J Comp Physiol B (1984) 154:105–111

Journal of Comparative Physiology B Biochemical, Systemic, and Environmental Physiology

Implications of the large surface area to body mass ratio on the heat balance of the greater glider (*Petauroides volans:* Marsupialia)

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Accepted May 9, 1983

Summary. 1. In a study of thermoregulation in the greater glider, a small arboreal marsupial with large gliding membranes, metabolic rate (MR), skin and deep body temperature (T_{sk}, T_b), and respiratory and total evaporative heat loss (E_{ex}, E_{tot}) were measured in relation to ambient temperature (T_a).

2. Although the surface area is twice that of marsupials of similar body weight, MR was not significantly different from the average marsupial metabolic rate. This must be attributed to an excellent thermal insulation and behavioural factors.

3. At T_a above the thermoneutral point, at 20 °C, the greater glider became hyperthermic. T_b increased from 35.4 °C at 20 °C T_a to 39.1 °C at 40 °C. At 30 °C, 55% of MR was dissipated by evaporation. This proportion increased to 105% at 35 °C and 132% of MR at 40 °C. The increase in E_{tot} was accompanied by intense licking of extremities and the ventral body surface. E_{ex} dissipated only 12% of MR at 40 °C irrespective of an 8-fold increase in respiratory frequency from a basal value of 18 breaths · min^{-1}.

4. It is concluded that the greater glider can utilize its gliding membranes to reduce heat losses by increasing the insulative layer around the body surface. At high T_a, a clear contrast between the inefficient use of water for evaporative thermolytic processes, mainly salivation, and the limited availability of water in its arboreal habitat becomes evident.

Introduction

The greater glider (*Petauroides volans*) is a small arboreal marsupial living in the dense eucalypt forests of the east coast of Australia, from the subtropical climate of Victoria to the tropical areas of North Queensland. Like other members of the family *Petauridae* they are strictly nocturnal and do not emerge from their sleeping sites in hollow branches of large eucalypt trees before sunset. Their feeding habits are very similar to those of the koala (*Phascolarctos cinereus*) who feed almost exclusively on the foliage of a few species of eucalypt.

Large gliding membranes enable the greater glider to move from tree to tree with minimal climbing. Although a distinct advantage in an arboreal habitat, these gliding membranes may result in considerable heat loss in a cold environment. Brown and Lasiewsky (1972) found the metabolic rate of cold stressed weasels with their high surface area to body mass ratio to be 50 to 100% higher than that of normally shaped mammals of similar body weight. Energetic efficiency, however, is more likely to be sacrificed in small carnivores for it can easily be compensated by improved predatory ability. Small herbivores, especially those depending on microbial fermentation processes as an important source of energy may easily be confronted with the problem of limited energy intake, which clearly requires adaptational cold defence strategies. The sugar glider (*Petaurus breviceps*), a smaller member of the same family, enters torpor to overcome periods of restricted food intake and low ambient temperature (Fleming 1980). This has never been observed in the greater glider.

Although well armed for the defence against cold, the heavily furred greater glider may be in a potentially dangerous compromise under conditions requiring the dissipation of heat during exposure to high ambient temperatures or during exercise. On the other hand, the large surface area may provide a selective advantage as a heat sink, comparable to the wings of bats which were found not only to increase thermal insulation of the body

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shell, but are also used for cooling during exposure to heat (Bartholomew et al. 1964). Wing temperature can be as low as 5 °C at low ambient temperatures but close to T_b at high T_a. A direct comparison between the bat wing and the gliding membranes of the greater glider may prove difficult due to the dense fur on the upper side of the gliding membranes which may inhibit effective nonevaporative heat loss. However, the inner sides of these membranes clearly show a lower density of hair which lead us to the assumption that these areas may be involved in the control of body temperature by behavioral and autonomic mechanisms. The present work therefore was undertaken to study the heat balance and the methods of heat conservation and dissipation used by the greater glider in the ambient temperature range of 5 to 40 °C.

