

HEAT TOLERANCES OF AUSTRALIAN MONOTREMES AND MARSUPIALS

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Summary

Heat tolerances of monotremes and marsupials have been compared by exposing the animals in a hot room, on different days for 7-hr periods, to various combinations of dry-bulb temperature ranging from 86° to 108·5°F with absolute humidity from 15 to 40 mm v.p.

Changes in their various physiological responses during heat exposure were examined.

Animals studied included the echidna, platypus, bandicoot, possum, cuscus, koala, wallaby, and wallaroo.

Results show an evolutionary trend in homeothermism. The monotremes possess the most primitive type of heat regulation, relying primarily on metabolic regulation to maintain body temperature. Sweat glands on the snout and over the body of the platypus give it a slight advantage over the echidna in hot, dry atmospheres.

Marsupials show a distinct advance on monotremes in heat regulation in employing both respiratory and non-respiratory evaporative mechanisms to an increasing degree, in the following ascending order: bandicoot, possum, cuscus, koala, wallaby, wallaroo. The cuscus, which inhabits the coastal regions of tropical Queensland and New Guinea, has a more effective evaporative mechanism than the more widely distributed possum.

Animals which rely to a large extent on evaporative methods for heat disposal are more distressed in humid atmospheres than those which favour other methods of heat disposal.

I. INTRODUCTION

Towards the close of the last century, isolated observations were made on the body temperatures of monotremes and marsupials (Miklouho-Maclay 1884; Semon 1894; Vernon 1898). Then appeared two important papers, first that of Sutherland (1896) recording body temperature at different air temperatures, and later Martin's (1903) valuable metabolic studies during heat exposure.

As an outcome of these experiments, several investigators, notably Sutherland (1896), Vernon (1898), and Martin (1903, 1930), pointed out that these two groups of animals present a stage of physiological development intermediate between the close approaches to homeothermism of the higher mammals and the rudimentary indications of this in lower vertebrates. Further details were added when daily body temperature variations in the echidna were recorded by Wardlaw (1918).

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Although in recent years some detailed studies of heat regulation have been carried out on American marsupials (Morrison 1946; Schmidt-Nielsen and Schmidt-Nielsen 1952), there has been a dearth of similar work in Australia. Since Australian lower mammals, particularly the monotremes, hold such an interesting position in the phylogenetic development of thermo-regulation, it was felt that this deficiency of knowledge should be remedied and to meet this need the present study was undertaken. In this investigation the heat tolerances of monotremes and marsupials are compared and changes in several physiological parameters during heat exposure are recorded.

II. METHODS

(a) Atmospheres

The animals were exposed for 7 hr, twice a week, to 11 combinations of dry-bulb temperatures varying from 86° to 108.5°F with absolute humidities between 15 and 40 mm v.p. Air movement remained constant at an average velocity of 60 ft/min.

(b) General Conditions

The animals remained in the air-conditioned room in which the required temperature and humidity had been produced for 7 hr or until a rectal temperature of 101°F for monotremes or 103°F for marsupials had been reached. Just above these temperatures signs of heat stroke begin to appear (Robinson and Lee 1946). Free access to water was allowed during the heat exposure period. The animals were fed before but not during the experimental period.

The species, as classified by Troughton (1941) and Wood Jones (1923), and number of animals used in the experiment were:

Monotremes:

Platypus (*Ornithorhynchus anatinus*): four animals
(two male, two female).

Echidna (*Tachyglossus aculeatus*): four animals
(two male, two female).

Marsupials:

Bandicoot (*Perameles nasuta*): five animals
(three male, two female).

*Possum (*Trichosurus caninus*): four animals
(two male, two female).

Cuscus (*Spilocuscus nudicaudatus*): five animals
(one male, four female).

Koala (*Phascolarctos cinereus*): two animals
(two female).

Wallaby (*Petrogale penicillata*): one animal
(female).

* The initial 'o' has been omitted deliberately to distinguish it (a diprotodont) from the American or true opossums, which belong to the polyprotodont sub-order of marsupials (Troughton 1941).

