THE UNIVERSITY OF WESTERN AUSTRALIA

DEPARTMENT OF ZOOLOGY

Thesis

GROWTH AND BIOENERGETICS OF THE CHUDITCH, DASYURUS GEOFFROII

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"'Native cat' is a misnomer," remarked the Senator, as we climbed the bank. "The animal belongs to the Dasyuridae, not to the Felidae. The distinction is an extremely far-reaching one; it is more than specific, it is generic. Worth knowing, that the Dasyuridae are peculiar to Australia, Tasmania, and New Guinea; whilst Australia, Madagascar and the Antilles are the only parts of the world destitute of indigenous Felidae. Apparently, however, the native cat is ichthyophagous upon occasion, like the domestic cat."

"Well, no; he ain't," replied Dixon, politely captious toward a rival pedant. "He's always spotted - white on top o' yallerish grey. Now an' agen, he's spotted white on top o' black, but that's on'y a case of exceptio probat (adj.) regulam, as the sayin' is. Curious thing, Rigby, the natey cat he'll eat any (adj.) thing, and no (adj.) thing'll eat the natey cat."

Joseph Furphy Rigby's Romance

First published in the "Barrier Truth" 1905-6

SUMMARY

1. Dasyurus geoffroii produces litters of six after a gestation period of 15-17 days. The neonates weigh about 15 mg. Young are born in late autumn or winter (May-July) and become independent of the parent in the spring (September-November). Reproductive maturity is reached in the first breeding season after birth.

2. Age-relative growth of three measurable features, development of topographical features and tooth eruption sequence provide "landmarks" for comparison with other species and a means of aging pouch-young.

3. Juveniles are homeothermic at 16 weeks when the pelage is fully developed.

4. Adult thermoregulation is efficient at ambient temperatures of 0° to $40^{\circ}C$.

5. Body temperature is variable below the thermal neutral zone and shows a circadian cycle in which temperature is lowest during the morning and highest in early evening or pre-dawn.

6. Torpor was occasionally observed. Arousal from torpor was accompanied by shivering as body temperature rose at a rate of 0.1-0.3 degrees per minute to "normal" levels (35°-$38^{\circ}C$).

7. Rates of O_2 consumption, breathing, evaporative water loss and heart rate within the thermal neutral zone (27°-$33^{\circ}C$) are comparable with values determined for other marsupials.

8. Long periods when O_2 consumption falls close to the basal level occur below the lower critical temperature. Such periods are accompanied by falling body temperatures. This phenomenon must result in savings in energy usage.

9. Body temperature increases at ambient temperatures above 30°C until it equals ambient temperature at 39°C. Thus a gradient is maintained from the body to the environment so that non-evaporative heat loss can occur until 39°C. Evaporative heat loss, facilitated by panting, can exceed heat production at higher ambient temperatures.

10. Rates of O_2 consumption and evaporative water loss are significantly correlated with body temperature.

11. Thermal conductance below the thermal neutral zone approximates McMillen and Nelson's (1969) empirical relationship for the dasyurids.

12. The mean of weight-relative blood volumes of individual animals falls within the normal range of blood volumes of eutherian mammals.

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Mr. Alex Baynes of the Western Australian Museum provided me with information about the distribution of the species and gave permission to use the maps, Fig 2.1 and Fig 2.2.

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ABBREVIATIONS USED IN THE TEXT

ABBREVIATION	EXPLANATION
T_a	Ambient Temperature: air temperature in the immediate environment of the animal.
T_b	Body Temperature: measured by a thermistor probe or a mercury-in-glass thermometer inserted through the cloaca to a depth of 8-10 cms in the colon.
SMR	Standard Metabolic Rate: Mean resting rate of O_2 consumption at T_a 30.0°-30.9°C, taken to be the centre of the thermal neutral zone. SMR is expressed as ml O_2/kg.min. or, assuming a respiratory quotient of 0.8 and a caloric equivalent of 4.8 cal/ml O_2, as kcal/day.
HP	Heat Production: calculated from O_2 consumption assuming the caloric equivalent of O_2 as above.
EWL	Evaporative Water Loss: The combined evaporative water loss from the skin and the respiratory surfaces, whether insensible loss in the absence of thermal stress or with pulmonary loss facilitated by high breathing rates.
I.W.	Insensible Water Loss: the combined water loss from the skin and respiratory surfaces in the absence of thermal stress, i.e. below the panting and/or sweating threshold.

DEFINITIONS

STANDARD METABOLIC RATE

The rate of oxygen consumption (as an index of the rate of metabolism) measured when the animals were resting during the daytime, fasted for at least 24 hours, and in a thermal neutral environment.

THERMAL NEUTRAL ZONE

The ambient temperature at which metabolism is minimal, below which and above which the rate of metabolism rises; the ambient temperature at which the resting animal expends least thermoregulatory effort while body temperature is maintained above torpid levels.

LOWER CRITICAL TEMPERATURE

The ambient temperature below which the rate of metabolic heat production of a resting, thermoregulating animal increases by shivering and/or nonshivering thermogenic processes to maintain thermal balance (Bligh and Johnson, 1973).

UPPER CRITICAL TEMPERATURE

The ambient temperature above which the rate of metabolic heat production of a resting animal increases above minimal levels and active evaporative cooling commences (as measured by increase in the breathing rate above the minimal level).

TORPOR

A state of inactivity and reduced responsiveness to stimuli associated with a reduction in metabolism and body temperature (Bligh and Johnson, 1973). Animals with body temperatures below $30^{o}C$ were considered to be torpid.

CHAPTER I

INTRODUCTION

Studies of the Western Australian carnivorous marsupials are few although there are nine contemporary species which occur in the south-west of the state. This is due to their cryptic behaviour, rarity and difficulty of capture. Furthermore they are difficult to maintain and breed in captivity. The Western Native Cat, or Chuditch, Dasyurus geoffroii is one such native carnivore which has been little studied.

The species is of special interest because its range extends from the temperate south-western corner of the Australian continent, through the dry sclerophyll woodland, to the arid interior (Ride, 1970). Thus it can be expected to display adaptations which would fit it to life under stringent environmental conditions. A further reason for studying aspects of the biology of the species is its apparent rarity. The meagre evidence available suggests that it is at present much less common than earlier in the period of European settlement.

It was apparent that the success of a field study would be uncertain because resources were too limited to mount an effective investigation of this rare species. Instead, attention was turned towards establishing and maintaining a captive colony of D. geoffroii from which

animals could be drawn for laboratory studies on aspects of the energy metabolism. At the time when the study was started it was becoming clear that the herbivorous macropodid marsupials had lower energy requirements than analagous eutherian mammals, but that the kangaroos and wallabies could in no way be regarded as less efficient or 'second-class' mammals. I set out to determine whether the same could be said for the carnivorous Dasyurus geoffroii. Since that time much evidence has accumulated to show that species from all of the marsupial groups have lower resting metabolic levels than most eutherian mammals, and at the same time display patterns of energy usage which fit them for diverse environments.

The study centred on a study of thermoregulation of the species, in particular:

1. the effectiveness of temperature regulation, and
2. the 'cost' of maintaining body temperature as it could be measured by rates of oxygen consumption and evaporative water loss over a range of environmental temperatures which approximated that likely to be encountered by the species in the wild.

The breeding colony founded to supply adults for metabolic studies provided the opportunity to document the growth and development of the species and aspects of the breeding biology. The results of this portion of the study permit comparison with other marsupial species and provide a means of estimating the age of the pouch young.

CHAPTER II

MATERIALS AND METHODS

The Animal

Dasyurus geoffroii Gould, 1841 (Marsupialia; Dasyuridae) is a nocturnal carnivore. Its distribution extends from the west coast of Australia south of the Fitzroy River, as far east as the Great Dividing Range (Ride, 1970). Figs 2.1 and 2.2 were provided by Mr. Alex. Baynes of the Western Australian Museum. Fig 2.1 shows the distribution of live and fossil specimens collected since European colonization in the nineteenth century. Fig. 2.2 shows localities of live specimens captured since 1957, and indicates that present distribution of the species appears to be restricted to the temperate and semi-arid south-western region of the Australian continent. Shortridge (1909) considered that it did not extend far inland from the west coast and 'was killed off as much as possible in the agricultural and more thickly populated districts on account of being so destructive of poultry'. Although people who have had long associations with rural areas in the south-west of Western Australia comment that it used to be well known, particularly for its depredations on poultry yards, it is now rarely seen. Nevertheless, it still extends into semi-arid areas. I obtained one live specimen from Hyden in 1969, 350 km east of Perth, and a sighting was reported in 1973,

Fig 2.1 Map of Australia showing localities at which Dasyurus geoffroii has been captured since European exploration and settlement or at which fossil material has been found.

Fig 2.2 Map of Australia showing localities at which live specimens of D. geoffroii were captured in the years 1957-1973.

Symbols:

- ● modern specimen
- ◘ fossil specimen
- ■ both modern and fossil specimens

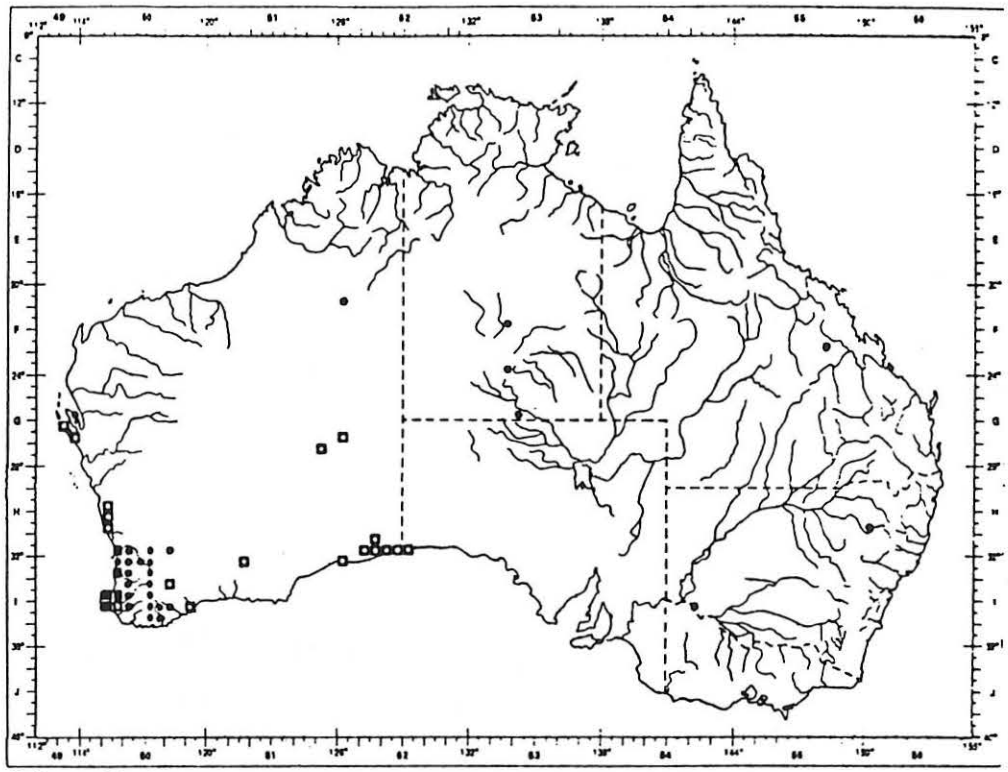


Fig. 2.1

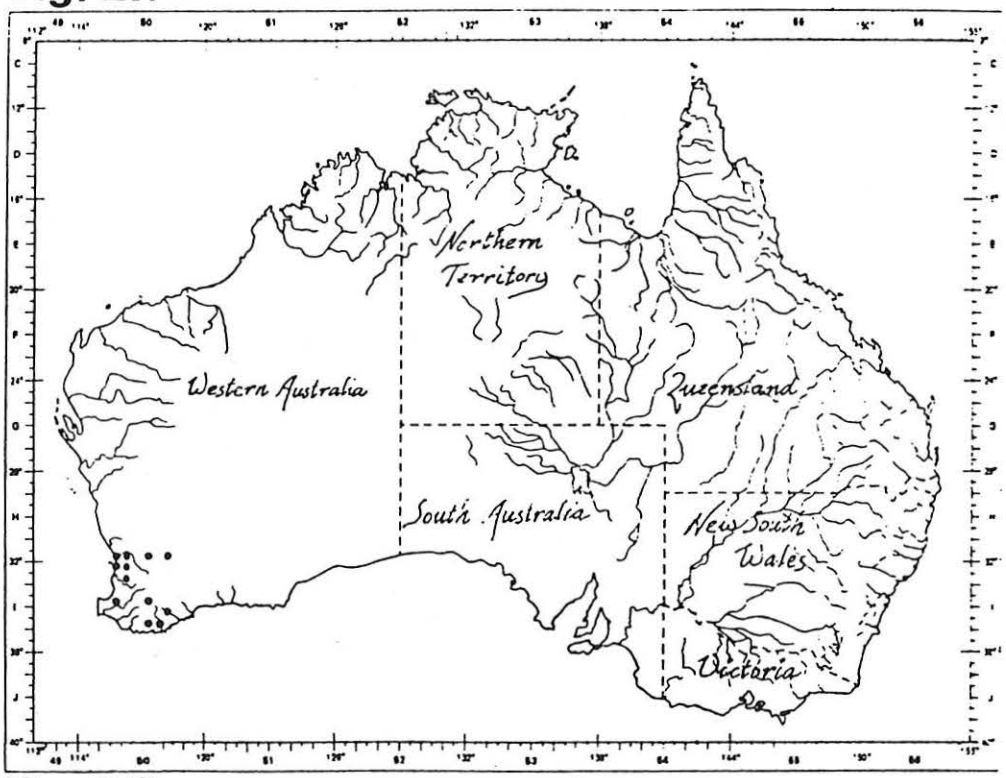

Northern Territory
Western Australia
Queensland
South Australia
New South Wales
Victoria

Fig. 2.2

by a reliable source, from Ravensthorpe, 560 km south-east of Perth.

It was thought that words used to describe the animal in Aboriginal languages may indicate the distribution of the species. However, the only words which clearly refer to it come from Njungar, a collection of survivors of dialects from south-western Australia. These words are transliterated as tjutidj, or djuditj meaning native cat, and wiyu meaning spotted native cat. There appears to be no known word for the animal in the inland languages in which wiyu is applied to the feral domestic cat (Douglas, 1968).

The common name of Dasyurus geoffroii is 'western native cat' or 'chuditch'. Shortridge (1909) gave chuditch as the name used by aboriginals of the Beverley area (130 km east of Perth). The name chuditch is obviously derived from the Njungar word and is generally recognized by people familiar with the animals. It has been used as a common name for the species by Ride (1970). Chuditch will be used throughout this study as a recognized common name for Dasyurus geoffroii. Its use avoids confusion which may arise from the use of the word 'cat' with feral domestic cats which are now widespread in many parts of Australia.

Source of Animals used in the Study

The localities from which animals were obtained for the captive colony are shown on Fig 3.1. The first

opportunity to form the colony arose when a female with a pouch litter, trapped by Mrs. Slater at Karragullen, and a second female with a litter, from Collie, were obtained in 1966 and 1967 respectively. These two females with their litters and a further five females and six males, captured in the forest areas within 170 km of Perth, together with a male obtained by Mrs. Feehan of "Hyridge", East Hyden, formed the basis of the colony. Six of the females had a total of 31 pouch-young when taken from the wild. During the study, 33 animals were born in captivity. The birth dates of 23 of these were known with some accuracy. The colony was supplemented from time to time by animals which were trapped near poultry runs following reports of losses of chickens. The chuditch being protected by law, such damage was reported to the Department of Fisheries and Fauna which agency made the information available to me and gave permission to trap in the vicinity.

Maintenance of Animals

The animals were caged singly, in male/female pairs or in small groups consisting of a female and her litter. It was found to be necessary to remove males from cages containing females with litters as the males often killed the young animals when they began to move about the cage away from the female.

The cages were of two sizes, either 2 m x 2 m x 2 m, or 1 m x 3 m x 3 m. They were roofed, had concrete floors

and were enclosed on at least one side with glass or galvanized iron. The remaining sides of the cages were enclosed with wire-netting. A nest-box was placed within each cage, together with a stout tree-branch on which the animals could climb. The animals were fed on raw meat, fresh fish and eggs. Drinking water was freely available at all times.

I found the animals difficult to handle at first. The cost of early experience was badly lacerated hands, either from slashing strokes of the canines, or from rapid repeated bites from the molariform teeth. With practice, however, it was possible to handle them without gloves, and without undue disturbance either to the animal or the handler.

Observations on Breeding

In the first autumn after the colony was founded, copulation was observed between litter mates reared in captivity, but no young were born. In the next two years litters were born to captive animals. Observations on the animals maintained in the colony as well as on animals captured from the wild were used to obtain information about the breeding biology of the species.

Season of birth.

The season of birth in captivity was determined from the observed birth dates of six captive-born litters. Birth dates estimated from body weights and linear measurements of

six litters of females trapped in the wild with pouch litters were used to estimate the breeding season in the wild.

Reproductive maturity.

When the birth dates of animals were known from observation, or could be closely approximated by measurements, it was possible to determine the ages of reproductive maturity by determining the date of birth of their first litters. This was possible in the case of three females and two males.

Gestation period, birth weight, litter size and sex ratio.

Observations of copulations by caged pairs in the yard colony and regular examinations of the pouches of the females enabled estimates of the gestation period to be made for four different animals. In three instances the gestation period was estimated from the date of the last observed copulation of continuously associated pairs to the first observation of a pouch litter. In a fourth instance a female, which had been in a cage on her own for nine weeks and then caged with a male for only six days, gave birth to a litter 15-17 days after its separation from the male.

Six litters were born in captivity. One animal was removed from each of four of these litters immediately the litter was first observed in the pouch. Pouch young removed from these four litters were weighed to the nearest 0.1 mg. These weights were used to approximate the mean and range of birth weight.

The number of individuals in each of the six litters born in captivity and in a further six litters taken from the wild, was recorded to allow the calculation of mean litter size.

It was not possible to determine the sex of very young animals from external features and there was considerable mortality of pouch young between early examination of the pouch and subsequent observations. The sex of the animals could be determined at about six weeks of age. Insufficient observations were made to establish whether it could have been determined earlier. When the sex of the animals could be determined on the first observation (i.e. in litters taken from the wild) or when there was no mortality between the first count of the litter and that at which the sexes could be distinguished, the numbers of males and females were recorded for a preliminary estimate of the sex ratio.

Growth and Development of Pouch-young

Growth.

Animals from three litters of known age were weighed and head and pes lengths were measured repeatedly in order to establish three growth vs. age relationships. Only a few measurements were made on animals younger than seven weeks because it was found early in the study that they were unable to reattach to the maternal teat after they had been removed for measurement. Weights of four new-born animals and a single

set of measurements from each of three animals aged between 14 and 42 days were obtained. These seven animals did not survive. Two animals removed from the pouch for measurement at 49 days of age survived. Eight animals aged between 56 and 126 days of age were weighed and measured at weekly intervals. Subsequently these eight animals were weighed and measured less frequently until they were 365 days of age.

Weights and measurements of these eight animals when aged one year, and weights and measurements of 11 animals, known to be aged two years or older, were taken to calculate the mean adult weight, head length and pes length of males and females.

Weights and measurements of the known-age animals, when they were aged one year or less, were displayed as scatter diagrams vs. age, and smoothed curves were fitted by eye.

Instantaneous (or geometric) growth rates for weight, head length and pes length were calculated using the formula:

$$\frac{\ln V_2 - \ln V_1}{t_2 - t_1} \times 100 = k$$

where V_1 and V_2 are values of consecutive measurements, $t_2 - t_1$ is the time interval in days between the measurements, and k is the instantaneous, or geometric, growth rate, per cent per day (Brody, 1945).

Mean daily increments (arithmetic growth rates) in body weight, head length and pes length were calculated for the age interval 0-32 weeks.

Smoothed growth curves for body weight, head length and pes length, in conjunction with geometric and arithmetic growth rates, were used as a means of relating growth to stages in development and to provide a basis for comparison with other species.

Development of pelage, topographical features, dentition and motor responses.

When known-age animals were weighed and measured, notes were also made on the development of the pelage, of topographical features, of the tooth eruption pattern, and the development of motor responses.

(a) Development of the pelage.

Serial observations of the growth of under-fur and guard hairs on individuals enabled estimates of the ages at which under-fur:

(i) first appeared on the head,

(ii) first appeared on the dorsum, and

(iii) covered the whole body;

and the ages at which guard hair:

(i) first appeared on the head,

(ii) first appeared on the dorsum,

(iii) extended to the base of the tail, and

(iv) covered the entire body.

(b) Topographical features.

Note was taken of whether: vibrissae were visible or not; lips were fused laterally, or free; eyes were

closed or open; and ears adhered to the side of the head, or erect. These observations enabled the development of these topographical features to be determined.

(c) Dental eruption sequence.

The ages at which all incisors and canines, and the cusps of the molariform teeth first appeared through the oral membranes were recorded, enabling the pattern of dental eruption to be established.

(d) Motor responses.

The ages at which certain motor responses became established were observed. These were the ability to:

(i) crawl,

(ii) right themselves when placed on their backs,

(iii) stand erect on four feet,

(iv) perceive and avoid precipices,

(v) display co-ordinated locomotion,

(vi) snarl and show teeth when teased,

(vii) inflict painful bites to handler,

(viii) run when unrestrained,

(ix) chew meat.

Estimates of Age

Weights and head and pes length measurements of known-age animals were used to construct growth trends which were used as a means of estimating the ages of animals whose birth dates were not known. The curves were constructed

from the weekly mean values of body weight, head length and pes length graphed against age.

In order to assess the age-predictive accuracy of these curves, age estimated from body weight and length measurements of animals of known-age, not used to construct the curves, were compared with their actual ages. These known-age animals came from a single litter which consisted initially of six animals. One of these was removed to determine birth weight. Four of the remaining five animals survived to 51 days of age when pes length of one animal was measured. A complete set of measurements was obtained from one animal at 64 days of age. At 84 days of age only three survived and all were weighed and measured. By 91 days, when only two remained, both were weighed and measured. These two animals were also weighed and measured when aged 108 days. These nine sets of measurements were compared with the growth curves to see how closely the age estimates so obtained agreed with known ages.

Sets of measurements, one from each of four young litters taken from the wild, were compared with the growth curves in order to estimate the date of birth of each of the litters.

Members of two litters from the wild were weighed and measured at regular intervals over several weeks and these serial measurements were compared with the growth curves in order to assess the variation likely to arise in age estimates derived from the growth curves.

