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GLAUCOMYS VOLANS

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Glaucomys volans is nocturnal, active during the winter, and has a low metabolic rate and conductance for its size. Body mass of *G. volans* was greater in winter than in summer, but there were no seasonal differences in basal metabolic rate or conductance. Energetic constraints may partially explain why many life-history characteristics of this species are relatively conservative compared to diurnal tree squirrels and to other mammals of similar mass.

Key words: *Glaucomys volans*, metabolism, energetics, life history

The southern flying squirrel (*Glaucomys volans*) resembles other North American tree squirrels (*Tamiasciurus, Sciurus*) in that all are arboreal, consume principally hard mast, and remain active and euthermic during winter (Dolan and Carter, 1977; Flyger and Gates, 1982; Obbard, 1987). *G. volans,* however, differs from these species by being nocturnal and a glider, traits that subject it to potentially high thermoregulatory costs while exposed to the coldest daily temperatures. Behavioral mechanisms employed by *G. volans* to reduce exposure during winter include forming large aggregations inside nest-lined tree cavities and reducing outside activities at low ambient temperatures (Muul, 1968). It is not known, however, whether *G. volans* uses physiological adjustments for energy conservation. I studied the winter and summer energetics of *G. volans* in southern New Hampshire and compared my results with metabolic information from throughout the distribution of this species. My objectives were to evaluate possible seasonal and geographic variation in energetics of *G. volans,* and ascertain whether a nocturnal, gliding lifestyle contributes to differences in the energetics between *G. volans* and sympatric diurnal squirrels. Be-

cause energetics and life-history traits are generally correlated (McNab, 1980), I also examined potential relationships among the energetics of *G. volans* and other tree squirrels, and certain aspects of their respective life histories.

MATERIALS AND METHODS

Squirrels were live-trapped in southern Strafford Co., New Hampshire, in spring and summer 1989 and housed in a large outdoor pen at the University of New Hampshire Wildlife Research Facility in Brentwood, New Hampshire. Squirrels were provided with nest boxes (12.8 by 15.2 by 25.4 cm) for shelter and fed a diet of sunflower seeds, acorns, apples, and walnuts ad lib. Metabolism experiments were conducted from 16 December 1989 to 24 February 1990 (winter) and from 4 to 13 July 1990 (summer), and were performed during daylight hours (0700 to 1630 h) when feeding activity had ceased and squirrels presumably were inactive. The same nine adult animals (five males, four females) were used in both seasons.

Oxygen consumption was measured at ambient temperatures (T_a) from 12 to 35°C in summer and from 8 to 35°C in winter. Squirrels were fasted for at least 3 h, weighed, and placed into 4.9-l metabolism chambers constructed of 0.6 cm Plexiglas that had been painted dark brown. Temperature was monitored inside each cham-

ber using a copper-constantan thermocouple fixed 5 cm from the top. Three chambers were placed in a large, darkened cabinet, with ambient temperature (T_a) initially set at 30–35°C. Temperature was lowered by 4–5°C every 2 h, and squirrels were allowed 1 h to adjust to each T_a before measurements were resumed. Air was drawn from the chamber at the rate of 1.1 l/min (corrected to standard temperature and pressure for calculations), with flow rates maintained using a Cole-Parmer factory-calibrated flowmeter (150 mm; accurate to ±2°). A Beckman paramagnetic oxygen analyzer (Model 755A) measured the oxygen concentration of effluent air for 25 min; these data were recorded continuously and summarized every 5 min by an Apple IIE microcomputer. The minimal oxygen concentration during the last three 5-min intervals was subtracted from the average value of surrounding cabinet air (measured during temperature adjustment periods) to determine the amount of oxygen consumed. Rates of oxygen consumption, calculated using equation 3a of Withers (1977), were divided by the average body mass during the trial to calculate metabolic rates (cm^3 O_2 g^{-1} h^{-1}).

