Effects of Helium/Oxygen and Temperature on Aerobic Metabolism in the Marsupial Sugar Glider, *Petaurus breviceps*

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Accepted 10/16/00

ABSTRACT

Helox (79% helium and 21% oxygen) has often been used for thermobiological studies, primarily because helium is thought to be metabolically inert and to produce no adverse effects other than increasing heat loss. However, these assumptions have been questioned. As basal metabolic rate (BMR) represents maintenance energy requirements for vital body functions, potential physiological effects of helox should be reflected in changes of BMR. In this study, sugar gliders were subjected to both air and helox atmospheres over a wide range of T_a's, including the thermoneutral zone (TNZ), to determine (1) whether helox has any influence other than on heat loss and (2) the maximum heat production (HP_{max}) and thermal limits of this species. Although thermal conductance in the TNZ increased in helox, BMR was similar in air and helox (0.55 ± 0.07 and 0.57 ± 0.06 mL g^{-1} h^{-1}, respectively). The TNZ in helox, however, was shifted upwards by about 3°C. Below the TNZ, sugar gliders were able to withstand an effective temperature of -24.7 ± 7.3°C with an HP_{max} of 3.14 ± 0.36 mL g^{-1} h^{-1}. The low effective temperature tolerated by sugar gliders shows that they are competent thermoregulators despite their apparent lack of functional brown fat. Similarities of BMRs in air and helox suggest that the effect of helox is restricted to an increase of heat loss, and, consequently, helox represents a useful tool for thermal physiologists. Moreover, the lack of increase of BMR in helox despite an increase in thermal conductance of sugar gliders suggests that BMR is not a function of body surface.

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Physiological and Biochemical Zoology 74(2):219–225. 2001. 1522-2152/2001/7402-0092$03.00

Introduction

For almost 50 yr, helox, a gas mixture of approximately 79% helium and 21% oxygen, has been used in thermobiological studies. Since the conductivity of helium is approximately 6.5 times that of nitrogen (Hodgman et al. 1955), animals in a helox atmosphere have an increased rate of heat flux and thermal conductance, which is about twice that of animals in air (Thomas et al. 1998). Thus animals exposed to helox react as if they are exposed to a substantially lower ambient temperature (T_a) than they really are. Utilising this property of helox, researchers have been able to elicit maximum heat production (HP_{max}) of animals without the risk of freezing injury to tissues (Rosenmann and Morrison 1974; Rosenmann et al. 1975; Smith and Dawson 1985; Dawson et al. 1986; Dawson and Olson 1988; Hallam and Dawson 1993; Chappell et al. 1995; Fournier and Thomas 1999).

While helium is widely assumed to be an inert carrier gas, there have been a number of reports that conflict with this concept (see Brice and Welch 1983). However, as almost all measurements using helox have been conducted at the low end of the thermal range of animals to quantify HP_{max}, possible metabolic side effects were difficult to distinguish from the general thermogenic response. Given that basal metabolic rates (BMR) represent the total maintenance requirements for all physiological processes (Hainsworth 1981), potential side effects of helox on aerobic metabolism should become obvious when BMR is determined in a helox atmosphere. However, to our knowledge, effects of helox on BMR and the thermoneutral zone (TNZ) have not been investigated in detail. Such measurements should also be useful in addressing the question of whether the allometric relationship between BMR and body mass is affected by an animal's surface area (Schmidt-Nielsen 1984) because heat loss and surface area are related (Dawson and Hulbert 1970; Bradley and Deavers 1980). If surface area and BMR were related, BMR in the helox atmosphere should increase with thermal conductance.

The experimental animal for our study was the sugar glider, *Petaurus breviceps*, a small marsupial (120–160 g; Suckling 1995). This species forages among trees at night, when T_a is low, with the aid of a gliding membrane, and it is likely that heat loss is substantial (Geiser and Stapp 2001). Sugar gliders have a wide distribution along the east coast of Australia, including cool-temperate regions. Nevertheless, although sugar gliders are known to be regularly confronted with energetic and thermal challenges in the wild (Körtner and Geiser 2000) and

have a surface area that is well above that predicted for their size (Dawson and Hulbert 1970), little is known about their thermoregulatory performance when exposed to thermal extremes.