Measurement of Body Temperature

Two methods were used to measure body temperature:

1. Single measurements using quick-recording mercury-in-glass thermometers.

This method was used to measure body temperature of pouch-young and juvenile animals, of adults when they were maintained at constant ambient temperatures, and of adults before entry into, and on removal from, the metabolism chamber. Depth of insertion of the thermometer through the cloaca was 1-2 cms for young animals. Initially, during a trial when body temperatures of adults were measured in the cages in which they were normally resident to provide comparison with body temperatures of juveniles (see p. 5.3 below), the thermometer was inserted to a depth of 4 cms into the rectum. The values obtained are considered to represent 'rectal temperature'. Subsequently thermometers were inserted to 5-6 cms to give body temperatures which more nearly represented deep body or 'colonic temperature'.

2. Continuous records of body temperature using thermistor probes.

Continuous records of body temperature of animals confined within the metabolism chamber were obtained by inserting a thermistor probe through the cloaca into the colon to a depth of 8-10 cms. The probe lead was covered by a flexible metal sheath to prevent the animals biting or scratching at it, and was taped firmly to the base of the tail with adhesive tape. The animals were unrestrained within the

metabolism chamber, apart from the thermistor probe connection, and could change position freely. The thermistor probe was connected to a telethermometer (Yellow Springs Instrument Company) from which values could be read directly from the dial. A continuous recording of body temperature was also obtained by means of which general trends in levels of body temperature could be monitored.

Establishment of Homeothermy

The development of the ability to maintain a stable body temperature was investigated in three groups of animals:

1. five pouch litter-mates caught in the wild, whose ages were estimated by comparison with growth curves,
2. eight captive-born animals of known age, and
3. six members of a second litter from the wild which were fully furred and semi-independent and estimated to be 17-19 weeks of age.

Individuals from the first wild-captured litter were taken from the pouch or nest-box at weekly intervals and placed in small wire cages in the laboratory at room temperature. They were otherwise unrestrained. Rectal temperatures were measured immediately after removal from the pouch or nest-box, and again after one-hour and three-hour sojourns in the cages. These measurements were carried out weekly for eight weeks and twice subsequently at intervals of three weeks. The estimated age of the animals at the beginning of this procedure was 12 weeks.

The eight animals of known age were treated similarly but body temperatures were measured at ten-minute intervals over a period of one hour. Rectal temperatures of these eight animals were measured in this way at weekly intervals from 11 weeks to 17 weeks of age. Five of the animals were treated in this way at 10 weeks and three at 18 weeks of age.

Members of the second wild-captured litter were judged to be homeothermic. The rectal temperatures were measured in the cage in which they were normally resident six times daily (0600, 0900, 1200, 1500, 1800 and midnight) for three days in order to determine whether, in the period immediately following the establishment of homeothermy, body temperature fluctuated with environmental temperature or whether it followed the adult pattern which is independent of environmental temperature variations. At the same times, as a control and for comparison, rectal temperatures of four adults were measured in their 'home' cages. Air temperature within the cages was also recorded.

Determination of mean Body Temperature and Circadian Cycle in Body Temperature

Six adult animals, three males and three females, were kept in a constant temperature room at ambient temperatures of 11°, 15°, 20° and 30°C. Variations in air within the constant temperature room was of the order of ±1° at 11°C, ±0.5° at 15° and 20°C, and ±2° at 30°C. A 12-hour photoperiod was maintained in the room by means of a

time switch which turned lights on at 0600 hours and off at 1800 hours. During the 12 hours of darkness a 10W blue-painted light bulb provided faint illumination in the room. The animals were kept singly in small cages (1 m x 50 cm x 50 cm), each of which was provided with a nest-box. They were fed on kangaroo meat, fish and eggs. Clean drinking water was provided ad libitum. One group of animals was maintained under these conditions for periods ranging from three to seven weeks at the one ambient temperature from March through July. A second group of six animals, three males and three females, was kept under the same conditions at an ambient temperature of 15.0 ±0.5°C in October-November.

Body temperature of the animals was measured with a mercury-in-glass thermometer inserted into the colon to 5-6 cm. Two people were required to make the measurements; one captured and held the animals, and the other inserted the thermometer and recorded the temperatures. The animals were measured in varying sequence and care was taken to move about quietly in the room. In order to minimise disturbance of the animals the room was entered no more than twice, and usually only once, daily, the animals being fed and given fresh water immediately after temperature measurements had been made.

Body temperatures were recorded at least once for each animal at each hour of the day and night. In a few cases, when animals were difficult to catch or were very aggressive, high body temperatures were recorded due to

activity. Such values were discarded. Mean values, standard deviations, standard errors and coefficients of variation were calculated using no more than one value per animal per hour. A number of additional body temperature measurments were made during the morning hours (at the same times on different mornings) in order to determine when the animals were to be found in torpor. These additional values were not included in the daily means as the low and variable temperatures recorded would have produced spuriously low mean values.

The amplitude of the circadian cycle in body temperature for males and females was calculated as the difference between the highest and lowest hourly mean temperature for the 24-hour period.

Mean body temperatures were also calculated for the three-hour period when the animals showed greatest activity and for the four-hour period when they showed the least activity and were usually asleep.

On four occasions when animals were found in a torpid condition body temperatures were recorded at frequent intervals during arousal from torpor to determine the rate at which temperature approached normal levels. This procedure was followed twice with one female and once with each of two other females. The former animal was also found torpid in the laboratory on several occasions and its body temperature during arousal was recorded twice.

Body temperature measurements in the metabolism chamber.

At first body temperatures were measured with mercury-in-glass thermometers before entry to, and after removal from, the metabolism chamber. Subsequently continuous records of body temperature were obtained from animals confined within the chamber. Thus it was possible to relate body temperature directly to rates of oxygen consumption, evaporative water loss and breathing rate while ambient temperature was either maintained at constant levels or raised slowly.

Oxygen Consumption

All animals were deprived of food but not of water for 24 hours before they were placed in the metabolism chamber. They were weighed immediately before they entered the chamber.

Oxygen consumption was measured while animals were confined in a stainless steel metabolism chamber of about six litres capacity. This chamber was enclosed in a jacket through which temperature-controlled water was circulated. The water was maintained at the required temperature by alternate duty cycles of a refrigerator coil and an immersion heater controlled by a contact thermometer in the jacket of the chamber. Air was passed through glass cylinders which contained about 500 g of silica gel and 500 g of drierite (granular, anhydrous $CaSO_4$) to remove water vapour. It was then led into the metabolism chamber

via a copper coil in the water jacket to bring it to chamber temperature. Flow rates of 900 ml/min to 5000 ml/min were used, depending on the size of the animal and the temperature of the chamber. The flow rate was measured by a calibrated flow meter and converted to standard temperature and pressure. A fraction of the effluent air (100 ml/min) was passed through two drierite columns, each containing about 250 g drierite, and the partial pressure of oxygen measured by a paramagnetic gas analyser (Beckman Model E2). The calibration of this instrument was checked regularly with reference gases. In some cases trends in oxygen consumption were monitored by a temperature-compensated oxygen electrode placed in the effluent air duct and the output coupled to a D.C. amplifier and strip-chart recorder.

At chamber temperatures between 0^{o}-30^{o}C, with dry air input, chamber humidity remained low. Above 30^{o}C flow rates were increased to lower the humidity. When a hygrometer became available it was possible to maintain the relative humidity in the chamber below 30 per cent. Relative humidity within the chamber was assumed to be the mean of relative humidities of outflow and inflow.

Oxygen consumption rates of the animals were calculated from the flow rate and the partial pressure of oxygen in the effluent air. Rates were expressed as mls O_2/kg. minute, using the weight of the animal measured before entry to the chamber. Rates of oxygen consumption

were converted to rates of heat production in calories assuming a respiratory quotient of 0.8. This assumption has been made in many recent studies on mammal energetics (e.g. Scholander et al, 1950; W. Dawson & Bennett, 1970; T. Dawson, 1973; Hudson & Deavers, 1973; Hulbert & Dawson, 1974). The caloric equivalent of 1 ml O_2, at R.Q. = 0.8, is 4.8 calories (Brody, 1945).

The animals responded well to confinement within the metabolism chamber and generally remained quiet, except for brief periods of activity. Measurements of oxygen consumption made during these periods of activity were not included in the calculations of mean values. Animals did not suffer any apparent ill-effects from their confinement in the chamber.

Breathing Rates

Respiratory movements of the animals were counted either by direct observation through the transparent face-plate of the metabolism chamber, or by observation of oscillations of the fluid in a manometer connected to the effluent air duct. In the ambient temperature range 0° to $36^{\circ}C$, breathing rates could be determined accurately but with the onset of panting, with breathing rates in excess of 150 breaths/minute, some inaccuracy arose in the counts.

Evaporative Water Loss

Evaporative water loss was measured concurrently with body temperature and oxygen consumption while animals were confined within the metabolism chamber. Humidity sensors connected to an electronic hygrometer (Hydrodynamics Inc.) were inserted into the air ducts and readings were converted to relative humidity using calibration curves provided by the makers of the apparatus. The calibration curves were checked against standard humidity solutions (Winston and Bates, 1960). After passing through drying columns the relative humidity of the air entering the chamber was less than three per cent. Relative humidity of the outflowing air was maintained at levels below 60 per cent by adjustment of the flow rate.

Using tables giving the density of pure water vapour at saturation over water (List, 1958) in conjunction with the temperature, the flow rate and the relative humidity of the air streams, the amount of water vapour entering and leaving the chamber was calculated. The difference between the water in outflow and inflow was taken as a measure of the evaporative water loss of the animal. For comparative purposes the weight-relative rate of evaporative water loss (mg H_2O/kg. min.) was used. No attempt was made to partition the pulmonary and cutaneous components of the water loss. Loss of body heat due to evaporation was calculated, taking the latent heat of evaporation to be 0.58 calories per mg of water.

evaporated (Schmidt-Nielsen, 1964). The ratio of evaporative heat loss to heat production, estimated from oxygen consumption, could then be calculated for any ambient temperature.

As the animals rarely defaecated or urinated while they were in the chamber, no problems arose from water vapour from these sources. On the two occasions when an animal urinated while in the chamber, no further measurements were made.

Response to Water Deprivation

A short trial was carried out to observe the response of two animals to water deprivation. Two animals, one male and one female, were confined separately in small cages in the laboratory. Each animal was provided with fresh meat each evening and for the first four days of confinement had clean water *ad lib*. For the following nine days no water was provided. Weighed quantities of fresh kangaroo meat and beef fat were placed in the cages at 5 p.m. each evening. The remaining material was removed the following mornings at 9 a.m. and weighed. Samples of meat left in the laboratory were found to lose about 5 per cent of weight due to dehydration over-night. Weight of the remaining meat in the cages was adjusted for a 5 per cent weight loss. This represents a rather crude approximation to real weight loss. The animals were weighed each morning. After nine days without access to free water the animals were again provided

with water ad lib and maintained under the same feeding regimen for a further six days, in order to compare body weight and food intake in absence and presence of water. Air temperature in the laboratory ranged from 14.5°-22°C during the trial.

Heart Rate

Attempts were made to measure heart rate of three animals at the same time as oxygen consumption rate, skin temperature and colonic temperature. ECG electrodes made from surgical suture clips were attached to the skin of fore and hind limbs and of the ventral thorax. As the animals would attempt to remove the clamps by biting and scratching they were restrained by means of a perspex (plexiglass) frame consisting of a collar which immobilized the head and flanges to which fore and hind feet were bound with adhesive tape. The frame was designed so that the animals could assume a normal crouching position. A flat-tipped thermistor probe was fixed to a shaved area of the flank and a thermistor probe was inserted to a depth of eight cm into the colon. The animals were placed into the metabolism chamber through which air was flowed at the rate of 1-2 litres per minute. Heart rates were recorded on a Beckman Dynograph. Colonic and skin temperatures and oxygen consumption were measured as previously described. The animals did not respond well to restraint; they did not settle readily into a resting condition and

two of them showed prolonged periods of activity, high oxygen consumption and, as a consequence, elevated body temperature.

Blood Volume

Blood volume determinations were made under the guidance of Associate Professor I. Kaldor, of the Department of Physiology. Professor Kaldor devised the technique and prepared the marker solution. Calculations were made using a computer program written by Mr. K.C. Lee.

The blood volumes of ten animals were measured, including three males and seven females. All the animals were mature, being aged $1\frac{1}{2}$ years or more, and had been in captivity for at least six months. Those captured six months previously had been adult at the time of capture. The body weights of the animals were: mean and range for 10 animals: 0.985 kg, 0.70-1.90 kg; mean and range for 3 males: 1.34 kg, 0.95-1.9 kg; mean and range for 7 females: 0.831 kg, 0.70-1.075 kg.

Preparation of the marker mixture.

A marker mixture was prepared by injecting a donor animal two weeks before the determinations were carried out with 60 μCi of Fe^{59} ($FeCl_3$ solution, specific activity 3-30 mCi/ml) intravenously. On the day of the determinations the donor was exsanguinated under ether anaesthesia, using heparin to prevent coagulation of the blood. The blood

sample was centrifuged lightly and the plasma was set aside. The red cells were washed twice with ACD solution and the final supernatant was removed and discarded. The plasma was labelled by addition of a small volume of I^{125} labelled serum albumin (RIHSA-I^{125} - Radioiodinated human serum albumin). The in vivo labelled red cells were then re-suspended in the labelled plasma and the resulting marker mixture was kept on a rotating mixer until used. The haematocrit value of the mixture was 39 per cent.

Injection of the marker mixture.

During blood volume measurements the animals were restrained by hand, having been injected 30-60 minutes earlier with Diazepam - Valium Roche 5 mg/ml (1 ml/kg) intramuscularly. This dosage had previously been found to make the animals tranquil. They remained reasonably quiet throughout the procedure of injection and subsequent sampling.

A volume of 0.5-1.5 ml of the marker mixture, depending on the size of the animal, was withdrawn into a polythene cannula of 2 ml displacement volume with a 26 gauge injection needle at the tip. The cannula was attached to a 2 ml syringe which was used only to control volume displacement. The cannula and syringe combination was weighed on an analytical balance, the mixture was injected into a marginal ear vein of a study animal and the syringe and cannula were re-weighed after delivery of the mixture.

The cannula was washed and dried between injections. Injection standards, one at the beginning and one after all animals had been injected, were prepared by delivering a volume of the marker mixture into a volumetric flask using the cannula and syringe in the same way as described above. Dilutions of the injection standard were prepared for radioactivity counting.

Blood sampling and processing for analysis.

Fifteen minutes after injection, a marginal vein on the contralateral ear was nicked with a scalpel blade. A 300 µl aliquot of the issuing blood was run into a microlitre pipette and eight to ten microhaematocrit capillary tubes were also filled. The blood from the pipette was washed into a radioactivity counting vial containing 2 ml distilled water. The capillary tubes were flame-sealed, centrifuged and the haematocrit value was read (Hawksley microhaematocrit Centrifuge, 14,000 r.p.m. for five minutes and Hawksley Microhaematocrit Reader). The capillary tubes were cut at the cell-plasma boundary and duplicate 50 µl aliquots of plasma were run into micropipettes and subsequently washed into counting vials containing 2 ml distilled water. With five of the animals, sampling was also carried out 60 minutes after injection.

Radioactivity counting.

Counting was done in a dual channel Packard Auto-spectrometer, using optimal setting for Fe^{59} and I^{125}

for the two channels respectively. Pure standard solutions of the two isotopes were used to determine the rate of cross-counting between them and to derive a correction which was subsequently applied to all raw counts. Counting times were chosen to maintain a sampling counting error of less than five per cent.

Calculation and expression of results.

The number of counts of each isotope injected into individual animals was calculated, using the counts determined on injection standards and the ratio of weight of injection mixture injected to that in the standard. Red cell volume was calculated from the ratio of Fe^{59} counts injected to counts in the whole blood sample, using the haematocrit value to express the actual volume of red cells in the sample. The total haematocrit value was corrected for trapped plasma, assuming a trapped plasma fraction of 10 per cent (Shield, 1971). Plasma volume was calculated in a similar way to red cell volume, using the injected count to sample count ratio of I^{125} and the percentage haematocrit value to express the actual volume of plasma in the sample. Plasma volume was also calculated from the ratio of injected counts to counts in the separated plasma sample for I^{125}. Results were expressed as:

$$\text{relative red cell volume, ml/kg} = \frac{\text{red cell volume, ml}}{\text{body weight, kg}}$$

$$\text{relative plasma volume, ml/kg} = \frac{\text{plasma volume, ml}}{\text{body weight, kg}}$$

$$F_{cells}\ \text{factor} = \frac{\text{total body haematocrit}}{\text{large vessel haematocrit}}$$

where total body haematocrit =

$$\frac{\text{red cell volume, ml}}{\text{red cell vol, ml + plasma vol, ml.}}$$

All calculations were done with the aid of a computer program written for the purpose.

Accuracy of Measurements

The level of accuracy of measurements made in this study is listed below:

MEASUREMENT	LEVEL OF ACCURACY
Body Weight	
newborn animals	0.0001 g
up to 20 g	0.01 g
20 - 500 g	0.1 g
more than 500 g	10 g
Length	
pes and head length	0.1 mm
Temperature	
rectal, colonic and chamber	telethermometer probe and mercury thermometer accurate to 0.2°C; readings approximated to 0.1°C.
Oxygen Consumption	0.01 per cent O_2 tension
Evaporative Water Loss	relative humidity read to nearest one per cent; converted to absolute amounts of water using chamber temperature and meteorological tables (List, 1958).

CHAPTER III

THE CLIMATE IN SOUTH-WESTERN AUSTRALIA

A brief description of the climate of the region in which the chuditch occurs is included to show the conditions with which it must contend. This account relies on macroclimatic data and does not take into account the microhabitat of the species which was not studied.

The climatic factors which may prove limiting to a species are not readily indicated by average conditions. This information is more likely to be gained from data on extremes of temperature and aridity and the frequency with which such extremes are likely to occur. I have chosen to illustrate extremes by tabulating, in addition to average annual or monthly values, average rainfall in the driest months, the average number of days on which maximum air temperature exceeds 37.8°C (100°F) and the average number of days in which minimum air temperature (in meteorological screen) falls below 2.2°C (36°F), i.e. in which frosts are likely to occur. Table 3.1 shows climatic data for six representative meteorological stations within, and at the outer limits of, the area of south-western Australia from which chuditches were drawn for this study (see Fig. 3.1 for position of meteorological stations).

The south-west of the Australian continent has a reliable winter rainfall and dry summers. The mean

variability of the rainfall from the annual average is less than 20 per cent (Leeper, 1960). The winter temperatures are mild and the summers are hot. Highest mean maximum temperatures occur in January when average rainfall is very low.

Inland from the coast the rainfall is reduced, its variability is increased and the trend is from a largely winter rainfall to an increasing proportion of rainfall in late summer. There is an increasing frequency of high summer temperatures and, because of reduced cloud cover in the winter months, an increasing frequency of frosts.

The apparent range of the chuditch at present is in the least climatically stringent portion of its range as determined by collections made during the early part of European settlement.

Table 3.1

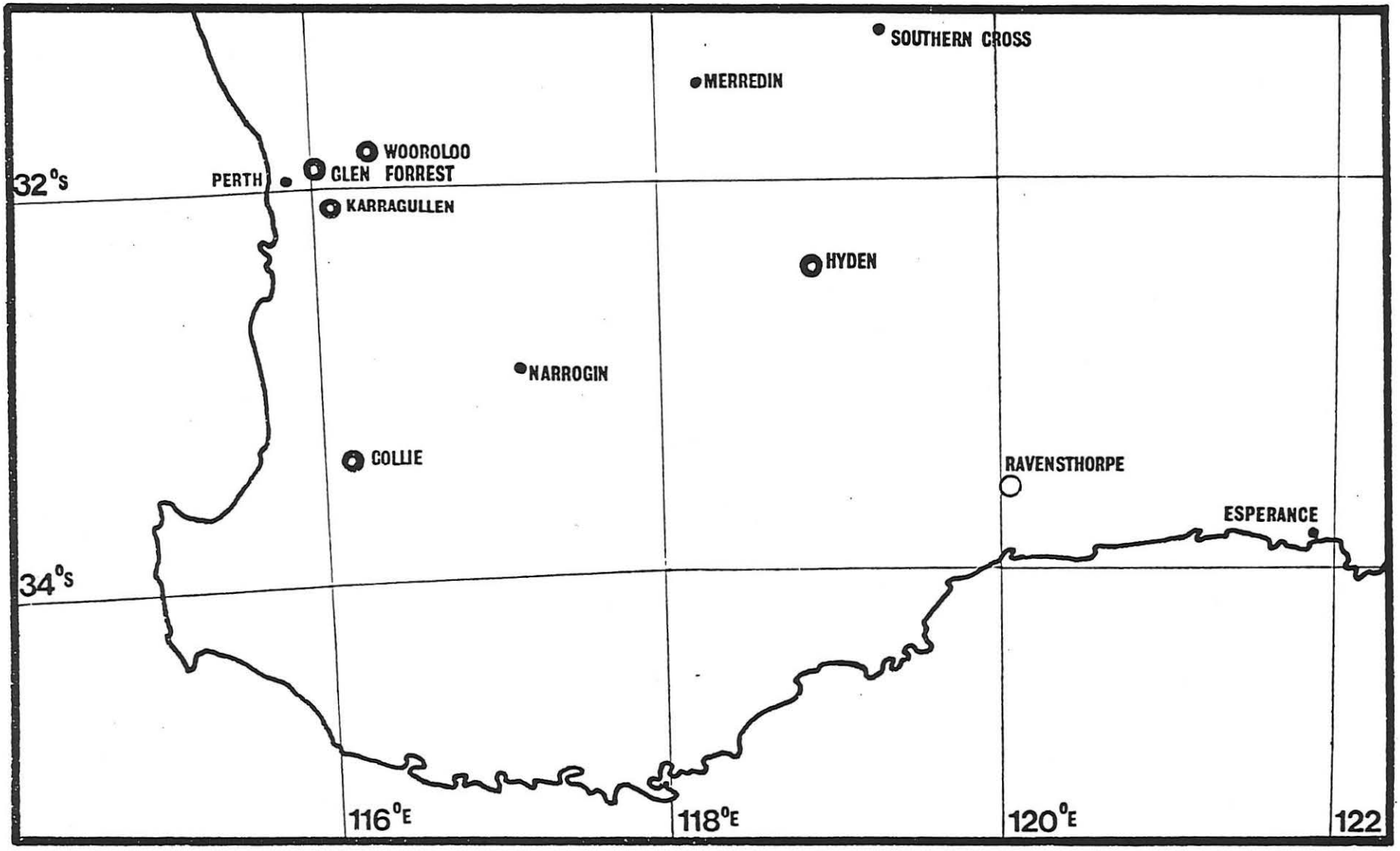
Climatic data from six representative locations in south-western Australia (Bartlett, 1974)

Location	Rainfall (mm)		Temperature (^{o}C)			
	Annual Average	Average Total for 3 driest months	Mean Maximum in hottest month	Mean Minimum in coldest month	No. days when max. > 37.8°C	No. days when min. < 2.2°C
Collie	987	45 Dec-Feb	30.2 Jan	3.9 Jul	5.5 Nov-Mar	36.6 Mar-Dec
Esperance	676	51 Dec-Feb	25.3 Jan	7.4 Jul	3.8 Nov-Mar	2.5 Jun-Jul
Merredin	326	36 Nov-Jan	33.8 Jan	4.6 Aug	17.0 Oct-Apr	26.2 Apr-Oct
Narrogin	506	37 Nov-Jan	30.8 Jan	5.1 Jul-Aug	5.3 Nov-Feb	18.6 Apr-Dec
Perth	880	31 Dec-Feb	29.7 Jan	8.8 Jul	5.0 Nov-Mar	0.2 Jun-Jul
Southern Cross	281	40 Nov-Jan	34.6 Jan	3.9 Jul	27.4 Oct-Apr	32.2 Apr-Oct

Fig 3.1 Map of south-western Australia showing localities to which reference is made in Chapters II and III.

