

Energetic savings and the body size distributions of gliding mammals

Roman Dial*

*Department of Environmental Science, Alaska Pacific University,
4101 University Drive, Anchorage, AK 99508, USA*

ABSTRACT

Natural selection should favour gliding when it is energetically favourable. I use published allometric relationships to determine an upper limit for body mass in mammalian gliders (flying squirrels, marsupial gliders, colugos and anomalurids). The energetic cost to walk distance D scales as body mass raised to the $2/3$ power. To glide distance D using the glide angle θ , a glider must climb to height H , where $H = D \tan \theta$. The energetic cost of climbing to height H scales linearly with body mass. Most published accounts put glide angle at about 25° . I use this angle to compare the energetic costs of walking D metres with climbing H metres to glide D metres. A gliding mammal that weighs 0.4 kg achieves the greatest savings over walking, whereas a 2.5 kg mammal expends the same energy walking as climbing to glide. These masses compare favourably with published body mass distributions of independent glider faunas from Africa (6 species), Borneo (15 species) and Australia (6 species). In each of these three assemblages, the largest glider is ~ 2 kg and the mean glider mass is ~ 0.5 kg. Gliding mammals may have fairly straightforward constraints on their body size.

Keywords: body size, body size distribution, energetics, mammalian gliders.

INTRODUCTION

Gliding mammals include arboreal members of three eutherian and three marsupial families. These animals climb and launch themselves to glide at an angle $\theta < 45^\circ$ below the horizontal using membranes stretched between limbs and sometimes tail. Gliding has evolved among the mammals (two extinct and two extant families of Rodentia, three families of Diprotodontia, and Dermoptera) on at least seven and possibly eight separate occasions (Stafford *et al.*, 2002). However, gliding is efficient for transport over some given distance, D , only so long as the energy expenditure in walking D is greater than that required in climbing to height $H = D \tan \theta$ and gliding to D . Using a simple comparison of walking and gliding energy, I show that the difference in energy cost between gliding and walking is a function of distance travelled, glide angle and body mass. The difference between walking

* e-mail: roman@alaskapacific.edu

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and gliding energy may explain, in small part, the body size distributions of gliding mammals. At least one review of macroecology claims determinants of body size distributions among mammal species are not clear (Blackburn and Gaston, 1996). Another suggests that energetics, resource distribution and habitat structure play important roles (Brown, 1995). Empirically, among large, diverse assemblages of animal species, log-body mass distributions are frequently skewed to the right (Brown *et al.*, 1993; Brown, 1995; Gaston and Blackburn, 2000). In contrast, distributions of log-body sizes for non-volant, arboreal mammal communities from each of five zoogeographic regions (Australian, Nearctic, Ethiopian, Oriental, Neotropical) suggest a left skew (Smith and Lee, 1984; Emmons, 1995; Carey, 2000). A left skew is also seen among the gliding marsupials and eutherians (Fig. 1; Jackson, 1999). While maximal body masses in arboreal animals as a group often exceed 6 kg, the maximum glider biomass has an apparent ceiling at ≤ 3 kg (Emmons, 1995; Jackson, 1999).

Figure 1 shows that mammalian glider communities with different phylogenies have similar log-body mass distributions. Australian marsupial gliders (Fig. 1a–c), African anomalurids (Fig. 1d–f) and Bornean sciurid gliders (Fig. 1g–i) all show a bimodal distribution with similar minimum (10–30 g) and maximum (1000–3000 g) size classes. Although similar to each other, these distributions differ from body mass distributions of other related species in higher taxonomic groups from the same regions. Figure 1b shows the marsupial gliders are smaller than most Australian diprotodontid species (all marsupial gliders are in the order Diprodontia). Compared with the wet forest rodents of Africa, the anomalurid gliders are large (Fig. 1e). And compared with all the gliding sciurids of Eurasia, the Bornean gliders are bimodal (Fig. 1h). To quantify these distributional differences, I sampled six log-body masses (with replacement) randomly 1000 times from all Australian mammals, all marsupials, all diprotodontids all arboreal diprotodonts and arboreal diprotodonts without gliders (Table 1). Using each sample of six, I calculated three distribution statistics (mean, skew, maximum) and compared these with the corresponding Australian glider statistics. For the Australian fauna, at least one of the three distribution statistics for gliders was more extreme than 900 of the 1000 samples from each of the non-glider groups. I found similar results when comparing west Africa's anomalurid gliders with all African rodents, all African rain forest rodents, and all African rain forest arboreal rodents without gliders, but not for arboreal rodents with gliders or rainforest arboreal rodents with gliders (Table 1). These comparisons suggest glider mass distributions are not a random sample of related mammal body mass distributions. Their body mass distributions may instead reflect the gliding habit.