The aims of our study were twofold: first, to investigate whether helox affects the BMR and TNZ of sugar gliders and second, providing that helox has no effect on BMR, to determine the thermogenic capacity of the gliders and the effective minimum temperature that they can tolerate.

Material and Methods

Sugar gliders were captured in the New England Tablelands region of New South Wales near Armidale, Australia, and maintained in outdoor aviaries under natural photoperiod and temperature conditions at the University of New England. Excess food and water were provided daily. Food consisted of a mixture of high protein cereal, honey, and water, which was occasionally supplemented with vitamins (Pentavite infant vitamins). Fresh apple and carrot were given every second day, while mealworms (*Tenebrio* larvae) were also provided occasionally.

Resting metabolic rates (RMR) of 10 sugar gliders were measured as rate of oxygen consumption ($\dot{V}O_2$) using open-flow respirometry during spring (September–November). Animals were placed individually into 3-L respirometry chambers within a temperature-controlled cabinet (± 0.5°C). Flow rates of dried air, 40–50 L h^{-1}, were controlled with rotameters and measured with mass flowmeters (Omega, FMA 5606, Stamford, Conn.). With these flow rates and the size of the chambers, the system was in 99% equilibrium after about 17–20 min. Oxygen content of the dried expired air was measured with a single-channel oxygen analyser (Ametek Applied Electrochemistry, S-3A/I, Pittsburgh) fitted with a high-resolution output board. Solenoid valves switched channels in 3-min intervals. This permitted the measurement of up to three animals and a reference (outside air) in succession, with each channel measured once every 12 min when all chambers were occupied.

Presentation of T_a's to the gliders was dependent on whether heating or cooling experiments were performed. Animals were placed in the respirometry chambers late in the afternoon (between 1600 and 1700 hours), at T_a's between 10° and 25°C, and allowed to settle overnight. The following morning, during the gliders' inactive phase, T_a was either raised or lowered to the desired T_a, and RMR was determined. T_a was then raised or lowered in 2°–5°C steps, and the process was repeated. A maximum of four T_a measurements (usually two or three) were taken during 1 d. Animals were in the chambers for a maximum of 23 h. For the extreme hot and cold T_a, RMRs were measured in the morning, and the gliders were removed by midday. Food and water were not available to the gliders during the measurements. At least 5 d was allowed for gliders to recover between measurements. The whole process was repeated for each animal over the T_a range 0°–39°C, or to that T_a where the animal became hypothermic.

At each T_a, RMR was first measured in air. Air was then replaced with helox, and time was allowed (at least 30 min) for the chamber to equilibrate before determination of RMR in helox using corrected flow rates. Air was then pumped through the system while the T_a was changed. The gliders were weighed before and after each testing period, and a constant rate of mass loss was assumed for calculation of mass-specific RMRs.

RMRs were calculated from the mean of at least three consecutive lowest diurnal $\dot{V}O_2$ values (i.e., over at least 30 min) in normothermic, resting individuals at each T_a. BMRs were determined as the minimum RMR within the range of T_a measured.

Body temperatures (T_b) were measured simultaneously with RMR using temperature-sensitive transmitters (single-stage FM, model EPX76, Sirtrack). These transmitters were calibrated to the nearest 0.1°C against a precision mercury thermometer in a water bath. The wax-coated transmitters weighed 2.5–4.5 g (battery life approximately 9 mo) and were implanted intraperitoneally under isoflurane anaesthesia at least 2 wk before measurements. Transmitter signals were received using a VHF/UHF scanning receiver (Yaesu, FRG-9600). T_a was measured to the nearest 0.1°C with a calibrated thermocouple inserted 1 cm into the respirometry chamber. Thermocouple output was amplified by a digital thermometer (Omega, DP116).

