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ENERGY METABOLISM AND THERMOREGULATION OF THE SPECTACLED HARE WALLABY (LAGORCHESTES CONSPICILLATUS)[1]

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Spectacled hare wallabies (*Lagorchestes conspicillatus*) have a basal metabolic rate (0.32 $cm^3\ O_2 \cdot g^{-1} \cdot h^{-1}$) that is about 70% of the value that would be anticipated for most eutherian mammals of corresponding size (2.66 kg). The body temperature and heart rate of these marsupials are also relatively low by eutherian standards. *Lagorchestes* regulates its body temperature well in environments as cool as 6 C, relying on augmented heat production and heat conservation resulting from effective insulation and peripheral heterothermy involving the tail and distal portion of the limbs. The minimal heat-transfer coefficient for this wallaby is 1.1 kcal $(m^2 \cdot h \cdot C)^{-1}$, a value similar to those reported for other macropodids. Hare wallabies cope with heat stress by a combination of controlled hyperthermia and evaporative cooling. The latter involves panting; breathing rates exceeding 400 cycles/min were noted in individuals tested in environments at 43 C. Panting resulted in a slight increase in blood pH after 2–4 h. Licking behavior also appears to contribute to evaporative water output at high temperatures. Cutaneous water loss is not an important component of this output, at least in the resting animals utilized in this study. Hare wallabies are nocturnal in nature and spend the day protected from solar radiation and high air temperatures within shelter provided by porcupine grass (*Triodia angusta*). Behavior thus serves to minimize requirements for evaporative output of water on hot days. The physiological performance of the hare wallaby is compared with that of the jackrabbit, an animal of similar size and ecology occupying North American deserts.

The family Macropodidae (wallabies and kangaroos) is one of the conspicuous faunal elements of Australia. Its members live in a broad assortment of environments from tropical rain forests to deserts. Deserts comprise the dominant feature of the Australian subcontinent, and the suite of behavioral and physiological characteristics that have enabled certain macropodids to come to terms with intense heat and scanty and often unpredictable rainfall is of considerable interest. Several studies provide information on thermoregulation and related behavior and on water and electrolyte balance of the red kangaroo (*Megaleia rufa*) and euro (*Macropus robustus*), two of the larger desert macropodids (Dawson and Denny 1969*a*, 1969*b*; Dawson and Brown 1970; Russell 1971; Dawson 1972*a*, 1972*b*, 1972*c*, 1973; Denny and Dawson 1975*a*, 1975*b*). Comparable studies of this type on smaller members of the family Macropodidae have been mainly confined to

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the tammar wallaby, *Macropus eugenii* (Dawson, Denny, and Hulbert 1969; Dawson and Rose 1970), the quokka, *Setonix brachyurus* (Bartholomew 1956; Bentley 1960; Shield 1966), and the rat-kangaroo, *Potorous tridactylus* (Hudson and Dawson 1975; Nicol and Maskrey 1977), none of which is associated with extreme desert conditions. Because of the relatively limited information available on wallabies, which may differ from their larger relatives, the kangaroos, with respect to rates of exchange of energy and materials, access to shelter from heat, and mobility, we felt it would be desirable to study aspects of the thermoregulation and behavior in the field of a true desert species. We were fortunate in this regard in obtaining spectacled hare wallabies (*Lagorchestes conspicillatus*) for investigation at the University of Western Australia. We report here the full extent of our laboratory and field observations. A preliminary report on aspects of the energy metabolism and evaporative water loss of this species has been presented previously (Dawson and Bennett 1971).

MATERIAL AND METHODS

LABORATORY OBSERVATIONS

Source of experimental subjects.—The spectacled hare wallaby was formerly distributed widely in the tropical deserts of Australia. It now appears confined mainly to a few islands off the northwest coast of Western Australia. Our eight experimental animals were obtained from Barrow Island (20°45′ S 115°25′ E). They were brought to the animal yards of the Department of Zoology, University of Western Australia, in Nedlands, where they were studied in the austral spring, summer, and fall (October–April) of 1969–1970. The animals adjusted well to captivity, grew or maintained body mass, and in some cases reproduced successfully. Body masses of the adults used in our studies ranged from 1.9 to 3.2 kg (mean 2.66 kg).

The spectacled hare wallaby represents an approximate ecological equivalent of the black-tailed jackrabbit (*Lepus californicus*) of North America. Both are nocturnal herbivores that spend the day in shallow forms in the shelter of vegetation, which in the case of *Lagorchestes* on Barrow Island was the porcupine grass *Triodia angusta*.

Oxygen consumption.—Measurements of oxygen consumption ($\dot{V}O_2$) by hare wallabies were made on individuals that had rested 4–6 h at a particular test temperature in a Perspex metabolism chamber. The animals had been fasting for 48 h at the time of introduction into the chamber, and measurements were made over a period of at least 30 min between 1500 and 1700. Ambient temperature (T_a) was controlled during tests by maintaining the metabolism chamber in a controlled temperature cabinet. The metabolism system, which included a Beckman F-3 paramagnetic oxygen analyzer, was of the general open circuit type described by Dawson and Fisher (1969). Details of procedure are given by Dawson and Bennett (1971).

Evaporative water loss. Measurements of total evaporative water loss were carried out in conjunction with those on oxygen consumption. The gravimetric method employed is described in Dawson and Bennett (1971). Rates of air flow through the metabolism chamber were adjusted so that vapor pressure for water within the chamber was maintained below 10 torr in all the experiments. Above 30 C the vapor pressures were between 5 and 10 torr. In these experiments the animals rested on a wire mesh platform over a 2-cm layer of paraffin oil, which served to cover any

urine or feces voided in the course of an experiment, thereby preventing these waste products from adding water vapor to the system.