Symbols

- ◎ localities from which chuditches were obtained
- ○ 1973 sighting
- • meteorological station (Table 3.1)


SOUTHERN CROSS
MERREDIN
WOOROLOO
32°S
PERTH
GLEN FORREST
KARRAGULLEN
HYDEN
NARROGIN
COLLIE
RAVENSTHORPE
ESPERANCE
34°S
116°E
118°E
120°E
122

CHAPTER IV

BREEDING BIOLOGY

Preamble

Marsupials in temperate regions normally have restricted breeding seasons. Sharman, Calaby and Poole (1966) concluded that diprotodont marsupials living in the coastal areas of southern Australia are adapted to breed at a time which ensures that pouch emergence occurs in the spring. The flush of green feed at this time of the year provides favourable conditions for the young animals as they approach independence. Tyndale-Biscoe (1973), in reviewing the breeding patterns of marsupials, has pointed out that whereas eutherians with seasonal breeding usually give birth in the spring when conditions are most conducive to survival of the young, for marsupials it is emergence from the pouch which is so timed.

Species from arid or wet tropical climates show different breeding patterns. The desert kangaroos, Megaleia and Macropus robustus, (Sharman, Calaby and Poole, 1966) breed continuously throughout the year so that young animals are available to take advantage of pasture growth that follows sporadic rainfall. Some tropical marsupials have extended breeding seasons. Biggers (1966) found that Philander opossum and Didelphis marsupialis tabascensis in Nicaragua were reproductive for the greater part of the year,

whereas Didelphis marsupialis virginiana from Pennsylvania exhibited a more restricted breeding season.

An exception to the generalization that marsupials from temperate regions have restricted breeding seasons is found in the quokka, Setonix brachyurus. A population of this species on Rottnest Island has a season of birth restricted to six months, from January to August, whereas a mainland population from the same latitude breeds continuously throughout the year (Shield, 1965).

It would be expected that Dasyurus geoffroii from south-western Australia, where seasons are well-defined and there is a reliable winter rainfall, would have a restricted breeding season like other dasyurids from temperate regions. Antechinus stuartii (Marlow, 1961; Woolley, 1966), Dasyurus viverrinus (Hill and O'Donoghue, 1913; Fleay, 1935; Green, 1967) and Sarcophilus harrisii (Green, 1967; Guiler, 1970) have all been shown to have short breeding seasons restricted to the autumn and winter months. Some dasyurids from desert regions, on the other hand, are capable of breeding over a greater part of the year. This capacity enables them to breed at any time when environmental conditions are suitable in a region where the climate is very variable. Ewer (1968) found that female Sminthopsis crassicaudata may breed continuously without intervening anoestrus. Godfrey (1969) found that S. froggatti (larapinta) has a breeding season

of eight months duration with the possibility of producing two or three litters per year. Michener (1969) and Sorenson (1970), however, found that another desert species, Dasycercus cristicauda, had a restricted breeding season and Sorenson considered that this was also true for Dasyuroides byrnei.

Where the breeding season is restricted to a small part of the year the age at which reproductive maturity is reached is governed by seasonal, as well as developmental, factors. It would therefore be expected that reproductive maturity is reached either in the first or second breeding season after birth when the animals are approaching either 12 months or two years of age. Woolley (1966), in a survey of data on reproduction in the Dasyuridae from various sources, listed five species with restricted breeding seasons which were reproductively mature at one year, while Sarcophilus is probably reproductively mature at two years. Sminthopsis froggatti in captivity was found to come into oestrus at four months and males had sperm in the urine at $7\frac{1}{2}$-9 months (Godfrey, 1969), so that this species with its less restricted breeding season lacks the seasonal constraints on the attainment of reproductive maturity.

A restricted seasonal breeding pattern places a further constraint on breeding; it limits the animal to a single litter per year. This is particularly true of marsupials with their prolonged pouch-life.

Gestation periods in marsupials are short, ranging from $12\frac{1}{2}$ days for Isoodon macrourus (Lyne, 1974) to 38 days for Potorous tridactylus (Hughes, 1962). Gestation in the dasyurids ranges from $12\frac{1}{2}$ days for Sminthopsis froggatti (Godfrey, 1969) to 26-35 days for Antechinus stuartii (Woolley, 1966).

The dasyurids are all polytocous. Woolley (1966) tabulated data on reproduction in the group from various sources, showing that pouches contain from four (e.g. Sarcophulis, Myrmecobius) to twelve nipples (e.g. Antechinus flavipes, Planigale) and that all nipples may be occupied at one time by pouch-young.

Results

Breeding Season

The following results show that the chuditch has one breeding season per year, both in captivity and in the wild. Young were born in the captive colony only during the months of May and June. Estimated birth dates of litters taken from the wild showed that births occurred in June and July. Table 4.1 shows known birth dates of litters born in captivity and estimated birth dates of those captured from the wild. Animals in the colony were observed to copulate in April and May and also in August, but no young were born as a result of the late matings.

Table 4.1

Known birth dates of animals born in captivity
and estimated birth dates of litters taken from the wild

Litter No.	Birth date of litters born in captivity	Litter No.	Estimated birth dates of litters taken from the wild
3.	22.v.1968	1.	21.vii.1966
4.	27.v.1968	2.	1.vii.1967
5.	3.vi.1968	9.	6.vi.1969
6.	28.v.1969	10.	9.vi.1969
7.	10.vi.1969	11.	13.vi.1969
8.	28.vi.1969*	12.	14.vi.1969

* Estimated from body measurements.

The pouches of the captive females showed a marked change as the breeding season approached. During spring and summer (September through February) the pouches of juvenile females were inconspicuous and were covered with dense white fur like the remainder of the ventral surface. At about the beginning of March a reddish, waxy secretion appeared on the fur of the pouches of some animals. By mid-April this secretion was generally observed in the pouches which had become much deeper, the posterior rim being enlarged and swollen. The nipples were enlarged at this stage. Pouch development reached a maximum in May and June. Pouches were then very deep, they were markedly glandular with long, sparse hair, and the red secretion was no longer present. As the nipples increased in size they were surrounded by a swollen rim of tissue. The cloacal region became swollen and there was a marked reduction in the fur in the mid-line between pouch and cloaca.

In animals which had not given birth the pouch was regressing by mid-July; the posterior rim became less swollen and the fur returned to the condition of that covering the remainder of the ventral surface. By the end of July the pouches had returned to the non-breeding condition. One pair of animals was observed to mate in mid-August; the pouch of the female, which had previously regressed following enlargement during autumn, was again observed to be in a fully developed condition.

Age at Reproductive Maturity

Of animals born or reared in captivity, four females produced litters and two males sired offspring in the first breeding season after their birth. Captive animals therefore are reproductively mature when they are slightly less than 12 months of age. It was not possible to age females taken from the wild with litters in their pouches to determine whether they too were reproductive at one year of age.

Gestation Period

Table 4.2 shows the time intervals between the last observed copulation, or of separation of the parents, and the discovery of litters in the pouches of four captive females. For litters 3, 4 and 6, where the male/female pairs were continuously associated, the gestation period was estimated as the interval from the last observed copulation to the discovery of the litter, taking into account the interval since the pouch was previously examined and found to be empty. For litter 5, the male was associated with the female for six days and was removed 17 days before the litter was first observed. The female was examined 15 days after removal of the male when its pouch was found to be empty. Examination on the seventeenth day revealed a litter. The minimum duration of the gestation period, therefore, was 15 days and the maximum duration, assuming that fertilisation occurred very soon after the male was placed with the female, was 23 days.

Table 4.2

Observations on the gestation periods of four litters born in captivity

Litter No.	Age of litter at first observation (days)	Days since last observed copulation	Gestation period (days)
3.	0 - 4	16	12 - 16
4.	0 - 2	18	16 - 18
5.	0 - 2	15-23*	15 - 23
6.	0 - 1	18	17 - 18

* Copulation not observed, female caged with male for six days.

The overlap of these four different observations suggests that the gestation period is 15-17 days.

Litter Size and Sex Ratio

All of the females examined had six nipples in the pouch.

Table 4.3 shows the numbers of young first observed in each of six litters born in captivity and of six litters taken from the wild. Five of the six captive-born litters were aged less than four days when first examined (Litter nos. 3-7) and the sixth (Litter No. 8) was estimated to be between eight and nine weeks old. The most common number of young per litter in these 12 litters was five with a mean of 5.3

Table 4.4 shows the numbers of males and females in five litters which suffered no mortality between the time when they were first examined and the time that sex could be determined. More than twice as many females as males were observed (17 females : 8 males) but the sex ratio is not significantly different from parity ($\chi^2_{(1)} = 2.56$, using Yate's Correction, $p > 0.1$).

Though it appears that all nipples are usually occupied in young litters, there was some mortality of pouch-young in captive litters, even when they were handled only rarely. There is some evidence that mortality also occurs in wild litters. One female captured from the wild

Table 4.3

Numbers of individuals in six litters born in captivity and six litters taken from the wild

Litter No.	Litters born in captivity	Litter No.	Litters taken from the wild
3.	5	1.	6
4.	6	2.	5
5.	6	9.	5
6.	6	10.	4
7.	5	11.	5
8.	5	12.	6
Totals:	33		31
Means:	5.50		5.17
Overall mean:		5.33	

Table 4.4

Numbers of males and females in five litters in which sex could be determined on complete litters (i.e. in which no mortality occurred between first observation and observation when sex could be determined)

	Litter No.	No. of individuals	Males	Females
Captive-born litter	7.	5	2	3
Litters taken from the wild	1.	6	3	3
	2.	5	1	4
	10.	4	1	3
	11.	5	1	4
	Totals:	25	8	17
	Means:	5.0	1.6	3.4

in January 1968, had only five of the six nipples elongated, indicating that she had suckled five young in the previous breeding season. Another female, found killed on the road in August 1971, had only three of its six nipples elongated with surrounding mammary tissue enlarged and was probably suckling only three young when she was killed.

Longevity

Twenty-three animals survived in captivity for two years or longer. Of these, two known-age animals (one male, one female) died at $3\frac{1}{2}$ years of age, one known-age female was killed by her mate at four years of age, another female died when $4\frac{1}{2}$ years and one male died at $5\frac{1}{2}$ years of age. Two males and two females captured in the wild as adults survived in captivity for four years so that they must have been at least five years old when they died.

One female, caught as a pouch-young in the wild and reared in captivity, gave birth to litters in two successive breeding seasons when she was aged one and two years respectively.

From these observations it appears that animals are likely to survive for at least two years and may live for $5\frac{1}{2}$ years or more. It appears that females have the potential to produce more than one litter during their lifetime. If this is the case then the animals have a reproductive potential sufficient to maintain or increase existing populations.

Discussion

The chuditch, in the reliable rainfall area of south-western Australia, has its breeding season restricted to autumn and winter (May to July) so that young animals emerge from the pouch from August to November, during the spring and early summer (Chapter V, Growth and Development). The breeding season was not changed by conditions in which the captive colony was maintained. The related species from south-eastern Australia, D. viverrinus, throughout the whole of its range, appears to have a breeding season similar to that of the chuditch. Hill and O'Donoghue (1913) reported that D. viverrinus in New South Wales has one breeding season a year which begins at the end of May or early June and extends to the first fortnight of August; Fleay (1935) described the observation of a pouch litter born in mid-June in Victoria; Green (1967) found that of 13 females captured in north-eastern Tasmania in July, 12 had young pouch litters.

At least some animals in the captive colony of D. geoffroii were reproductively mature in the first breeding season after birth. Fleay (1935) made a similar observation for D. viverrinus.

The factors which determine the onset of the breeding season in D. geoffroii have not been determined. As the breeding season commences when days are shortening with the approach of the winter solstice, photoperiod is a

likely factor in determining when breeding will begin.

The gestation period of the chuditch cannot be established with precision from the observations available as additional matings may have occurred after fertilisation and observations of nocturnal matings were not made. The most precise statement that can be made is that gestation cannot be shorter than 15 days nor longer than 23 days in the one case where a male was caged with a female for a limited time. Other observations suggest that it is closer to 15 than to 23 days.

There is confusion about the length of gestation of the related species D. viverrinus. This has arisen from differences in definition of the gestation period, either as the time from copulation to parturition or as the time from ovulation to parturition. Hill and O'Donoghue (1913) found that ovulation in D. viverrinus was spontaneous and quite independent of copulation and that the time interval between copulation and the finding of unsegmented ova in the uteri ranged from four to eight days, the average interval between copulation and ovulation being about five or six days. They reported one case, which they regarded as being 'perfectly trustworthy', of a female in which the young were born 16 days after copulation. Subtracting five days (the average interval from copulation to ovulation) from the sixteen day period between copulation and parturition, they concluded that the gestation period

is about eleven days and that from evidence available '...the gestation period in Dasyurus is not less than eight, and does not exceed fourteen days'. Waring, Moir and Tyndale-Biscoe (1966) and Woolley (1966), quoting Hill and O'Donoghue (1913) cited the gestation period of D. viverrinus as being 8-14 days. Tyndale-Biscoe (1973) stated that there is no doubt that the gestation period of D. viverrinus is nine days but gives no reference to subsequent observations. Hill and O'Donoghue described, in considerable detail, one case in which a female newly captured from the wild was observed to copulate immediately with a captive male and to give birth to a litter eight days later. In spite of their statement '...that a female once served will not under normal circumstances again copulate', they suggested that this female may have been fertilised earlier and did not regard this record as absolutely conclusive as to the length of the gestation period. The possibility that the particular animal had previously copulated in the wild is given more credence by the observation that D. geoffroii, in captivity, will copulate on several successive days. I think that D. geoffroii and D. viverrinus probably have similar gestation periods, from copulation to parturition, of about 16 days duration.

Observations of new-born chuditch litters suggest that normally all nipples are occupied to give a full complement of six young, though there may be some mortality during subsequent pouch development. No female was found

to have supernumery neonates as described for D. viverrinus by Hill and O'Donoghue (1913), but it is possible that such occurrences were not observed. Hill and O'Donoghue described two cases in which eighteen and ten newborn animals respectively were observed. They also found that a much greater number of ova were discharged at each ovulation than could be accommodated in the pouch in either D. viverrinus or D. maculatus. Godfrey (1969) reported that Sminthopsis froggati (larapinta) produces large numbers of ova per ovulation. Didelphis marsupialis virginiana is also known to produce more young than can be accommodated on the nipples (Hartman, 1923; Reynolds, 1952).

The observed ratio of males to females in young pouch litters of D. geoffroii suggests an excess of females. Observations of Fleay (1935) and Green (1967) also showed more females than males in litters of D. viverrinus, and Guiler (1970) found a predominance of females compared with males in pouch young of the Tasmanian devil, Sarcophilus harrisi. In all four cases samples are very small and chi-squared tests show the sex-ratio to be not significantly different from parity.

Shield (1962) put forward the thesis that, as marsupials have a short uterine life compared with eutherians and lack the heavily male-biased causes of death in utero and at birth which have been demonstrated

for some eutherian species, the sex-ratio of new-born pouch young would closely approximate the primary sex-ratio of the species being investigated (i.e. the sex-ratio at conception). As estimates of the primary sex-ratios of a number of eutherian species show a significant excess of males to females it might also be expected that a high proportion of males to females might be found in marsupial pouch-young if similar determinants of sex-ratios act in the two groups. The sex-ratio at birth for eutherians (secondary sex-ratio) is closer to parity than the primary sex-ratio, due to the relatively high mortality of males in utero. If pouch life in marsupials is equated to uterine life in eutherians, it might be expected that differential mortality during pouch-life would be reflected in changes in the sex-ratio at birth compared with sex-ratios to be observed later in pouch-life.

Shield (1962, 1968) found that the sex-ratio of quokka joeys aged 40 days or less was close to parity while that for joeys of more than 100 days was significantly different from that in the young joeys, with a deficiency in males compared with females. Caughley and Kean (1964) found a significant excess of males to females in a sample of grey kangaroo joeys from south-western Queensland, but a 1:1 sex-ratio in joeys of Megaleia rufa from the same area. In reviewing data for five other marsupial species (including Shield's data for the quokka, cited above)

they were unable to demonstrate that these species showed a significant disparity between the frequencies of male and female pouch-young. Poole (1973) found that the sex-ratio of 713 young grey kangaroos from Mt. Hope in New South Wales was not significantly different from parity. Neither Caughley and Kean (1964) nor Poole (1973) found evidence of differential mortality of male and females during pouch-life.

It can be concluded that the shorter gestation period of marsupials does not in general favour a high sex-ratio and that the primary sex-ratios at fertilisation are probably not significantly removed from parity, as has been suggested by some eutherian studies.

CHAPTER V

GROWTH AND DEVELOPMENT

Preamble

A study of the growth and development of the pouch-young of Dasyurus geoffroii was undertaken for two reasons. Firstly it was necessary to establish a calendar of development and thereby a means of aging pouch-young captured in the wild. As a corollary this made possible comparisons between the development of this species and that of other marsupials whose development has been documented. These aspects will be considered in this chapter. The second, more relevant aspect of development in respect of the energetics of the species was the determination of the age at which the young animals were able to maintain a stable body temperature. The ontogeny of the establishment of homeothermy will be considered in Chapter VI.

Marsupials, when compared with eutherians, are characterised by a proportionately small birth weight, but when they emerge from the pouch they are as fully developed as many neonatal eutherians. Consequently pouch development of marsupials has been compared to foetal development of eutherians. This cannot be strictly correct as a number of functions not required by the foetal eutherian must necessarily be established early in pouch life (e.g. motor activity necessary to move into the pouch,

respiration, alimentation and suckling). A calendar of pouch development distinguishes between precociously developed features and those upon which little demand is placed because of the protection afforded by incubation and nursing within the pouch.

This section of the study is concerned with the documentation of growth from birth to adult status using body weight, two linear measurements, five external features and the development of motor responses. These data are presented as a calendar of development and will subsequently be used as a means of aging pouch-young and a comparison with other marsupials and eutherian perinatals.

Results

New-born Animals

Table 5.1 shows the body weights of four individuals, from four separate litters, measured when the litters were first observed in the pouches. The maximum possible age, in hours, of each of the animals is also shown. As it is known for certain that one neonate weighing 15.4 mg was less than 24 hours old, it is likely that the two animals weighing less than 15 mg were also less than one day old. The remaining animal, weighing 25 mg, could have been as much as 54 hours old. From these data, the neonatal weight of *Dasyurus geoffroii* is estimated as between 14 and 15 mg. Insufficient numbers were available to estimate the variation in birth weight.

Table 5.1

Neonatal weight and maximum age when weight determined for four pouch-young from four litters born in captivity

Litter No.	Body weight (mg)	Maximum age when weight measured (hours)
3.	14.5	96
4.	14.7	44
5.	25.0	54
6.	15.4	24

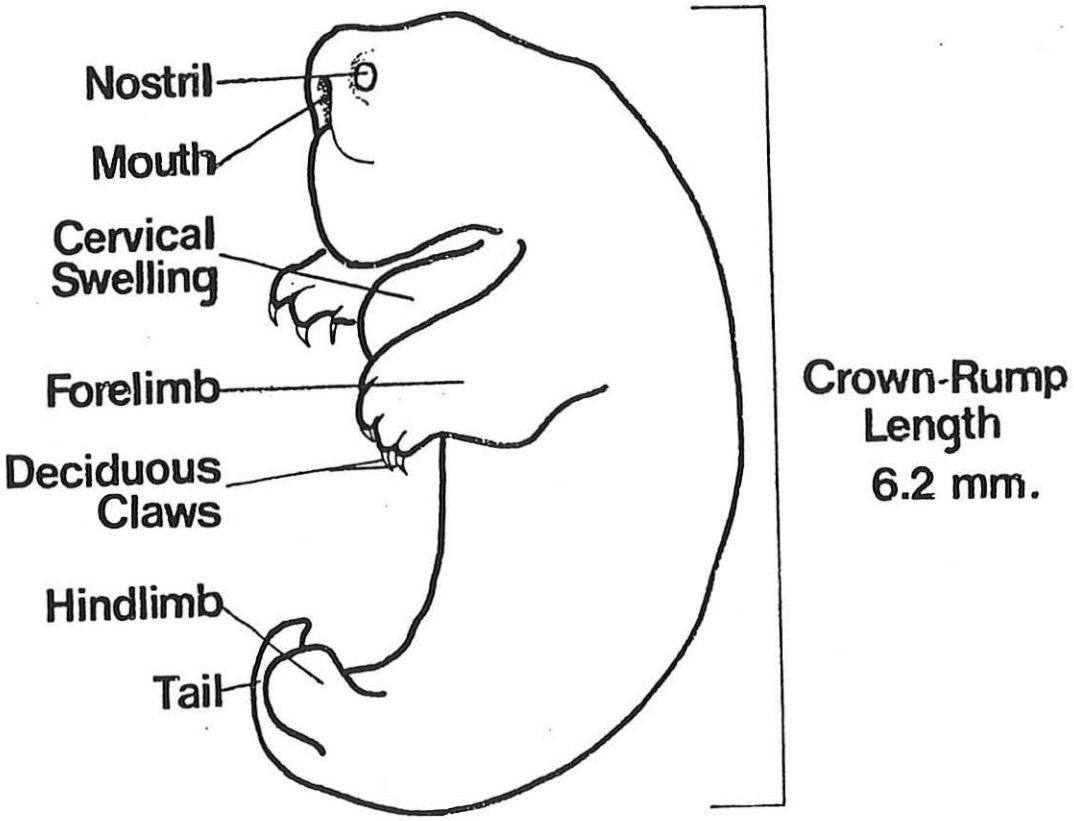
One new-born animal had a crown-rump length of 6.2 mm (weight 15.4 mg). A second new-born animal had a crown-rump length of 6.5 mm (weight 14.7 mg).