MODEL

In this paper, the energetic cost of climbing to height $H = D \tan \theta$ (to glide distance D) is subtracted from the energetic cost of walking distance D for a similar-sized mammal. This is one way to compare the cost of walking with the cost of gliding. Previous investigators considered the *ratio of mass-specific* expenditures (Scholey, 1986; Keith *et al.*, 2000; J.S. Scheibe *et al.*, unpublished manuscript). I consider *differences in whole-animal* expenditures. Because no-one has published energetic measurements of animals climbing to glide, I will use general allometric relations for horizontal motion and vertical climbing motion documented by Schmidt-Nielsen (1986). One remarkable result is that the energy required to propel quadrupeds a horizontal unit distance is mass specific but independent of speed.

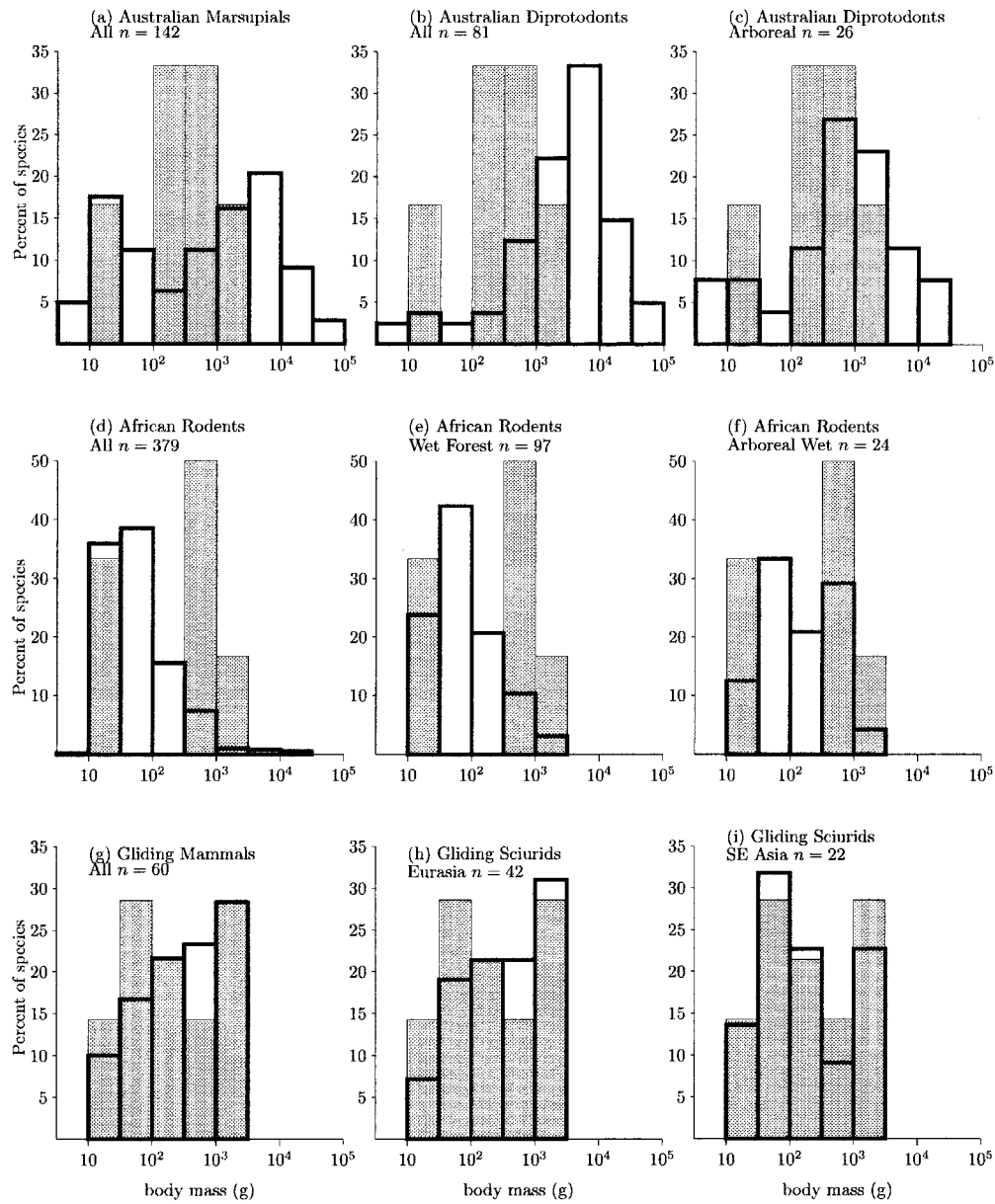


Fig. 1. Log-body mass distributions for mammal faunas (bold outlines) compared with gliding assemblages (shaded distributions) from the same regions. Number of species given by n . (Top row) Australian mammal body masses from Strahan (1998) with all 6 marsupial gliders compared with (a) 142 Australian marsupial species, (b) 81 Australian diprotodont species and (c) 26 Australian arboreal diprotodont species. (Middle row) African body masses from Kingdon (1997) with all 6 anomalurid gliders compared with (d) 379 African rodent species, (e) 97 African wet forest rodent species and (f) 24 African wet forest arboreal rodent species. (Bottom row) Glider body mass data from Jackson (1999) with 14 gliding scuriids of Borneo compared with (g) all 60 worldwide gliding species, (h) all 42 gliding scuriids from Eurasia and (i) all 22 Southeast Asian gliding scuriids.

Table 1. Descriptive statistics for Australian mammal \log_{10} body size distributions and the probability of sampling these statistics at least as extreme as the glider fauna statistics from random samples of size $n = 6$ from these distributions (based on 1000 random samples for maximum and skew and on t -distribution for mean). For each distribution, except the next to last column, the gliders are included in the distribution