Basal metabolic rate, defined as energy expenditure of a fasted, inactive animal under thermoneutral conditions, was calculated as the mean of the lowest metabolic rates obtained for each squirrel. Lower critical temperature was first visually estimated by inspection of a plot of metabolism on T_a, and then calculated by using a linear regression equation of metabolism and temperature (below the estimated lower critical temperature) and solving for the calculated basal metabolic rate. The slope of this curve provided an estimate of thermal conductance. Analysis of covariance was used to examine seasonal differences in conductance (Zar, 1984).

RESULTS AND DISCUSSION

There were no significant intersexual differences in body mass or basal metabolism (*t*-tests, $P > 0.15$), so data for males and females were pooled in both seasons. Body mass was greater in winter ($\bar{X} \pm SE = 67.0 \pm 2.3$ g) than in summer (61.5 ± 2.1 g; paired *t*-test, $P = 0.049$), but mass-specific basal metabolic rates did not differ significantly between seasons (winter, 0.95 ± 0.04; summer, 1.05 ± 0.02 cm^3 O_2 g^{-1} h^{-1}; paired *t*-test, $P = 0.086$). Total metabolic rates (cal

animal^{-1} h^{-1}), which incorporate seasonal changes in both mass and metabolism, differed by only 1.4% (winter, 302.2 ± 9.9; summer, 310.4 ± 13.3; paired *t*-test, $P = 0.622$), indicating that differences in metabolism were not biologically significant.

Many small mammals that inhabit seasonal environments undergo winter reductions in either mass or metabolism (Merritt, 1984), strategies that apparently are not employed by *G. volans*. Similarly, whereas winter-acclimatized animals often possess lower rates of heat loss (Hart, 1971), I found no significant seasonal differences in conductance (Fig. 1; interaction of T_a and season, $P = 0.08$), or in metabolic rates at any T_a (*t*-tests, $P > 0.05$). Lower critical temperature was slightly lower in winter (26.3°C) than in summer (27.6°C).

The slope of the metabolism-temperature curve provides a reasonable estimate of thermal conductance under the assumptions that body temperature (T_b) and conductance remain constant below thermoneutrality and that the curve extrapolates to T_b when metabolic rate equals zero (Bradley and Deavers, 1980). Body temperature was not monitored in this study, but Neumann (1967) reported little variation in T_b for *G. volans* at ambient temperatures from 30 to −2°C, and no differences between winter and summer. Assuming that T_b remained constant at 39°C, extension of the curves in Fig. 1 to the abscissa indicated that the summer data provided a relatively good estimate of conductance, but that the winter slope underestimated T_b by ca. 10% (4°C). This discrepancy suggests either some error in the method used to measure or calculate conductance or that body temperature or conductance changed with decreasing temperature. Muul (1968) reported low body temperatures in wild squirrels (*G. volans*) in Michigan during an extremely cold period, but torpor has not been studied experimentally in *G. volans*. Additional simultaneous measurements of metabolism and body temperature at low temperatures, therefore, are needed before the relationships among
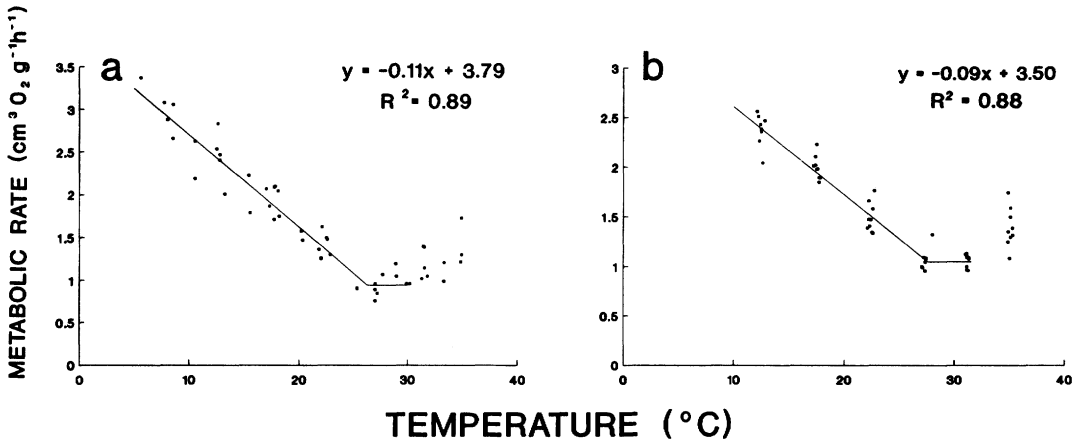
FIG. 1.—Metabolic rate as a function of ambient temperature for *Glaucomys volans* during, a) winter, and b) summer in southern New Hampshire. Regression equations describe the relationship below thermoneutrality.