We attempted to determine the contribution of cutaneous water loss from either sweating or diffusion through the skin on the naked surfaces of the paws and tail in heat-stressed wallabies. Plastic bags containing preweighed packages of Drierite (anhydrous $CaSO_4$) were secured to the limbs and/or tail of an animal which was then exposed to high T_a's for 1–2 h. The bags prevented these surfaces being licked and were tolerated well by the animals. They were removed at the end of the heat exposure and water loss determined by weighing the Drierite packages.

Body temperature.—Body temperature (T_b) of hare wallabies was usually determined at the conclusion of metabolic experiments, using a thermistor probe in conjunction with a YSI Telethermometer. The probe was inserted into the rectum to a depth of 10 cm. An attempt was also made to determine the extent of diurnal fluctuations in T_b by telemetry. A temperature transmitter was placed in the pouch of a female hare wallaby which was housed in an outdoor enclosure of approximately 40 m^2. Pouch temperature of hare wallabies in metabolic tests at moderate T_a tended to fall 0.4–0.7 C below simultaneous rectal temperatures. Initial trials were complicated by the animal's removing the unit from the pouch. We subsequently prevented this by covering the opening of the pouch with an athletic supporter, which was attached to the animal by means of the elastic bands. While giving the wallaby a widely commented upon appearance, these bands did not appear to impede its movements.

Heart rate, breathing rate, and blood pH.—Heart rates were determined electrocardiographically using safety pin electrodes attached to the sides of the thorax. The electrodes were connected via shielded cable to a Grass P-5 a.c. preamplifier used in conjunction with a Sanborn 299 recording oscillograph. For electrocardiographic determinations, the animals were housed in a cage placed in a 240-liter chamber. This chamber was immersed in a propylene glycol-water mixture that could be maintained at any desired temperature between 0 and 50 C.

Breathing rates were determined visually in some of the metabolism experiments. However, most were measured in conjunction with electrocardiographic measurements in the large chamber mentioned above. Adjustment of the low-frequency filter network on the Grass P-5 preamplifier to its lowest setting allowed registration of slow potentials corresponding to thoracic movements during breathing. This method of counting respiratory movements was indispensable in determining the higher breathing frequencies utilized by hare wallabies.

Another series of experiments was performed to determine whether prolonged panting during heat stress produces alkalosis in hare wallabies. Initial blood samples were taken by heart puncture on animals exposed to room temperature. The wallabies were then fitted with broad cardboard collars to restrict licking behavior and placed in the 240-liter metabolism chamber at 39.7-41 C for 2–4 h. Final blood samples were obtained at the end of the exposure to heat. Blood pH was measured at 38.5 C with a Beckman microblood pH electrode used in conjunction with a Beckman 160 Physiological Gas Analyzer. Coagulation of samples was prevented by the addition of a few crystals of Na-heparin.

FIELD OBSERVATIONS

Interpretation of laboratory results required observations on the situations in which hare wallabies exist in the field. We were particularly interested in determining the extent of the protection afforded the animals by the vegetation in which they spend the day. Accordingly, we spent several days on Barrow Island in early November 1969. This period was selected as offering hot weather yet occurring safely before the cyclone season in northwestern Australia. We captured three hare wallabies at night by netting them while they were temporarily immobilized in the beam of a spotlight on our vehicle. Following capture the animals were fitted with collars containing temperature transmitters that used a blocking oscillator circuit. The hare wallabies were then released at the point of capture. The signals from the collar transmitters were received with a loop antenna that made it possible to locate the animals on the following days when they were concealed in their forms in clumps of vegetation. The pulse frequency provided a rough indication of the temperature in the form with the animal present. After a form was located and the animal had left as we approached, observations were made on the orientation of the entrance. Surface temperatures of the soil and walls of the structure were estimated using a Barnes PRT-10L infrared thermometer. A few determinations of humidity within the form were made with a dew point hygrometer.

RESULTS

LABORATORY OBSERVATIONS

Oxygen consumption.—The standard $\dot{V}O_2$'s for the hare wallaby during daytime are plotted against T_a in figure 1. The zone of thermal neutrality for this

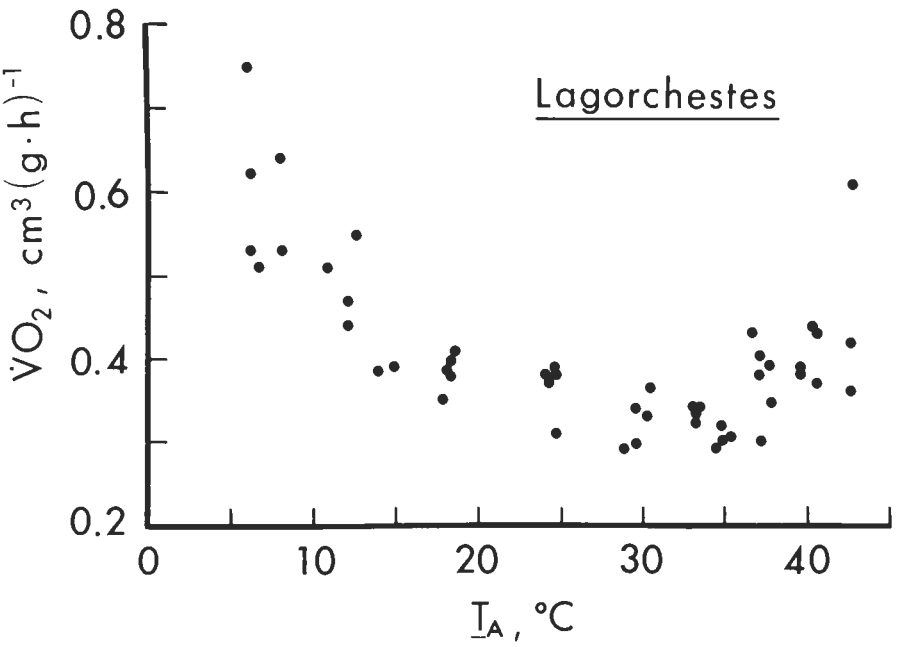

FIG. 1.—Relation of standard $\dot{V}O_2$ by postabsorptive *L. conspicillatus* to T_a. Measurements pertain to resting animals in inactive phase of their daily cycle. All gas volumes have been converted to standard temperature and pressure, dry.