Materials and methods

Animals. Two male and three female greater gliders weighing between 985 and 1,250 g (mean 1,141 g) were used. The animals were caught during a logging operation in Nowendoc State Forest, 100 km south east of Armidale, N.S.W., and kept initially in an open outdoor enclosure. The animals were captured and held under the provisions of Licence No. SIF 52 from the National Parks and Wildlife Service and permit No. 079 from the Forestry Commission of New South Wales. Some weeks before the experiments were started the animals were housed individually in wire cages of $30 \times 60 \times 60$ cm in a temperature-controlled room. Each cage contained a wooden sleeping box ($15 \times 15 \times 20$ cm). Mean room temperature was 22 ± 3 °C, relative humidity ranged between 38 and 53% and lighting followed the natural cycle. The animals were fed once per day, between 15.00 and 18.00 h. The diet consisted of eucalypt leaves (*Eucalyptus radiata*) which were collected once per week and stored in plastic bags in a cold room until used. Water was always available ad libitum.

Surface area. The body surface of three greater gliders killed for other purposes was measured by slightly stretching the skin and plotting the outlines on graph paper. The surface areas were 2,664, 2,895 and 2,910 cm^2 for animals weighing 1,100, 1,230 and 1,140 g, respectively. The gliding membranes thereby accounted for 41, 49 and 46% of the total surface area, the ears for 2%.

Oxygen consumption. Measurements of oxygen consumption were made between 08.00 and 18.00 h during the resting period of the animals. The animals were fed the evening before the experiments and thus were not postabsorptive. The long retention time of food in the gut together with the fact that caecum volatile fatty acid production rates are constant throughout a 24 h cycle (Foley 1983) makes it unlikely that the animals will become postabsorptive within the usual 24 h. Attempts to fast the animals for longer periods, however, caused the animals to collapse presumably because these animals have no long term energy stores which is confirmed by the low level of liver glycogen and whole body fat (Dash and Hume, unpublished). O_2 consumption was measured in an open flow system, using a polystyrene-insulated glass chamber with a volume of 31 l. Temperature inside the chamber was maintained by perfusing water of constant temperature through two copper coils with a large surface area, fitted on both inner sides of the chamber. The air in the chamber was circulated by means of a small fan. Temperature inside the chamber was measured with mercury thermometers at two different sites at a distance of 1 and 2 cm from the chamber wall. Humidity of the chamber air was measured with a wet bulb thermometer. All temperatures were measured to the nearest 0.1 °C. Air flow through the system was maintained between 2.5 and 3.7 $l \cdot min^{-1}$ using a membrane pump. The flow rate was measured using a calibrated wet gas meter. At chamber temperatures exceeding 30 °C a part or all of the inflowing air was dried over silica gel. The water vapour pressure gradient between body surface and chamber air which determines the evaporative heat transfer coefficient thus could be maintained at a level of 31.3 ± 5.1 mmHg between 5 and 35 °C and at 22.0 ± 2.7 mmHg at T_a's above 35 °C, respectively. Part of the air leaving the chamber was dried over Drierite, and the flow rate was held constant using a flowmeter and a needle valve. After CO_2 absorption, O_2 concentration in this sample was measured with an E2 Beckman oxygen analyser. No readings were taken until steady state conditions were clearly reached, which usually occurred within 2 to 3 h. After that, measurements were taken at 5 min intervals. Total heat production was calculated according to McLean (1972), using a caloric equivalent of 20.46 $J \cdot ml\ O_2^{-1}$.

Deep body temperature (T_b) and skin temperature (T_{sk}). Body temperature was measured using small radio transmitters ($0.8 \times 1.2 \times 0.5$ cm, weight 7 g) designed according to Mackay (1963). They were calibrated in a water bath to the nearest 0.1 °C. The clicking rate of these transmitters was received by a commercial AM radio and the time for 100 clicks was measured with a stop watch. Plans to implant the transmitters into the peritoneal cavity were abandoned after two other animals implanted with transmitters died after four and six days. Cause of death was not clear, but may have been due to toxic effects of the antibiotics used postoperatively. In the experiments transmitters were placed in the pouch of the three female animals, where they remained for at least one day and apparently caused no discomfort. This method for the estimation of T_b was validated by measuring rectal and pouch temperatures simultaneously over the temperature range of 8 to 30 °C using copper-constantan thermocouples inserted 5 cm into the rectum and into the pouch of three animals. Temperatures were recorded with a recording potentiometer. Rectal and pouch temperatures were similar at and above 20 °C. Pouch temperatures were 0.4 °C below rectal temperature at 8 °C, however, only when the animals moved. In sleeping animals in the typical curled position the difference between pouch and rectum decreased to less than 0.2 °C. Skin temperatures in the respiration chamber experiments were also measured with transmitters attached to the skin with medical silicone.