TABLE 1
MEAN 9 A.M. READINGS WITH STANDARD DEVIATIONS

	Monotremes		Marsupials					
	Echidna	Platypus	Bandicoot	Possum	Cuscus	Koala	Wallaby	Wallaroo
No. animals	4	2	5	4	5	2	1	1
No. observations	39	10	49	46	50	22	11	5
Body wt. (kg)	3.8±0.3	0.75±0.12	4.6±1.5	3.5±0.9	3.2±1.1	3.4±0.2	16.4±0.8	37.2±0.5
Rectal temp. (°F)	83.1±3.3	86.0±2.7	95.7±1.2	94.5±1.5	94.8±1.5	97.0±1.2	97.8±1.4	93.4±0.4
Rectal temp. (°C)	28.4±1.8	30.0±1.5	35.4±0.6	34.7±0.8	34.9±0.8	36.1±0.6	36.5±0.8	34.1±0.2
Pulse rate/min	96±13	115±5	158±24	226±25	142±43	79±10	73±11	64±8
Resp. rate/min	11±3	19±1	82±25	75±24	92±26	38±9	64±8	48±10

Wallaroo (*Macropus robustus*): one animal
(female).

All animals were healthy young adults and their body weights are set out in Table 1. Food supplied to the platypus consisted of prawns and worms; and a pool with bank of sand was available for swimming and burrowing during non-experimental periods. The echidnas were fed bread and milk, finely minced meat, and hard-boiled eggs. A vegetable diet comprising gum leaves, fruit, and root and leafy vegetables was provided for the marsupials.

The following observations were made immediately before the animals entered the hot room and at hourly intervals thereafter: rectal temperature—by clinical thermometer; pulse rate—by stethoscope over the heart or manual palpation of the femoral artery (wallaby, wallaroo); respiratory rate—by observing movements of the flank. Animals were weighed hourly on a Sauter balance sensitive to 1 g. Urine and faeces were collected; the water consumed was measured; and evaporative weight loss was determined by difference.

III. RESULTS

(a) Rectal Temperature

The mean 9 a.m. ante-room rectal temperature for each species, with standard deviation and number of estimations, is given in Table 1. The experiments were carried out in autumn, winter, and spring, when the 9 a.m. dry-bulb air temperatures ranged from 57° to 77°F.

The values fall into two distinct groups: the monotremes with a low body temperature and a considerable range of variation (S.D. $\pm 2.7^\circ$ to $\pm 3.3^\circ\text{F}$), the marsupials with a higher body temperature and a restricted variation (S.D. $\pm 0.4^\circ$ to $\pm 1.5^\circ\text{F}$).

As with most other animals when exposed to heat (Lee and Robinson 1941), the rectal temperature rose during the first 2 hr, the rise being much greater in monotremes (3.5°F/hr) than in marsupials (1°F/hr) (Fig. 1A, B). By comparison, Lee and Robinson found that in Eutheria, under resting conditions, rectal temperature rises only with shade air temperatures above 90°F, and then the rate of rise in the first 2 hr varies between 0.5° and 1°F/hr. Unless the conditions were too severe, a new equilibrium between heat gain and loss was reached by marsupials at a higher rectal temperature than normal. This equilibrium was approached but rarely achieved by the monotremes.

The effect on heat tolerance of varying dry-bulb temperature at constant humidity and varying humidity at constant dry-bulb temperature is shown in Table 2. It will be noted that heat tolerance is much lower in monotremes than marsupials, and in addition the separate effects of dry-bulb temperature and humidity differ in the two subclasses. The monotremes are greatly stressed by rising dry-bulb temperatures, whilst rising humidity at 90.5°F is fairly well tolerated. With the marsupials, both dry-bulb temperature and humidity play a part in producing heat stress but the evolutionarily more primitive types,