these parameters is completely understood. However, if I assumed no variation in T_b (39°C) and calculated conductance (C) by the equation: C = metabolic rate/$(T_b - T_a)$ (Bradley and Deavers, 1980), mean conductance in the present study was 0.09 cm³ O_2 g^{-1} h^{-1} °C^{-1} in both seasons.

Comparisons within and among species were facilitated by expressing parameters in terms of their residual variation (the ratio of observed values to those expected based on mass—McNab, 1983), which removes the effect of body size. An examination of the residual variation in the energetic parameters investigated here (metabolism, f_m; conductance, f_c; lower critical temperature, f_t) indicated that *G. volans* has relatively low rates of metabolism and conductance relative to other mammals of similar mass (Table 1). The differences between observed and expected basal metabolic rates in this study were statistically significant (Mann-Whitney *U*-test; *P* = 0.001). Further, at northern latitudes *G. volans* has a high temperature differential (the difference between body temperature and lower critical temperature; McNab, 1974), which serves as a measure of the ability of an organism to thermoregulate efficiently. One can speculate that such mechanisms, particularly low rates of metabolism and heat loss, permit this species

to persist in a lifestyle in which the energetic costs may be prohibitively high.

My results demonstrate that *G. volans* does not adjust to seasonal environmental changes by changing metabolism or heat production but instead sustains inherently low maintenance costs to reduce energy use in winter and summer. However, total energy use in winter may be considerably greater than in summer; e.g., if one calculated total minimum energy expenditures (E) by the equation E = Conductance × ($T_b - T_a$), using the values in Table 1 and conservative estimates for T_a of 5 and 15°C in winter and summer, respectively, energetic costs would be 89% greater in winter than summer (1,202.8 and 637.6 cal/h, respectively). *G. volans* apparently reduces these costs through behavioral adjustments such as reducing foraging activity at low temperatures, and huddling in nests inside tree cavities (Muul, 1968). Neumann (1967) reported that nest temperatures surrounding huddled squirrels (*G. volans*) remained above lower critical temperature at T_a = -5°C, whereas Stapp et al. (1991) calculated daily energy savings of 26–33% for six squirrels huddled in a nest compared to an individual nesting alone. *G. volans* also hoards large quantities of hard mast during autumn, which provides an easily located

source of energy rich food for winter use (Muul, 1968).

Although distributed across ca. 20° of latitude and a variety of habitat types (Dolan and Carter, 1977), there appears to be little geographic variation in the basal metabolism or conductance of *G. volans* (Table 1). Lower critical temperature, however, increased with decreasing latitude, as demonstrated by the reduction in f_t in more southerly regions. A higher f_t may be necessary for efficient thermoregulation at colder latitudes, assuming that body temperature remains seasonally constant at all localities.

In contrast with this study, Neumann (1967) found a higher basal metabolic rate in winter than summer, whereas Muul (1968) reported no seasonal differences in metabolism, but did not provide metabolism values for flying squirrels during summer. Metabolic rates during winter from these two studies were 36% higher than that in the present study, a discrepancy that may be due to differences in methods. For example, Muul (1968) measured metabolism at temperatures below the lower critical temperature found in the other studies (Table 1; $T_a \leq 26°C$), which suggests that basal conditions may not have been achieved.