The analog outputs from the mass flowmeter, oxygen analyser, scanning receiver, and digital thermometer were interfaced to a personal computer. Data acquisition and processing were performed with software written by G. Körtner, B. Lovegrove, and T. Ruf. Rates of $\dot{V}O_2$ were calculated using STPD volumes and equation (3a) of Withers (1977). Apparent thermal conductance was calculated using the equation

$$\text{conductance} = \frac{\text{metabolic rate}}{(T_b - T_a)}.$$

HP_{max} in helox was defined as the point where RMR and/or T_b could be maintained for at least 1 h and was just above the T_a where hypothermia, as demonstrated by either a falling RMR or T_b, was induced. Because the effective temperature at which HP_{max} occurred in helox could not be ascertained directly, it was derived by extrapolating the regression line for an individual's RMR in air to the intercept with its HP_{max} (see Fig. 1). The factorial metabolic scope of this species was determined by dividing HP_{max} by BMR (Dawson and Dawson 1982).

All numerical values are expressed as mean ± SD of the number of individuals (N) measured. Sample variances were tested for homogeneity using an F_{max}-test (Zar 1984). Paired observations underwent paired t-tests (Zar 1984). After standardised residuals were plotted to ensure homoscedasticity, lines were fitted using least squares regression analysis (Zar

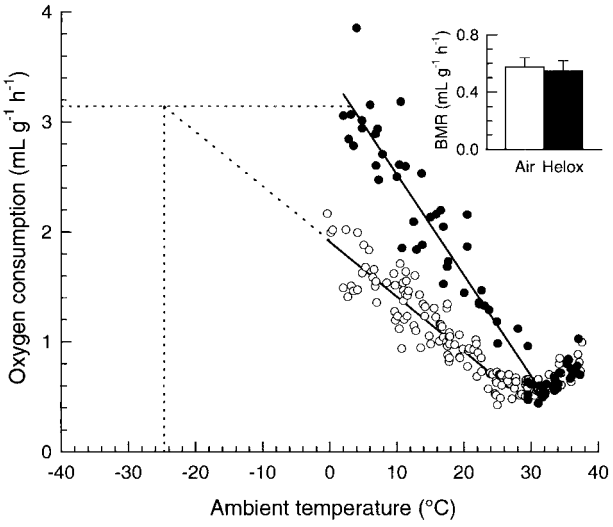

Figure 1. Resting metabolic rates (RMR) over entire range of ambient temperatures measured for *Petaurus breviceps* in air (*open circles*) and helox (*filled circles*). Mean maximum metabolic rate (HP_{max}; *horizontal dashed line*) was substituted into the regression line for RMR in air to determine the effective temperature (*vertical dashed line*) the gliders can tolerate. *Inset graph*, mean basal metabolic rates (*BMR*) in air and helox. These did not differ significantly, and the overall mean BMR was 0.56 ± 0.06 mL g^{-1} h^{-1}.

1984). Values at a given T_a ± 1.0°C are for different individuals, with the same individuals repeated at different T_a's. Slopes and elevations were compared using ANCOVA (Zar 1984). The lower and upper critical temperatures (T_{lc} and T_{uc}, respectively) at which RMR showed a significant increase were determined by calculating a regression equation for the increasing values for each individual and determining the intercept with the mean BMR for that individual. The critical T_a at which T_b began to increase was determined as the intercept of the regression for the increase in T_b at high T_a and the mean T_b below T_a of 25°C of individuals. Differences were considered significant at $P < 0.05$.

Results

Sugar gliders in air and helox displayed qualitatively similar thermoregulatory patterns. However, several quantitative differences were observed.