In an additional series of experiments the effect of ambient temperature on T_b and T_{sk} was measured simultaneously in a climatic room after the animals had been adapted to the temperature for 2 to 3 h. T_{sk} was measured with thermocouples at midside trunk, upper and lower side of the gliding membranes and the ears. The thermocouples were glued to the skin with plastic glue (Tarzan's Grip).

Respiration parameters were measured using the barometric method described by Drorbaugh and Fenn (1955). The pressure inside the chamber was recorded with a Sanborn differential gas pressure transducer (Mod. 270) and a Sanborn carrier preamplifier Mod. 350, 1100B. One end of the transducer was connected to the chamber, and the other end to a reference chamber with a volume of about 20 l, which was part of the

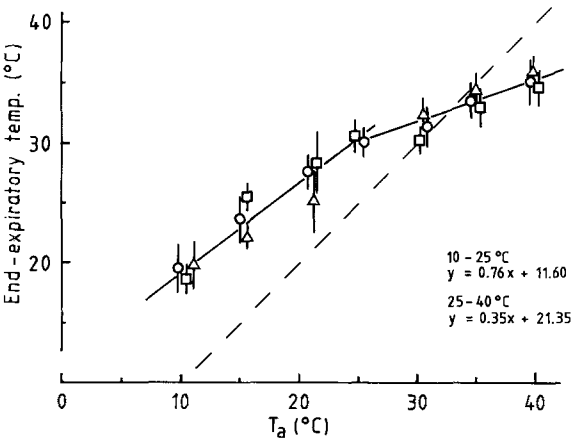

Fig. 1. End expiratory nasal temperatures in three individuals at different ambient temperatures. Each point represents the mean ± SD of 4 to 9 measurements

respiration chamber and maintained at the same temperature as the respiration chamber itself. A narrow hypodermic needle between the two chambers allowed the equilibration of pressure differences with a long time constant caused by small temperature changes which otherwise could cause a steadily drifting baseline. Tidal volumes (V_T) were calculated from the formula given by Drorbaugh and Fenn (1955):

$$V_T = P_t/P_k \times V_k \times T_b(P_B - P_C)/(T_b(P_B - P_C) - T_a(P_B P_b))$$

where P_k and P_t are the pressure deflections in mm caused by the injection of a measured volume (V_k) of air and due to respiration, respectively. T_b and T_a are deep body temperature and chamber temperature, P_B is the barometric pressure, P_C the water vapor pressure inside the chamber, and P_b the saturation water vapor pressure at body temperature. Based on the theoretical considerations of Epstein and Epstein (1978) that only the transition from alveolar to nasal conditions is fast enough to contribute to the phasic pressure changes we have used the formula of Jacky (1980) to retrospectively correct the V_T-values for changes in the ratio of respiratory to total breath duration, and for the temperature of expired air (T_N). T_N was measured in unrestrained animals with a fast responding thermistor (1 kΩ, 0.2 mm diameter) sealed at the tip of a thin flexible wire which was used to position the thermistor about 2 mm inside the nostril of the animal. The signal was processed in a Devices thermistor preamplifier (3553) and recorded over periods of 15 to 45 s on a Devices recorder (M 19) with a frequency response of >100 Hz. Readings were taken as soon as end-expiratory air temperatures reached similar level which indicated the proper position of the thermistor in the air stream. Defense movements of the animals occurred often but could be reduced by bringing the extremely thin thermistor leads in contact with the nasal wall which supported the thermistor and helped to avoid the tickling movements. T_N plotted as a function of T_a is shown in Fig. 1. The saturation water vapour pressures P_b, P_C and P_N which refer to T_b, T_a and T_N were calculated from the expression: $\log P_{H_2O} = 0.7109 + 0.02657 \times T$. Minute volume ($V_E$) was calculated as $V_T \times$ respiratory frequency (f).

Respiratory evaporative heat loss (E_{ex}) was calculated from the formula: $E_{ex} = V_E(P_{ex} - \varnothing_a P_{in})\lambda$, where P_{in} is the saturated density of inhaled air at ambient temperature, $\varnothing_a$ is the percent relative humidity divided by 100 and λ is the latent heat of vaporization of water (Gagge et al. 1969). In modification of the original formula, P_{ex} is the saturated density of exhaled air at the end-expiratory temperature (T_N).