Whereas conductance is considered a function of environmental severity, with lower conductances adaptive in cold climates or microhabitats (Bradley and Deavers, 1980), the relative magnitude of basal metabolism is thought to be related to food habits, climate, and activity (McNab, 1980). For instance, most mammals that feed on seeds and nuts, notably *Tamiasciurus* and *Sciurus,* have high basal rates (i.e., $f_m >$ 100), a factor related to the relatively low perishability, high energy content, and temporal availability of hard mast (McNab, 1986a; Reynolds, 1985). These species also tend to have higher conductances than expected by mass (Reynolds, 1985), in contrast to the low conductance exhibited by *G. volans*. The exceptions to this pattern are desert granivores, which require low met-

TABLE 1.—*Energetic parameters of Glaucomys volans throughout its distribution. Residual variation (observed × 100/expected) parameters: f_m = basal metabolic rate × 100/3.42$M^{-0.25}$ (Kleiber, 1961; McNab, 1983), f_c = conductance × 100/0.76$M^{-0.43}$ (Bradley and Deavers, 1980), f_t = temperature differential ($T_b - T_{lc}$) × 100/3.42$M^{0.25}$ (McNab, 1974); where M = mass, T_{lc} = lower critical temperature, and T_b = body temperature = 39°C. Items without values either were not measured or not reported.*

Locality	Season	n	Mass (g)	Basal metabolic rate (cm³ O₂ g⁻¹ h⁻¹)	f_m	Conductance (cm³ O₂ g⁻¹ h⁻¹ °C⁻¹)	f_c	Lower critical temperature (°C)	f_t	Source
New Hampshire	winter	9	67.0	0.95	79	0.11	87	26.3	130	This study
	summer	9	61.5	1.05	86	0.09	69	27.6	119	This study
Michigan	winter	1	70.0	1.29	109	0.06[a]		19–20	197	Muul (1968)
Massachusetts			75.0	1.10	95					Pearson (1947)
Virginia	winter	10	61.2	1.30	107	0.11	85	28.0	115	Neumann (1967)
	summer	10	62.8	1.06	88	0.11	86	30.0	93	Neumann (1967)
North Carolina		6	67.1	0.97	81					VanVoorhes (1976)
Florida	summer	5	70.7	0.87	74	0.11	89	32.0	71	Dolan (1975)
	summer	7	62.8	1.04	86	0.11	86	35.0	41	Dolan (1975)

[a] Conductance to 6°C. Muul (1968) reported that conductance <6°C was 0.11 cm³ O₂ g⁻¹ h⁻¹ °C⁻¹.

TABLE 2.—Residual variation (observed × 100/expected) in life history parameters of the tree squirrels occurring in eastern North America. f = residual variation and o = observed values for each parameter and M = mass. Data are from Eisenberg (1981), Flyger and Gates (1982), Innes and Lavignes (1979), Niethammer (1990), Obbard (1987), Ouellet and Ferron (1985), Pauls (1981), Stapp and Mautz (1991), Zullinger et al. (1984), and this study.

Parameter	Glaucomys volans f	Glaucomys volans o	Glaucomys sabrinus f	Glaucomys sabrinus o	Tamiasciurus hudsonicus f	Tamiasciurus hudsonicus o	Sciurus carolinensis f	Sciurus carolinensis o	Sciurus niger f	Sciurus niger o	Equation	Source
Mass (g)		64		138		190		425		850		
Basal metabolism (cm^3 O$_2$ g^{-1} h^{-1})	82	1.00			127	1.12	133	0.92			$3.42M^{-0.25}$	Kleiber (1961)
Gestation (days)	167	40	134	37	119	35	128	44	115	45	$10.86M^{0.19}$	Kihlström (1972)
Conception-to-weaning period (days)	169	96	140	97	120	91	112	104	94	105	$19.30M^{0.26}$	McNab (1986b)
Fecundity (young female^{-1} year^{-1})	65	5.8	83	6.0	91	6.0	106	5.6	127	5.6	$27.28M^{-0.27}$	McNab (1986b)
Neonate mass (g)	91	4.1	55	5.0	62	7.5	65	16.5	33	16.0	$0.10M^{0.92}$	Blueweiss et al. (1978)
Growth rate constant (1/day)	86	0.032	57	0.017[a]	82	0.022	109	0.023	106	0.018	$0.13M^{-0.30}$	Zullinger et al. (1984)
Age of first reproduction (days)	202	330	165	330	151	330	121	330	101	330	$53.00M^{0.27}$	Blueweiss et al. (1978)
Maximal lifespan (years)	181	12	175	13	154	12	274	24	154	15	$3.54M^{0.15}$	Prothero and Jürgens (1987)

