Role of Sweating from the Tail in the Thermal Balance of the Rat-kangaroo *Potorous tridactylus*

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Abstract

Among the marsupials the thermoregulatory response of sweating is uncommon and has only been described in the larger macropodids. Sweating in kangaroos is very unusual in that it only occurs in response to an exercise heat load. The thermoregulatory responses of a smaller, more generalized rat-kangaroo *Potorous tridactylus* were therefore examined to obtain a more general appreciation of sweating in macropodids. The pattern of heat balance at low and neutral temperatures was characteristic of that previously found for macropodids; body temperature was $35 \cdot 9 \pm 0 \cdot 52$ (mean $\pm$ SD). Standard metabolism was only slightly higher than the predicted level for marsupials and minimal conductance was low, *c.* $1 \cdot 3$ W m^{-2} per degree Celsius. At moderate air temperatures heat was primarily lost by vasodilation and panting. The thermoregulatory responses at high air temperatures (near or above body temperature) also included copious sweating from the tail, but not from the body generally. Sweating rates of 600–650 g water per m^2 per hour were obtained; these are about twice the generally reported rates for eutherians such as cows and horses.

Introduction

Since the initial studies of Sutherland (1897) and Martin (1902) there has been controversy about the 'primitiveness' of the thermoregulatory abilities of marsupials. The thermoregulatory responses which now have been described led Dawson (1973*a*) to suggest that the pattern of marsupial thermoregulation should be regarded as a mosaic of primitive and advanced characteristics. Marsupials do have the relatively low metabolic rates and body temperatures which appear typical of various groups of primitive mammals, but superimposed upon these characteristics are a range of thermoregulatory responses which are as efficient as those of advanced eutherian mammals (Dawson 1973*a*). Bartholomew and Hudson (1962) reached similar conclusions with regard to the capacity for hibernation in the pygmy possum, *Cercartetus nanus* (Desmarest).

Panting appears to be the major form of evaporative heat loss in the marsupials (Dawson 1973*a*), but two other forms, licking and sweating, may be utilized and there has been disagreement about their relative importance. This problem has been largely resolved, at least for the large kangaroos in which both licking and sweating play an additional role to panting. Special vascular structures exist in the kangaroos' forelimb to facilitate heat loss during licking (Needham *et al.* 1974), and sweating occurs as an auxiliary means of water loss during the high heat loads encountered during sustained exercise (Dawson 1973*b*; Dawson *et al.* 1974). Licking is widespread in marsupials but sweating appears uncommon and has been demonstrated as significant only in the larger macropodids and then only during exercise. Other

families of marsupials do not appear to sweat, at least at rest. Recent studies have failed to observe sweating in species from the Dasyuridae (Hulbert and Rose 1972), the Phalangeridae (Dawson 1969) and the Peramelidae (Hulbert and Dawson 1974). Although these studies were on resting animals, it is unlikely that exercise-induced sweating, associated with occasional bouts of struggling, would have passed unobserved. Since Robertshaw and Taylor (1969) reported that sweating is of major thermoregulatory importance only in the large (> 50 kg) ungulates, by analogy significant sweating in marsupials may be confined to the larger macropodids. That sweating may be more widespread among the Macropodidae is suggested, however, by observations of Bentley (1960) on the quokka, *Setonyx brachyurus* (Quoy & Gaimard), one of the smallest (3–4 kg) of the wallabies.

In view of the unusual energetic requirements of hopping (Dawson and Taylor 1973) and the occurrence of sweating with exercise in kangaroos (Dawson *et al.* 1974), it is possible that hopping and sweating are related evolutionary developments in the Macropodidae. The Macropodidae are divided into two subfamilies, the Macropodinae, which includes the kangaroos and wallabies, and the Potoroinae, the smaller, more generalized rat-kangaroos. The only information about the Potoroinae is from the work of Robinson and Morrison (1957), who examined *Potorous tridactylus* (Kerr) in their survey and concluded that of the macropodids 'the smallest and most primitive member, the rat-kangaroo, relied least on evaporative cooling and its reaction to heat was greater'. Some of the data of Robinson and Morrison have been questioned in respect to other species (Hulbert and Rose 1972), and it would appear that a further examination of the thermoregulatory responses of the Potoroinae is necessary before generalized conclusions about macropodid and marsupial thermoregulation can be attempted.