animal extends from approximately 25 to 35 C. The oxygen consumption within this interval averages 0.32 cm^3 $(g \cdot h)^{-1}$ (SD = 0.22), or 1.79 W/kg. Below thermal neutrality $\dot{V}O_2$ rises with decreasing T_a. A regression line fitted to metabolic values between 5 and 18.5 C has the following equation: $\dot{V}O_2 = 0.72 - 0.019\ T_a$, where $\dot{V}O_2$ is in cm^3 $(g \cdot h)^{-1}$ and T_a is in degrees Celsius. The line described by this equation extrapolates to zero metabolism at a T_a of 37.9 C. The rate of oxygen consumption also rises perceptibly with T_a above 35 C.

Evaporative water loss.—Evaporative water loss by hare wallabies increases relatively little with T_a between 6 and 35 C (fig. 2). At $T_a < 20$ C, minimal rates of evaporation average 0.40 mg H_2O $(g \cdot h)^{-1}$ (SD = 0.08), representing a rate of heat loss of 0.27 W/kg. Above 35 C, the rate of this function rises rapidly, reaching a maximum of 7.8 mg $(g \cdot h)^{-1}$ or 5.27 W/kg, at 42.8 C in our experiments.

Rates of water loss from bagged extremities during heat stress are reported in table 1. This avenue of water loss did not make a large contribution to the total water output at high T_a's in our experiments. Calculated values of percutaneous water loss for animals 2 and 3 are only 2%–6% of total water loss for animals at 42–43 C (see fig. 2). It should be emphasized that these experiments, which required use of Drierite, will tend to maximize cutaneous water loss by maximizing the vapor pressure deficit of the air around the extremities. Values for limbs which ordinarily would be wet by licking would probably be much lower.

Body temperature.—A complex relation exists between T_b and T_a in hare walla-

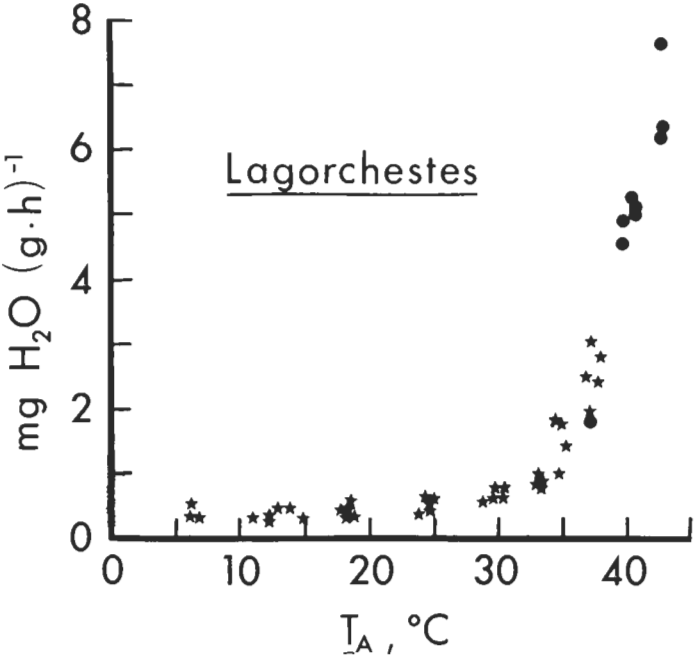

FIG. 2.—Relation of evaporative water loss by *L. conspicillatus* to T_a. Values represented by circles were obtained in tests in which the animals were observed to engage in licking behavior; those represented by stars refer to tests from which such behavior was absent. Measurements of evaporative water loss were made in conjunction with those on standard oxygen consumption.

bies (fig. 3). Temperature of the body core is essentially stable between 6 and 25 C, averaging 36.0 C (SD = ±0.6 C). However, temperatures of the sparsely furred extremities decline noticeably with decreasing T_a over this range. For example, surface temperatures of the tail of animals exposed to 6.2 and 12.1 C were 13.2 and 16.7 C, respectively. Between 25 and 35 C, the zone of thermal neutrality, the body temperature rises 2 C and ultimately stabilizes at approximately 39 C at T_a's between 38 and 43 C.

TABLE 1

RATES OF PERCUTANEOUS WATER LOSS

Animal No.	T_a (°C)	Structure[a]	Rate of Water Loss mg/h	Rate of Water Loss mg/(g^b ·h)
1.....	37.4	Tail	123	.042
2.....	42.6	Right forepaw	41.4	.018
		Right hind limb	68	.030
3.....	43.0	Right forepaw	137	.057
		Right hind limb	249	.104
		Left hind limb	236	.098
		Tail	145	.060
		Total for animal 3[c]	904	.377

[a] Extremities were enclosed in plastic bags containing Drierite.
[b] Body mass.
[c] Calculated for all limbs and tail.