Metabolic Rates

The response of RMRs to changes in T_a of sugar gliders exposed to helox was very similar to that of the same individuals in air. The TNZ was bounded on both sides by rising RMRs (Fig. 1). However, in the helox atmosphere, the TNZ was shifted upwards by 3°–4°C (air: 26.9° ± 1.4° to 30.8° ± 1.2°C; helox: 31.0° ± 1.0° to 33.0° ± 1.7°C). The thermal range of the TNZ did not differ significantly between the two atmospheres.

Within the respective TNZs, BMRs of gliders in the two atmospheres were almost identical (air: 0.57 ± 0.06 mL g^{-1} h^{-1}, body mass = 129.9 ± 15.0 g, $N = 10$; helox: 0.55 ± 0.07 mL g^{-1} h^{-1}, body mass = 130.5 ± 15.4 g, $N = 10$; Fig. 1). The total BMR were 74.36 ± 10.15 mL h^{-1} and 70.78 ± 8.39 mL h^{-1} in air and helox, respectively. The overall mean BMR was 0.56 ± 0.06 mL g^{-1} h^{-1} (total BMR: 72.57 ± 8.27 mL h^{-1}, body mass = 130.2 ± 15.1 g, $N = 10$). Above the TNZs, the RMRs of gliders in air and helox were also similar and in both atmospheres increased curvilinearly with T_a ($y = 0.002x^2 - 0.10x + 1.61$, $P < 0.001$, $r^2 = 0.55$; Fig. 1).

Below the TNZs, RMRs of sugar gliders in both atmospheres displayed a linear increase with decreasing T_a (air: $y = 1.91 - 0.05x$, $P < 0.001$, $r^2 = 0.83$; helox: $y = 3.43 - 0.09x$, $P < 0.001$, $r^2 = 0.89$). However, the RMRs of sugar gliders in helox were approximately 1.8 times higher than in air, with the slope for the linear regression for RMR versus T_a in helox significantly steeper than air ($P < 0.001$; Fig. 1).

The mean HP_{max} for the sugar glider was 3.14 ± 0.36 mL g^{-1} h^{-1}, $N = 6$ (Fig. 1), and, consequently, the mean factorial metabolic scope was 5.45 ± 0.32. With this HP_{max}, sugar gliders were able to withstand an effective minimum temperature of −24.7° ± 7.3°C (Fig. 1).

Thermal Conductance

In both atmospheres, thermal conductance was a curvilinear function of T_a. The point where conductance began to rise markedly was near the TNZ for both atmospheres (Fig. 2).

Within the TNZs, the thermal conductance of sugar gliders in the helox atmosphere was 22% greater (0.11 ± 0.01 mL g^{-1} h^{-1} $°C^{-1}$, $N = 4$) than in air (0.09 ± 0.01 mL g^{-1} h^{-1} $°C^{-1}$, $N = 4$; $P < 0.05$). At T_a's below the TNZs, thermal conductance of gliders in helox was, like RMR, approximately 1.8 times higher than in air ($P < 0.001$; Fig. 2). Above 31°C, however, no difference in conductance between gliders in the two atmospheres was apparent.

Body Temperature

Within the TNZs, the mean T_b's of gliders in air, 36.3° ± 0.5°C ($N = 4$), and helox, 36.8° ± 0.5°C ($N = 4$), did not differ. However, as the TNZ in helox occurred at a higher T_a, the differential between T_b and T_a was nearly 2°C higher for animals in air (air: 6.8° ± 0.4°C, helox: 4.9° ± 0.5°C; $P < 0.01$).

Below the TNZs, T_b and T_a in both atmospheres were not related (Fig. 3). Although only differing by 0.7°C, mean T_b of gliders in air below the critical T_a at which T_b began to show a significant increase, 35.0° ± 0.1°C ($N = 4$), was significantly lower than when in helox, 35.7° ± 0.3°C ($N = 4$; $P = 0.018$).