	Non-aquatic, non-volant, mammals ^a	Marsupials ^a	Diprotodonts ^a	Arboreal diprotodonts ^b	Arboreal diprotodonts (no gliders) ^b	Gliders
Number of species	204	142	81	27	21	6
Log ₁₀ mean mass (s.e.)	2.435 (0.43)	2.70 (1.12)	3.34 ^c (0.86)	2.65 (0.94)	2.74 (1.00)	2.32
Skew in distribution	0.34 ^c $P(m_6 \leq -1.24) = 0.009$	-0.14 ^d $P(m_6 \leq -1.24) = 0.06$	-1.04 $P(m_6 \leq -1.24) = 0.13$	-0.53 ^d $P(m_6 \leq -1.24) = 0.08$	-0.67 $P(m_6 \leq -1.24) = 0.14$	-1.24
Log ₁₀ max mass	4.71 ^d $P(m_6 \leq 3.07) = 0.09$	4.71 ^c $P(m_6 \leq 3.07) = 0.03$	4.71 ^c $P(m_6 \leq 3.07) \leq 0.001$	4.04 $P(m_6 \leq 3.07) = 0.13$	4.04 ^d $P(m_6 \leq 3.07) = 0.06$	3.07

^a Significantly different at $P = 0.05$ in at least one statistic.

^b Significantly different at $P = 0.10$ in at least one statistic.

^c Significantly different at $P = 0.05$.

^d Significantly different at $P = 0.10$.

s.e. = standard error.

Table 2. Descriptive statistics for African rodent body size distributions and the probability of sampling these statistics at least as extreme as the glider fauna statistics from random samples of size $n = 6$ from these distributions (based on 1000 random samples for maximum and skew and on t -distribution for mean). For each distribution, except the next to last column, the gliders are included in the distribution

	Rodents ^a	Rain forest rodents ^a	Arboreal rodents	Arboreal rain forest rodents	Arboreal rain forest (no gliders) ^a	Glider
Number of species	379	97	32	24	18	6
Log ₁₀ mean mass (s.e.)	1.78 ^b (0.54)	1.89 ^b (0.54)	2.08 (0.54)	2.17 (0.58)	2.12 (0.50)	2.37
Skew in distribution	1.17 ^c $P(m_6 \leq -0.85) = 0.10$	0.53 $P(m_6 \leq -0.85) = 0.13$	0.31 $P(m_6 \leq -0.85) = 0.17$	-0.07 $P(m_6 \leq -0.85) = 0.27$	-0.038 ^c $P(m_6 \leq -0.85) = 0.10$	-0.85
Log ₁₀ max mass	4.29 ^b $P(m_6 \geq 3.19) = 0.03$	3.44 $P(m_6 \geq 3.19) = 0.12$	3.19 $P(m_6 \geq 3.19) = 0.18$	3.19 $P(m_6 \geq 3.19) = 0.23$	2.89 ^b $P(m_6 \geq 3.19) < 0.001$	3.19

^a Significantly different at $P = 0.05$ in at least one statistic.