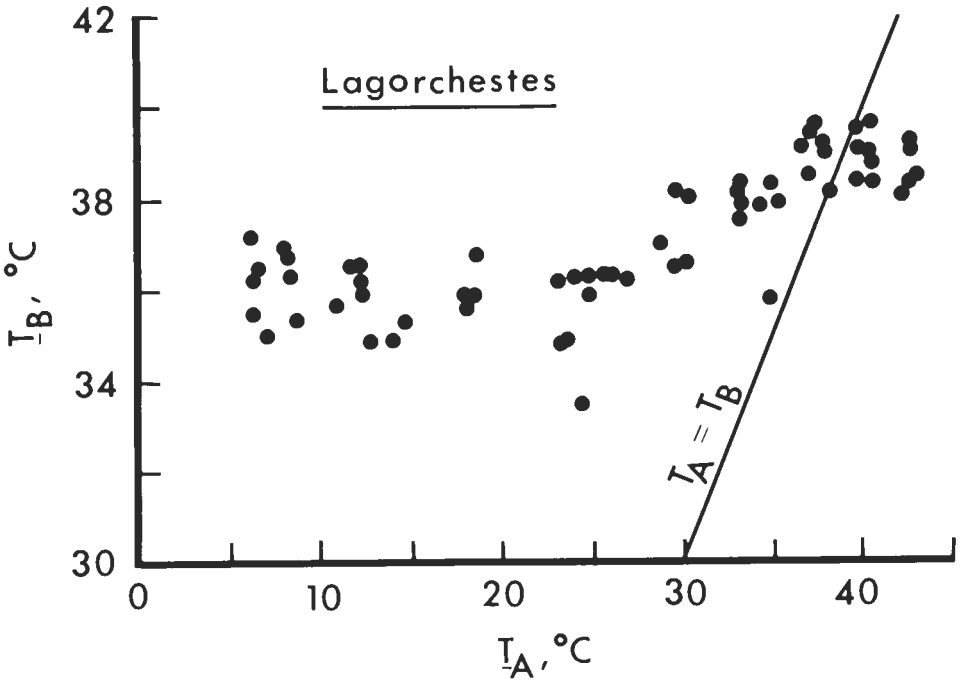

FIG. 3.—Relation of T_b to T_a in postabsorptive *L. conspicillatus*. Measurements pertain to resting animals in the inactive phase of their daily cycle. Most of these were made in conjunction with metabolic tests.

The telemetry of pouch temperature occurred on 2 days in April while the female wallaby equipped with the transmitter was undisturbed in an outdoor pen. Air temperatures during the periods of measurement ranged between 13.2 and 18.5 C. Body temperature underwent a diurnal cycle. During the afternoon and evening (1430–2400), T_b averaged 36.6 C (SD = $\pm$0.2, range = 36.0–37.0 C). At night and during the morning (0200–1330), lower pouch temperatures were recorded (mean = 35.1 C; SD = $\pm$0.3; range = 34.8–35.5 C). As noted previously, pouch temperatures for female wallabies resting at moderate T_a's ran 0.4–0.7 C cooler than simultaneous rectal temperatures.

Heart rate, breathing rate, and blood pH.—Heart rates of animals resting at room temperature (T_a = 23.1–25.0 C) average 73.5 beats/min. During prolonged exposure to heat stress (T_a = 38.4–43.7 C), those rates increased, presumably reflecting the cost of active heat defense (mean value = 108 beats/min; SD = $\pm$12; range = 84–116 beats/min).

Breathing rate of hare wallabies at T_a's in and slightly below the zone of thermal neutrality (22.5–34 C) averages 22 cycles/min, being relatively independent of T_a (fig. 4). However, beyond the upper bound of thermal neutrality, this physiological activity rises sharply with increasing ambient temperature, and the rates increase about eightfold between 35 and 44 C. The values obtained at T_a's of 41–44 C are between 325 and 435 cycles/min. Hare wallabies evidently do not rely on a single breathing frequency during panting.

Prolonged panting for 2–4 h consistently produced moderate aklalosis. Blood pH increased from an average value of 7.33 (SD = $\pm$0.05) before heat

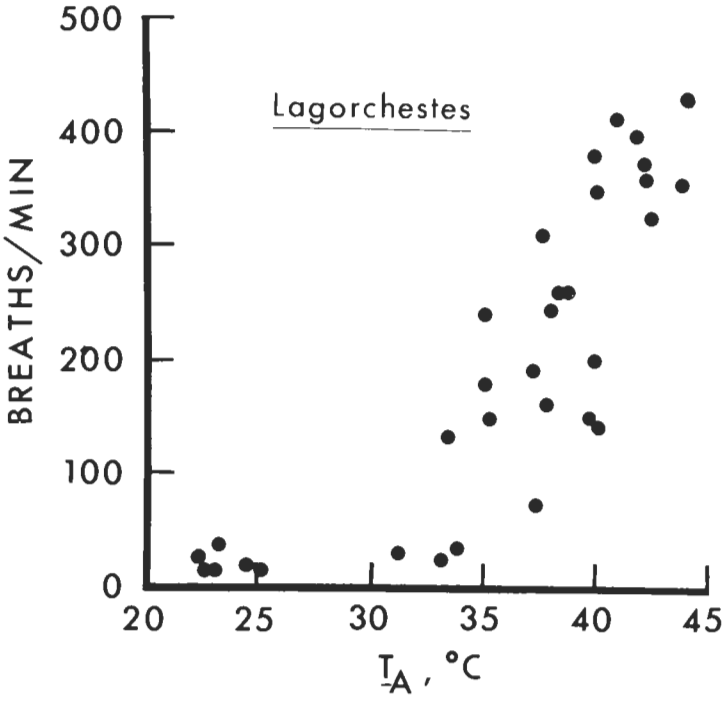

FIG. 4.—Breathing rates for resting *L. conspicillatus* at various T_a's

exposure to 7.44 (SD = ±0.06) after exposure. Individual increments in blood pH ranged from 0.02 to 0.15 U (mean = 0.09; SD = ±0.05).