TABLE 2
HEAT TOLERANCES*

	Atmosphere		Monotremes		Marsupials					
	Dry-bulb Temperature (°F)	Humidity (mm v.p.)	Echidna	Platypus	Bandicoot	Possum	Cuscus	Koala	Wallaby	Wallaroo
Varying dry-bulb temperature at constant humidity	86	20		53	96	63	83	85	88	81
	90.5	20		14	84	67	79	79	92	
	95	20		-57						
	86	30	23	53	73	62	64	73	84	
	90.5	30	2	20						
	95	30	-128							
	99.5	30			60	53	60	69	83	
	104	30	-170		42	45	58	65	77	58
	103.5	30			5	37	52	52	76	
	93	40	-120							59
	95	40								56
	101	40								22
Varying humidity at constant dry-bulb temperature	90.5	15	13							
	90.5	17	11							
	90.5	20		14						
	90.5	25	13							
	90.5	30	2	20						
	95	30	-128							
	95	40	-102							
	104	15								
	104	20								
	104	25								
	104	30	-170							
	104	35								
	104	40								
					59	56	—	74	83	
					58	46	59	71	87	
					44	34	54	71	73	
					42	45	58	65	77	
					38	36	49	61	40	
					25	28	38	51	27	

* Heat tolerance coefficient = $100 - (\text{average rectal temp. in room} - \text{average ante-room rectal temp.}) \times 10$.

without efficient evaporating cooling, are more affected by dry-bulb temperature than are the more advanced types. The somewhat primitive bandicoot is more stressed by high dry-bulb temperature than humidity; the possum, cuscus, and koala equally affected by both; whilst humidity, particularly in the higher ranges, is more distressful to the wallaby, which is placed high on the evolutionary scale.

R values, which represent the areas under the reaction curves, have been used to compare the effect on each species of a particular combination of dry- and wet-bulb temperature. The values were derived from the following expression:

$$R = (a/2 + b + c + \dots + p/2) I,$$

when a, b, c, \dots, p are successive average measurements at equal time intervals, I , commencing with ante-room value assumed at zero time.

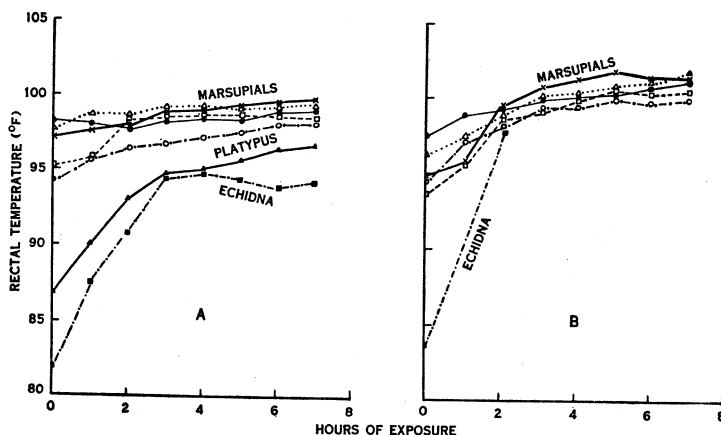


Fig. 1.—Effect of (A) 90.5°F dry-bulb temperature and 30 mm. v.p., and (B) 104°F dry-bulb temperature and 30 mm v.p. on rectal temperatures of monotremes and marsupials.

If the animal had to be removed before the period of exposure was complete, the adjusted R value was obtained by extrapolation as follows:

$$R = (a/2 + b + c + \dots + l/2) I + lt + t^2 \frac{(l-k)}{2I},$$

where k and l are the second last and last average measurements respectively, and t is the unexpired portion of the exposure.

R values for rectal temperatures of monotremes and marsupials are recorded in Tables 3 and 4.

Both echidna and platypus withstood exposure to 90.5°F for 7 hr but, when the dry-bulb temperature was increased to 95°F, the regulating mechanism became inadequate and body temperature rose rapidly to 101°F.