^b Significantly different at $P = 0.05$.

^c Significantly different at $P = 0.10$.

s.e. = standard error.

Schmidt-Nielsen (1986) reviews eight studies to find that the energetic cost of quadrupedal motion is given generally as

$$E_D = am^b D \quad (1)$$

where $0.6 \leq b \leq 0.8$ (Schmidt-Nielsen suggests $b = 0.67$ based on scaling considerations) and $2.45 \times 10^{-3} \leq a \leq 8.46 \times 10^{-3}$. The units are energetic cost E_D in millilitres of oxygen for an animal of mass m grams travelling distance D metres. Schmidt-Nielsen (1986) also reviews work on the energetic costs of vertical climbing E_V (ml O_2), giving

$$E_V = \beta m H \quad (2)$$

for an animal of size m grams to climb a vertical distance H metres, with empirical estimates of $1.36 \times 10^{-3} \leq \beta \leq 2.0 \times 10^{-3}$. For the coefficient β , the upper bound $\beta = 2 \times 10^{-3}$ was hypothetical and the lower bound $\beta = 1.36 \times 10^{-3}$ was measured.

Once a glider reaches its launch height H , it can glide a horizontal distance $D = H \cot \theta$, assuming that it glides at an overall (from point of launch to landing) angle of θ below the horizontal. Empirical and theoretical work by Keith *et al.* (2000) suggests that launch energy is small compared with other costs. Although no-one has estimated the energy expenditure in maintaining the gliding posture, I assume it to be negligible. Equations (1) and (2) also omit basal metabolic rate (BMR). Basal metabolic rate would be included if there is a BMR trade-off for gliding versus non-gliding in mammals. However, there is no evidence of a trade-off in BMR, because double log regressions of BMR on m are indistinguishable between gliding and non-gliding mammals (Geiser and Stapp, 2000). Assuming that equation (2) is a fair representation of energetic expenditures for gliding mammals of size m to travel horizontal distance $D = H \cot \theta$, I address the question: 'For what sized mammals is walking D more energetically costly than climbing and gliding to D ?' The answer may be approached by considering the energetic difference, $S(D, m, \theta)$, between walking (equation 1) and gliding (equation 2):

$$S(D, m, \theta) = E_D - E_V = D(am^b - \beta m \tan \theta) \quad (3)$$

RESULTS AND DISCUSSION

The energetic savings given by equation (3) depend linearly on D and non-linearly on glide angle θ and mass m (Fig. 2a). The linear dependence on D supports the hypothesis that gliding is favoured for transport in more open habitats (Emmons and Gentry, 1983; Archer, 1984; Emmons, 1995; Moffett, 2000). This follows if more open habitats have a higher average distance between canopy elements, such as found in tall forests. Tall forests are usually less dense and more open, allowing for both higher launch points and less cluttered glide paths, each of which would lead to greater horizontal glide distances and increased energetic savings. Certain anomalurids are even known to prune their glide paths (Kingdon, 1997). Consistent with this are spatial measurements from six sites in four different biogeographic regions (Nearctic, Neotropical, Australian, Oriental). Sites with high glider richness are more open than sites with low glider richness (Dial *et al.*, in press).

The dependence on glide angle θ can be investigated by setting $S(D, m, \theta) = E_D - E_V$ (equation 3) equal to zero and determining the glide angle as a function of body mass that makes gliding as energetically favourable as walking, $E_D = E_V$:

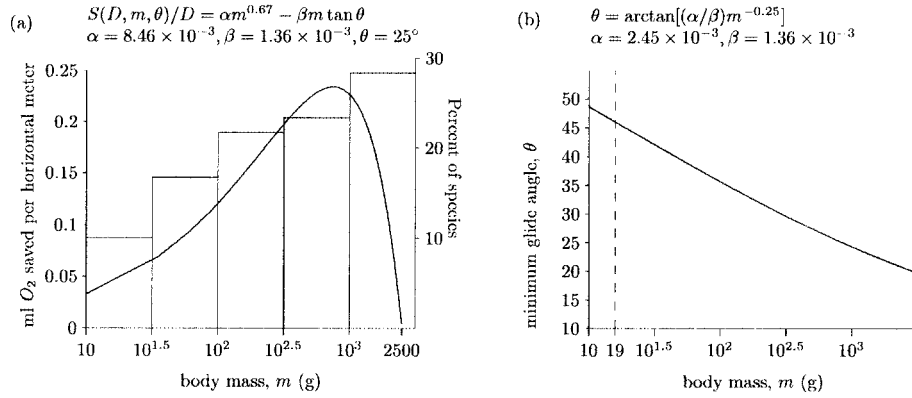


Fig. 2. (a) The curve (equation 3 with parameters in the figure) shows the difference between walking and gliding energy expended to travel 1 m horizontally as a function of log₁₀-body mass. The histogram shows the percentage of all species in the log-body size classes from Jackson (1999). At 2500 g the difference in energy expenditures is zero and for body masses greater than 2500 g it is less costly to walk than to climb and glide. (b) Minimum glide angle as a function of body mass (equation 4 with parameters in the figure). Only glide angles below the theoretical curve are energetically favourable over walking for a mammal of *m* grams.

$$\theta = \arctan\left(\frac{\alpha}{\beta} m^{b-1}\right) \quad (4)$$

For glide angles less than θ , gliding will be energetically favourable over walking. In general, the relationship between glide angle and body mass suggests that larger gliders must glide at flatter angles than smaller gliders to save energy over walking (Fig. 2b). Several glider studies have shown that longer glides generally have flatter overall glide angles (Scholey, 1986; Jackson, 1999; Vernes, 2001; Stafford *et al.*, 2002); thus larger gliders might be expected to make longer glides to affect more cost-effective glides. This is the standard result reported elsewhere (Scholey, 1986; Scheibe and Robins, 1998). Thus, short distances may be reached using quadrupedal motion more often by large gliders than small ones. Small gliders can be energetically favourable with much steeper glides than larger gliders and so glide short distances more often. An interesting point raised by Fig. 2b is that for sufficiently small mass, the ‘glide angle’ need no longer be less than 45° to be cost-effective. In other words, sufficiently small mammals may climb and jump $D = H \cot \theta$ with $\theta \geq 45^\circ$ and still expend less energy than required to walk. We can solve equation (4) for the mass that gives a glide angle $\theta \geq 45^\circ$ – that is, where ‘parachuting’ is sufficient for a small mammal. Using the range of parameter values reviewed by Schmidt-Nielsen (1986), $0.6 \leq b \leq 0.8$, $2.45 \times 10^{-3} \leq \alpha \leq 8.46 \times 10^{-3}$ and $\beta = 1.36 \times 10^{-3}$, suggests a maximum body mass of $m \leq 19$ g. Below 19 g for observed parameter values, the ‘glide angle’ (perhaps better called ‘angle of descent’) need not be less than 45°. The implication is that gliding membranes are unnecessary for very small mammals. Jackson (1999) lists 10–13 g as the smallest glider body size.

Glide angles estimated in a variety of studies tend to be $20^\circ \leq \theta \leq 30^\circ$ for most observed mammal gliders, most of the time (Scholey, 1986; Jackson, 1999; Vernes, 2001; Stafford *et al.*, 2002). Supposing, then, that $\theta = 25^\circ$, $b = 0.67$, $2.45 \times 10^{-3} \leq \alpha \leq 8.46 \times 10^{-3}$

and $1.36 \times 10^{-3} \leq \beta \leq 2 \times 10^{-3}$, the question of largest mass for an energetically favourable glider can be estimated using equation (3) set to zero and $\tan\theta = \tan(25^\circ) = 0.466$ to find

$$m_{\max} = \left(\frac{\alpha}{\beta \tan\theta} \right)^{1/(1-b)} \leq 2573 \text{ g}$$

