg)	Reference
Glaucomys volans	33	Scheibe and Robins, 1998
Glaucomys sabrinus	36	Scheibe et al., 2006
Petaurista leucogenys	18	Stafford et al., 2002
Petaurus breviceps	30	Jackson, 2000
Petaurus gracilis	28	Jackson, 2000
Galeopterus variegatus	15	Present study

Descent angle was calculated as arcsin(height change/glide distance).

Unfortunately, no previous study has examined the relative costs of moving in an arboreal environment *versus* on the ground. However for colugos, because the cost of climbing is so much greater than the estimated cost of horizontal movement, even increases in metabolic cost for arboreal movement similar to those on sand (Lejeune et al., 1998) would not change the general conclusions of this study.

Colugos climbed a total distance in excess of 2 km and glided nearly 8 km during the sampling period of approximately 18 nights. The mean angle of descent over the entire sampling period was 15 deg. Although not specifically an aerodynamic glide angle because it is averaged over all climbs and glides, this measure is analogous to some glide angles presented in the literature (e.g. Jackson, 2000). This angle of descent is lower than mean glide angles reported for other gliding mammals, including flying squirrels and marsupial gliders (Table 1).

Despite climbing a relatively short distance on average to initiate glides, the cost of climbing to glide requires approximately 1.5 times more energy than moving a distance equivalent to the glide distance by quadrupedal locomotion. This is a result of the nearly 10 times greater mass-specific metabolic cost of transport for vertical climbing compared with running. This evidence suggests that for the colugo, gliding is not an economical mode of locomotion and thus does not support the hypothesis that gliding evolved as a means of energetically inexpensive movement through the forest. Furthermore, because colugos have a lower average angle of descent than many other gliding mammals (Table 1), it is unlikely that gliding is an economical form of locomotion for any mammal over ecologically relevant time scales. Therefore, locomotor costs likely result more from some other aspect of the animal's locomotor ecology than from maximizing locomotor economy (Reilly et al., 2007).

Examining the locomotor ecology of gliding mammals reveals further evidence against the locomotor economy hypothesis. Colugos spend a very small fraction of their daily time budget climbing (<1%) and gliding (<0.25%) (Byrnes et al., 2011). Therefore, despite the high cost of climbing, little of an individual's daily energy balance is expended climbing. For example, field metabolic rate (FMR, kJ day^{-1}) in mammals scales following the expression FMR=4.82$m_b^{0.734}$ (Nagy, 2005); therefore, a 1 kg colugo would be predicted to expend 795 kJ day^{-1}. On average, colugos expend 12 kJ climbing each day, only 1.5% of their estimated daily energy expenditure. More conservatively, if an individual consumed energy at its BMR (mlO$_2$ g^{-1} h^{-1}) based on the scaling relationship for arboreal folivores, $\dot{V}_{O_2}/m_b$=2.71$m_b^{-0.302}$ (McNab, 1986), when not climbing, it would spend only 8% of its daily energy expenditure climbing. Therefore, locomotor economy may not have a large influence on the ecology of extant colugos and by inference the evolution of gliding in mammals.

Similarly, time budgets for two marsupial gliders from independent lineages, the greater glider (*Petauroides volans*) and the yellow-bellied glider (*Petaurus australis*), use locomotion minimally, spending approximately 6% (Comport et al., 1996) and 4% (Goldingay, 1989) of their daily time budget engaged in locomotor activities, respectively. Furthermore, based on a study using doubly-labeled water, *P. volans* expends approximately 520 kJ day^{-1} (Foley et al., 1990). If *P. volans* were to move similar distances to those reported here, locomotor costs would total just 2.5% of the total daily energy budget.

If gliding is not an economical form of locomotion, what factors have driven the origins of gliding? First, gliding is a rapid form of locomotion. Time itself is a salient pressure that shapes behavior (Dunbar and Dunbar, 1988; Dunbar, 1992) and by gliding, colugos, like other gliders (Goldingay, 1989; Comport et al., 1996; Scheibe et al., 2006), minimize the time spent travelling between foraging trees. In contrast, moving through the canopy is slow and indirect, with narrow, often compliant substrates that must be negotiated at the terminal branches of trees. Although the horizontal velocity of colugos while moving through the trees is not known, the velocities of other similarly sized arboreal mammals on narrow substrates are relatively slow, approaching 1 m s^{-1} (Delciellos and Vieira, 2007; Stevens, 2008). In contrast, gliding colugos can travel at velocities in excess of 10 m s^{-1} (Byrnes et al., 2008), reducing travel time 10-fold or more. Therefore, although climbing and gliding may not maximize locomotor economy, moving quickly between trees allows for more of the active period of an animal to be spent foraging, possibly increasing the net energy balance. Specifically, colugos have rapid rates of digesta passage, requiring large amounts of forage to be consumed (Wischusen et al., 1994). Therefore, maximizing foraging time within the active period could be particularly important in this group. Second, the fitness benefits of gliding as a means of escaping predators might also be an important component. For example, in eiders, sea ducks that forage by diving and not flying, flight is retained as a result of its fitness benefits, despite high costs. Eiders partially overcome this high cost by only rarely engaging in energetically costly locomotor behaviors (Pelletier et al., 2008). Similarly, colugos use high-velocity leaps from trees to initiate glides (Byrnes et al., 2008) and could realize fitness benefits from this locomotor behavior even if encounters with predators are infrequent. Finally, gliding might provide access to foraging patches not easily accessible by moving through the canopy. The high cost of gliding results from the cost of climbing to sufficient height to glide, so the energetic costs could be even greater in cases in which an animal descends to the forest floor and then climbs an adjacent tree to access resources available there. Therefore, in forests that are taller, more

open or have limited connectivity between the canopies of adjacent trees, gliding might be more likely to evolve (Emmons and Gentry, 1983; Dudley and DeVries, 1990).

By using empirical data collected over an ecologically relevant time scale, we found that the cost of climbing to glide is significantly higher than the cost to travel the same distance horizontally through the forest canopy. This evidence, coupled with data on the locomotor ecology of colugos and other gliding mammals, does not support the long-standing hypothesis that locomotor economy drove the evolution of gliding. The ecological relevance of locomotor behaviors should be taken into account when examining their costs because, in many cases, it might outweigh the need to maximize economy.

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