Figure 5.1 shows a line drawing of a new-born animal, from Litter 6, known to be less than 24 hours old. The head of the neonate was set at right angles to the trunk. The mouth was a triangular orifice with laterally fused lips. The nostrils were lateral in position. There was no external evidence of eyes or ears. The animal was pale in colour and translucent, with blood vessels visible through the skin. The forelimbs were strongly developed in comparison with other features and four digits bore deciduous claws. There was a pronounced cervical swelling situated on the ventral surface below the head and between the forelimbs. The hindlimbs were small buds with no evidence of joints or digits. The tail was extremely small and curved between the hindlimbs.

Growth of Known-age Animals

Three metrical characters, body weight, head length and pes length, were selected to typify the growth of the chuditch. Figs 5.2, 5.4 and 5.5 are scatter diagrams of log body weight, head length and pes length respectively vs. age for known-age animals during the first year of life. Trend lines were fitted by eye, and separate trends for males and females are shown when sexual dimorphism in

Fig 5.1 Lateral view of a neonatal chuditch.


Nostril
Mouth
Cervical Swelling
Forelimb
Deciduous Claws
Hindlimb
Tail
Crown-Rump Length
6.2 mm.

size becomes apparent in juvenile animals. Growth rates, per cent per day, for individual animals are also shown with associated trend lines. Fig 5.3 shows a smoothed curve of body weight vs. age, on linear axes, together with mean daily increments in body weight calculated both as per cent per day and as grams per day. Fig 5.6 shows smoothed curves for both head length and pes length vs. age, together with mean increments in per cent per day and in mm per day. Growth trends and growth rates for the three variables measured are considered in turn below.

Body Weight.

Fig 5.2 is a scatter diagram showing body weight (log scale) vs. age of fifteen known-age animals (from Litters 3, 4 and 5) between birth and 365 days of age. Equivalent-age males and females of less than about 120 days of age showed no difference in body weight. For animals older than about 120 days, males consistently weighed more than females of the same age. The mean body weights of four males and four females, when they were one year of age, were 1300 g and 864 g respectively. Percentage increments in body weight, per day, were calculated from successive measurements of individual animals (except for young animals for which calculations were made using weights of different animals). These growth rates are shown as individual points on Fig 5.2 and the eye-fitted trend line through these points shows the decline in growth rate which accompanied the increase in age.

Fig 5.2 Scatter diagram of body weight (log. scale) vs. age (days) for known-age chuditches, and growth-rates (per cent/day).

Symbols:

◐ sex unknown

● male

○ female

• growth rate

——— eye-fitted trend line of weight vs. age

– – – eye-fitted trend line of growth rate vs. age

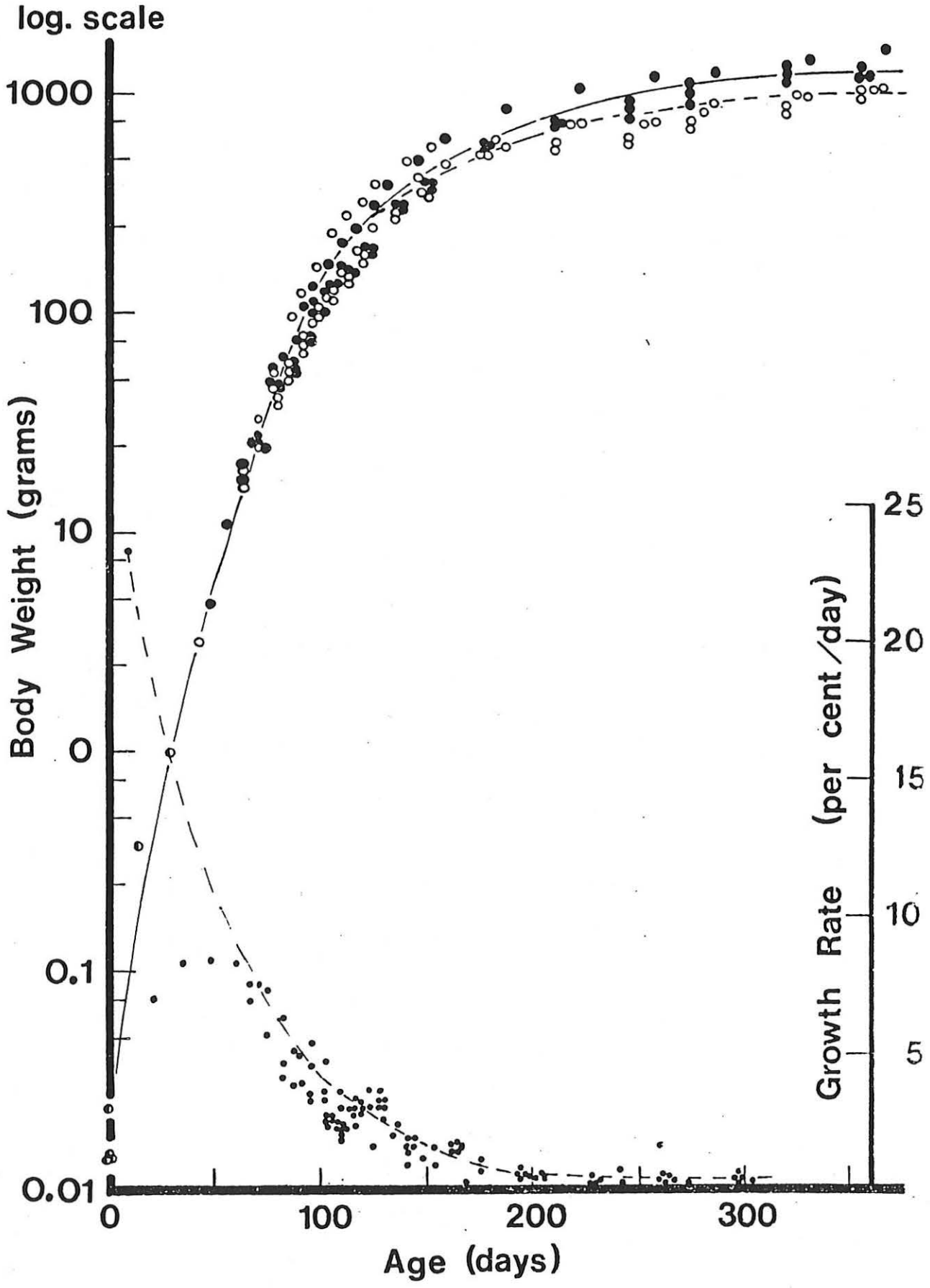

log. scale
1000
100
10
0
0.1
0.01
Body Weight (grams)
25
20
15
10
5
Growth Rate (per cent/day)
0
100
200
300
Age (days)

Fig 5.3 shows the smoothed curve of body weight (linear scale) vs. age compared with the mean daily percentage growth rates and the mean daily increments in body weight from early pouch life to 32 weeks of age. The growth curve shows its inflection at 20-22 weeks of age. The mean percentage growth rate fell rapidly from about 21 per cent/day between birth and two weeks of age to 7.7 per cent/day between two and six weeks, and thereafter fell more slowly to between 2 and 3 per cent/day between 14 and 20 weeks of age. By 32 weeks the mean daily percentage growth rate had fallen to 0.2 per cent/day. The mean daily increment in body weight rose from less than 0.05 g/day between birth and two weeks of age to more than 2 g/day from 10 weeks to 30 weeks, after which it fell to 1.4 g/day at 32 weeks. From 18 to 26 weeks of age the mean daily increment in body weight was greater than 6 g/day. Thus the greatest daily increments in body weight occurred when the percentage growth rate was about 2.5 per cent per day and at about 20 weeks of age, corresponding to the inflection of the growth curve.

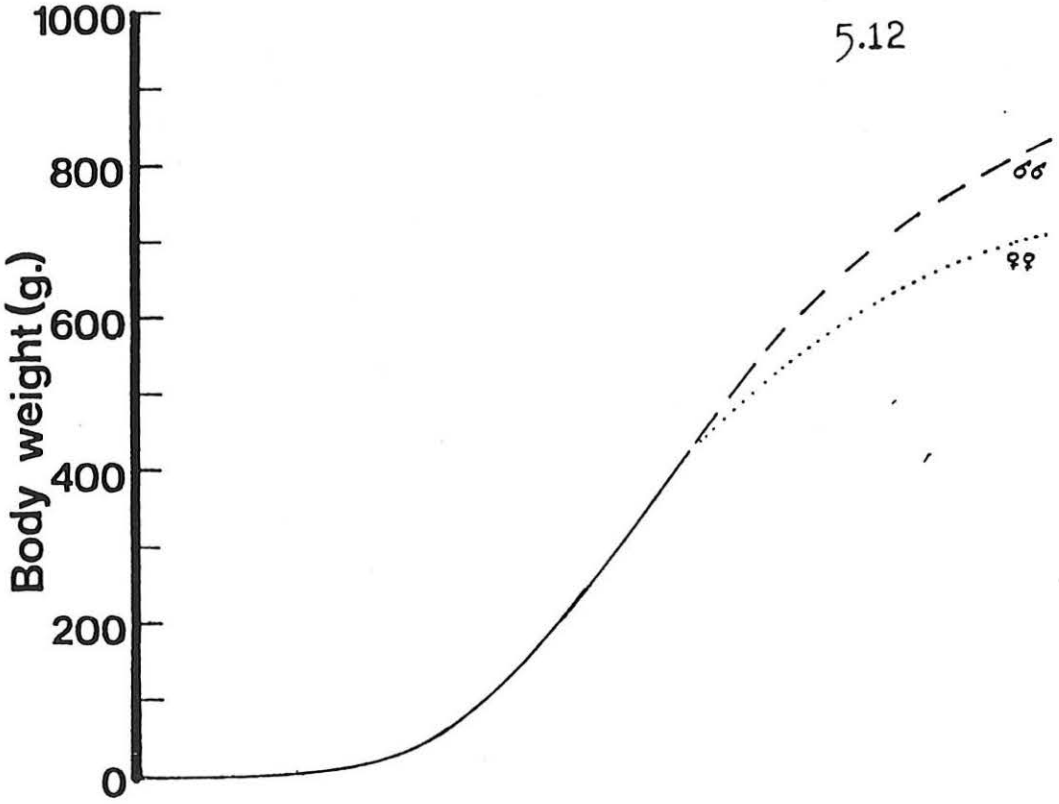
Head Length.

Head length measurements of 11 animals aged from 14 days to 365 days of age are shown on Fig 5.4 with eye-fitted trend curves. As was the case with body weight, from about 120 days of age males tended to be larger than females of equivalent age. Mean head length at one year

Fig 5.3 Trend line of body weight (linear scale) vs. age (weeks) and mean geometric and arithmetic growth rates in body weight for known-age chuditches.

Symbols: ●——● mean geometric growth rates linked by trend line

○----○ mean arithmetic growth rates linked by trend line


1000
800
600
400
200
0
Body weight (g.)
♂♂
♀♀

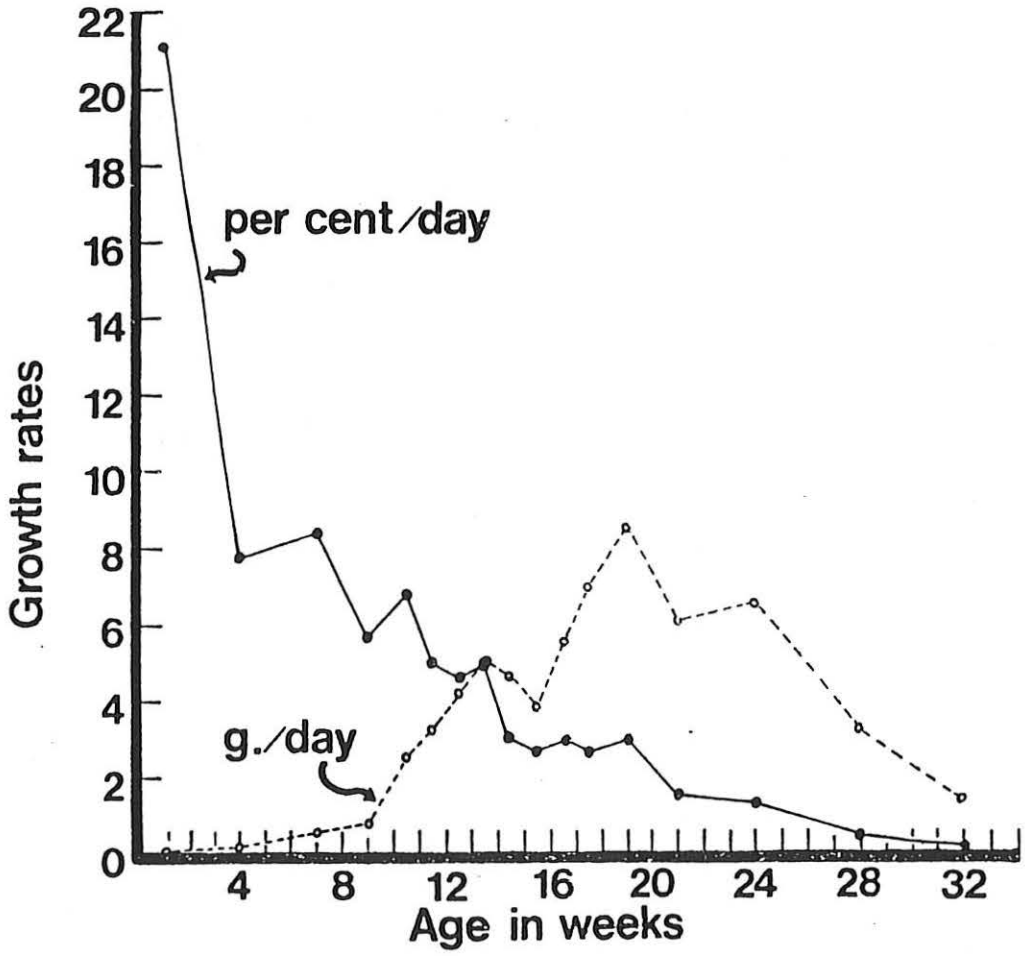

22
20
18
16
14
12
10
8
6
4
2
0
Growth rates
per cent/day
g./day
4
8
12
16
20
24
28
32
Age in weeks

Fig 5.4 Scatter diagram of head length (mm) vs. age (days) for known-age chuditches, and growth rates (per cent/day).

Symbols: as for Fig 5.2

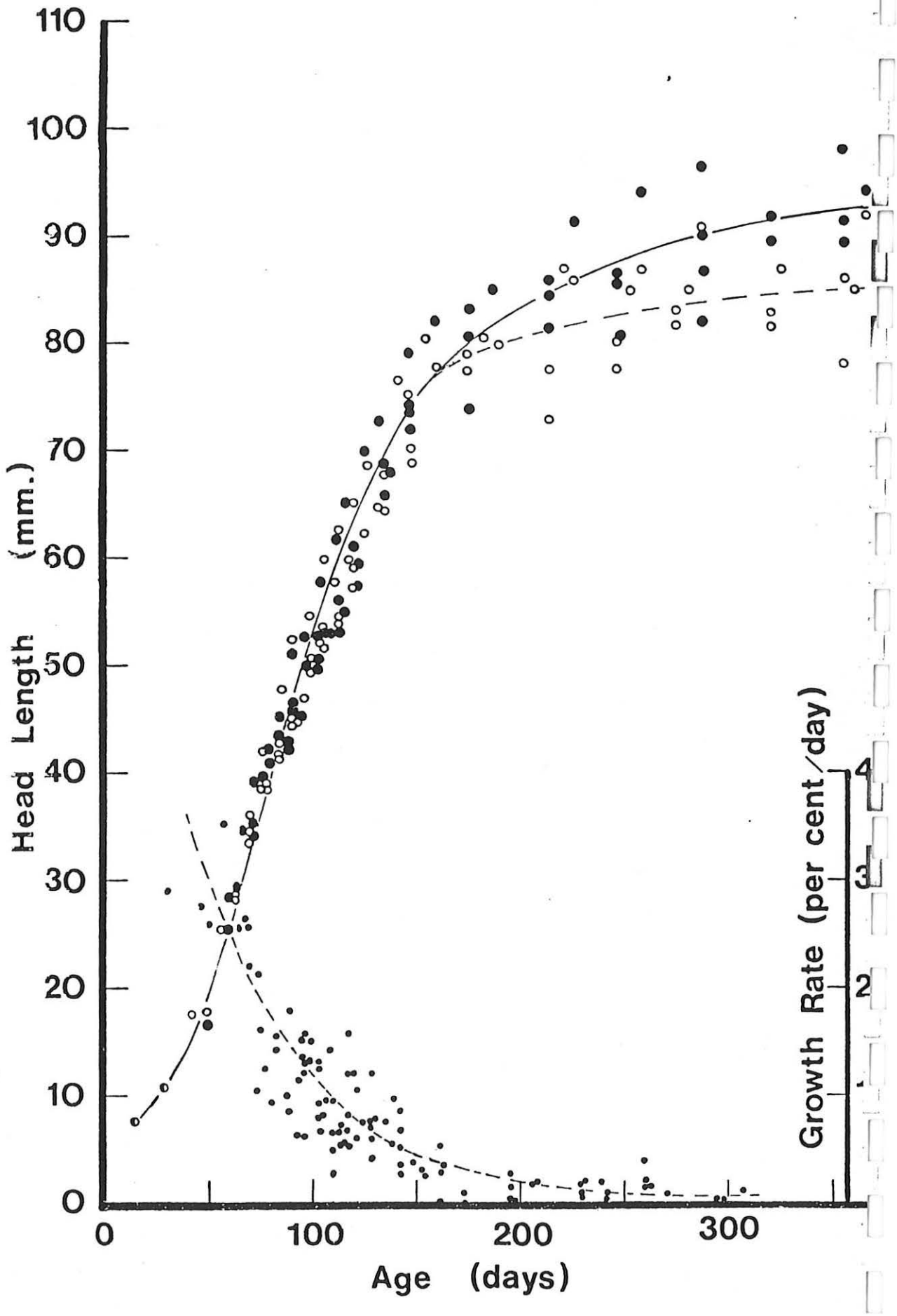
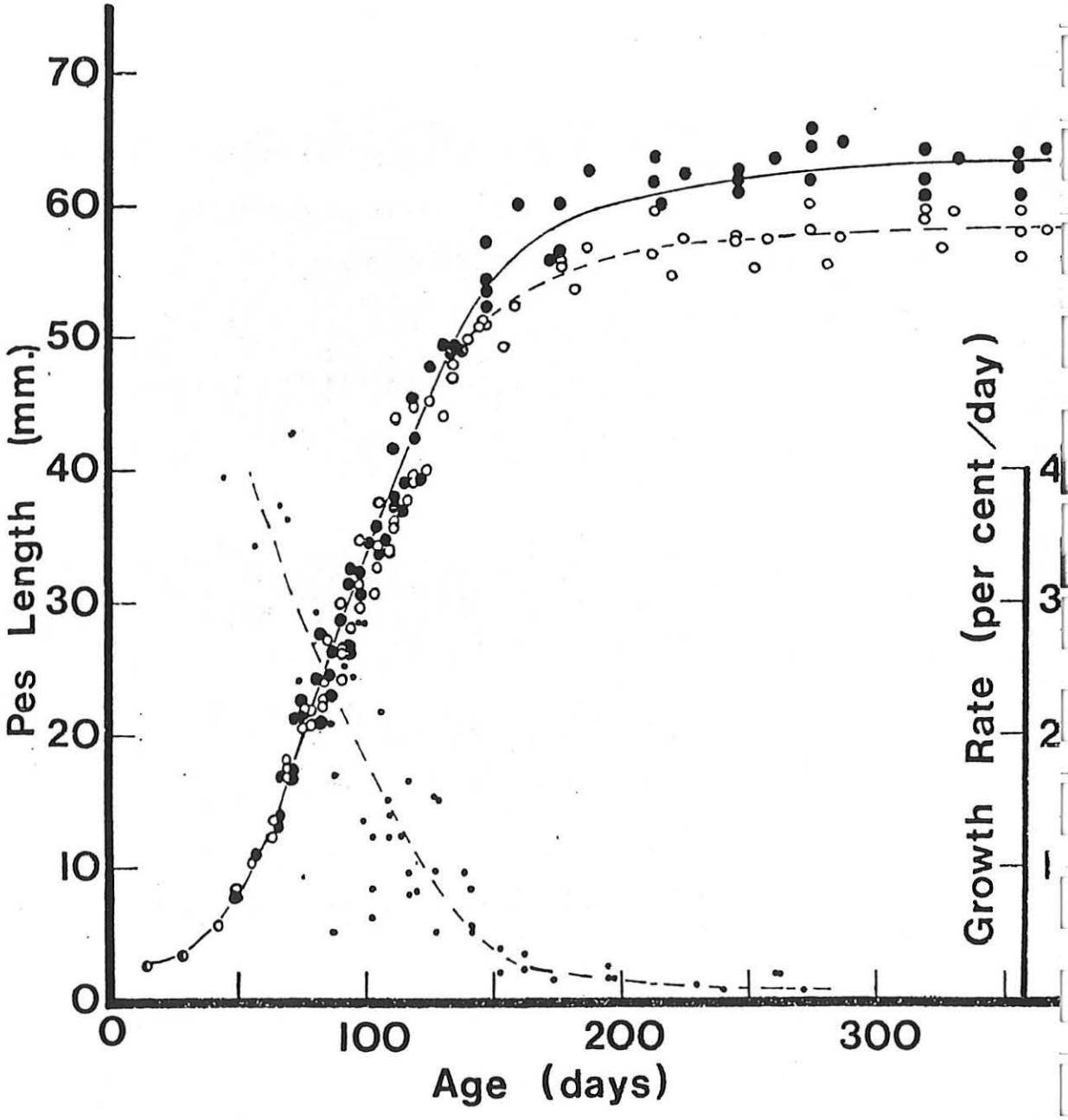

110
100
90
80
70
60
50
40
30
20
10
0
Head Length (mm.)
0
100
200
300
Age (days)
4
3
2
Growth Rate (per cent/day)

Fig 5.5 Scatter diagram of pes length (mm) vs. age (days) for known-age chuditches, and growth rates (per cent/day).