E_{tot} was measured in a climatic chamber by weighing the animals to the nearest 0.1 g over one hour periods after an adaptation of 1 to 2 h. The experiment was terminated when the animals lost faeces or urine. Regression lines were calculated using the method of least squares, and values are given as mean ± standard deviation (SD). Significance of difference between means was estimated using Student's t-test.

Results

Deep body (T_b) and skin (T_{sk}) temperature

Figure 2 shows the pattern of T_b and T_{sk} measured at the upper side of the gliding membranes, over an ambient temperature range of 5 to 40 °C. T_b was relatively constant between 5 and 20 °C T_a, the mean being 35.4 ± 0.4 °C (n=22). Mean T_{sk} in this range varied considerably, increasing from 29.1 ± 3.9 °C at T_a=5 °C (n=4) to 32.1 ± 2.2 °C (n=7) at T_a=20 °C. Due to the large standard deviations the difference is not statistically significant. There was no difference in T_{sk} between the different sites of measurement on the dorsal side of the gliding membranes and the trunk skin. Above 22 °C there was a linear increase in T_b with T_a, and the maximum T_b reached after a 3-h exposure to a T_a of 40 °C was 39.1 ± 0.4 °C (n=8).

Above a T_a of 22 °C, T_{sk} approximated T_b, and both temperatures were nearly identical at T_a > 35 °C. The relatively large standard deviation in T_{sk} below 20 °C T_a coincided with the behaviour of the animals which showed a curled posture, the long furred tail wound around the body. The temperature recording then highly depended on the position of the thermocouple. At a T_a above 35 °C the animals became restless. They mostly sat upright and exposed the sparsely furred ventral sides of their gliding membranes to the air. At T_b > 38 °C this behaviour was associated with intense licking of hindlimbs, forelimbs and face, which soon became visibly wet.

Simultaneous recordings of T_b, and skin temperatures at different sites of the body surface showed relatively small variations in the temperatures on the dorsal and ventral sides of the gliding membranes (Fig. 3), larger variations being mostly caused by changes in the position of the animals. The ear temperature showed spontaneous oscillation at T_a=20 °C and to a minor degree at 15 and 25 °C. Whenever the animals became active, at 20 or 25 °C, T_{sk} increased almost immediately and nearly reached T_b. At and above T_a=25 °C, T_b began to rise at a rate of 0.3 °C · h^{-1} at 25 °C, 0.6 °C · h^{-1} at 30 °C, and 1.3 °C · h^{-1} at 35 °C. A significant increase in respiratory frequency (f),

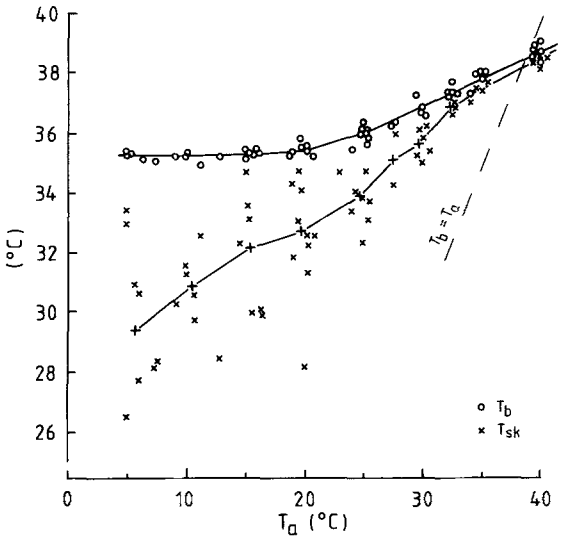

Fig. 2. Relation of deep body and skin temperature to ambient temperature in five individual greater gliders