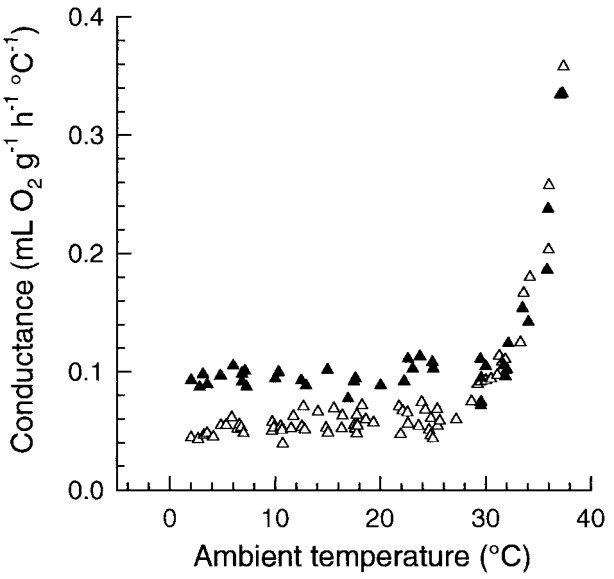

Figure 2. Thermal conductance for *Petaurus breviceps* in air (*open triangles*) and helox (*filled triangles*) over the entire range of ambient temperatures (T_a) measured. Thermal conductance of animals in helox was significantly higher ($P < 0.001$) than those in air only at T_a's below 30°C.

Further, the critical T_a at which T_b started to increase occurred at a significantly higher T_a in helox (29.9° ± 0.3°C, $N = 4$) compared to air (27.1° ± 1.0°C, $N = 4$; $P = 0.015$; Fig. 3). Above these T_a's, T_b's increased linearly in both atmospheres (air: $y = 23.7 + 0.42x$, $P < 0.001$, $r^2 = 0.91$; helox: $y = 18.7 + 0.57x$, $P < 0.001$, $r^2 = 0.92$). However, T_b's rose at a steeper rate when the gliders were in the helox atmosphere ($P < 0.001$; Fig. 3).

Discussion

Our study shows that *Petaurus breviceps* are competent thermoregulators and are able to withstand a range of effective temperatures from about –25° to at least 39°C. Sugar gliders responded to helox gas in a manner akin to that of animals in air, with RMR, T_b, and thermal conductance all showing a similar qualitative pattern in the two atmospheres. However, significant quantitative physiological differences were observed, especially below the TNZs. Interestingly, the BMR of sugar gliders was not affected by helox, although thermal conductance increased within the TNZ, suggesting that there is no side effect on aerobic metabolism.

Common uses for helox gas include the prevention of nitrogen narcosis in divers (Baddeley and Flemming 1967), increasing aerosol delivery of medication in nebulizers (Weber et al. 1994), induction of hypothermia (Werner 1992; Osborne and Milsom 1993), elicitation of maximum metabolic rates without the risk of tissue injury (Rosenmann and Morrison 1974; Hinds et al. 1993; Fournier and Thomas 1999), and investigations into various aspects of torpor (Osborne and Milsom 1993; Geiser et al. 1996). Therefore, it is an important requirement that helox does not have any physiological side effects. The data presented here suggest that the only physiological variable that was altered during helox exposure was heat