Symbols: as for Fig 5.2


70
60
50
40
30
20
10
0
Pes Length (mm.)
0
100
200
300
Age (days)
4
3
2
1
Growth Rate (per cent/day)

of age was 94.1 mm for four males and 84.1 mm for four females. Growth rates (per cent per day) calculated from individual measurements, are also shown on Fig 5.4 and indicate a decreasing growth rate tending to zero by 300 days of age.

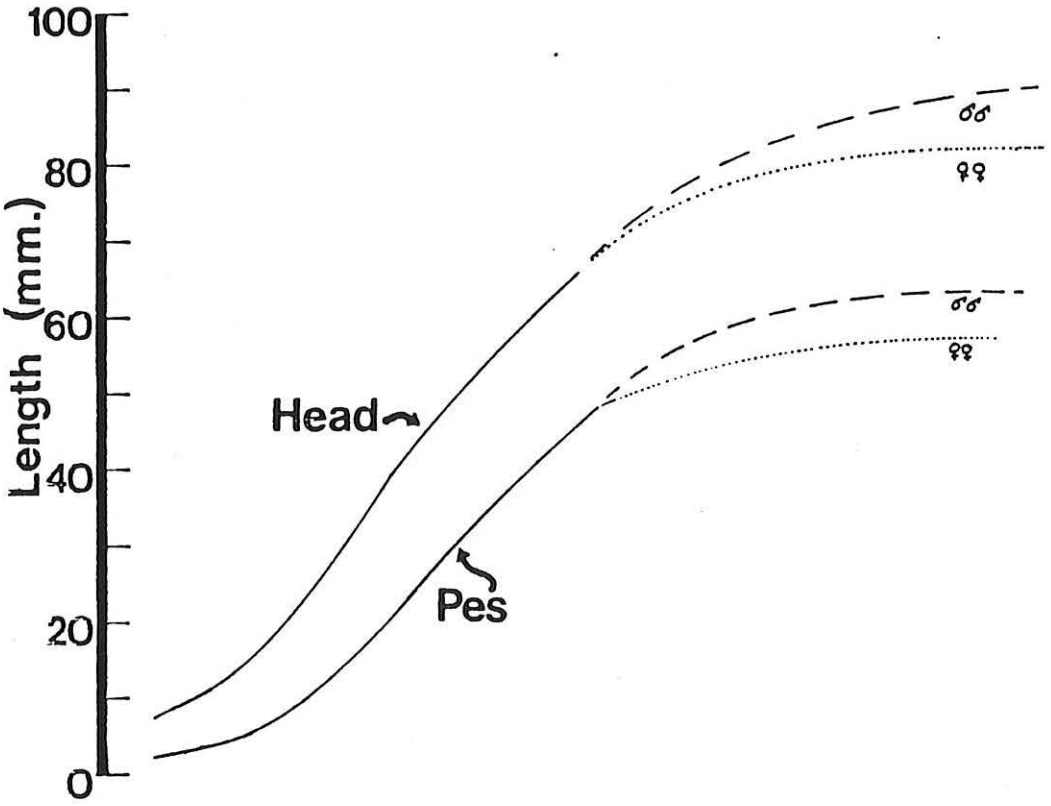
Pes Length.

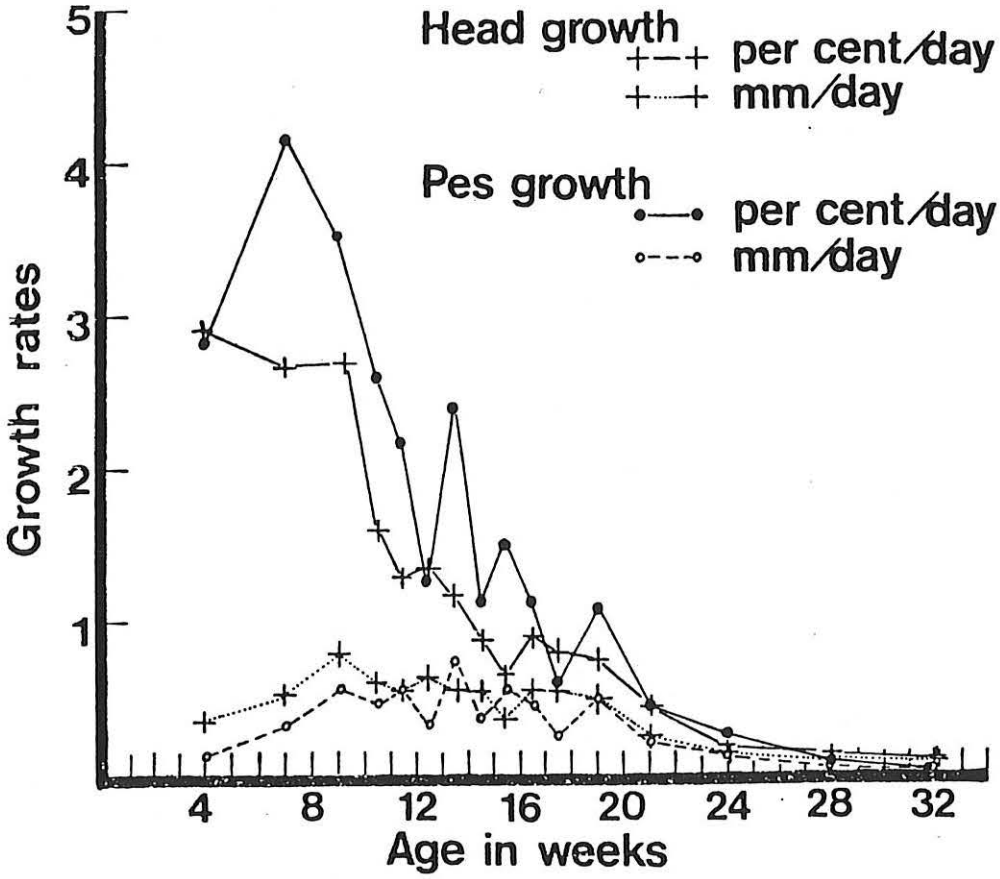
Fig 5.6 shows the smoothed growth curve for pes length together with daily increments in length (per cent/day and mm/day). As for head length the pes growth curve passes through its inflection at about 10-12 weeks of age. Daily growth rates (per cent/day) rose from less than three per cent/day between weeks two and six, to a peak in excess of four per cent/day between weeks six and eight. Thereafter the growth rate was variable but showed a decreasing trend. At the age when the growth curve passed through its inflection the mean percentage daily increment was 1-2.5 per cent/day; at 18-20 weeks it was about 1 per cent/day and by 32 weeks it was less than 0.05 per cent/day. The calculated daily increment in pes length (mm/day) was also rather variable, ranging from 0.11 mm/day at 2-6 weeks, 0.32-0.72 mm/day in the age range 8-20 weeks, falling to 0.23 mm/day at 20-22 weeks and to 0.02 mm/day at 32 weeks. Relatively large increases in pes length therefore occurred at the age when the growth curve was inflected.

Body weight, head and pes lengths of adult animals.

Table 5.2 shows means, standard errors and ranges of

Fig 5.6 Trend lines of head length and pes length (mm) vs. age (weeks) and mean geometric and arithmetric growth rates in head and pes length for known-age chuditches.


100
80
60
40
20
0
Length (mm.)
Head
Pes
♂♂
♀♀
♂♂
♀♀


5
4
3
2
1
Growth rates
Head growth
per cent/day
mm/day
Pes growth
per cent/day
mm/day
4
8
12
16
20
24
28
32
Age in weeks

body weight, head length and pes length of captive adult animals. There is little difference in either head length or pes length between one-year-olds and older animals but both males and females of two years or more weigh about 200 g more than animals of one year. The relatively greater weights of older captive animals may be due to the rather sedentary life they lead in captivity, rather than to a real difference from the younger animals. At one year of age then, when captive animals are known to be reproductively mature, they are close to their maximum linear measurements but are 15-20 per cent lighter than animals of two years or more.

Development of other Features

The progressive development during pouch life of the pelage, of topographical features such as the lips, eyes, ears and claws, of the dentition, and of motor responses, was documented in order to provide some easily identifiable landmarks in the calendar of development of the species. Information on developmental events which occurred during the first seven weeks of pouch life is incomplete because the animals were examined infrequently to minimize the loss of pouch-young due to disturbance of the mother.

Pelage.

Under-fur was first seen on the head at 28 days of age, it could be seen on the dorsal body surface at 49 days, and by 60 days it covered the entire body. The

Table 5.2

Means, ± 1 standard error of means, and ranges of body weight, head length and pes length of captive male and female Dasyurus geoffroii aged one year, and two years or more.

Age	Body Weight (g)	Head Length (mm)	Pes Length (mm)
One year			
males	1300 ± 71.4	94.1 ± 2.9	63.6 ± 0.4
	1175 - 1500	87.5 - 101.5	63.0 - 64.8
	(n=4)	(n=4)	(n=4)
females	864 ± 59.5	85.1 ± 2.5	57.1 ± 0.9
	705 - 960	79.6 - 90.3	54.6 - 58.5
	(n=4)	(n=4)	(n=4)
Two years or more			
males	1523 ± 157.0	95.1 ± 2.5	64.2 ± 0.8
	1190 - 2075	81.9 - 108.8	62.4 - 66.7
	(n=5)	(n=5)	(n=5)
females	1047 ± 50.1	89.0 ± 1.9	58.4 ± 0.5
	965 - 1285	81.9 - 93.3	56.4 - 59.8
	(n=6)	(n=5)	(n=6)

thicker and longer guard hairs also appeared progressively, being first observed on the head between 77 and 84 days of age, and on the dorsum between 84 and 91 days. The body was completely furred, both with under-fur and guard hairs, to the base of the tail by 91-98 days of age and during this time long black hairs appeared on the tail. By 105-112 days the pelage of the animals resembled that of adults except that the juvenile fur appeared longer and more dense. Fig 5.7A shows the ages at which certain stages in development of the coat are reached.

The follicles of the vibrissae were clearly visible at 28 days of age. The first observation of erupted vibrissae was made on an animal aged 42 days.

Topographical features.

Until 49 days of age the lips were fused except around the nipple which remained permanently in the mouth. At about this age the lips began progressively to separate until at 70 days all animals had the lip-line free to the angles of the mouth. Two neonates and three animals aged 14, 28 and 42 days respectively, failed to reattach when removed from the nipple and then replaced in the pouch. The first successful re-attachment occurred at 49 days of age. This coincided with the age at which the lips started to separate.

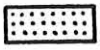
No external vestige of eye or ear was visible at birth. The eye rudiment was apparent as a pigmented ring

Fig 5.7 A. Development of pelage vs. age for known-age chuditches.

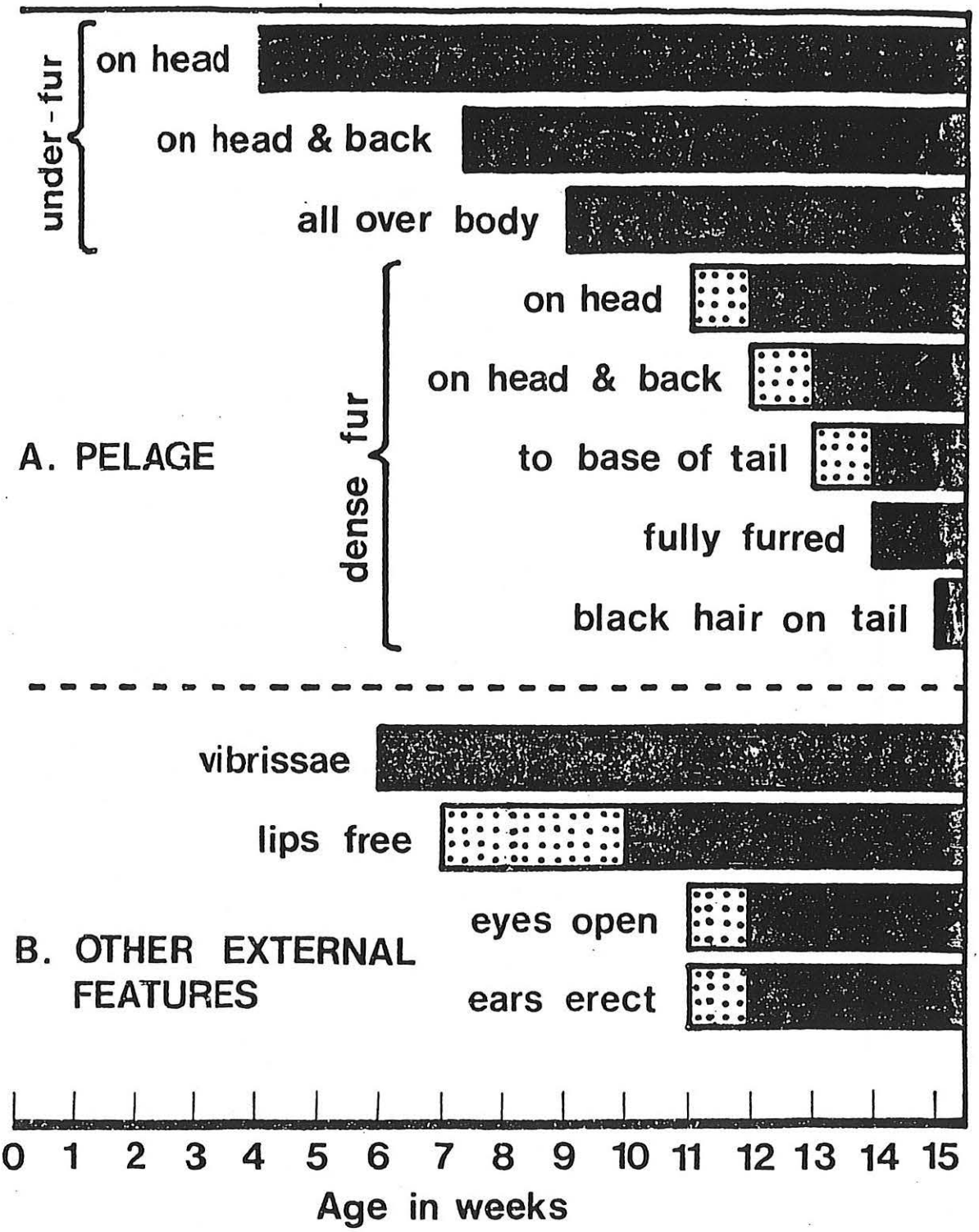
B. Development of other external features vs. age for known-age chuditches.

Symbols:

feature established



feature established partially or in some animals but not in others


under-fur
on head
on head & back
all over body
dense fur
on head
on head & back
to base of tail
fully furred
black hair on tail
A. PELAGE
vibrissae
lips free
eyes open
ears erect
B. OTHER EXTERNAL FEATURES
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Age in weeks

beneath the skin of the head at 14 days of age. The line of the fused eyelids was visible at 28 days and by 42 days the eyelids were well formed and the follicles of the eyelashes could be detected. The eyelids remained fused until about 77 days but all animals had their eyes open by 84 days of age. At 14 days of age the ear orifice was not visible but the pinna could be detected as a small ridge. The earfold was present but the ear canal was still not perforated by 28 days. By 42 days the pinna was pigmented and lay flat over the ear orifice. The pinna became erect when the animals were aged 77-84 days.

By 14 days of age the deciduous claws of the neonate were no longer present. The ankle joint and the digits of the hind-foot were then formed. Permanent claws were present on the digits of the forelimbs by 28 days of age, and by 42 days of age claws were present on all digits except the first digit of the hind foot which characteristically does not bear a claw in the adults of this species. (The first digit of the hindfoot is absent from the eastern native cat D. viverrinus).

Fig 5.7B shows the ages at which certain of the features described above become established. Only those features for which the age of establishment could be determined to within one week are included.

Dentition.

The incisors first became visible through the oral

membrane when animals were aged between 70 and 77 days. At 84 days of age four of the eight animals had at least one erupted incisor. At 91 days all animals had one pair of upper incisors and one to three pairs of lower incisors. The lower canines had pierced the oral membrane in all animals by 98 days of age. At 105 days there were two or three pairs of upper incisors and three pairs of lower incisors. Both upper and lower canines and the cusps of some of the molariform teeth were visible at this age. At 119 days of age all animals had three pairs of incisors in each jaw. The fourth pair of upper incisors erupted between 133 and 147 days of age. The time sequence of the eruption of the teeth is shown in Fig 5.8A.

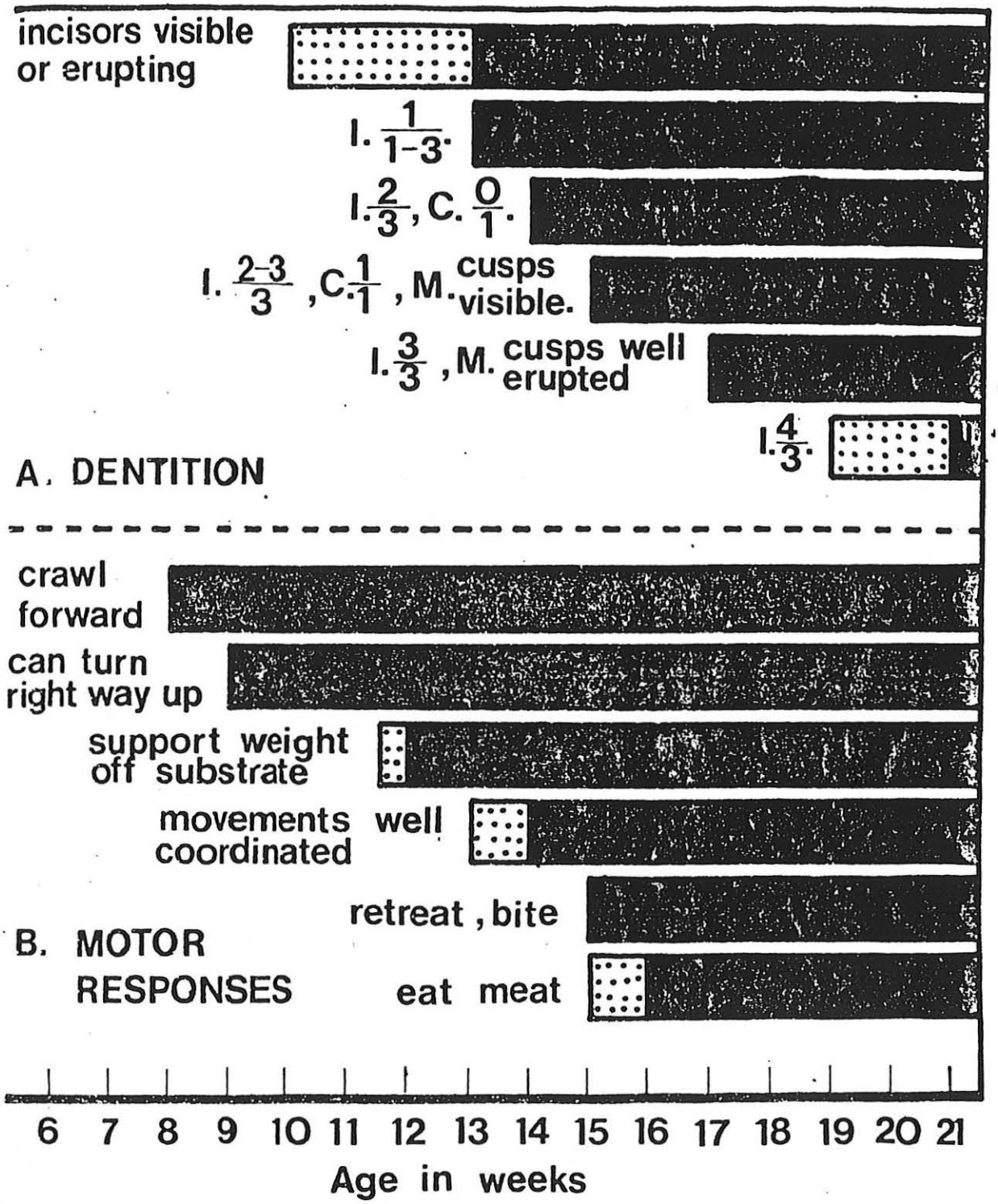
The development of motor responses.

The development of the ability of the pouch-young to progress and to co-ordinate movements occurred as follows:- they were able to crawl forward at 56 days; to right themselves when placed on their backs at 63 days; to shiver at 70 days: to stand erect on four legs, and to show awareness of heights at between 80 and 84 days; they were capable of well-coordinated movements and exhibited threatening behaviour when 90-98 days of age, and at 105 days they would retreat or bite when handled. They were first observed to eat meat at 105-112 days of age. This corresponds with the first observation of dark faecal deposits in their cages. The time sequence of the ontogeny of these developments is shown in Fig 5.8B.

Fig 5.8 A. Eruption of teeth vs. age in known-age chuditches.