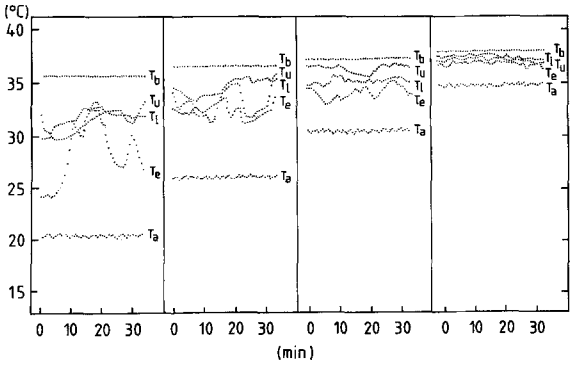

Fig. 3. Continuous recordings of T_a, T_b and T_{sk}, measured at the dorsal (T_u) and ventral side of the gliding membranes (T_l) and the ear (T_e)

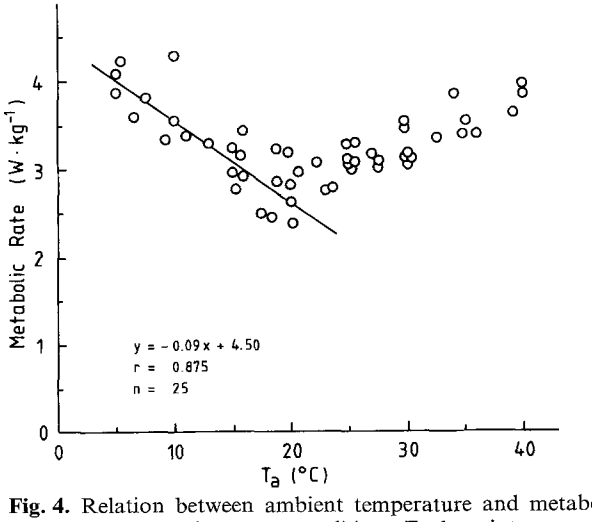

Fig. 4. Relation between ambient temperature and metabolic rate measured in four greater gliders. Each point represents the mean of one experiment

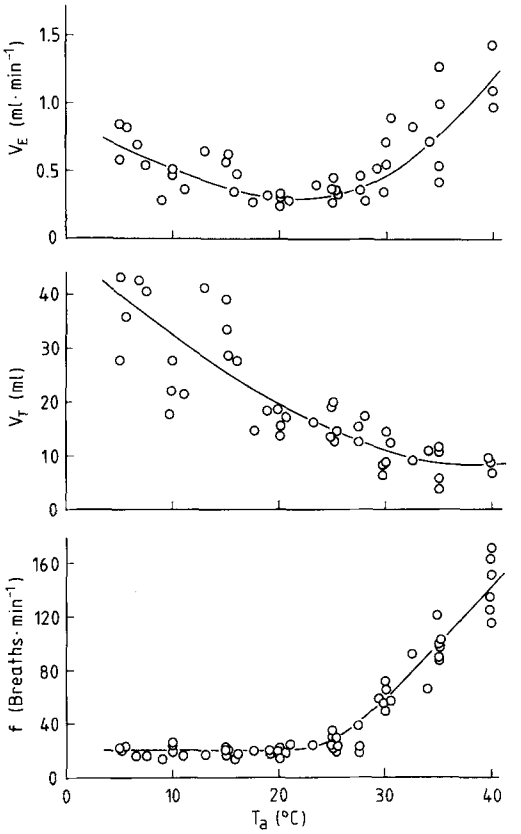

Fig. 5. Respiratory frequency (f), tidal volume (V_T) and minute volume (V_E) plotted against ambient temperature. All lines were fitted by eye

however, was not noted until T_b reached about 37 °C.

Metabolic rate

The metabolic rate (MR) decreased linearly with increasing T_a up to a temperature of 20 °C (Fig. 4). The regression line fitted to the values between 5 °C and 20 °C was $y = -0.09X + 4.50$ ($r = 0.875$, $n = 25$). The intercept with the X-axis, when the metabolic rate was zero, was 51 °C. At 20 °C, the thermoneutral point, the minimum metabolic rate was 2.81 ± 0.33 W · kg^{-1} ($n = 9$) or 2.90 ± 0.33 W · kg$^{-0.75}$, when expressed in terms of metabolic body weight. Above thermoneutrality, MR increased linearly with T_a. The whole body Q_{10}, calculated from the Arrhenius plot was found to be 2.3 ($r = 0.885$, $n = 26$).