The bandicoot was the only marsupial unable to withstand 104°F 30 mm v.p. for 7 hr. With the exception of the Macropodidae, the remainder of the

TABLE 3
R VALUES FOR MONOTREMES OVER 7-HR EXPOSURE PERIOD

Figures in brackets have been weighted as described in the text. The number above the bracket indicates how many animals had to be removed with a body temperature of 101°F before 7 hr had elapsed; and that below, the hours that the animals remained in the room. When the animals had to be removed before sufficient figures required to estimate evaporative loss had been obtained, a blank appears in the column. An approximate mean value for rectal temperature, pulse rate, or respiratory rate may be obtained by dividing the appropriate figure by 7, and for evaporative loss by dividing by 6.

	Atmosphere		Rectal Temp. (°F)		Pulse Rate (no./min)		Respiration Rate (no./min)		Evaporative Weight Loss (g/kg)	
	Dry-bulb Temp. (°F)	Humidity (mm v.p.)	Echidna	Platypus	Echidna	Platypus	Echidna	Platypus	Echidna	Platypus
Varying dry-bulb temperature at constant humidity	86	20				801		135		35
	90.5	20		634.8		860		118		58
	95	20		662.0		(1026)		(185)		—
	86	30	635.3	(712.1) ^{2.5} _{3.5}	664	809	141	130	6	40
	90.5	30	650.6	634.8	800	759	257	137	5	58
	95	30	(741.6) ^{4.2.8} _{2.2}	657.7	(1088)		(472)		—	—
	104	30	(770.9) ^{4.2.2} _{2.2}		(1182)		(992)		—	—
Varying humidity at constant dry-bulb temperature	90.5	15	642.4		738		151		7	
	90.5	17	644.1		798		169		13	
	90.5	20		662.0		860		118		58
	90.5	25	642.4		764		143		10	
	90.5	30	650.6	657.7	800	759	257	137	—	58
	95	30	(741.6) ^{4.2.8} _{2.8}		(1088)		(472)		—	
	95	40	(723.0) ^{4.2.9} _{2.9}		(1014)		(449)		—	

group had to be removed with signs of heat stroke at a dry-bulb temperature of 108.5°F .

It is interesting to note the superiority of the cuscus over the possum in hot atmospheres (Table 4 and Fig. 1). Both animals belong to the Phalangeridae.

(b) Pulse Rate

Normal values for pulse rates at rest in the absence of heat stress are given in Table 1. As with most poorly sweating animals (Lee and Robinson 1941), the pulse rate of monotremes and marsupials shows little rise with continued exposure to a room temperature which produces a marked rise in rectal temperature. Neither change in humidity nor change in dry-bulb temperature has a significant effect (Tables 3 and 4).

(c) Respiratory Rate

Monotremes respire at a much slower resting rate than marsupials (Table 1). Martin (1903) showed that respiratory rate changed little when the monotremes were exposed for short periods (30 min) to different temperatures. Even after 7 hr exposure in our experiments, the rate of respiration remained slow, except at the highest range of temperature. Open-mouthed panting did not occur.

As a marked contrast, the rate of breathing increases rapidly in marsupials during heat exposure, particularly in hot, dry atmospheres (Table 5). With more stressful conditions, the mouth opens slightly to allow increased evaporation from the buccal cavity. Panting is minimal in the cuscus but particularly marked in the wallaroo, where it resembles the panting of a dog.

(d) Evaporative Weight Loss

Weight loss has been estimated as g/kg body weight in order that a comparison may be made between species.

The following findings are recorded in Tables 3 and 5:

- (i) The platypus has a higher rate of evaporation than the other mammals.
- (ii) Monotremes show very little change of weight with rising temperature.
- (iii) In marsupials, evaporative loss increases markedly as dry-bulb temperature rises but remains fairly constant with changing humidity. This correlates highly with respiratory rate. The cuscus, however, does not lose water proportionally to respiratory rate.

The apparent increase in values with some of the highest humidities may be explained by increased loss through drooling.