B. Development of motor responses vs. age in known-age chuditches.

Symbols: as in Fig 5.7


incisors visible or erupting
I. 1/1-3.
I. 2/3, C. 0/1.
I. 2-3/3, C. 1/1, M. cusps visible.
I. 3/3, M. cusps well erupted
I. 4/3.
A. DENTITION
crawl forward
can turn right way up
support weight off substrate
movements well coordinated
retreat, bite
B. MOTOR RESPONSES
eat meat
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
Age in weeks

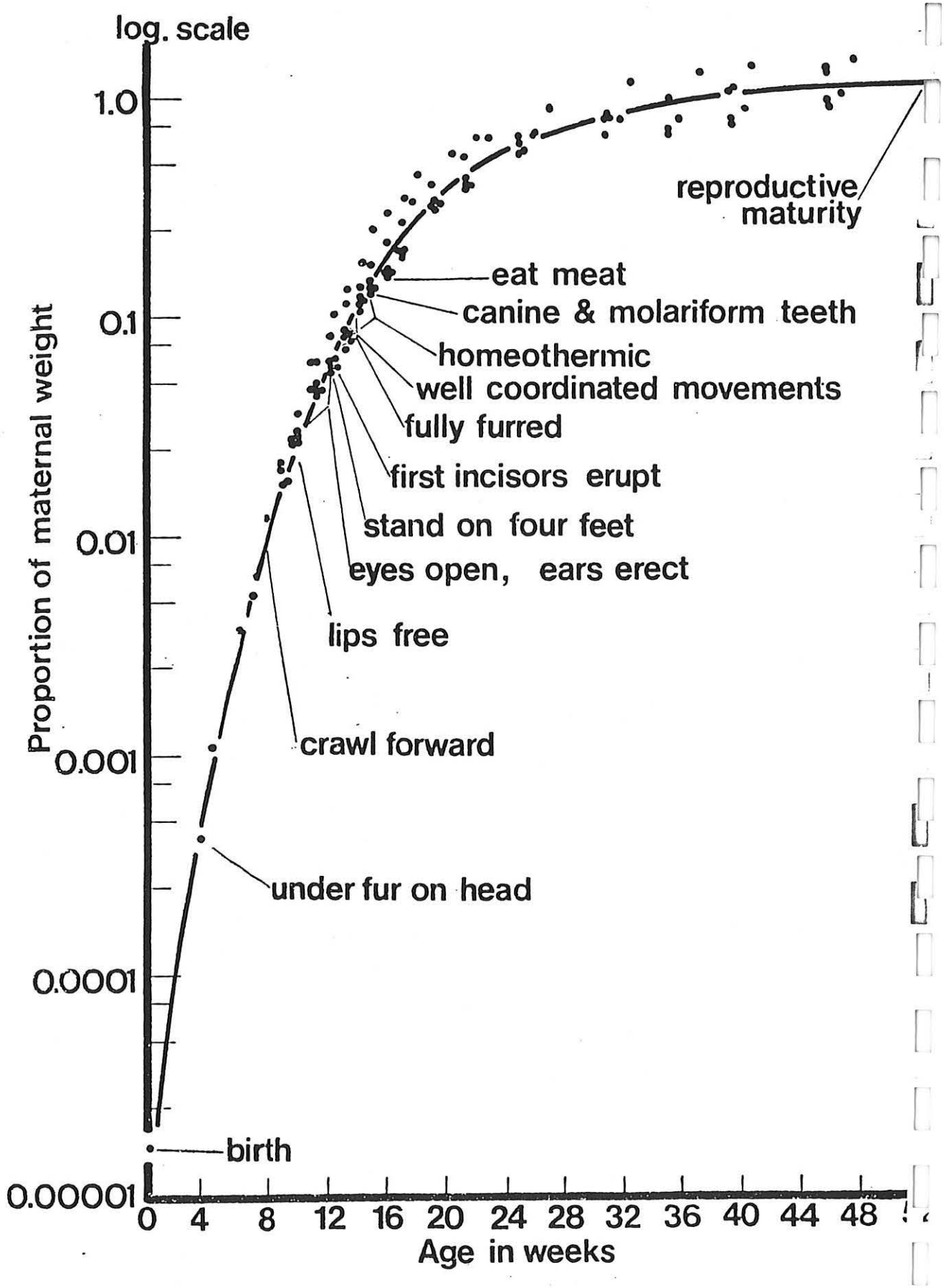
Emergence from the pouch.

Emergence from the pouch is a gradual process. Even when the pouch-young are still permanently attached to the nipples they tend to protrude from the pouch aperture. They apparently detach themselves from the nipples and move about in the pouch from about 10-11 weeks of age and may crawl around on the ventral and dorsal surface of the mother, clinging onto her fur with the fore- and hindfeet. At eleven weeks the total weight of a litter of six is 250-300 g, or more than one-quarter of maternal weight. The females appear first to leave their litters for short periods during the day when the young are aged about 90 days. By this time the pouch will not accommodate the full litter. The weight of a full litter of six is then more than 500 g, or about one-half of maternal weight. The age when the animals ceased to suckle was not determined. Captive animals of 120 days of age or more were observed to suckle occasionally.

Development in relation to Body Weight expressed as proportions of Maternal Weight

Fig 5.9 is a scatter diagram in which body weights of known-age animals, expressed as proportions of maternal weight, are shown vs. age. The trend line was fitted by eye and significant developmental events are indicated on the trend line.

Fig 5.9 Body weight as a proportion of maternal weight for known-age animals vs. age, with eye-fitted trend line. The developmental sequence of certain features are indicated against the trend line.


log. scale
1.0
0.1
0.01
0.001
0.0001
0.00001
Proportion of maternal weight
reproductive maturity
eat meat
canine & molariform teeth
homeothermic
well coordinated movements
fully furred
first incisors erupt
stand on four feet
eyes open, ears erect
lips free
crawl forward
under fur on head
birth
0 4 8 12 16 20 24 28 32 36 40 44 48
Age in weeks

The new-born chuditch has a body weight which is equivalent to 0.000015 or 1/65,000 of maternal weight. The animals remain permanently attached to the nipples in the pouch for the first seven or eight weeks of pouch life. The first successful reattachment of a pouch young occurred at 49 days when the animal was about 1/210 (0.005) of maternal weight and by 56 days of age, when the animals were first able to crawl forward, they were about 1/84 (0.012) of maternal weight. During the interval when animals were 10 weeks to 18 weeks of age, their proportion to maternal weight increased from 1/33 to 1/3 (0.03-0.33). This period could be equated to the perinatal period of eutherian mammals (see Discussion p. 5.50).

Age Estimates

Trend lines connecting weekly mean values of body weight, head length and pes length of known-age animals were used as the basis for estimating the ages of young animals, rather than smoothed curves fitted by eye. It was considered that the resulting relationships would represent mean weekly growth increments more accurately than would the smoothed curves.

Fig 5.10 shows weekly mean body weights, $\pm$ two standard errors and ranges vs. age from birth to 19 weeks of age for known-age animals. Mean values are connected by the trend line. Fig 5.11 shows head and pes lengths

treated similarly. Mean body weights, head lengths and pes lengths at weekly intervals, together with characteristic developmental events are given in detail in Appendix A.

To test the accuracy of age estimates obtained from the growth trends shown in Figs 5.10 and 5.11, measurements of body weight, head length and pes length were made of members of one captive-born litter of known age. These measurements were not used in construction of the growth curves. The measurements were compared with the growth trends in Figs 5.10 and 5.11 to obtain age estimates. Table 5.3 shows the measurements of the animals together with their known ages on the dates on which measurements were made, age estimates derived from each measurement and means of the estimates from the three separate measurements.

Means of estimates based on the three measurements provided age estimates which were within $\pm$ four days of known age. The greatest single errors arose in estimates based on body weight alone (+2 to +10 days) and the smallest errors arose in estimates based on pes length alone (-5 to +1 days). Estimates derived from the means of the estimates from the three separate measurements were more reliable than those obtained from single measurements. Again, when measurements of body weight, head length and pes length of these known-age animals are compared with the weekly means in Table 5.3 to obtain estimates of age to the nearest week, both head length and body weight tend to overestimate age

Fig 5.10 Weekly mean body weight (g) vs. age (weeks) for known-age chuditches.

Symbols: Horizontal lines: weekly means

Boxes: ± 2 s.e's of means

Vertical lines: ranges

The trend line connects means.

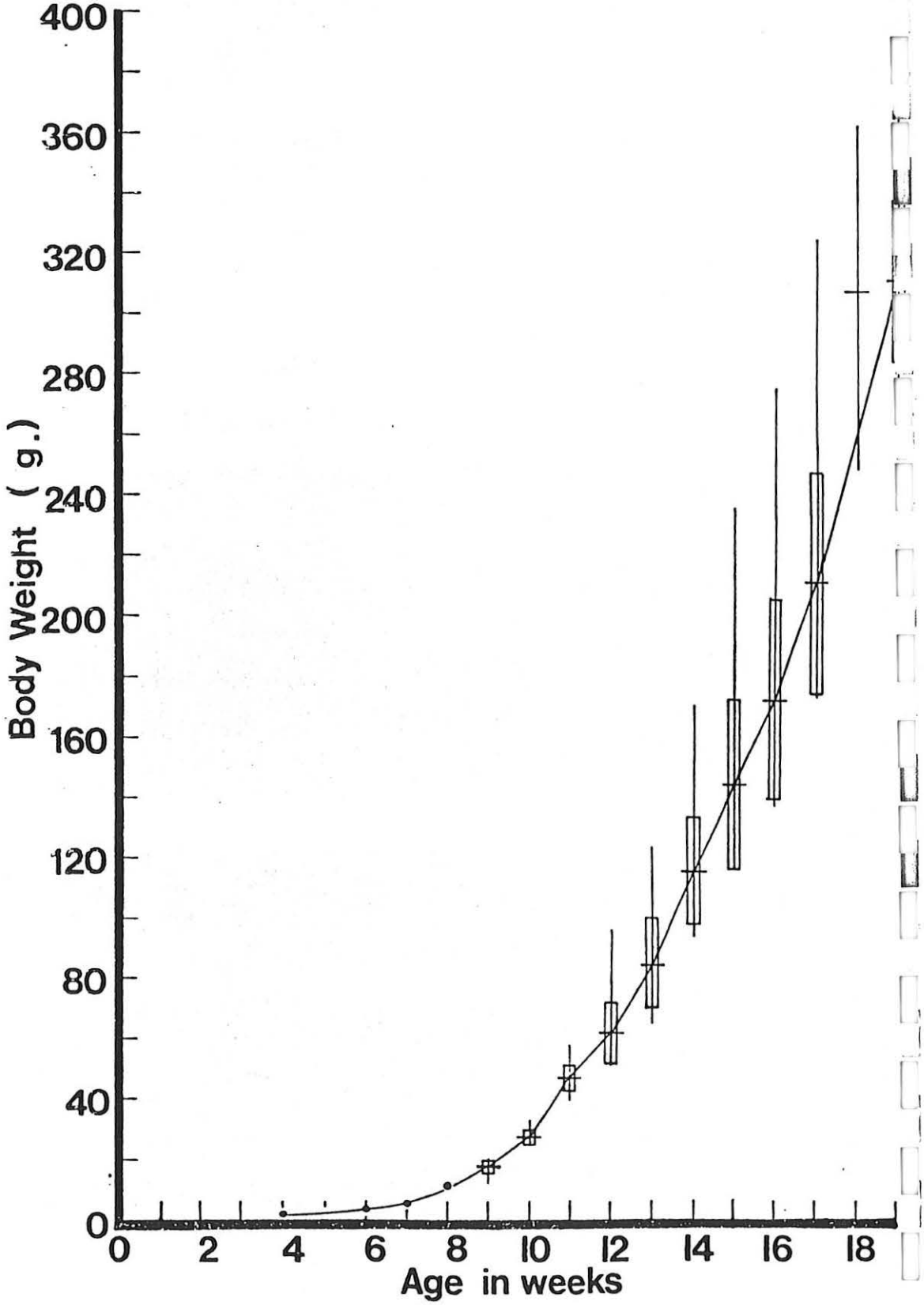
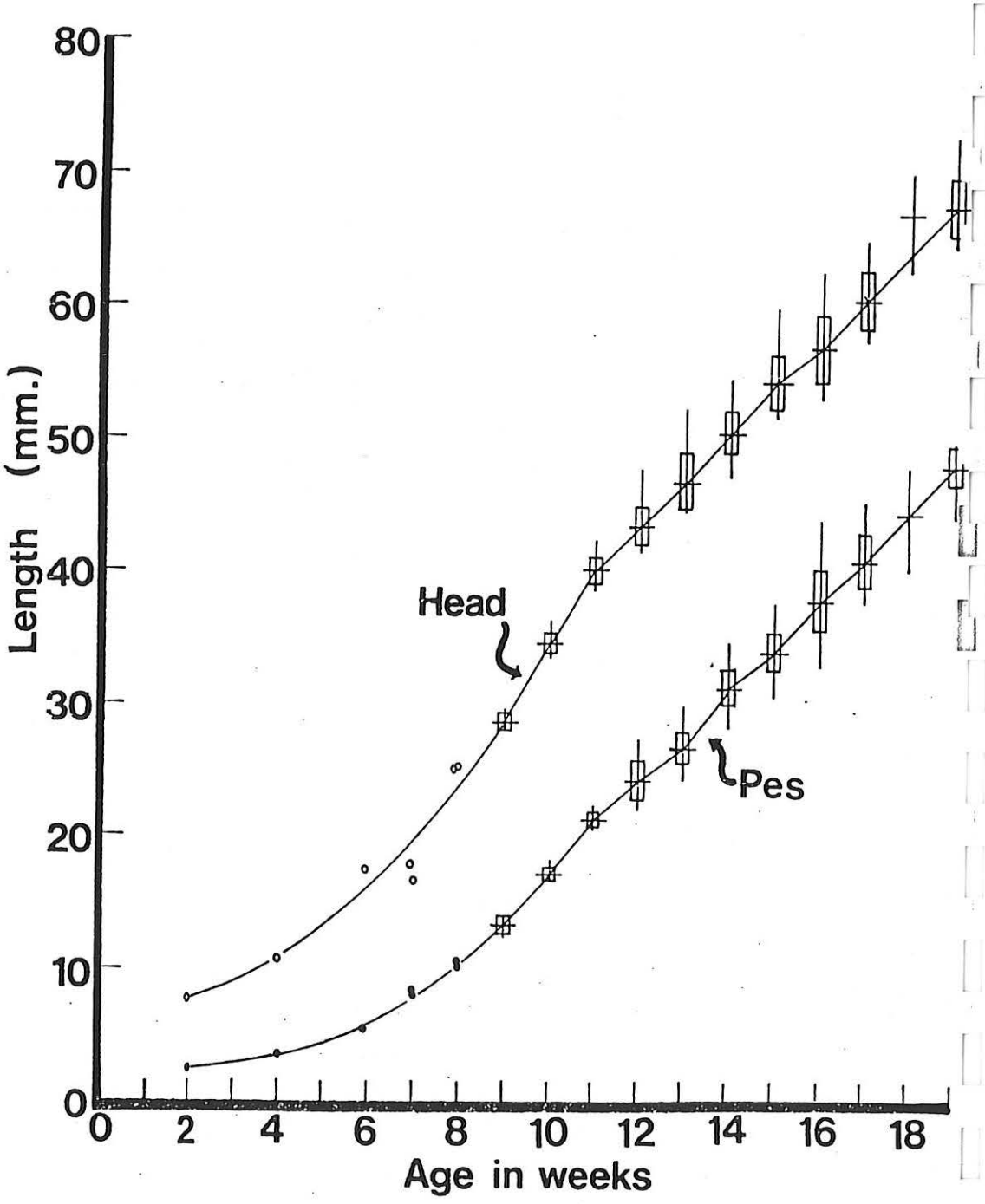

400
360
320
280
240
200
160
120
80
40
0
Body Weight (g.)
0
2
4
6
8
10
12
14
16
18
Age in weeks

Fig. 5.11 Weekly means of head length and pes length (mm) vs. age (weeks) for known-age chuditches.

Symbols: as for Fig 5.10


80
70
60
50
40
30
20
10
0
Length (mm.)
Head
Pes
0
2
4
6
8
10
12
14
16
18
Age in weeks

while pes length gives estimates correct to the nearest week.

The growth trends were used to estimate the ages of two litters captured in the wild. In order to determine whether age-dependent variation in age estimates would arise, estimates were made from successive sets of measurements made over a period of several weeks.

The six members of one litter of juveniles, captured with their mother from the wild as pouch-young in 1966 (Litter 1), were measured six times over a seven-week period. The mean values of body weight, head length and pes length for the six animals were compared with the growth trends shown in Figs 5.10 and 5.11 to obtain estimates of their age. For comparison with the age estimates obtained from each set of measurements, ages based on earlier and later estimates were also calculated. The results of this procedure are shown on Table 5.4.

Differences in age estimates based on body weight alone were within 14 days of those based on pes length while those based on head length fell between these two extremes. Variation was also apparent between initial estimates and estimates based on succeeding measurements. For instance, according to the estimates based on the first set of measurements, the animals were about 14 days older than estimates based on the last set of measurements would suggest. Nevertheless, estimates differed by less than 10 per cent in the age range concerned.

Table 5.3

Body weights, head lengths and pes lengths of pouch-young of known age from 52 to 108 days of age (Litter No.6), together with ages estimated from growth-trends of a different group of known-age animals.

Date	Known age (days)	Weight (g)	Head (mm)	Pes (mm)	Age estimate (days) based on:				Diff. between known age and estimated age (days)
					Weight	Head l.	Pes l.	Mean of 3 estimates	
19.vii.69	52	—	—	7.5	—	—	48	—	-4
1.viii.69	65	22.02	31.6	14.9	65	67	66	66	+1
20.viii.69	84	71.5	44.6	24.7	87	86	85	86	+2
20.viii.69	84	72.0	45.7	24.6	87	89	85	87	+3
20.viii.69	84	66.4	44.7	23.0	86	86	80	84	0
27.viii.69	91	92.4	48.5	27.6	93	93	92	93	+2
27.viii.69	91	102.7	44.9	27.1	95	87	91	91	0
13.ix.69	108	205	57.4	33.2	118	113	104	112	+4
13.ix.69	108	165	54.0	32.8	110	105	103	106	-2

Table 5.4

Mean body weight, head length and pes length of 1966 litter (Litter No.1) for a seven-week period, together with estimates of age determined from growth trends of known-age animals.

Date	Mean measurements			Age estimate based on: (days)				Estimated age using successive estimates					
	Weight (g)	Head l. (mm)	Pes l. (mm)	Weight	Head	Pes	Mean	1st	2nd	3rd	4th	5th	6th
14. x.66	127.5	55.3	39.5	101	108	115	108		104	103	104	98	96
21. x.66	135.2	58.3	39.8	103	115	116	111	115		110	111	105	103
28. x.66	171.0	58.3	42.8	112	115	123	117	122	118		118	112	110
4. xi.66	203	62.4	47.5	118	124	132	125	129	125	124		119	117
18. xi.66	262	66.5	50.5	126	132	140	133	143	139	138	139		131
2. xii.66	406	71.0	53.0	147	141	147	145	157	153	152	153	147	

Table 5.4

Mean body weight, head length and pes length of 1966 litter (Litter No.1) for a seven-week period, together with estimates of age determined from growth trends of known-age animals.

Date	Mean measurements			Age estimate based on: (days)				Estimated age using successive estimates					
	Weight (g)	Head l. (mm)	Pes l. (mm)	Weight	Head	Pes	Mean	1st	2nd	3rd	4th	5th	6th
14. x.66	127.5	55.3	39.5	101	108	115	108		104	103	104	98	96
21. x.66	135.2	58.3	39.8	103	115	116	111	115		110	111	105	103
28. x.66	171.0	58.3	42.8	112	115	123	117	122	118		118	112	110
4. xi.66	203	62.4	47.5	118	124	132	125	129	125	124		119	117
18. xi.66	262	66.5	50.5	126	132	140	133	143	139	138	139		131
2. xii.66	406	71.0	53.0	147	141	147	145	157	153	152	153	147	

The five members of another litter, captured in the wild with their mother in 1967, were measured at seven-day intervals over an eight-week period in their initial period of captivity. When the first set of measurements were made the animals still had closed eyes; underfur was present all over the body but guard hairs had not yet appeared on the head; the righting reflex was present but they were not able to support their weight on four feet. From the calendar of development of known-age animals they were considered to be between 63 and 77 days of age. Table 5.5 shows mean body weights, head lengths and pes lengths for these five animals during the eight-week period together with age estimates based on separate measurements and comparisons of estimates made in successive weeks.

The age estimates obtained for the 1967 animals were much more consistent than those obtained for the 1966 litter. For each of the nine sets of measurements used, differences of from two to five days occurred between estimates made from the three separate measurements. However, according to the first two sets of measurements the animals were about ten days younger than estimates from the last five sets of measurements indicate.

No systematic differences between estimates made at different ages could be detected. For the 1966 litters variations in the order of 10-15 per cent arose in estimates based on separate measures in any one week but

Table 5.5

Mean body weight, head length and pes length of 1967 litter (Litter No.2) at weekly intervals for an eight-week period, together with estimates of age determined from growth trends of known-age animals

Date	Mean measurements			Age estimate in days based on:				Estimated age using successive estimates								
	Weight (g)	Head (mm)	Pes (mm)	Wt.	Head	Pes	Mean	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
4. ix. 67	24.3	32.7	15.2	69	68	66	68		68	71	72	76	76	78	77	77
11. ix. 67	42.8	38.6	19.0	77	76	73	75	75		78	79	83	83	85	84	84
18. ix. 67	69.2	43.7	24.0	87	84	84	85	82	82		86	90	90	92	91	91
25. ix. 67	103.3	48.1	27.3	95	93	92	93	89	89	92		97	97	99	98	98
2. x. 67	148.8	53.1	32.9	106	103	102	104	96	96	99	100		104	106	105	105
9. x. 67	181.4	55.5	37.9	113	108	112	111	103	103	106	107	111		113	112	112
16. x. 67	227.4	61.4	40.0	121	121	117	120	110	110	113	114	118	118		119	119
23. x. 67	256.8	63.4	45.5	126	125	128	126	117	117	120	121	125	125	127		126
30. x. 67	310.0	66.6	48.8	133	131	135	133	123	123	127	128	132	132	134	133	

estimates based on the first and last sets of measurements differed by less than 10 per cent. For the 1967 litter age estimates based on separate measures made at the same time differed by from 1 to 5 per cent while differences between the first and last sets of estimates again differed by about 10 per cent.

Discussion

In many respects the new-born of Dasyurus geoffroii resembles the neonatal Dasyurus viverrinus as described by Hill and Hill (1955). The birth weight of D. viverrinus is 12.5 mg (Hill and Hill) which is comewhat lower than the birth weight of D. geoffroii (14-15 mg). Birth weights for both species were determined from small numbers of animals and, further, it is possible that Hill and Hill measured birth weight after spirit fixation. It seems likely that larger samples would show that the birth weights of the two species are very similar.

The birth weight of the chuditch is about 1/65,000 of maternal weight so that a litter of six new-born animals is equivalent to 1/10,800 of the mother's weight. This neonatal:maternal weight ratio is extremely small when compared with that of other marsupials. For example:- Megaleia 1/33,800; Setonix 1/7,200; Perameles 1/3,700; Antechinus 1/1,900. For multiparous species, when litters rather than individual neonates are considered, a litter of five Perameles nasuta represents 1/750 of maternal

weight and a litter of eight Antechinus represents 1/236 of maternal weight. (References: Megaleia Sharman and Pilton, 1964; Setonix Shield, 1968; Perameles nasuta Lyne, 1964; Antechinus Marlow, 1961). Only D. viverrinus has a birth weight:maternal weight ratio as low as that of the chuditch. Tyndale-Biscoe (1973) pointed out that marsupial birth weights are correlated with log maternal weight but D. viverrinus is well removed from the general trend in his graphical representation of this relationship.

The weights of neonatal eutherians are of a different order of magnitude than those of marsupials. Leitch, Hytten and Billewicz (1959) recorded neonatal and maternal weights for 114 species of eutherian mammals. Neonatal weights as fractions of maternal weights for some small eutherian mammals are: rabbit 1/40, domestic cat 1/24, house mouse and rat 1/20, guinea pig 1/7.