Respiration and evaporative heat loss

Respiratory frequency, V_T and V_E are plotted in Fig. 5 as a function of T_a. The respiratory frequency was constant between 5 and 22 °C and

Table 1. Metabolic heat production (MR), respiratory (E_{ex}) and total evaporative heat loss (E_{tot}) in the greater glider at ambient temperatures above 30 °C. * $p<0.05$, ** $p<0.01$, *** $p<0.005$

	Ambient temperature		
	30 °C	35 °C	40 °C
T_b (°C)	36.9 ±0.3***	37.7 ±0.3**	39.1 ±0.4
ΔT (°C)	6.9	2.7	− 0.9
MR (W kg^{-1})	3.18±0.16	3.55±0.21*	3.80±0.12
E_{ex} (W kg^{-1})	0.22±0.07	0.17±0.05**	0.62±0.06
E_{tot} (W kg^{-1})	1.74±0.16***	3.72±0.34**	5.03±0.69
$E_{tot/M}$ (%)	55	105	132

showed a linear increase above 25 °C. V_T was highest at 5 °C (37.9±6.5 ml) and reached a minimum of 7.6±2.5 ml at $T_a>35$ °C ($P<0.001$). Corresponding to the rise in V_T below 20 °C, V_E also increased. Above 20 °C V_E increased from 0.30±0.05 l·min^{-1} up to 1.06±0.5 l·min^{-1} at 40 °C ($P<0.001$), due to the increase in f. At 30 °C respiratory evaporative heat loss (E_{ex}) amounted to 13% of total evaporative heat loss (E_{tot}) and 7% of total heat production (Table 1). E_{ex} was similar at 35 °C, while the total amount of heat dissipated by evaporative means increased significantly to 105% of total heat production. At 40 °C, E_{ex} was doubled ($P<0.01$) compared to the value at 35 °C and contributed with 12% to total evaporative heat loss. At this temperature 132% of metabolic heat production was dissipated by the evaporation of water.

Discussion

The unusual high surface area to body mass ratio of the greater glider obviously has no effect on deep body temperature, which is stable during exposure to cold and affects its metabolic rate only to a minor degree. Although 21% higher than the basal metabolic rate predicted for a marsupial of similar body mass (Dawson and Hulbert 1970; Kinnear and Shield 1975) it must be borne in mind that our animals were not postabsorptive due to the reasons mentioned in the methods section. Measurements after 24 h starvation showed that the metabolic rate in greater gliders was identical to the BMR of marsupials of similar body mass (Foley 1983). The inability to reach a steady postabsorptive metabolic rate, however, makes it doubtful whether this value should be defined as the 'true' BMR. On the other hand, the BMR of the sugar glider (*Petaurus breviceps*), a similarly shaped, closely related species with a clearly defined BMR was found to be only 2% higher than the BMR predicted for a marsupial of similar body mass (Fleming 1980; Kinnear and Shield 1975) whereas Dawson and Hulbert (1970) could not find any difference at all. This clearly confirms our assumption that the metabolic rate in the greater glider is not significantly affected by their unusual body shape.

In contrast, *Mustelinae* and *Herpestinae*, both small eutherian carnivores which also have a high surface area to body weight ratio, have been reported to have a BMR more than twice that predicted from Kleiber's equation (Brown and Lasiewski 1972; Iversen 1972; Kleiber 1961), whereas the metabolic rate of the slender mongoose was similar to the predicted value despite their large surface area to volume ratio (Kamau et al. 1979). These conflicting results must be attributed to the fact that a high surface area to volume ratio need not necessarily be accompanied by high heat losses, since some of these species can reduce their effective surface area. In the greater glider in a sitting and especially in curled position the effective surface area is presumably small, as indicated by its low weight specific thermal conductance which is significantly below the value predicted for an animal of similar body weight (Bradley and Deavers 1980; Kinnear and Shield 1975). With regard to the uncertainty of our basal metabolic rate, which may be an overestimate, we cannot give absolute conductance values. On the other hand, if the specific dynamic action does affect thermal conductance, the true conductance values would even be lower and when related to surface area, would be smaller than that of the koala in winter (Degabriele and Dawson 1979).