Materials and Methods

The potoroo or long-nosed rat-kangaroo, *Potorous tridactylus*, is one of the smallest species in the family Macropodidae, being about 1 kg in weight. They are surface-dwelling and are now restricted to the wetter regions of south-eastern Australia. They are found in coastal heath, dry sclerophyll and wet sclerophyll forest areas, relatively thick ground cover being one of their major habitat requirements. Four animals were loaned by Dr P. J. Johnstone of Macquarie University. Three had been collected near Gosford, N.S.W., while the fourth was a laboratory-bred cross between adults collected near Gosford and in Tasmania. This latter individual appeared to carry more fur than the others. The potoroos were kept in small pens and given a diet of rabbit pellets, bread and apples. Water was supplied *ad libitum*. Food was withheld for approximately 36 h prior to measurements of metabolism and evaporative water loss.

Oxygen consumption and pulmocutaneous water loss estimations at various temperatures were carried out in a small climate room. Animals were weighed, placed in a 30 by 20 by 20 cm perspex chamber with an airtight lid and containing a wire mesh platform over a 2-cm layer of mineral oil. The mesh was small enough to keep the relatively long tail of the potoroo out of the oil. The lid of the chamber contained inlet and outlet connections at opposite ends. A T-piece in the outlet port permitted the introduction of thermocouples through a seal. Chamber temperature could be controlled to ±0·5°C.

Body temperature was measured as deep rectal or colonic temperature using 32-SWG copper–constantan thermocouples and a Honeywell Electronik 15 recording potentiometer. The thermocouples were inserted to a depth of 10–12 cm and taped to the tail. Since the potoroos were not restrained, they at times broke the thermocouples, so that not every animal was measured at each temperature. However, a reasonable range of measurements was made for each animal. Skin tempertaures were obtained with 38-SWG unsheathed thermocouples cemented to the skin with Cyanobond 5000 adhesive,

Oxygen consumption and total evaporative water loss were estimated by an open-circuit technique which was modified after the technique used by Dawson *et al.* (1969) with the use of filtered, compressed air. Oxygen consumption was measured with a Beckman Model F3 paramagnetic oxygen analyser. Dry air flowed through the metabolic chamber at a constant rate, between 0·5 and 17 l min^{-1}, and was measured with a calibrated dry gas meter. Water loss was continuously monitored with Hygrodynamics hygrometer indicators, Model 15-3001, and appropriate wide-range hygrosensors. The vapour pressure of the air leaving the chamber was kept below 15 torr. When water loss reached stable low values, total water loss was estimated gravimetrically for a 15- to 30-min period with U-tubes of indicating drierite.

In studies on the relative water loss from the tail, head and body, the potoroos were blindfolded and restrained in a light open fishnet. Previous experience had shown that kangaroos tended to become quiet under these conditions and the potoroos similarly appeared to relax. The evaporative loss from the tail was estimated by use of the humidity indicators and a perspex chamber 21 cm long and 3 cm diameter. The tail was enclosed in this chamber and room air was drawn along the tail at constant rates between 1 and 10 l min^{-1}. Respiratory evaporation was similarly measured using a ventilated face mask. Cutaneous water loss was estimated with a small, 27-mm diameter, ventilated capsule (flow rate 0·5 l min^{-1}) glued to a clipped area of back skin. Respiratory rate was measured with a Gilson polygraph Model M5P and a Sanborn Model P23BB pressure transducer attached via 2 mm tubing to a small pneumograph taped to the thorax. Skin thermocouples were attached halfway along the tail and under the trunk fur. The surface area of the tail enclosed in the chamber was calculated, on the assumption that the tail represented part of a cone.
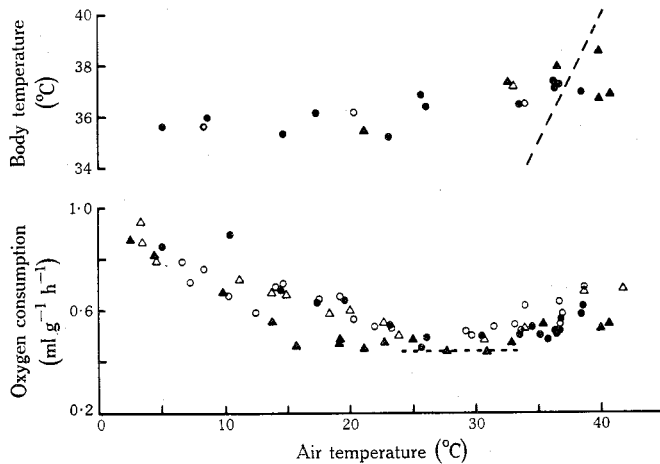

Fig. 1. Rectal temperatures and oxygen consumption of potoroos in equilibrium with various air temperatures. Symbols represent four different animals. Oblique line, equal body and air temperatures. Horizontal dashed line, the standard metabolic rate of a marsupial of the average weight of the potoroos, predicted by use of the data of Dawson and Hulbert (1970) (i.e. $2·4\ W^{-0·25}$).