Leitch et al found a straight-line relationship between log maternal weight and log total weight of new-born young for eutherian mammals. This line is described by the equation

$$\log_{10} N = 0.83231 \log_{10} M - 0.32628$$

where N = total weight of new-born young and M = maternal weight, both in grams. If this relationship is compared with data for marsupials (Fig 5.14) the difference between the two groups with respect to birth weight is graphically apparent. References for birth weights and litter sizes

of the 11 marsupial species included on the graph are:- Didelphis marsupialis, Hartman, 1928; Dasyurus viverrinus, Hill and Hill, 1955; Isoodon macrourus, Mackerras and Smith, 1960; Antechinus stuartii, Marlow, 1961; Potorous tridactylus, Hughes, 1962; Trichosurus vulpecula, Pilton and Sharman, 1962; Megaleia, Sharman and Pilton, 1964; Perameles nasuta, Lyne, 1964; Setonix, Shield, 1968; Bettongia lesueur, Tyndale-Biscoe, 1968; Dasyurus geoffroii, this study.

A regression fitted to log maternal weights vs. log total weights of new-born young of marsupial species is described by the equation

$$\log_{10}N = 0.29414 \log_{10}M - 1.29264$$

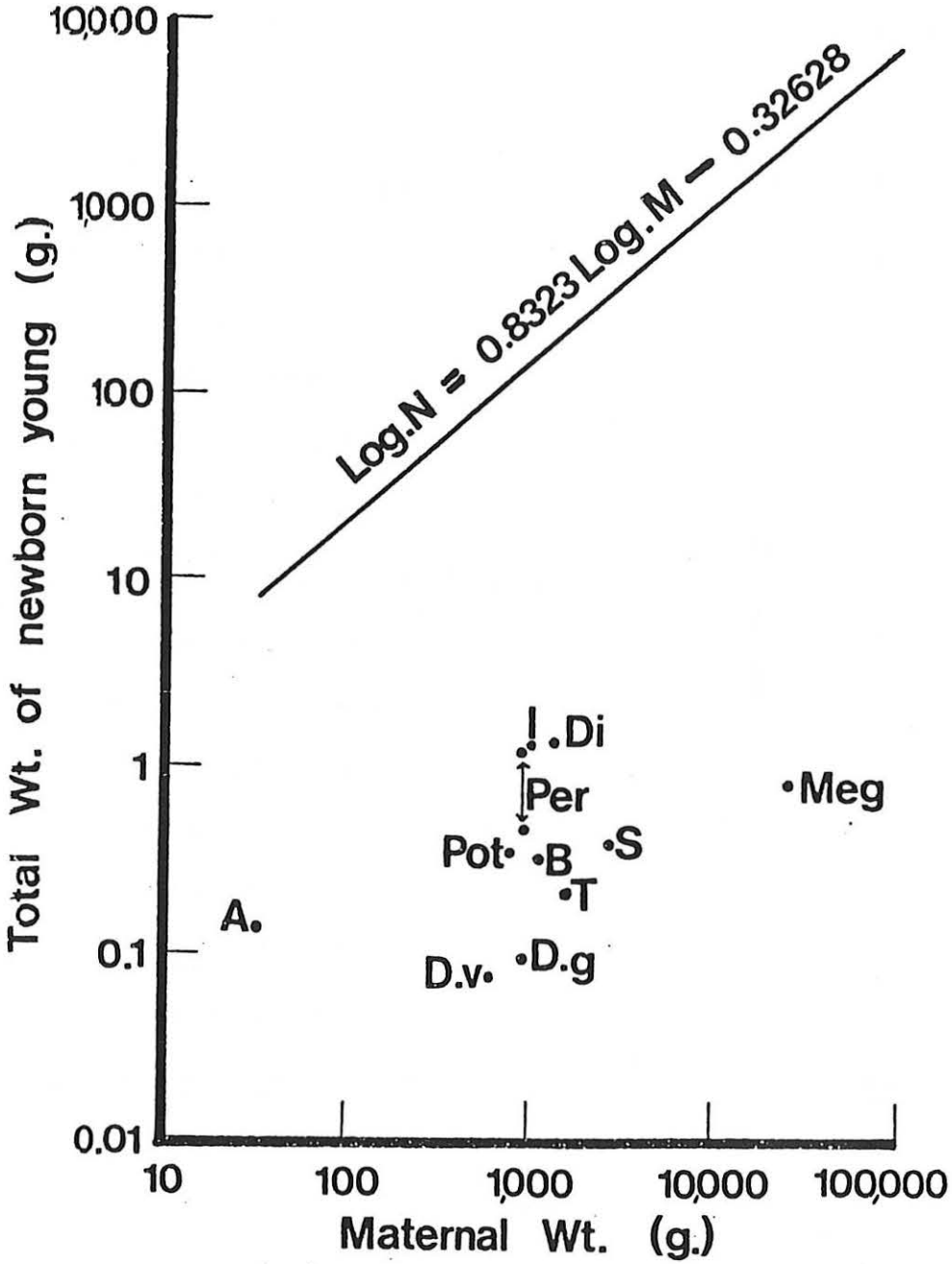
where N = total weight of new-born young and M = maternal weight, both in grams. The correlation coefficient of these values is, however, non-significant so that the regression cannot be said to be descriptive of marsupials in the same way that the regression of Leitch et al is descriptive for eutherians.

The curve of growth versus age typically follows a sigmoid curve, be it describing the growth of a single organism, or that of a population (Brody, 1945). The growth curve of eutherian mammals, from birth, as illustrated by many examples in Brody's discussion of growth, represents only the upper part of the sigmoid curve, the lower part being completed in utero. Waring, Moir and

Fig. 5.12 Total weight of neonates (g) vs. maternal w weight (g) (log scales) for eleven species of marsupials together with the interspecific regression of total neonatal weight vs. maternal weight for eutherian mammals (Leitch et al, 1959).

Key: Di = Didelphis; D.v = Dasyurus viverrinus; I = Isoodon macrourus; A = Antechinus stuartii; Pot = Potorous tridactylus; T = Trichosurus vulpecula; Meg = Megaleia rufa; Per = Perameles nasuta*; S = Setonix brachyurus; B = Bettongia lesueur; D.g = Dasyurus geoffroii.

* Two values for Perameles refer to litters of three and eight individuals.


10,000
1,000
100
10
1
0.1
0.01
Totai Wt. of newborn young (g.)
Log.N = 0.8323 Log.M − 0.32628
Di
Per
Meg
Pot
B
S
T
A.
D.v.
D.g
10
100
1,000
10,000
100,000
Maternal Wt. (g.)

Tyndale-Biscoe (1966), in reviewing the literature on marsupials, stated that 'at birth, the young marsupial is at a stage equivalent to the eutherian at the end of the embryonic phase of gestation when all the main organs are differentiated, but little growth has occurred'. Hartman (1928), with reference to Didelphis, observed that the early part of the growth curve of the pouch young exhibits a form which is typical of the foetal eutherian. This statement may be applied to the marsupials in general. The curve of growth during pouch life takes the shape of the lower portion of the typical sigmoid growth curve. Thus growth and development during pouch life of marsupials may be equated in many respects to uterine growth and development of eutherians.

Brody (1945) divided the curve of growth from conception versus age into two principal segments. The first part, of increasing slope, he designated the 'self-accelerating phase of growth' and the second part, in which the slope is decreasing, he designated the 'self-inhibiting phase of growth'. The inflection of the curve, at the change from increasing slope to decreasing slope, is accompanied by the greatest arithmetic increments in size and by declining geometric growth rates. Brody considered that this point of inflection could be equated with puberty in animals and could be used as a 'geometric referent' for the comparison of age equivalence in different species. Throughout his discussion he used

body weight as a measure of growth.

Simpson, Roe and Lewontin (1960), in discussion of the statistical treatment of growth data, also pointed out that the point when the arithmetic plot of size against age becomes inflected occurs when the increment in the measurement per unit time, the arithmetic growth rate, is greatest. However they equated the inflection point of the growth curve with birth rather than with puberty. Thus the earlier part of the curve, when arithmetic increments increase more and more rapidly, is mainly embryonic, while the latter part, with arithmetic increments decreasing, is mainly or wholly post-natal. Presumably Simpson, Roe and Lewontin were referring particularly to eutherian mammals in this discussion although they do not explicitly state this. From the examples used they were also dealing particularly with linear measurements rather than with body weight.

For the chuditch the growth curve for body weight is inflected at 20-22 weeks of age. At this age the animals have completely emerged from the pouch and are at least partially independent of the mother. It is at about this age that differences in body size between males and females become apparent with the males being generally larger than the females.

On the other hand, curves of growth in head length and pes length vs. age are inflected at 10-12 weeks after

birth. The inflections coincide with high arithmetic increments in length and with falling percentage growth rates. At 10-12 weeks of age the guard hairs first appear on the head, the animals detach from the nipples and move around free in the pouch, the eyes open and the ears become erect, and they have the righting reflex established and become capable of standing erect. Shivering is also observed at about this age. Eutherian mammals differ greatly in their stages of development at birth and the extremes can be indicated by the hamster and the rat at the one extreme, and the guinea pig at the other. The new-born hamster and rat are hairless, the righting reflex is just established and both have prolonged tolerance to anoxia whereas the guinea pig is fully furred, is homeothermic, has righting and postural reflexes established, and has poor tolerance of anoxia (Reynolds, 1949). The 10-12 week chuditch is equivalent to a new-born rat in its fur and reflex development, whereas at 15 weeks it has reached a stage of development which can be equated with that of the neonatal guinea pig with well-developed coat, postural reflexes, and good thermal regulation (Chapter VI).

Lyne and Verhagen (1957) compared growth curves of the brush-tailed possum, Trichosurus vulpecula, mouse, sheep, cow and man, using comparable scales of 'ultimate linear equivalence' ($\sqrt[3]{}$ body weight) versus the time taken

from conception to reach half of the ultimate linear equivalence. They demonstrated that the curves for Trichosurus, mouse, sheep and cow were essentially similar but differed from that of man. The curves for the species other than man coincided at about the points of inflection, close to birth for the mouse, sheep and cow, and at about 150 days of pouch life for Trichosurus, shortly before its complete emergence from the pouch.

Examination of growth curves for some marsupial species, Setonix (Shield and Woolley, 1961), Trichosurus (Lyne and Verhagen, 1957), Bettongia lesueur (Tyndale-Biscoe, 1968), Perameles nasuta (Lyne, 1964), Macropus parma (Maynes, 1972) reveals that the inflection of their growth curves of linear measurements vs. age occur some time before complete emergence from the pouch, whereas the inflection of the growth curves of body weight occur shortly after emergence from the pouch.

Medawar (1950) considered that undue significance should not be placed upon the inflection of the arithmetic plot of growth versus age. Nevertheless scrutiny of the above growth curves, in conjunction with observation of the maturation of certain external features does bear out the generalisations of Brody, and Simpson, Roe and Lewontin in providing referents for inter-specific comparison.

Estimates of age of pouch young based on measurements of head and pes length and body weight of known age animals together with the stage of development of certain

external features are reliable to within 10 per cent for a small group of animals of known age. Linear measurements provided more consistent estimates of age than did body weight. This is to be expected as linear measurements would be less affected by levels of feeding than would body weight. Successive age estimates of animals of unknown age showed some inconsistencies but again they were within 10 per cent. The data should prove adequate for aging pouch young but are not sufficient to age animals after they have assumed adult pelage and have fully emerged from the pouch. The one event of use in aging juveniles once they are fully furred is the emergence of the fourth upper incisor between 19 and 21 weeks of age.

CHAPTER VI

THE DEVELOPMENT OF HOMEOTHERMY

Preamble

The development of thermoregulatory mechanisms is of low physiological priority during the early pouch life of marsupials as the young are incubated in the pouch at high and constant temperatures for many weeks after birth. In contrast, many new-born eutherian mammals must be able to regulate body temperature within a few hours or days of birth and even those species which remain in an insulative nest for a time after birth develop the capacity to regulate body temperature within two or three weeks.

Young Dasyurus geoffroii were subjected to mild temperature stress, in order to determine the age at which the pouch-young became able to maintain their body temperature above ambient temperature, and whether a circadian cycle in body temperature comparable with that of adults was present soon after the establishment of homeothermy.

Results

Response of Young Animals to mild Temperature Stress

Animals of estimated age.

Mean body temperatures and mean body weights of five litter-mates aged from about 12 to 25 weeks, before

Table 6.1

Estimated age, means and standard errors of body weight and body temperature for five litter-mates (Litter No.2). Body temperature was measured immediately on removal from cage and after one hour and three hours of exposure in the laboratory to the specified environmental temperature

Estimated Age (weeks)	Mean body wt. ±1 s.e. (g)	Environ. Temp. °C	Body Temperature °C			No. animals
			Initial	After 1 hour	After 3 hours	
12	69.2 ± 1.27	20	31.4 ± 0.33	25.5 ± 0.18	—	5
13	103.3 ± 1.49	20	31.7 ± 0.45	29.0 ± 0.61	—	5
14	148.8 ± 1.89	21	34.5 ± 0.56	34.7 ± 0.30	—	5
15	181.4 ± 4.71	20-22	33.4 ± 0.24	36.1 ± 0.27	35.8 ± 0.33	5
16	227.2 ± 6.02	22	35.9 ± 0.13	37.3 ± 0.20	36.5 ± 0.15	5
17	256.8 ± 8.19	22	35.6 ± 0.25	36.7 ± 0.22	36.2 ± 0.07	5
18	310.0 ± 15.37	22	35.7 ± 0.24	36.6 ± 0.21	35.1 ± 0.26	5
19	367 ± 14.3	23-25	35.7 ± 0.37	35.8 ± 0.35	34.9 ± 0.47	5
22	500 ± 60.6	25	36.4 ± 0.47	37.1 ± 0.17	36.4 ± 0.35	4
25	683 ± 44.1	26	36.5 ± 0.34	35.9 ± 0.50	35.2 ± 0.24	5

and after exposure to ambient temperatures of 20°-26°C, are shown in Table 6.1. At 12 weeks of age the mean body temperature decreased six degrees to 25.5°C during one hour of exposure to 20°C. These animals were observed to shiver when first removed from the pouch but during the last 30 minutes of exposure they shivered only when disturbed by noises in the laboratory. At the end of one hour they were replaced in the pouch and immediately began to suckle. At 13 weeks of age they were found, for the first time, out of the pouch and away from the mother, but huddled together in the nest-box. Initial mean body temperature was slightly higher than that recorded in the previous week and, during this hour of exposure to 20°C, the mean body temperature decreased less than two degrees. The animals shivered almost continuously during the hour. At 14 weeks of age they were able, for the first time, to maintain body temperature 14° above air temperature during one hour of exposure to 21°C. At 15 weeks of age, mean body temperature was more than two degrees above the mean initial value after three hours of exposure at 20°-22°C. All animals older than 15 weeks maintained or increased body temperature during three hours of exposure to the environmental temperatures prevailing in the laboratory (22°-26°C).

Known-age animals.

Mean body temperatures of eight known-age animals

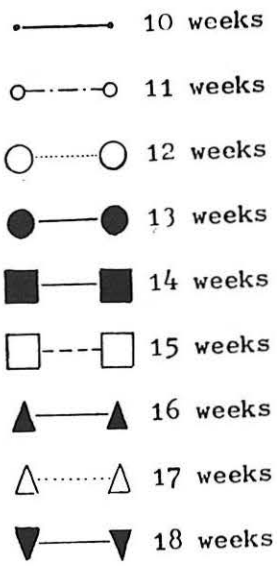
from three different litters (Litter Nos. 3, 4 and 5), aged from 10-18 weeks are shown in Fig 6.1. Temperatures were measured at 10-minute intervals for one hour after removal from the pouch or nest-box.

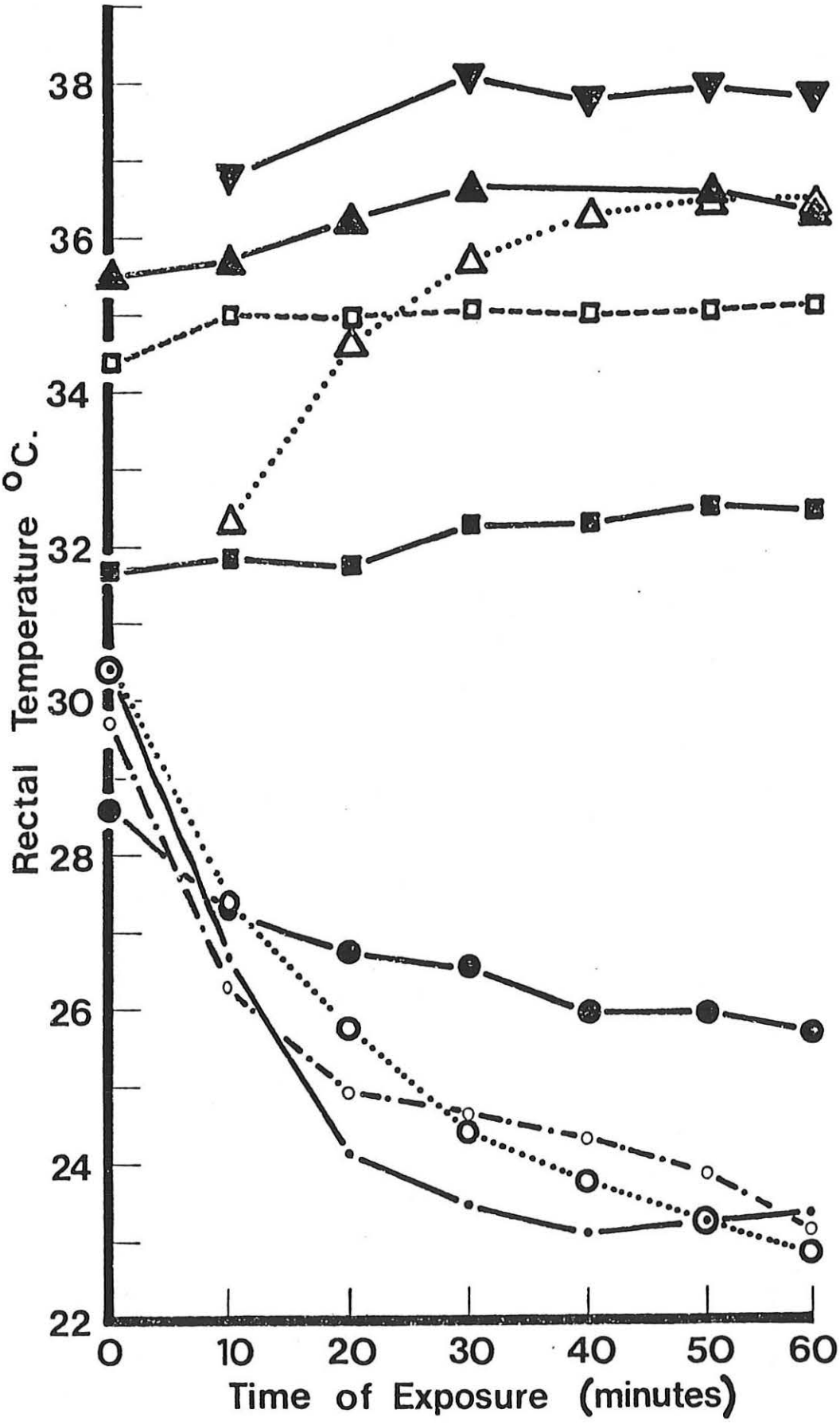
At 10 weeks of age, mean body temperature fell seven degrees, from 30.4° to 23.4°C, during the first 30 minutes of exposure to an ambient temperature of 19°C and then stabilised at about four degrees above ambient temperature. The animals did not shiver during the first 30 minutes but during the second half-hour slight shivering and accelerated breathing rates were observed. A similar response pattern was observed for the next two weeks, during which time mean body weight almost trebled (24.7 g at 10 weeks; 63.6 g at 12 weeks). When the animals were 13 weeks old they were occasionally found away from the mother in the nest-box. At this age body temperature decreased by less than three degrees over a period of one hour of exposure to ambient temperatures of 17°-19°C. At 14 weeks of age mean body temperature rose steadily from 31.7° to 32.5° during one hour of exposure to 18°-20°C. Animals older than 13 weeks showed a continuous rise in the level of controlled body temperature, from 32°C at 14 weeks to 37°-38°C at 18 weeks.

The use of mean body temperatures, as plotted on Fig 6.1, does not show the variation which was observed. Consequently mean body temperatures, standard errors and

Fig 6.1 Mean body temperature of known-age chuditches at 10-minute intervals during one hour of exposure to room temperature when aged from 10 to 18 weeks.