(e) Behaviour

Details of the behaviour of echidna, bandicoot, possum, cuscus, and wallaroo in hot atmospheres are described in an earlier publication (Robinson and Lee 1946).

The outstanding feature of the behaviour of the platypus when exposed to heat is drowsiness. It lies at first curled up in a ball, but as body temperature rises to 95°F its posture changes. It then rolls over on to its back with under surface exposed and legs outstretched but still remains inactive. There is a slight increase in respiratory rate but no attempt at panting. With higher body temperatures, the platypus becomes very restless and a slight tremor develops over its entire body, suggesting some impairment of neuro-muscular coordination. During heat exposure, this animal neither salivates nor increases evaporation from the body surface by coat licking.

The koala curls up and remains asleep at external temperatures of 86°F. At higher temperatures, which cause only a slight rise in body temperature, respiratory rate increases rapidly. When body temperature approaches 99°F, it begins licking its front and hind paws, the pads particularly, and it rubs their wet surfaces over its face. At this temperature, it also sits back like the possum, exposing its chest and abdomen. Later panting commences but the mouth opens only slightly and, although there is some dribbling on to the chin and abdomen, it is less profuse than that of the possum. Troughton claimed that the koala never drinks water but in these experiments, when body temperature rose to 101°F, it would repeatedly move over to its drinking vessel and lap small quantities. Evidently this is a procedure adopted only under severe heat stress.

When first exposed to a hot climate, a wallaby sits quietly though less drowsily than the other marsupials. Increased respirations occur after slight rise in body temperature and, when this reaches 100°F, rapid respirations are replaced by open-mouthed panting. Around this temperature, the animal continually licks its forearms and body and wipes its face with the wet paws. At 101°F body temperature, dribbling is profuse. The wallaby repeatedly drinks small quantities of water, a 16-kg wallaby consuming 150-250 ml in the 7-hr exposure period. At a body temperature of 103°F heat staggers begin to develop in its hind legs. The behaviour of wallaroos closely resembles that of wallabies in a hot environment.

IV. DISCUSSION

These results are in agreement with Martin's findings that monotremes exhibit some degree of homeothermism although the stability of their heat regulating mechanism can be easily upset at air temperatures above 90.5°F. The platypus is somewhat better regulated than the echidna in this respect.

Monotremes do not pant and are devoid of vasomotor adjustments, as shown by the circulatory experiments of Martin (1903) and pulse rate figures in this study. The only method available therefore to prevent over-heating is metabolic regulation—the reduction of heat production (Martin 1903). This would thus seem to be the most primitive type of heat-regulating mechanism used by mammals. It necessitates an inactive existence during the daytime. The animals spend this period in burrows where air temperatures are lower (rarely exceeding 86°F, as shown by Vorhies (1945)), and so are able to

TABLE 5

R VALUES FOR RESPIRATORY RATE/MIN AND FOR EVAPORATIVE WEIGHT LOSS (g/kg) FOR MARSUPIALS OVER 7-HR EXPOSURE PERIOD

Figures in brackets have been weighted as described in the text. Blanks are explained in Table 3. Evaporative loss was not measured in the koala. An approximate mean value for respiratory rate or evaporative loss may be obtained by dividing the appropriate figure by 7 or 6 respectively