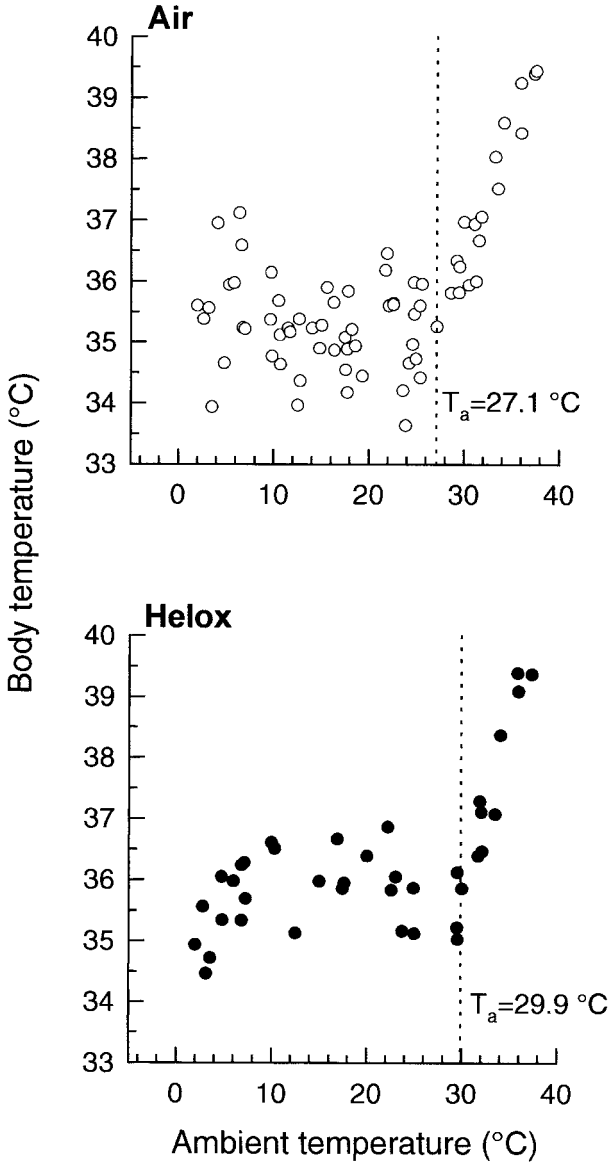

Figure 3. Body temperatures (T_b) of *Petaurus breviceps* in air (*open circles*) and helox (*filled circles*) over the entire range of ambient temperatures (T_a) measured. The dashed line indicates the critical T_a at which T_b started to rise in response to increasing T_a. The critical T_a for animals in helox was significantly higher than in air ($P < 0.05$).

loss, primarily via increased heat transfer through the surface insulation layer. Thus it appears that helox is indeed suitable for use in thermobiological and other studies.

The HP_{max} for the sugar glider, determined here over 1 h, was about 20% lower than the HP_{max} determined over 5 min by Hinds et al. (1993) and thus represents summit rather than peak metabolism (Dawson and Dawson 1982). Since the BMR measured by Hinds et al. (1993) was also somewhat higher than that measured here, the factorial metabolic scope was similar. The factorial metabolic scope of 5.5 determined in our study was at the lower end of that measured for other marsupials (metabolic scope: 5–13; Dawson and Dawson 1982; Smith and Dawson 1985; Dawson et al. 1986; Dawson and Olson 1988; Hinds et al. 1993). However, unlike those in previous studies, our values were for fasted animals. Since digestion may increase resting metabolism by as much as 30% (Hill 1976), it is possible that the HP_{max} values obtained here are underestimates.

Nevertheless, sugar gliders were able to withstand effective temperatures as low as −25°C. As the lowest recorded T_a in Armidale (New England Tablelands) is approximately −11°C, sugar gliders appear well able to cope with the cold T_a's experienced in this region. This cold limit also allows them a certain amount of latitude to withstand the effects of wind and rain, which can substantially reduce the effective temperature. Moreover, a good thermogenic capacity may be important during gliding episodes when heat loss is likely to be substantial. An estimate of the maximum temperature differential tolerable by an animal can be derived from dividing HP_{max} by the minimum conductance (Rosenmann and Morrison 1974). According to this calculation, sugar gliders should be able to tolerate a T_a range of 62.2°C, which is slightly under the range of effective temperatures (64°C) measured here.

Helox induced several predictable physiological changes. The upward shift of the TNZ in helox atmosphere and concomitant shift of critical T_a for T_b and thermal conductance were to be expected since the qualitative response to T_a of conductance was not changed. Therefore, to counteract the higher rate of heat loss of gliders in helox, metabolic rate had to increase at a higher T_a if the animal was to maintain a stable T_b. Further, the higher rate of heat loss also permitted the commencement of active cooling to be shifted to a higher T_a. Consequently, both the T_{lc} and T_{uc}, and thus the TNZ, are shifted to a higher T_a.