Most mammals have a zone of thermal neutrality wherein metabolic rate is minimal and T_b is controlled by vasomotor adjustments. A zone of thermoneutrality seems to be absent in the greater glider; the metabolic rate increased both below and above $T_a=20$ °C which may indicate that changes in thermal conductance alone were not sufficient to maintain a stable T_b over a wider range of T_a. This is unexpected because the slow increase in MR below the thermoneutral point, which does not intercept at 35.4 °C, shows that the animal still had the capacity to diminish its thermal conductance between 20 and 5 °C. Most of these changes in conductance can be attributed to the thermoregulatory behaviour of the glider which, in cold environments adopted a curled position, the long heavily furred tail wound around the body. In this position the gliding membranes cannot be seen because they are closely wrapped around the body.

This observation accords with the results of Bartholomew et al. (1964) and Carpenter and Graham (1967) who found comparable behaviour patterns in *Synconycteris australis* and *Leptonycteris sanborni*, both small Australian bats. As in the greater glider, thermoneutrality in these bats exists only at one point or within a very narrow zone, and thermal conductance decreases below thermoneutrality.

Heat dissipation

The greater glider responds to an increase in T_a with skin vasodilatation as indicated by the rise in skin surface temperature. At T_a's between 20 and 25 °C, regulation of T_b in resting animals obviously could be achieved by variation in the ear temperature while spontaneous oscillation in the temperature of the gliding membranes were not observed. Changes in the membrane surface temperature were mostly caused by positional changes when the thermocouples were either covered by skin folds or exposed to the air. It thus seems unlikely that the vasomotor adjustments of the gliding membranes are different from those of trunk skin.

Our initial hypothesis was that the overproportional large surface area of the gliding membrane may act as a heat sink at higher T_a. At first sight this assumption seems to be confirmed by several findings: a) the threshold for the onset of respiratory evaporative thermolytic processes was at a T_b of about 38 °C which would clearly favour nonevaporative heat loss. b) Although the greater glider showed a pattern of thermal polypnoea similar to panting animals like rabbits (Gonzales et al. 1971), sheep (Hales and Brown 1974) or the mongoose (Kamau et al. 1979), the respiratory evaporative heat loss was comparatively low, indicating a poorly developed ability for panting. c) It is further attractive to consider the passive rise in T_b with increasing T_a (see Fig. 2) as a useful adaptation to maintain a high temperature gradient between body and environment. This is supported by Heller (1980) who pointed out that the hypothalamic thermosensitivity in many species can vary significantly as a consequence of a specific adaptive response to the environment which enables an animal to tolerate a high heat load. d) At higher T_a the greater glider exposed the sparsely furred inner sides of the gliding membranes and the ventral body surface to the ambient air which presumably facilitates heat flow from body to environment at sufficiently high temperature gradients.

Surprisingly, however, our data on total evaporative heat loss indicate that the greater glider highly depends on evaporative cooling at high T_a. Table 1 shows that even at 30 °C, a temperature which is very common in its natural habitat, already 55% of the metabolic heat production had to be dissipated by evaporative means. At 35 °C this figure increased to 105% and at $T_a = 40$ °C total evaporative heat loss accounted for 132% of total heat production. Corresponding values for the fennec are 36%, 52% and 56% at $T_a = 32$, 36 and 38 °C, respectively (Noll-Banholzer 1979). This comparison clearly indicates that the evaporative heat defence strategies in the greater glider are not very effective. This may be attributed to the fact that these animals are salivating, which is commonly regarded as inefficient means of cooling especially when only fur is wetted. A comparatively high ratio of evaporative heat loss to heat production was found in the koala (Degabriele and Dawson 1979), a panting animal with excellent fur insulation which is also salivating when exposed to heat stress.

Ecological implications

There is no doubt that the greater glider is well adapted to the cool environmental temperatures during his nocturnal activity period but only poorly equipped for heat defence for prolonged periods. A study on the water economy of these animals (W.J. Foley, unpublished) revealed that the greater glider has to cover about 85% of its water requirements from preformed water in food and metabolic water. Only 15% of the total water intake was drinking water, presumably dew condensated at the leaf surface. The limited availability of free water and the low water content of *Eucalypt* foliage (50 to 55%) represent an obvious contrast to the inefficient use of water for thermoregulatory requirements which can only be illuminated by further ecological studies.

Acknowledgements. The authors wish to thank Dr. M.E.D. Webster and Dr. J.R.S. Hales for permission to use their equipment and for many helpful suggestions. This study was supported by grants from the Australian Research Grants Committee and the National Geographic Society. K. Rübsamen was supported by a Feodor Lynen Fellowship from the Alexander von Humboldt-Stiftung.

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