[a] Calculated from Ouellet and Ferron (1985) using the Gompertz equation in Zullinger et al. (1984).

abolic rates and low conductances for water conservation (McNab, 1986a), and G. volans. It is not clear why G. volans, which consumes principally acorns and nuts for most of the year (Harlow and Doyle, 1990), has such a low basal metabolism. This deviation may, in part, reflect the relative energetic and nutritional value of the mixed diet of G. volans in spring and summer (McNab, 1986a), which often contains a variety of other plant and animal matter (Dolan and Carter, 1977). However, diurnal tree squirrels also are more omnivorous during these seasons (Heaney, 1984) and still maintain high basal rates.

Further knowledge of the differences between G. volans and its diurnal relatives can be gained by comparing the residual variation in life-history traits of each species. Mammalian reproduction is correlated with the interaction between mass and basal metabolism (McNab, 1980), such that species with low basal metabolic rates are expected to be more reproductively conservative, or k-selected (MacArthur and Wilson, 1967) than those with high basal rates. Thus, based on its metabolic rate, one would predict that G. volans is more k-selected than its sympatric relatives. Such a prediction may be inappropriate when comparing life-history traits among sciurids of varying sizes (Armitage, 1981; Heaney, 1984), but the use of the residual variation in reproductive parameters, rather than the actual values, removes the effect of mass and permits a tentative evaluation of life-history patterns among closely-related species of different size.

In general, all of the tree squirrels in eastern North America are long-lived and have smaller young and longer gestation periods than other mammals of similar mass (Table 2). Interestingly, many life-history parameters (e.g., gestation, fecundity) are similar within this group, suggesting the presence of ecological pressures on arboreal squirrels that constrain reproduction independently of body size. Given these similarities and the potential risks of comparing life-history

tactics within phylogenies (Stearns, 1983), an analysis of the tradeoff between metabolism and reproduction among *G. volans* and other squirrels should be interpreted with caution. Nonetheless, compared to other sympatric tree squirrels, *G. volans* has a long period of maternal investment, slow rate of growth and maturity, large mass of neonates, and low annual fecundity. Again, note the relative differences in f_m between *G. volans* and *S. carolinensis* and *T. hudsonicus* (Table 2). Unfortunately, no comparable metabolic information was available for *S. niger* and *G. sabrinus*. Husband (1976) reported that the minimal daily energy requirements (per gram body mass) for *S. niger* were nearly identical to that for *S. carolinensis*, which suggests an even higher f_m for *S. niger*. One also might expect *G. sabrinus* to have a low basal metabolic rate based on its life-history traits (Table 2) and the fact that it inhabits colder climates and has a less energy-rich diet than *G. volans* (Wells-Gosling and Heaney, 1984).

It seems plausible then to interpret the differences in metabolic physiology between *G. volans* and diurnal tree squirrels as a consequence of the different microclimates encountered by these species. Because of its smaller size and nocturnal, gliding lifestyle, *G. volans* (and probably *G. sabrinus* as well) is subject to rapid heat loss and thus high energetic costs. Winter activity compounds this problem. *G. volans* is able to reduce energy expenditure by both physiological (low basal metabolism and conductance) and behavioral (aggregations in cavity nests, low foraging activity) adaptations. The need for efficient thermoregulation, however, has precluded *G. volans* from having a high basal metabolism and, perhaps, the high reproductive potential that might otherwise be permitted by its energy rich diet. The constraints on reproduction inherent with a low rate of metabolism, however, are effectively minimized by hoarding mast in autumn, which provides sufficient energy resources for both thermoregulation and reproduction (Stapp et al., 1991) during periods of unfavorable environmental conditions.

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