Results

The variation with air temperature of body temperature and resting metabolism (oxygen consumption) of potoroos is shown in Fig. 1. Below an air temperature of 32°C, body temperature was 35·9 ± 0·52 (mean ± SD) for nine determinations. This value is similar to most recently reported values for macropodid marsupials (Dawson and Hulbert 1970; Dawson and Bennett 1971; Dawson 1973b). At higher temperatures, up to 41°C, there was only a small increase in the equilibrium body temperatures.

The overall pattern of metabolism at various air temperatures (Fig. 1) was also similar to that previously reported for other smaller macropodids (Dawson *et al.* 1969; Dawson and Bennett 1971). The critical temperature was found to be relatively high, about 24°C, except in one animal, the hybrid (<20°C), which appeared to have relatively more fur insulation. The values for total body conductance, calculated in the manner of Dawson and Schmidt-Nielsen (1966), tend to confirm this, with the minimal conductance below the critical temperature being approximately $0 \cdot 93$ W $m^{-2} \, °C^{-1}$ for the hybrid and between $1 \cdot 14$ and $1 \cdot 74$ W $m^{-2} \, °C^{-1}$ for the three New South Wales animals.
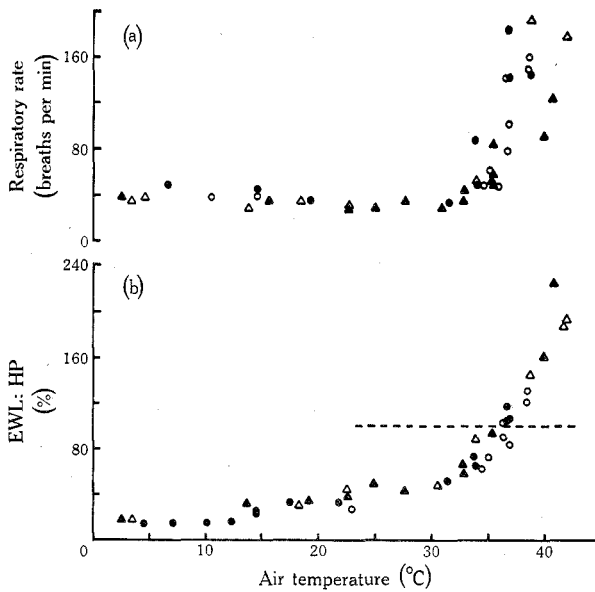

Fig. 2. (*a*) Respiratory rates of potoroos in equilibrium with various air temperatures. Symbols represent four different animals. (*b*) The proportion of the heat production of potoroos that is eliminated by the evaporation of water. Horizontal line, heat production (HP) equals evaporative water loss (EWL).

Minimal resting metabolism or standard metabolic rate (SMR) was attained between 24 and 32°C. The average SMR of the four potoroos was slightly higher (about 7%) than that which would be predicted from the equation of Dawson and Hulbert (1970), but was within the range of values obtained by them in the compilation of their relationship.

The data for body temperature and for the proportion of the heat production lost by evaporation (EWL : HP ratio, Fig. 2*b*) showed that potoroos were capable of maintaining a stable body temperature at high air temperatures by the evaporation of water. The picture for the respiratory response to various ambient temperatures (Fig. 2*a*) suggested that the increased evaporation in the resting potoroo was primarily associated with increased panting. It became apparent that the situation was more complex than this, however, because during initial experiments the tails of the potoroos