At T_a's below thermoneutrality, an increase in conductance at a given temperature must result in a proportional increase in metabolic rate (Herreid and Kessel 1967; Dawson and Olson 1988; Hallam and Dawson 1993; this study). Moreover, as the slopes (i.e., a measure of thermal conductance) of the regression lines of RMR versus T_a below the TNZ differ between air and helox, the differential between RMR in air and helox increases with a decreasing T_a (Rosenmann and Morrison 1974). These metabolic responses are due to the greater heat loss in the more conductive helox medium, which is equivalent to exposure to T_a's 20°–30°C lower than that actually measured. Consequently, helox elicits maximum metabolic rates at relatively high T_a's with a substantially reduced risk of freezing injury to the animals (Rosenmann and Morrison 1974; Rosenmann et al. 1975; Dawson et al. 1986; Dawson and Olson 1988; Hallam and Dawson 1993; Chappell et al. 1995; this study).

Since RMR was increased under helox gas in order to defend normothermic T_b, it was perhaps unexpected to find that mean T_b below the TNZ was also slightly higher in helox compared to air. However, two possible interpretations may explain this observation. First, the animals may have metabolically overcompensated for the substantial increase in conductance. Therefore, more heat was being produced than lost, and T_b increased. Second, it has been suggested that T_b may have a sigmoidal response to declining T_a (Lovegrove et al. 1991). From high T_a's, T_b decreases to the TNZ then slightly increases as T_a lowers below the TNZ before again declining towards hypothermia at very low T_a's (Lovegrove et al. 1991). Consequently, the higher mean T_b in helox may have been due to the sampling at effectively lower T_a's than in air. However, this response often becomes evident only when animals are measured over a wide range of T_a's encompassing their upper and lower thermal limits.

In contrast to T_a's below the TNZ, helox gas appeared to have little influence on either thermal conductance or metabolism of sugar gliders at T_a's above the TNZ. It should be pointed out, however, that in our study total heat flux was measured, that is, conduction, convection, and evaporative cooling. Therefore, the response above the TNZ was probably due to the greater contribution of evaporative cooling used at high T_a's. Sugar gliders, when exposed to high T_a's (above 34°C) initially spread saliva over their forelimbs (Robinson and Morrison 1957). As T_b's continue to increase, salivation extends to cover the hind limbs, abdomen, scrotal region, and underside of the tail and may be used in combination with vasodilation and open-mouthed panting (Robinson and Morrison 1957; Fleming 1980; this study). Consequently, since evaporative cooling is not affected by the helox atmosphere (Rosenmann and Morrison 1974), the predominance of evaporative cooling over thermal conductance by sugar gliders as a method to remove heat at T_a's above the TNZ means that in this thermal range helox causes only a little effect on aerobic metabolism.

The lack of difference in BMRs of *P. breviceps* in air and helox atmospheres is not only important for verification of the use of helox in studies of thermal physiology but also has implications regarding the allometric relationship between BMR and body mass. Because the exponent for BMR versus mass is similar to that of volume versus surface area (Schmidt-Nielsen 1984), it has been proposed that surface area may explain the allometric relationship of BMR with body mass (Rubner 1883; Heusner 1991). This interpretation appears plausible since thermal conductance is a negative function of surface area (Bradley and Deavers 1980). Our findings do not support this

interpretation. If surface area and thermal conductance were responsible for BMR, exposure of animals to helox should result in a change in BMR, which it did not. Thus our study does not support the notion that body surface area and BMR are related, and, consequently, alternative explanations are required to explain the allometric relationship between BMR and body mass.

Acknowledgments

This work was supported by a University of New England Zoology Department Postgraduate Internal Research Grant to J.C.H. and by a grant from the Australian Research Council to F.G.

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