FIELD OBSERVATIONS

During our November visit to Barrow Island, we found hare wallabies to be exclusively nocturnal. Our ability to locate the three female wallabies fitted with collars containing radio transmitters (fig. 5) allowed us to find the daytime retreats of these animals. They invariably utilized porcupine grass (*Triodia angusta*) for diurnal shelter. This particular grass is confined on Barrow Island to the vicinity of water courses, which are dry for much of the year, and to other places where the soil is relatively deep. Each of the three hare wallabies used a different clump of *Triodia* for shelter on November 18, 19, and 20. Two used still different ones on November 21, whereas the third wallaby was found in the clump in which it had sheltered on November 18. In all cases, the shift to a new clump of porcupine grass involved a move of at least 75 m from the site used on the preceding day. The total extent of these movements led A. A. Burbidge and A. R. Main (unpublished data) to estimate the home ranges of these female wallabies to be at least 5–10 acres in extent. In making observations on the shelters, we approached them closely enough to cause the animals to flee. Perhaps this was a factor in causing the wallabies to change their retreats daily. However, most of the shelters we inspected appeared to have been in use for some time, and we are unable to rule out the possibility that the animals may change retreats periodically even without disturbance.

The clumps of *T. angusta* used for

FIG. 5.—*L. conspicillatus* fitted with a collar radio transmitter, just prior to release

shelter by the three wallabies tended to be relatively large (fig. 6), their longest and shortest horizontal dimensions being 1.7–3.6 m and 0.6–2.2 m, respectively. The heights of these clumps ranged from 0.6 to 0.8 m. The entrance to the form from within the porcupine grass in which the wallaby rested was not oriented consistently from clump to clump, and entrances facing NW, NE, E, SSW, and WSW were found. The height of the cavities themselves did not exceed 0.3 m, and the distance between the back wall and the entrance ranged from 0.4 to 0.7 m. The form within which an animal rested was only slightly larger than its body, roughly 0.3 m on a side. The floors of these forms were slightly concave and consisted of soil with some limestone gravel.

The shelter utilized by hare wallabies is an effective barrier to thermal radiation. The temperatures of the floor and walls of their forms varied only from 32 to 34 C during the interval from 1200 to 1600. Temperatures as high as 58 C were simultaneously found on the surface of the soil in unshaded areas. The surface of the fur on the back of a wallaby exposed to the sun quickly reached 54 C and then, when air movement was restricted, rose to over 60 C. Temperatures reported by the collar transmitters with which the wallabies were fitted suggest that T_a within the cavities in the period referred to likewise remained between approximately 32 and 37 C. External T_a over the afternoon ranged from 31.6 to 38.4 C. Absolute humidities in the burrows ranged between 13 and 23 torr during the daytime in the period of November 18–21, during which our observations were made.

FIG. 6.—Clump of porcupine grass (*Triodia angusta*) used as shelter during daytime by *L. conspicillatus* on Barrow Island. Arrow indicates entrance to animal's form.

DISCUSSION

General metabolic considerations.—Views of the thermoregulatory and metabolic capacities of marsupials have changed substantially since Martin (1903) characterized these animals as physiologically intermediate between the "relatively primitive" monotremes and the more advanced eutherians. A number of workers in the past two decades have found, contrary to Martin's conclusions, that marsupials show extensive capacities for controlling body temperature by both physiological and behavioral means. While marsupials appear every bit as homeostatic as eutherians, this is not to say that they are identical with representatives of this group in various physiological dimensions, most notably basal metabolic rate (BMR). The BMRs of Australian marsupials tend to be about 70% of those of eutherians of comparable size (MacMillen and Nelson 1969; Dawson and Hulbert 1970), a pattern to which the hare wallaby conforms (table 2). Heart rates of marsupials are also lower than those of similar-sized eutherians, a relation borne out in the hare wallaby. The value for resting heart rate that we obtained for this macropod (73.5 beats/min) is 90% of that predicted from the equation of Kinnear and Brown (1967) relating heart rate and body mass in marsupials.

The overall thermoregulation of the spectacled hare wallaby does not restrict body temperature to a single value but confines it, instead, within a range of nearly 5 C, generally extending from 35 to 39.6 C over a span of T_a's reaching from 6 to 43 C. The higher T_b's were observed at T_a's above 35 C; the utility of this hyperthermia is considered below.

It seems most useful for comparative purposes to deal with values of T_b observed in animals resting and fasting during the day in or near the zone of thermal neutrality. The T_b under these conditions is in the same range as comparable values recorded for other macropodids (table 3). All these macropodids share the characteristic of distinctly lower levels of body temperature in the absence of thermal stress than most eutherian mammals (Dawson and Hulbert 1970).

With data on body temperature, metabolism, and evaporative water loss reported here, it is possible to calculate heat-transfer coefficients corrected for evaporative heat loss (dry thermal conductances), θ, for hare wallabies. The fact that the measurements pertain to situations in a metabolism chamber, where convective heat exchange is

TABLE 2

COMPARISON OF BMR OF THE HARE WALLABY WITH PREDICTED VALUES FOR EUTHERIANS AND AUSTRALIAN MARSUPIALS
(kcal/h)

Hare Wallaby (1)	2.66-kg Eutherian[a] (2)	(1/2)	2.66-kg Australian Marsupial[b] (3)	(1/3)
4.09	6.08	.67	4.25	.94

[a] Value for eutherian the size of a hare wallaby (2.66 kg) predicted from the equation kcal/h = 2.92 $m^{0.75}$, where m is body mass in kg (Kleiber 1961).