	Atmosphere		Bandicoot		Possum		Cuscus		Koala	Wallaby		Wallaroo	
	Dry-bulb Temp. (°F)	Humidity (mm v.p.)	Resp. Rate	Evap. Loss	Resp. Rate	Evap. Loss	Resp. Rate	Evap. Loss	Resp. Rate	Evap. Loss	Resp. Rate	Evap. Loss	
Varying dry-bulb temperature at constant humidity	86	30	329	2.8	490	12.6	521	6.9	254	17.8	392	19.1	
	90.5	30	384	5.0	585	11.4	326	10.6	940	19.4			
	95	30	758	12.4	564	16.3	361	12.8	1140	16.1			
	99.5	30	1113	12.6	852	20.0	707	15.0	1343	25.2			
	104	30	(1364)	(21.5)	1121	37.1	730	18.1	1436	36.2	1892	30.9	
	108.5	30	(1926)	—	(1348)	(39.4)	(935)	(40.0)	(1570)	39.6			
	93.0	40									1828	8.7	
	95	40									1956	20.4	
	101	40									1940	15.6	
Varying humidity at constant dry-bulb temperature	104	15	927	14.1	754	31.1			1157	46.6			
	104	20	1168	13.9	(1231)	(36.0)	732	21.3	1320	34.9	1178		
	104	25	(1561)	(18.0)	(1569)	(33.4)	626	17.8	1334	36.5	1464		
	104	30	(1364)	(21.5)	(1121)	(37.1)	730	18.1	1436	36.2	1607		
	104	35	(1531)	(32.4)	(1458)	(31.4)	1012	18.8	1543	—	(2027)		
	104	40	(1949)	—	(1887)	(36.8)	(1038)	(22.5)	(1623)	—	(1850)		

survive the hot Australian summers. Since evaporation is not an important cooling mechanism in monotremes, hot, wet climates with a lower dry-bulb temperature are preferred.

The slight superiority of the platypus over the echidna in heat regulation may be explained by differences in evaporative loss. The echidna has no sweat glands, whilst these are generously scattered over the snout of the platypus and in addition one apocrine gland opens into the follicle of each of the large hairs (Wood Jones 1923; Hardy 1944). Since neither animal alters respiratory rate significantly during heat exposure, the increased water evaporated from the platypus in hot, dry atmospheres is to be interpreted as increased activity of these sweat glands. Since they are confined to such a small area, their effectiveness is very limited.

Marsupials show a distinct advance in homeothermism, being able not only to vary heat production (Martin 1903) but heat loss as well. The higher body temperature would to some extent aid heat transfer by radiation but by far the greater loss arises from increased powers of evaporation (*a*) from the respiratory tract, and (*b*) from the body surface. The additional evaporation which takes place from the buccal mucosa during open-mouthed panting is evident when measurements of respiratory rate and evaporative weight loss are compared. Although, histologically, sweat glands can be demonstrated over the entire body surface of marsupials (Bolliger and Hardy 1945; Hardy 1947), they are of a primitive apocrine type and their poor functioning power is shown by the readiness with which these animals use saliva to aid evaporation, particularly from the abdomen, limbs, and tail. The cuscus appears to use a non-respiratory type of evaporative mechanism extremely well. Comparing it with the possum (a member of the same family), we find that, in hot, dry climates, evaporative weight loss rises much more steeply than does increase in respiratory activity. This is associated with a better heat tolerance response. It is interesting to note that the cuscus is restricted to the hot coastal regions of tropical Queensland and New Guinea whilst the possum abounds in more temperate parts. It is likely that this difference in evaporative power has been developed over the years as an adaptation to the thermal stress of the tropics. It could arise in one or both of two ways:

- (*a*) By a more efficient sweating mechanism; or
- (*b*) By a superior method of salivary application.

Histological studies should yield some information on the sweat glands, but they have not yet been examined in sufficient number. Skin sections taken from a single specimen of cuscus showed a fair number of sweat glands (one associated with each primary hair follicle) and these seemed to be functioning actively (Hardy, personal communication 1953). That sweating is probably the true explanation is suggested from evidence of Hardy (1947) that bandicoots from tropical districts tend to show better-developed sweat glands than those from colder areas. The constant licking of the bare tail would favour salivary cooling techniques whilst the peculiar posture adopted and the large water intake when body temperature rises would support both concepts.

The degree of development in marsupials of an evaporative mechanism for heat removal parallels structural evolutionary trends. Heat tolerance correlates with this evolutionary picture, increasing in the following ascending order: bandicoot, possum, cuscus, koala, wallaby, wallaroo. Evaporative cooling is more effective in hot, dry than in hot, wet climates and animals which rely most upon it are most affected by rising humidity. This method of heat transfer finds its highest development in man and the horse.

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