became wet at high temperatures. Licking and urination did not appear to be involved and copious sweating was apparent when the starch-iodine test of Wada (1950) was used. The sweat glands were observed to be in dense rings around the almost naked tail, between the dark tail scales. Sweat glands were also demonstrable over the body surface but were not numerous, nor were they as responsive to subdermal adrenaline injections as those on the tail. The importance of various avenues of evaporative water loss in the heat balance of a resting animal is shown in Fig. 3; similar results were
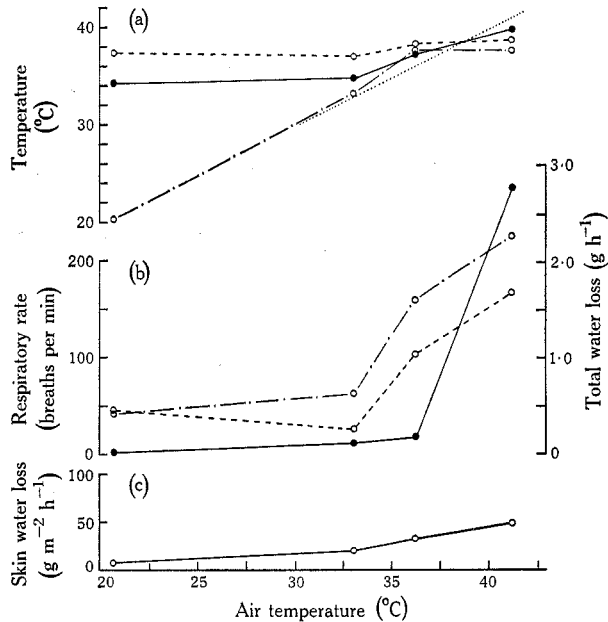

Fig. 3. (a) Skin temperature of tail (—·—·) and trunk (————), and rectal temperature (– – – –), of a potoroo in equilibrium at various air temperatures. ······ Rectal temperature equals air temperature. (b) Evaporative water loss from the head (—·—·) and tail (————) of a potoroo at various air temperatures; also included is respiratory rate (– – – –). (c) Skin evaporative water loss from clipped-back skin at various air temperatures.

obtained for the other animals. The relative rates of water loss from the tail and the respiratory system at various air temperatures vary markedly. At air temperatures below the body temperature respiratory water loss was much higher than tail water loss. At air temperatures close to or above body temperature, tail water loss increased markedly and in absolute amounts exceeded respiratory water loss at the highest air temperature at which measurements were made. The increase in the tail cutaneous water loss with increasing air temperature was not always as abrupt as indicated in Fig. 3. Further experiments at air temperatures between 33 and 39°C suggested that the increase in sweating rate was well regulated (Fig. 4). While it is difficult to accurately calculate the rate of sweat production per unit area, the rates do appear very high. We calculated the surface area of the tail by assuming that it was

equivalent to a cone with the apex cut off; the tail does not taper to a fine point. The values obtained agreed closely with the data on surface area given by Dawson and Hulbert (1970), which show that the tail of potoroos contributes approximately $9 \cdot 4\%$ of the animal's total surface area. The highest rates of sweating from the tail appear to reach 620–650 g m^{-2} h^{-1} in restless and struggling individuals at 40–41°C.

An interesting aspect of the data for tail skin temperatures (Fig. 3) is that the rise in tail skin temperature between 32 and $36 \cdot 2$°C air temperature indicates that tail vasodilation occurred before sweating commenced. All animals showed this response, which suggests that the tail is also a major area of non-evaporative heat loss as is the case for some other small mammals (Johansen 1962; Rand *et al.* 1965).
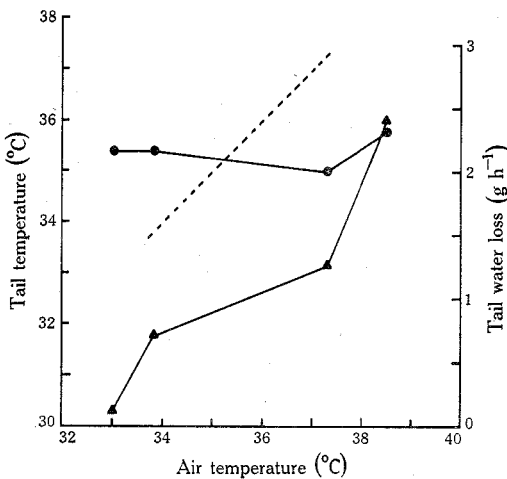

Fig. 4. Variation of sweating rate from the tail (▲) and of tail skin temperature (●) at high ambient temperatures. Oblique dashed line, tail temperature equals air temperature.

Water loss from the body surface does not increase markedly with increasing air temperature and, at first inspection of the results, appears to be a relatively unimportant component of total water loss when compared with the increased rate of sweating from the tail. The situation is, however, more complicated and the rate of water loss from the body is probably not at the levels indicated by the cutaneous water loss values (Fig. 3). The surface area of a 950-g potoroo is approximately $0 \cdot 1$ m^2. If body surface water loss occurred overall at the same rate as that given for skin loss at 41°C in Fig. 3c (i.e. 48 g m^{-2} h^{-1}), then total skin loss ($4 \cdot 8$ g h^{-1}) would be greater than the tail or head loss (Fig. 3b). The values for skin loss in Fig. 3c, while indicating the pattern of response to air temperature, are probably not applicable to the body surface generally but can be explained as simply representing the effect of the large increase in the vapour pressure deficit in the air circulated over the clipped skin beneath the capsule. That similar losses from the normally furred areas are unlikely is further indicated by the high trunk skin temperatures, which were taken beneath the fur.