Thus we should not expect gliders to exceed ~2.5 kg. Emmons (1995) noted that maximal body mass among each of the three glider orders Diprodontia, Rodentia and Dermoptera is ~2 kg, although Jackson's (1999) review lists two rodent gliders (*Petaurista nobilis* and *P. alborufus*) that have exceeded 3 kg. Equation (3) can also provide an estimate for the body mass of greatest energy difference between gliding and walking by taking the derivative of $S(D, m, \theta) = E_D - E_V$ with respect to mass and setting equal to zero:

$$\frac{dS}{dm} = \alpha b m^{b-1} - \beta \tan\theta = 0 \quad (4)$$

Again assuming a glide angle of $\theta = 25^\circ$, $b = 0.67$, $2.45 \times 10^{-3} \leq \alpha \leq 8.61 \times 10^{-3}$ and $1.36 \times 10^{-3} \leq \beta \leq 2 \times 10^{-3}$, provides the solution

$$6 \text{ g} \leq m_{\text{opt}} = \left(\frac{\alpha}{\beta \tan\theta} \right)^{1/(1-b)} \leq 806 \text{ g}$$

The midpoint of this range is $m_{\text{opt}} = 406 \text{ g}$. Figure 5 in Jackson (1999) shows the modal size class (30% of 60 species divided into five arithmetic classes) is 100–500 g. From Jackson's review I have chosen all gliders from Africa (Anomaluridae), Australia (Diprodontia) and Borneo (Sciuridae + Dermoptera). For each assemblage, the maximum body mass is ~2 kg and the mean mass is near the 'optimal' 400 g (Table 3).

The greatest energetic difference between walking and gliding locomotion occurs for mammals ~400 g. Gliding mammals substantially smaller and larger than 400 g should expend roughly similar energy climbing to glide as their non-gliding arboreal counterparts do walking. This suggests two aspects of glider biology should differ from that of non-gliders as a function of body size: home range size and diet. First, assuming home range size is limited by energy availability, extreme-sized gliders should have home range sizes similar to non-gliders. In contrast, mid-sized gliders (200–600 g) should have large home ranges compared with non-glider home ranges, since they can travel so much more efficiently. Goldingay (2000) reviews known home range data for 12 gliding mammals (six marsupial and six eutherian). The two species closest to the 400 g optimal body mass (*Petaurus australis* and *P. gracilis*) have very large home range sizes (> 20 ha), while nine of the other

Table 3. Body mass statistics for mammalian glider assemblages

	Borneo	Australia	Africa	Combined
Number of glider species	15	6	6	27
Mean mass (g)	544	419	560	520
Minimum mass (g)	13	12	16	12
Maximum mass (g)	1985	1175	1417	1985
Skew for $\log_{10}(\text{mass})$	-0.018	-1.24	-0.850	-0.339

ten species have home range sizes < 10 ha. A second hypothesis is that mid-sized gliders might best exploit calorie-poor diets compared with non-gliders of the same size. In contrast, very small (< 50 g) and very large gliders (> 1000 g) should feed on foods similar to their non-gliding counterparts, since they receive only small energetic gains by gliding. The food quality hypothesis may be supported by dietary data on arboreal marsupials. Smith and Lee (1984) show that the smallest marsupial glider (*Acrobates pygmaeus*), which feeds on nectar and insects, and the largest (*Petauroides volans*), which feeds on leaves, are more similar in their diet to other, non-gliding possums of similar sizes. The mid-sized marsupial gliders (*Petaurus australis*, *P. breviceps*, *P. gracilis*, *P. norfolcensis*), in contrast, feed more uniquely on plant exudates (Smith and Lee, 1984; Goldingay, 2000). Similarly, Kingdon (1997) states that bark predominates in diets of mid-sized anomalurids, while the same-sized, syntopic African giant squirrels (*Protoxerus stangeri* Sciuridae) feed on fruits and seeds. Goldingay's (2000) review shows the smaller *Glaucomys volans* (50–80 g) of North America has a typical, small-sized rodent (e.g. syntopic *Tamias* sp.) diet of 80% seeds, whereas the mid-sized *G. sabrinus* (110–185 g) generally specializes on fungi and lichens. Kawamichi (1997) lists a typical scansorial rodent diet of seeds, foliage and fruits for the large-sized sciurid glider *Petaurista leucogenys* (700–1500 g). Dumont (2000) describes both *Cynocephalus* species of Dermoptera (925–1750 g) as foliovores, and Mendoza and Custodio (2000) describe leaves and fruits as the diet of *C. volans*. These colugo foods are also typical of 2–4 kg arboreal primates. Thus the size-dependent observations of home ranges and diets for gliding mammals are consistent with the size-dependent energetic savings.