[b] Value for Australian marsupial the size of a hare wallaby (2.66 kg) predicted from the equation kcal/h = 2.04 $m^{0.74}$, where m is body mass in kg (Dawson and Hulbert 1970).

characteristically limited, influences the values of these coefficients (see Tracy 1972). However, they provide a convenient means of comparing basic insulative properties of *Lagorchestes* with those of various other mammals for which data have been obtained under comparable conditions. Minimal heat-transfer coefficients for the hare wallaby (fig. 7) occur between approximately 6 and 20 C, where θ equals 1.1 kcal $(m^2 \cdot h \cdot C)^{-1}$ (SD = ± 0.08) or 1.3 $W(m^2 \cdot C)^{-1}$. The minimum value of θ specified for *Lagorchestes* is identical with that ob-

TABLE 3

DEEP BODY TEMPERATURES OF SOME MACROPODID MARSUPIALS[a]

SPECIES	T_b (°C) Mean	T_b (°C) Range or (SD)	REFERENCE
Lagorchestes conspicillatus	35.8	(.63)	This study
Macropus eugenii	36.4	35.6–36.8	Dawson and Hulbert 1970
Megaleia rufa	35.9	35.4–36.8	Dawson and Hulbert 1970
Setonix brachyurus	37.0	36.7–37.6	Bartholomew 1956
Potorous tridactylus	35.9	(.52)	Hudson and Dawson 1975

[a] Values refer to individuals resting at T_a's between 20 and 35 C. The figures for *Lagorchestes* are based on measurements between 23 and 26 C to avoid the complication of the hyperthermia developing in the upper portion of the zone of thermal neutrality.

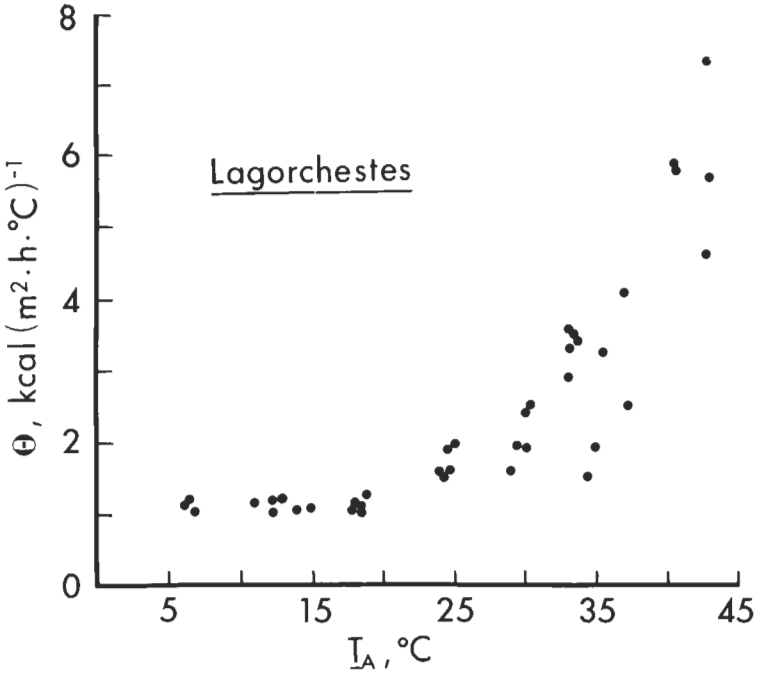

FIG. 7.—Values of θ for *L. conspicillatus* at various T_a's. These coefficients were calculated from results of metabolic tests and have been corrected for evaporation heat loss. Values of 4.8 cal/cm³ and 0.58 cal/mg have been utilized for converting data on $\dot{V}O_2$ and evaporative water loss, respectively, to thermal terms. Surface areas for the animals were estimated using the version of Meech's formula given for the tammar wallaby (*Macropus eugenii*) by Dawson and Hulbert (1970).

tained by Dawson et al. (1969) for the larger tammar wallaby (4.96 kg). This value also agrees closely with comparable ones during summer for the much larger euro (*Macropus robustus*) and red kangaroos (*Megaleia rufa*), 30 and 35 kg, respectively (Dawson 1972*c*).

Thermoregulatory repertoire.—In part as a consequence of their relatively low metabolic levels, hare wallabies show a narrow zone of thermal neutrality for a mammal of their size, the lower critical temperature approximating 25 C (fig. 1). The augmentation of heat production with decreasing T_a below thermal neutrality not only prevented a decline of core temperatures at the lowest temperature tested (T_a = 6 C); it may even have contributed to a slight rise in T_b that is suggested in data obtained below thermal neutrality. Such a rise is also suggested in data on body temperature obtained for other macropodids in cool environments (Dawson et al. 1969; Dawson 1973; Needham, Dawson, and Hales 1974). While core temperature does not drop in cool surroundings, temperature of the extremities does. This peripheral heterothermy resembles that noted in certain boreal eutherian mammals, in which it is regarded as a highly adaptive response serving to reduce the requirement for increased thermogenesis (Irving, Monson, and Krog, 1955). The facilities available to us did not allow full assessment of the capabilities of wallabies for cold defense. Many eutherian mammals can sustain rates of heat production in the cold that are three to four times BMR (Scholander et al. 1950; Gelineo 1964). Parameloid marsupials have been observed to increase thermogenesis at low T_a's to 3.7–4.4 times basal rates (Hulbert and Dawson 1974). If these multiples are representative for cold-stressed marsupials generally, *Lagorchestes* must have considerable reserve capacity at 6 C, the lowest T_a at which we conducted tests, for $\dot{V}O_2$ there was not even double BMR (fig. 1).