An observation which may be of significance in regard to the high rates of sweating from the tail is that at high temperatures (when sweating is taking place) the potoroos continually twitch their tail from side to side. Perhaps this is a mechanism to increase the rate of air movement across the tail and hence evaporation from it?

Discussion

Robinson and Morrison (1957), in their work on the reaction of marsupials to heat, stated that of the macropodids the 'smallest and most primitive', the potoroo, 'relied least on evaporative cooling and its reaction to heat was greater'. From the current study this would not appear to be the case, since body temperature remained relatively constant at air temperatures up to 40°C. This was the highest air temperature used by Robinson and Morrison (1957), and thermostability at such temperatures requires an adequate rate of evaporation because all heat has to be lost in this way. The doubtful conclusions of Robinson and Morrison seem to be due to observations on non-resting animals, as seen from the high 'control' body temperatures and respiratory rates. Also, they noted that potoroos did not lick significantly (as was also noted in this study) and presumed that this was a deficiency in their evaporative water loss capabilities.

The pattern of heat production of the potoroo at various temperatures was essentially similar to that of other smaller macropodids (Dawson *et al.* 1969; Dawson and Bennett 1971). The heat loss pattern in this study, however, adds sweating in a resting animal to the range of evaporative heat loss responses reported for macropodids. Panting still appears to be the primary response at lower temperatures but tail sweating becomes very important at air temperatures near and above body temperature. Some continuous observations under these conditions indicate that, although the rate of sweating is well regulated, it is probable that much of the fine control of the rate of evaporation is still by variation of respiratory loss. This is reasonable, since adjustments to the rates of ventilation of the evaporating surfaces are more easily made in the respiratory system.

The most interesting points about the sweating of the potoroo are: (1) that it occurs in such a small animal and from the resting animal, as distinct from the sweating of large kangaroos (Dawson *et al.* 1974); (2) that it occurs at such high rates from such a limited area. Among the ungulates only the larger species of more than 50 kg sweat (Robertshaw and Taylor 1969). Two reasons may be argued for this. One is that there are some limitations on respiratory loss in large animals, perhaps due to difficulties in oscillating the large mass of the respiratory system. The other is that because surface area increases only with $W^{0.67}$ and metabolism (i.e. heat production) increases with $W^{0.75}$, the proportion of surface area relative to heat production decreases with increasing size. Thus heat loss through the surface, even in moderate conditions, may need to be facilitated by sweating. This may especially be the case for the internally generated heat produced by exercise. In a small animal surface area relative to metabolism is large, and generally these animals face problems of heat conservation rather than loss, and carry reasonable fur insulation. This is particularly true for marsupials with their low resting metabolism. It can be easily calculated that, even at rates of surface evaporation considered insignificant in large animals, animals the size of potoroos could have major problems with heat loss. If augmentation of respiratory evaporation was required in potoroos, perhaps due to the unusual heat production characteristics of hopping at low speeds (Dawson and Taylor 1973), then this could best be met by sweating from specific regions. Such areas would need to be naked or lightly furred so that evaporation would not be slowed. Consequently these areas would also need to be easily isolated from the animal's core. The tail and the lower part of the feet would seem to be well suited for this purpose; next

to the tail, the lower parts of the hind legs had the highest concentration of sweat glands when examined by the starch-iodine technique of Wada (1950). The rate of sweating from the tail is very high, with rates in excess of $600\,g\,m^{-2}\,h^{-1}$ being recorded several times. These rates are about double the generally reported maximum rates for eutherian mammals such as cows and horses (Allen and Bligh 1969).

Since sweating has now been demonstrated in the Potoroinae as well as in the larger kangaroos, it now seems likely to occur under some conditions in most macropodids. Previous attempts to detect it have failed because of the relative rarity of these conditions. At this stage little can be said about the control of sweating in the potoroos except that the glands respond to an intradermal injection of adrenaline, but this response is common to most sweating animals (Robertshaw 1971). Before general statements can be made about the evolution of sweating in marsupials it will be necessary to reexamine some of the non-macropodid marsupials in the light of what is now known about the macropodids.

Acknowledgments

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