If gliding is such an efficient mode of travel, why are there only 60 gliding mammal species worldwide? At any one tropical site there can be at least half this many arboreal mammal species that do not glide. Two well-known instances may suggest a partial answer. The North American flying squirrel, *G. sabrinus*, is the primary food item for the spotted owl (Carey, 2000), and the Philippine *Colugo volans* for the Philippine eagle *Pithecophaga jefferyi* (Mendoza and Custodio, 2000). Perhaps gliding mammals are more susceptible to predation from avian predators than non-gliders (Scheibe *et al.*, 1990; Stapp, 1994), in contrast to the usual 'predation hypothesis' implied for selection for gliding (Norberg, 1985). Three pieces of evidence support this hypothesis: (1) Gliders are generally considered less agile climbers than non-gliders due to their gliding membranes, making them more vulnerable on limbs and boles (Harrison, 1973). (2) Gliding locomotion, while efficient, is constrained to descents, reducing degrees of freedom, so to speak. (3) A nocturnal habit is ubiquitous among mammalian gliders, with the usual interpretation that this helps avoid avian predation (Jackson, 1999). Consistent with the handicap hypothesis (Zahavi and Zahavi, 1997), gliders from three different orders are active in daylight only during courtship, when mates can potentially best advertise their fitness through predation. Another possibility is that the sensitivity of gliding efficiency to body mass may preclude gliders from having large litters. Indeed, Goldingay's (2000) review of 23 species of gliding mammals shows litter sizes are characteristically small. Only gliders < 250 g have litters of more than 1–2 young. The largest gliders have only a single young. Thus, while gliding may increase fitness through increased energetic efficiency for locomotion, it may reduce fitness in terms of survival due to predation and reproduction.

In summary, considering the difference in energetic expenditures between walking locomotion and climbing-to-glide suggests the following: (1) Open forests favour gliding in mammals. We may observe this in the geographic distribution of gliding mammals. (2) Larger-bodied gliders must glide at flatter glide angles (higher glide ratios) to be energetic-

ally favourable over quadrupedal motion. We may observe this as a higher frequency of long-distance glides and a higher frequency of quadrupedal motion when moving shorter distances in larger gliders than in smaller ones. (3) Very small mammals can even benefit from ‘parachuting’, obviating the need for gliding membranes. This may be observed in the smallest gliders ~10 g. (4) Assuming a glide angle $\theta \approx 25^\circ$ suggests that very small gliders and very large ones save little energy over quadrupedal motion. We may observe this in diets and home range sizes of extreme-sized gliders as similar to same-sized non-gliders, while mid-sized gliders consume poor-quality food and occupy very large home ranges. (5) There is a theoretical ceiling ~2.5 kg for gliding at $\theta \approx 25^\circ$. This may explain the maximum body mass in most gliding assemblages ≤ 3 kg. (6) The biggest energy savings between walking and gliding at $\theta \approx 25^\circ$ occurs at a body mass ~400 g. While the modal size is not 0.4 kg in most glider communities, the mean mass often is close to this value. Among all glider species combined, the modal size class is 100–500 g (Jackson, 1999).

The observed body size distribution in gliding mammals may result from null, random processes, from competition for nest holes or other limiting arboreal resources, the physics of glissant locomotion, or some combination of these factors and others. I have chosen to focus on a simple, first-order approach that considers the difference in scaling between the energetic costs of walking and climbing. However, it is difficult to view natural selection favouring an energetically based optimal body size among gliders, except in the first stages of evolution from non-gliding ancestors. Once evolved, the sizes of gliders are most likely subject to forces other than energetic optimization. For instance, consider a null, random evolutionary approach applied subsequent to evolution of an ancestral glider. Initially, the natural selection event would favour gliding to evolve for ~400 g animals as set by $dS(D,m,25^\circ)/dm = 0$. With subsequent speciation within a glider lineage, this distribution might approach a uniform distribution (Maurer, 1999) centred at ~400 g. However, assuming that body size evolution was random but subject to the ~2.5 kg ceiling set by $S(D,m,25^\circ) = 0$, an upper, reflecting limit at ~2.5 kg would preclude gliders from evolving larger. McShea (1994) has argued that a reflecting boundary in a random evolutionary process leads to skew opposite the boundary. In the case of gliders, an upper boundary would lead to left, or negative, skew, and a mean mass slightly higher than the optimal mass. The body size distributions for gliders shown in Fig. 1 are consistent with this scenario.

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