As noted previously, hare wallabies allow their T_b to rise during exposure to heat. However, this tendency toward hyperthermia first becomes evident within the zone of thermal neutrality, and T_b shows some direct dependence on T_a between approximately 25 and 38 C. It stabilizes at approximately 39 C, at T_a's between 39 and 43 C. The changes in T_b that occur at warmer T_a's are accompanied by vigorous evaporative cooling. The principal component of this appears to be respiratory water loss, the trends in breathing rate and total evaporative water loss being parallel. Neither of these functions changes appreciably at T_a's between 6 and 34 C. However, both rise dramatically above the hotter temperature, increasing approximately 10-fold between 34 and 43–44 C. Panting by hare wallabies at the hotter temperatures proceeds at approximately 400 cycles/min, which is of the same order observed in panting tammar wallabies under severe heat stress (440 cycles at a T_a of 46 C) (Dawson and Rose 1970). Protracted panting can result in a mild alkalosis due to increased respiratory release of carbon dioxide in these animals, judging by our observation on blood pH. Moderate heat stress and panting did not produce significant alkalosis in the tammar wallaby. However, more severe stress involving exposure to 46 C produced a statistically significant rise in arterial pH of approximately 0.08 U (Dawson and Rose 1970). Values reported for arterial pH of tammars at moderate T_a's are nearly 0.1 U higher than we obtained for non-heat-stressed hare wallabies, a discrepancy that we believe reflects the fact that blood samples

were obtained from indwelling catheters in the former animals, whereas they were procured by heart puncture in the latter.

Hare wallabies engage in licking behavior as well as panting in hot environments, as do most other macropodids (Bartholomew 1956; Dawson et al. 1969; Dawson 1973). The animals in our tests began licking at T_a's between 37.4 and 39.7 C. All animals tested engaged in licking behavior at T_a's above 39.7 C (fig. 2). Rectal temperature is a relatively poor predictor of whether a wallaby will engage in licking behavior. Some individuals initiated this behavior at T_b's near 38.3 C, whereas others refrained from it at T_b's as high as 39.5 C. One thing is clear from our observations: licking behavior by hare wallabies is not a last-ditch measure for heat defense. The animals generally licked in a quite leisurely manner and did not appear particularly stressed, a situation confirmed by the rather modest increments in heart rate observed in licking individuals. The animal exposed to the highest experimental temperature (43.7 C) maintained a heart rate of only 84 beats/min while licking profusely.

The importance of spreading saliva by licking as a means of evaporative cooling has been difficult to assess, for it is hard to separate experimentally from respiratory evaporation. Licking was regarded as a minor and inefficient mechanism for evaporative cooling in the tammar wallaby (Dawson et al. 1969). We believe that it is important in hare wallabies, which effectively spread saliva on the distal portions of the hind limbs, the abdomen, the scrotum, and the relatively thinly furred tail. Evaporation from these sites could result in substantial dissipation of body heat, assuming that vascular arrangements exist for transporting heat from other portions of the body to these evaporative sites. A profuse superficial venous network has been demonstrated in the forelimbs of red kangaroos (Needham et al. 1974), which lick portions of these appendages vigorously in hot environments. Blood flow to the forelimbs increases in such environments, and licking behavior appears temporally coordinated with this increased perfusion.

Cutaneous evaporation, in the form of sweating or percutaneous water loss, is of minor importance as a means of evaporation for hare wallabies during heat stress (cf. table 1, fig. 2). It appears relevant in this connection that the rate of cutaneous water loss seems unaffected by external heat load in other marsupials (Hulbert and Rose 1972; Dawson 1973).

By whatever means achieved, evaporative cooling stabilizes T_b near 39 C at high T_a's (38–43 C). Such cooling accounts for 1.4–2.0 times as much heat as metabolism produces at these T_a's (fig. 8). This performance is of the same general order as that noted at high T_a's for evaporative cooling by the red kangaroo, euro, and tammar wallaby (Dawson et al. 1969; Dawson 1973).

Interrelations of physiology and behavior of hare wallabies in their natural environment.—Our laboratory results permit characterization of the spectacled hare wallaby as an animal having a relatively low metabolic rate and low body temperature by eutherian standards. We infer from the relatively low metabolic rate that *Lagorchestes* probably has a far lower rate of water turnover than do eutherians of similar size under comparable conditions. Other macropodids show turnover rates that are only about 2/3 as high as the corresponding ones for eutherians (Denny and Dawson 1975*a*).

On the basis of the ratios of total evaporative water loss to oxygen con-

sumption plotted in figure 8, we can specify for the hare wallaby that evaporative water output exceeds metabolic production of this fluid at all but very cool ambient temperatures. Thus some dependence on preformed water obtained from drinking or in food is inevitable. The relative importance of metabolic water in the economy of hare wallabies is reduced even further at higher temperatures where evaporative output per unit of oxygen consumption is high (see fig. 8).

The relatively low metabolic rate of *Lagorchestes* is potentially advantageous in hot environments, for it produces a relatively low internal caloric burden. However, the relatively low T_b is potentially disadvantageous, for it renders hare wallabies more prone to gain heat in warm environments than most eutherians with their higher T_b's. While these general statements provide some background concerning the problem of existence by hare wallabies in the desert environment, a fuller understanding of their adjustments to these conditions must involve appreciation of behavioral as well as physiological considerations. Our field observations indicate that spectacled hare wallabies utilize a pattern of behavior widespread among desert animals, namely, confining their activity to the cooler nighttime hours when intense incoming thermal radiation is not a major problem. The wallabies couple this with use of shelter during the day. While our observations on temperature conditions on Barrow Island are confined to only a few warm days in late November, we feel they effectively document the utility of this

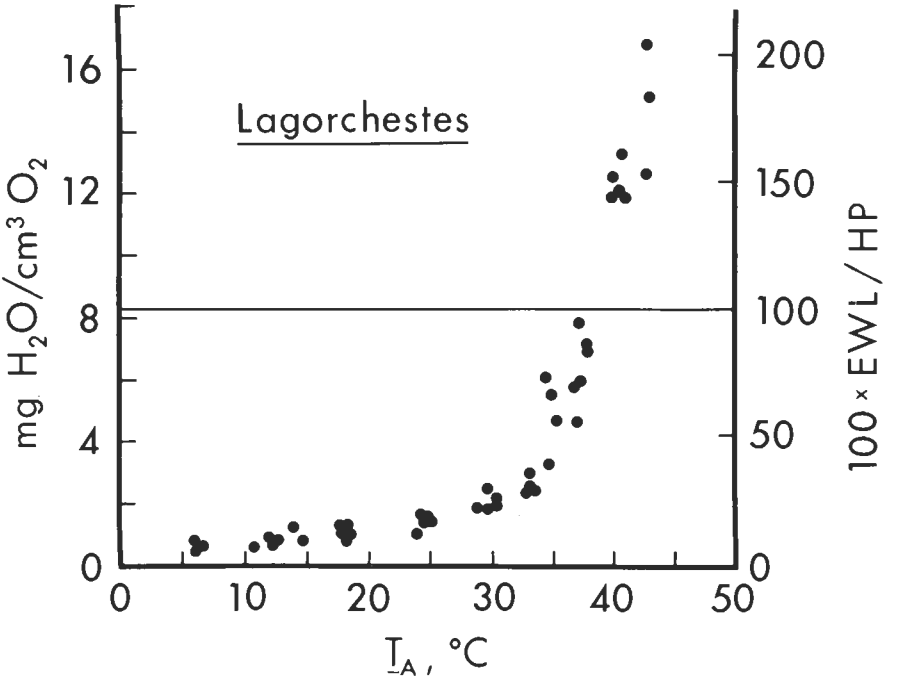

FIG. 8.—Ratios of evaporative water loss to $\dot{V}O_2$ in hare wallabies tested at various T_a's. The ratios of evaporative heat loss to simultaneous $\dot{V}O_2$ are indicated on the right-hand ordinate. Values of 0.58 cal/mg and 4.8 cal/cm³ have been used for converting values for O_2 consumption and evaporative water loss to thermal terms.

behavior. Use of forms within clumps of porcupine grass protects the animals from the intense solar radiation prevailing in open areas and maintains them under ambient thermal conditions at or just above the zone of thermal neutrality (34–37 C). Our laboratory measurements indicate that such temperature conditions foster some hyperthermia but little or, at most, modest efforts at evaporative cooling. These efforts would not require the licking response. The ability of hare wallabies to tolerate a 3 C rise in T_b obviously improves their position with regard to heat exchange in warm environments and thereby compensates for their inherently low T_b. The storage of the 6.8 kcal producing the 3 C rise of body temperature from levels maintained in the absence of heat stress also represents a potential saving of 11.7 g of water, an amount equivalent to the total water used for thermoregulation during exposure to 40 C for nearly 1 h (see fig. 2). This value also represents approximately 10% of the minimum daily requirement of 1.8-kg jackrabbits (*Lepus californicus*) for preformed water in summer under field conditions (Nagy, Shoemaker, and Costa 1976).

The climate of Barrow Island is ameliorated to some extent by the Indian Ocean, a fact impressed upon us by comparing maximum daytime temperatures at Onslow, on the nearby Western Australian coast, with those on the island (45 vs. 38 C). It appears unlikely that hare wallabies on Barrow Island are normally required to use their full powers of evaporative cooling in heat defense, owing to their success in reaching relatively undemanding thermal conditions in their forms. The distribution of hare wallabies formerly included much hotter desert regions on the Australian mainland, and it is possible that these capacities were called on more regularly there on especially hot days, even when shelter was used. The abilities of these animals for evaporative cooling may also play a role in thermoregulation during and immediately following vigorous muscular exertion. It is perhaps these considerations that fostered the evolution of extensive powers for heat dissipation. However, we believe that the basic tactic of hare wallabies involves minimizing the use of these powers through use of shelter during the day. Such a tactic, of course, allows the animal to be better able to cope with the other great challenge of a desert existence, the restricted availability of water.

Comparison of desert adaptations of hare wallabies and jackrabbits.—One of our prime interests in undertaking this study was to obtain comparative information on a marsupial that appears to be an approximate ecological equivalent of jackrabbits (*Lepus* spp.), inhabitants of North American deserts. Both animals are medium-sized herbivores that are nocturnally active. Both utilize forms within or beneath vegetation for daytime retreats. Both have well-developed capacities for evaporative cooling and can maximally dissipate heat at approximately twice the rate it is produced in metabolism, although this entails an evaporative output of no more than 8 g H_2O $(kg \cdot h)^{-1}$ in the wallaby (fig. 2) versus 13 g H_2O $(kg \cdot h)^{-1}$ in the black-tailed jackrabbit (*L. californicus*) with its higher level of metabolism (Schmidt-Nielsen et al. 1965).

One result of the study by Dawson and Schmidt-Nielsen (1966) that has attracted a good deal of attention among students of thermal regulation is the claim that the antelope jackrabbit (*Lepus alleni*) substantially reduces the

heat-transfer coefficient (θ) as T_a exceeds T_b (Dawson and Schmidt-Nielsen 1966). Such a capacity would retard heat flow into the body under these conditions. It was assumed that this decrease in the value of θ was primarily achieved by reducing blood flow to the pinnae. However, recently reported thermograms of these structures in black-tailed jackrabbits under heat stress fail to demonstrate any substantial vasoconstriction (Hill and Veghte 1976). Hind's (1977) observations of antelope jackrabbits indicate that θ does not rise significantly as T_a exceeds T_b. However, it was not found to decline dramatically, as claimed by Dawson and Schmidt-Nielsen (1966). Our analysis of θ in hare wallabies indicates that the value of this coefficient increases steadily from thermal neutrality through T_a's exceeding T_b. While the jackrabbit and hare wallaby differ in certain quantitative details of their physiological responses to heat, we believe that this difference pales in comparison to the similarities in the manner in which these medium-sized herbivores contend with desert conditions: nocturnality, extensive powers of heat defense, controlled hyperthermia, and use of forms in or beneath vegetation in evasion of the extreme conditions of their respective environments.

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