Symbols:



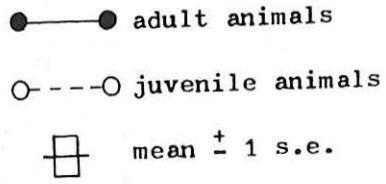

Rectal Temperature °C.
38
36
34
32
30
28
26
24
22
0
10
20
30
40
50
60
Time of Exposure (minutes)

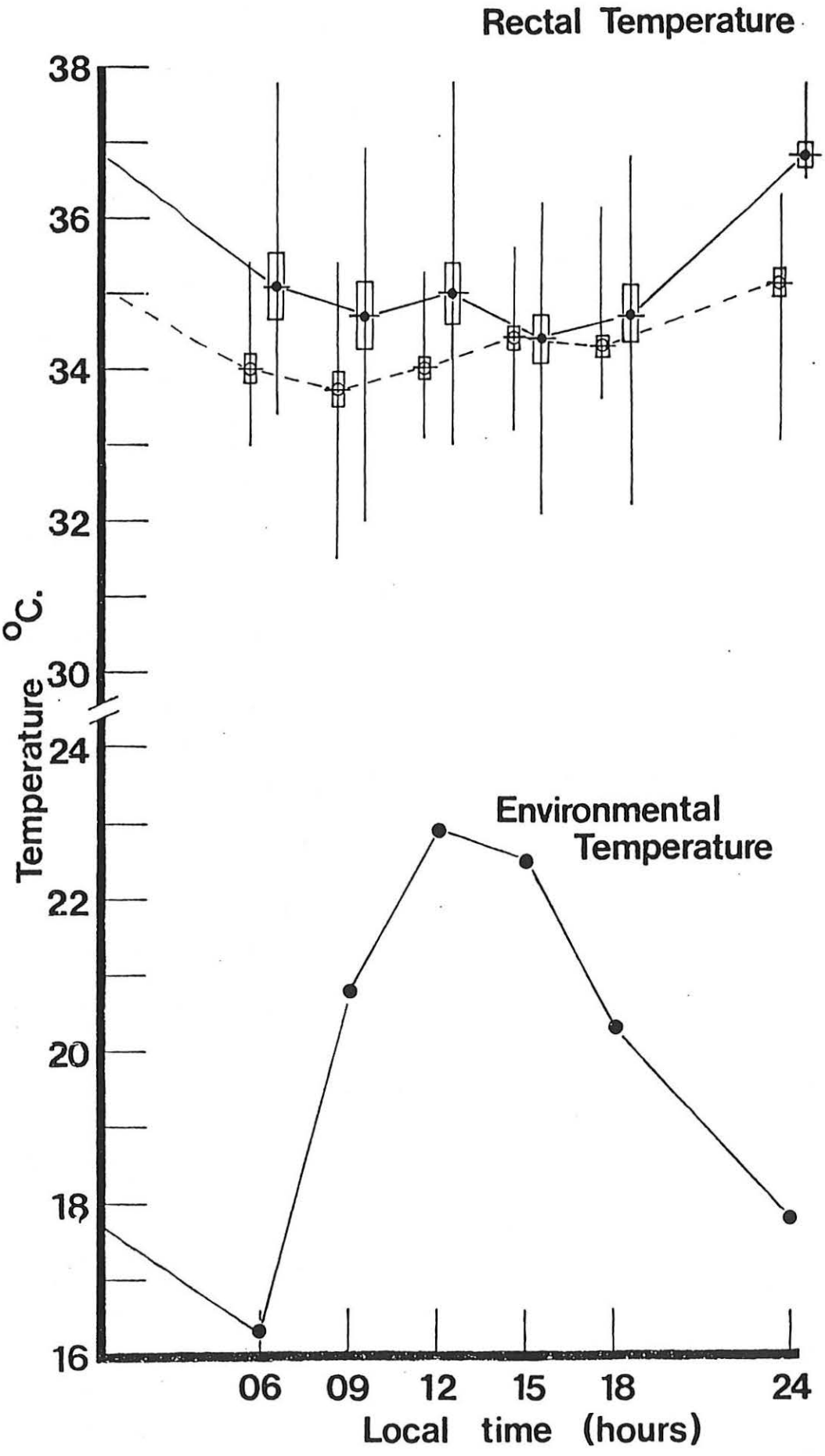
ranges of body temperature measured in this series of observations are tabulated in Appendix B. At 10 weeks of age the variation was low with standard errors of ± 0.14 - 0.33°C. The variation increased in subsequent weeks. For example, at 13 weeks standard errors were 0.73° - 1.30°C and the range of body temperatures measured at the end of one hour of exposure was 23.1° - 29.9°C. (The extremes were for animals from different litters). This indicates that while some animals displayed some ability to maintain body temperature, others still allowed body temperature to fall close to that of the environment. Variation remained high through weeks 14 and 15 but at 15 weeks animals from all three litters maintained body temperature above 30°C throughout the full hour of exposure to ambient temperatures of 17.9 - 20.8°C. For animals older than 15 weeks of age variation in body temperature was reduced, the animals maintaining body temperature between 34°-38°C which is within the normal range of body temperatures observed for adults (Chapter VII).

Responses of juveniles to diurnal changes in environmental temperature.

Fully furred juvenile animals, judged to be 17-19 weeks of age on the basis of physical measurements (Chapter V, p. 5.32), were found to maintain body temperature between 31.5°-36.6°C throughout a three-day period in November (austral spring) when the mean environmental

Fig 6.2 Mean trends in body temperature of juvenile and adult chuditches during three days in 'home' cages when the environmental temperature showed the diurnal range indicated.




Rectal Temperature
38
36
34
32
30
24
22
20
18
16
Temperature °C.
Environmental Temperature
06
09
12
15
18
24
Local time (hours)

temperature ranged from 16.2°C (6.00 a.m. local time) to 23°C (12 noon, local time). Mean body temperatures, with ranges and standard errors, of six juveniles (Litter No. 1), together with those of four adults measured at the same time, and mean environmental temperatures in the cages, are shown in Fig 6.2. These data are also tabulated in Appendix C. Mean rectal temperatures of the juveniles ranged from 33.7°C at 9.00 a.m. to 35.0°C at midnight. Body temperatures showed an approximately inverse relationship to environmental temperature. Rectal temperatures of the juveniles were generally lower than those of the adults, particularly at midnight when the range of rectal temperatures of the adults was higher than that of the juveniles. The variation of rectal temperatures, as shown by the ranges and standard errors, was generally less for the juveniles than for the adults.

Discussion

Chuditch pouch-young were first observed to shiver at 10 weeks of age, at ambient temperatures of about 20°C. At this age the shivering response was insufficient to prevent body temperature from falling to within 4° of ambient temperature over a period of one hour, although only a slight change occurred during the last 30 minutes of exposure suggesting limited thermal regulation. At this age the body weight is three per cent of maternal

weight. The body is covered with fine sparse hair but dense fur has developed on the head. The coat would therefore provide little insulation against heat loss even if the animals were capable of increasing heat production in response to reduced ambient temperature. At 13 weeks some animals showed a capacity to maintain body temperature above 29°C while others allowed body temperature to fall within a few degrees of ambient temperature. The animals shivered continuously during the hour of exposure. The coat is well developed by this age, the whole body surface being covered with dense fur, while the tail is still sparsely furred. The age at which the first marked thermoregulatory response occurs coincides with that at which females were first observed to leave their litters for fairly long periods during the day.

The animals showed a capacity to maintain body temperature above 30°C for one hour when they were 15 weeks of age. By this age the coat is fully developed and appears relatively thicker and longer than that of the adults. It is probable that, at this age, the coat is sufficient to provide effective insulation against heat loss from the body surface. The establishment of effective homeothermy at 15 weeks occurs at the age when young animals first eat meat and appear to be approaching independence from the mother.

Juvenile animals older than 15 weeks maintained

body temperature at levels above 31°C. Animals of 17-19 weeks were found to maintain body temperature close to adult levels during a three-day period. Though the body temperatures of these juveniles were very variable, they were generally less so than those of adults measured at the same time and the circadian cycle was not directly related to environmental temperature.

The capacity to maintain body temperature above ambient temperatures of about 20°C appears to be dependent upon the full development of the pelage at 13-15 weeks of age. Although shivering is observed some 20-30 days earlier, additional heat production from this source is apparently insufficient to balance the heat loss from the poorly insulated body surface of younger animals. Homeothermy is established at about the age when the animals begin to spend considerable periods of time away from the mother.

The development of the thermoregulatory response has been documented for two other marsupial species, the opossum Didelphis (Reynolds, 1952; Morrison and Petajan, 1962), and the quokka Setonix (Shield, 1966; Jones, 1970).

Reynolds (1952) concluded that for Didelphis pouch young, body temperature control begins between 75 and 85 days of age but is not effective over long periods (4-12 hours) at low environmental temperatures until the

young are 90-95 days of age. However oxygen consumption rates of animals as young as 62-65 days showed a peak at 25°C and were reduced at higher ambient temperatures, suggesting that, by this age, they were capable of displaying a metabolic response to moderate ambient temperatures. Morrison and Petajan (1962) found that the earliest evidence of thermal regulation in Didelphis occurred at 60 days of age at an environmental temperature of 30°C and that by 90 days they had good thermal regulation at 5°C.

Comparison can be made between Didelphis and the chuditch in the capacity to maintain body temperatures at ambient temperatures of about 20°C. Didelphis was able to prevent body temperature from falling below 29°C during one hour of exposure to 21°C when aged 76 days. This approximates the thermoregulatory response of the chuditch when aged 91-98 days. The opossum therefore appears to achieve an equivalent capacity for temperature regulation when it is about 2-3 weeks younger than the chuditch.

Shield (1966) found that the rate of oxygen consumption in Setonix joeys below 100 days of age increased directly with increase in ambient temperature though animals older than 20 days did show some reduction in oxygen consumption at temperatures of 35°C or higher. Joeys of less than 100 days had rectal temperatures slightly

lower than pouch temperatures whereas in older joeys rectal temperatures were above pouch temperatures, indicating that body heat generated by the joeys was sufficient to raise their temperature above that of the environment. At about 120 days of age, the rate of oxygen consumption at 20°C was about twice that of animals of less than 100 days. By 153 days, about 30 days before emergence from the pouch, a definite thermal neutral zone was established, with minimal oxygen consumption rates at ambient temperatures above 30°C.

Jones (1970) extended the investigation of the development of the thermogenic mechanisms in the quokka. She found that it utilizes only shivering thermogenesis during development. At no stage are brown fat deposits laid down and no significant rise in metabolic rate was observed in response to exogenous catecholamines. Increases in metabolic rate could be attributed to muscular activity, either as an activity response in younger animals or as shivering thermogenesis which is initiated at 113 days of age. The fur becomes a significant element in insulation at 150-160 days and the thermoregulatory response is fully established by 185 days of age, at pouch emergence. Shield (personal communication) has shown that the quokka joey can only maintain its body temperature at 35°C, when kept at an ambient temperature of 20°C, at the age of 165 days or older. Consequently the quokka is like the chuditch - it shivers long before

homeothermy is established and homeothermy ultimately depends upon adequate fur insulation.

Setonix weighs about 500 g, or 18 per cent of maternal weight at the time of emergence from the pouch. The chuditch, at 105 days of age, is homeothermic and about 16 per cent of maternal weight. Isoodon macrourus (Mackerras and Smith, 1960), Potorous tridactylus (Hughes, 1962), and Bettongia lesueur (Tyndale-Biscoe, 1968) have reached 19-21 per cent, 24-26 per cent and 22 per cent of maternal weight respectively at about the time they leave the pouch and are, presumably, homeothermic. Despite considerable differences in the duration of pouch life, different species appear to leave the pouch at approximately similar proportions of maternal weight. It is probable that, for marsupials generally, homeothermy is established just before pouch exit.

Unlike young marsupials which do not develop a capacity to respond to cold by increased heat production until late in pouch life, most eutherian mammals respond to a cold stimulus by an increase in heat production at birth. The metabolic response to cold may be due to increased muscle activity, either shivering or an increase in spontaneous activity, to local heat production by brown adipose tissue mediated by the sympathetic nervous system, or to a combination of these mechanisms. The ability of new-born eutherian mammals to maintain high and stable body

temperatures can be related to the maturity of the thermogenic mechanisms, to neonatal body size, to the insulative capacity endowed by the coat and vasomotor responses and, ultimately, to the environment with which the new-born animals must normally contend. Thus animals which are immature at birth are usually nurtured in an insulative nest for some time after birth and generally have a limited capacity for thermal regulation whereas animals such as the ungulates, which must be able to follow the mother within a few minutes of birth, have a fully developed thermal regulation. Examples from the literature on neonatal thermal regulation serve to illustrate differences which occur between some eutherian species.

Of the altricial eutherian species studied, only the golden hamster (Mesocricetus auratus) is apparently unable to raise its energy turnover at birth. From 0-11 days of age oxygen consumption increases linearly with temperature between 25 and 36°C. Brown adipose tissue deposits are not developed at birth and their maturation at about 11 days of age corresponds with the inflexion of the oxygen consumption rate - temperature curve at 30°C (Rink, 1969).

The rat and the mouse are also born at a very immature stage but new-born rats and mice both display an increase in the rate of oxygen consumption on exposure to cold (Taylor, 1960; Varnai and Donhoffer, 1970;

Pichotka, 1970). Brown adipose tissue in rats has its greatest functional capacity (in vitro) around the fifth day of postnatal life (Barnard, Skála, and Lindberg, 1970) whereas shivering develops sometime later. The early metabolic response to cold in mice is attributed to non-shivering thermogenesis whereas the capacity to shiver is only developed about 11 days after birth.

New-born rabbits are more developmentally advanced than rats and mice but like them are sparsely furred. They show a three-fold increase in the rate of oxygen consumption when exposed to cold but this is insufficient to maintain body temperature (Hull, 1964). Presumably this is due to lack of fur insulation. The metabolic response to cold is only partially related to muscle activity and can be mimicked by injection of exogenous catecholamines, particularly nor-adrenaline (Dawes and Mestyán, 1963). Local heat production in brown adipose tissue is considered to be the principal source of metabolic response to cold.

Species such as the guinea-pig, pig, sheep and ox are capable of effective thermoregulation at birth. Their reliance on the different thermogenic mechanisms varies but all are characterised by being relatively mature at birth. They have well developed motor responses and they have well developed coats. The new-born pig, sheep and ox are relatively large at birth but absolute

body size alone cannot account for their effective temperature control since the guinea-pig, though large relative to mature weight, is small compared with the other species. The maturity of the insulation, together with the maturity of the thermogenic mechanisms, combines to provide effective thermal regulation.

Non-shivering thermogenesis from brown adipose tissue is of major importance in the metabolic response of new-born guinea-pigs and its contribution to the response to cold is reduced with increasing age (Zeisberger, Brück, Wünnenberg and Wietasch, 1967 - English summary only). Both shivering and non-shivering thermogenesis are important in the new-born lamb. During acute cold exposure metabolic rate increases greatly. About 60 per cent of the maximum increase derives from shivering and 40 per cent from non-shivering thermogenesis, apparently from brown adipose tissue (Alexander and Williams, 1968). The contribution of shivering is apparently greater in the new-born lamb than in many other species although Alexander and Williams considered that the contribution of shivering, which apparently does not appear until the non-shivering thermogenic potential is approached, may not have been fully assessed in some species.

The new-born piglet and ox differ from other species studied in lacking adipose tissue and depending entirely on shivering thermogenesis in the metabolic response to cold

(Mount, 1968; Jenkinson, Noble and Thompson, 1968). Both species thermoregulate effectively within a few hours of birth.

It is concluded that Dasyurus geoffroii, in company with other marsupials, differs from the eutherians in the development of homeothermy. Unlike most eutherians, there is no capacity to increase heat production at birth and the animals are entirely reliant on pouch incubation for maintenance of body temperature until shivering is first observed at ten weeks of age. Lacking experimental evidence from the application of catecholamines it cannot be established that the chuditch is like the quokka in lacking chemical thermogenesis. Nevertheless, from the observation that shivering is established relatively early in development, at the same proportion of maternal weight as the quokka when shivering is established (about three per cent), it seems likely that shivering is the sole mechanism involved in the metabolic response to cold.

When shivering is first initiated in the chuditch the response is insufficient to maintain body temperature at high levels but it does retard the decrease in body temperature on cold exposure. Full homeothermy is achieved only when fur growth provides an effective insulative sheath at about the time that the animals emerge from the pouch at about 15 weeks of age. As birth occurs from late May to early July, a pouch-life of 15 weeks has the young animals approaching thermal

independence from mid-September to mid-October, during the austral spring when minimum air temperatures are rising.

The ontogeny of temperature regulation has been documented for relatively few marsupial species and only for the quokka have the mechanisms for heat production been investigated, demonstrating the absence of brown adipose tissue. Nevertheless it appears likely that marsupials as a group would not utilise brown adipose tissue as a site of heat production during pouch development. The pouch-young never suffer the rigours of nest life nor do they have to keep up with the mother at birth. Emergence from the pouch occurs when the animals are well insulated and have reached a considerable proportion of their adult body weight (15-25 per cent), and, no doubt, have a well developed capacity for shivering thermogenesis.

CHAPTER VII

BODY TEMPERATURE OF ADULT ANIMALS

Preamble

Early studies indicated that marsupials had lower body temperatures (Sutherland, 1897; Brown, 1909) and lower metabolic rates (Martin, 1903) than eutherian mammals. Martin's work was interpreted as showing that marsupials represented a level of physiological development lower than the 'advanced' eutherian mammals in that their capacities for thermal regulation were less highly developed. That many marsupial species have relatively low body temperatures has been amply confirmed. Morrison (1946) reported mean body temperatures for Didelphis marsupialis etensis and Metacheirus nudicaudatus to be 35.5°C and 33.8°C respectively; Morrison and McNab (1962) reported a mean level of 34.7°C (excluding torpor) for a single specimen of a Brazilian Marmosa; Morrison (1965) obtained mean values for seven species of Dasyurid marsupials of from 34.0°-37.0°C during the quiet period of their activity cycle and from 37.4°-38.8°C for their active periods; Dawson and Hulbert (1970) found mean resting body temperatures for eight species of Australian marsupials to range from 33.8°C for Sminthopsis crassicaudata to 36.4°C for Macropus eugenii; Hulbert and Dawson (1974a) reported mean body temperatures from

34.6°-36.1°C for six species of Perameloid marsupials. Comparison with mean body temperatures of 37°-39°C for many eutherian mammals (Spector, 1956) shows marsupials to be 2°-4°C lower.

Despite the relatively low level at which body temperature is maintained by many marsupials, they have nevertheless been shown to have a capacity to maintain their body temperature within normal limits over a wide range of ambient temperatures which is as good as that displayed by most eutherians (Bartholomew, 1956; Robinson and Morrison, 1957; Bentley, 1960; Morrison, 1962 and 1965).

Body temperatures of Dasyurus geoffroii were measured in order to determine:

1. the mean level of body temperature in a thermal neutral environment;
2. the effect of moderately low ambient temperatures on mean levels of body temperature;
3. whether there was a circadian cycle in body temperature, the amplitude of such a cycle and the effect of ambient temperature on the cycle;
4. the relationship between body temperature and oxygen consumption in the ambient temperature range 5°-40°C;
5. the relationship between body temperature and evaporative water loss at ambient temperatures within and above the thermal neutral zone.

Points 1-3 will be dealt with in this chapter; 4 and 5 will be discussed in Chapters VIII and X respectively.

The observation that animals occasionally become torpid at ambient temperatures below the thermal neutral zone led to an attempt to identify the stimulus causing entry into torpor. Observations were also made on body temperature of animals during arousal from torpor.

Results

Mean Body Temperature at Environmental Temperatures below and within the Thermal Neutral Zone

Daily mean values of body temperature were calculated from five sets of measurements made at different environmental temperatures. The animals were maintained in cages in a constant temperature room at environmental temperatures of 11°, 15.5° (two trials), 20.5° and 30°C. (Materials and Methods, p. 2.15). Table 7.1 shows daily mean body temperatures for males, females and for males and females together. Ranges, standard errors and coefficients of variability are also shown. Daily means for the males ranged from 35.0° at 20.5°C to 36.1° at 11°C environmental temperature. Daily mean values for the females ranged from 33.8° in the autumn trial at 15.5°C to 36.3° in the spring trial at the same environmental temperature.

Pearson's coefficient of variability (V) is used

Table 7.1

Mean colonic temperatures of chuditches maintained at constant ambient temperatures, together with measures of variability

	Environmental Temperature °C				
	10 - 12	15 - 16 (autumn)	15 - 16 (spring)	20 - 21	28 - 32
MALES (three animals)					
n	71	72	72	72	72
$\bar{x}$	36.12	35.31	35.48	35.00	35.87
s	1.350	1.421	1.543	1.835	1.372
s.e.	0.160	0.168	0.182	0.216	0.162
V	3.74	4.02	4.35	5.24	3.82
range	30.3-38.6	31.3-37.8	29.0-37.7	30.6-38.3	34.4-38.3
FEMALES (three animals)					
n	63	72	71	69	72
$\bar{x}$	34.84	33.82	36.35	34.88	35.90
s	3.336	3.359	1.303	2.788	1.308
s.e.	0.420	0.396	0.155	0.336	0.154
V	9.58	9.93	3.58	7.99	3.64
range	23.1-38.8	25.2-38.2	33.7-38.8	26.2-38.3	32.7-38.8
MALES & FEMALES (six animals)					
n	134	144	143	141	144
$\bar{x}$	35.52	34.57	35.91	34.94	35.89
s	2.571	2.684	1.493	2.351	1.346
s.e.	0.222	0.224	0.125	0.198	0.112
V	7.24	7.76	4.16	6.73	3.75
range	23.1-38.8	25.2-38.2	29.0-38.8	26.2-38.3	32.7-38.8

n = number of temperature determinations; $\bar{x}$ = mean;

s = standard deviation; s.e. = standard error of mean;

V = Pearson's coefficient of Variability.

as a measure of variation of body temperature during the twenty-four hour period. For males, body temperature showed the greatest variation when the environment was maintained at 20.5°C. Females tended to have more variable body temperatures at the lower environmental temperatures. Their tendency to become torpid contributed to this increased variation (see p. 7.25).

Daily Cycle of Body Temperature at Constant Environmental Temperature below and within the Thermal Neutral Zone

Colonic temperatures measured in five trials at environmental temperatures ranging from 10° to 30° are shown in Figs 7.1-7.6. The hourly mean temperatures for males and females are also shown, connected by trend lines. During the "light" period (0600-1800 hours) body temperature was generally lower and more variable than during the "dark" period (1800-0600 hours). Within the light period, body temperature was lower and more variable from 0800-1400 hours, thereafter showing a gradual increase which continued beyond the onset of darkness. During the dark period, body temperatures measured during the hours 1800-2200 were generally higher and less variable than those measured later.

The change from light to darkness and from darkness to light in the constant temperature room was an abrupt one. The change from light to darkness at 1800 hours

did not have a marked effect on the general rise in body temperature which commenced four to five hours earlier and reached a peak one to three hours after the onset of darkness. The abrupt change from darkness to light at 0600 hours did, however, coincide with transitory peaks in body temperature at air temperatures of 10^{o} and $15.5^{o}C$, suggesting that some disturbance of the falling trend in body temperature in the early morning hours may have occurred.

Fig 7.1 shows colonic temperatures measured while the environmental temperature was maintained at $11\pm1^{o}C$. The highest body temperatures occurred one hour after the onset of darkness (1900 hours) and again at the start of the light period. The peak which coincided with the lights switching on may have been an artifact but the peak at 1900 hours probably represents the activity peak of these nocturnal carnivores. Hourly mean body temperatures for the three females were generally lower than those for the males for most of the 24 hours and were markedly lower during the light period. During this time two females were found to be torpid at different times (see Table 7.4). No male was ever found in torpor, the lowest temperature recorded for a male being $30.3^{o}C$ at 0800 hours. Hourly mean body temperatures rose during the latter part of the light period, from 1400 hours, to a peak one hour after the onset of darkness. From this high level,

Fig 7.1 Rectal temperatures of three male and three female chuditches at 11°C (T_a) in a 12/12 hour light/dark regime. Hourly mean temperatures for males and for females are connected by trend lines.

Symbols:

● males

○ females

——— trend lines connecting hourly mean rectal temperatures for males

..... trend lines connecting hourly mean rectal temperatures for females

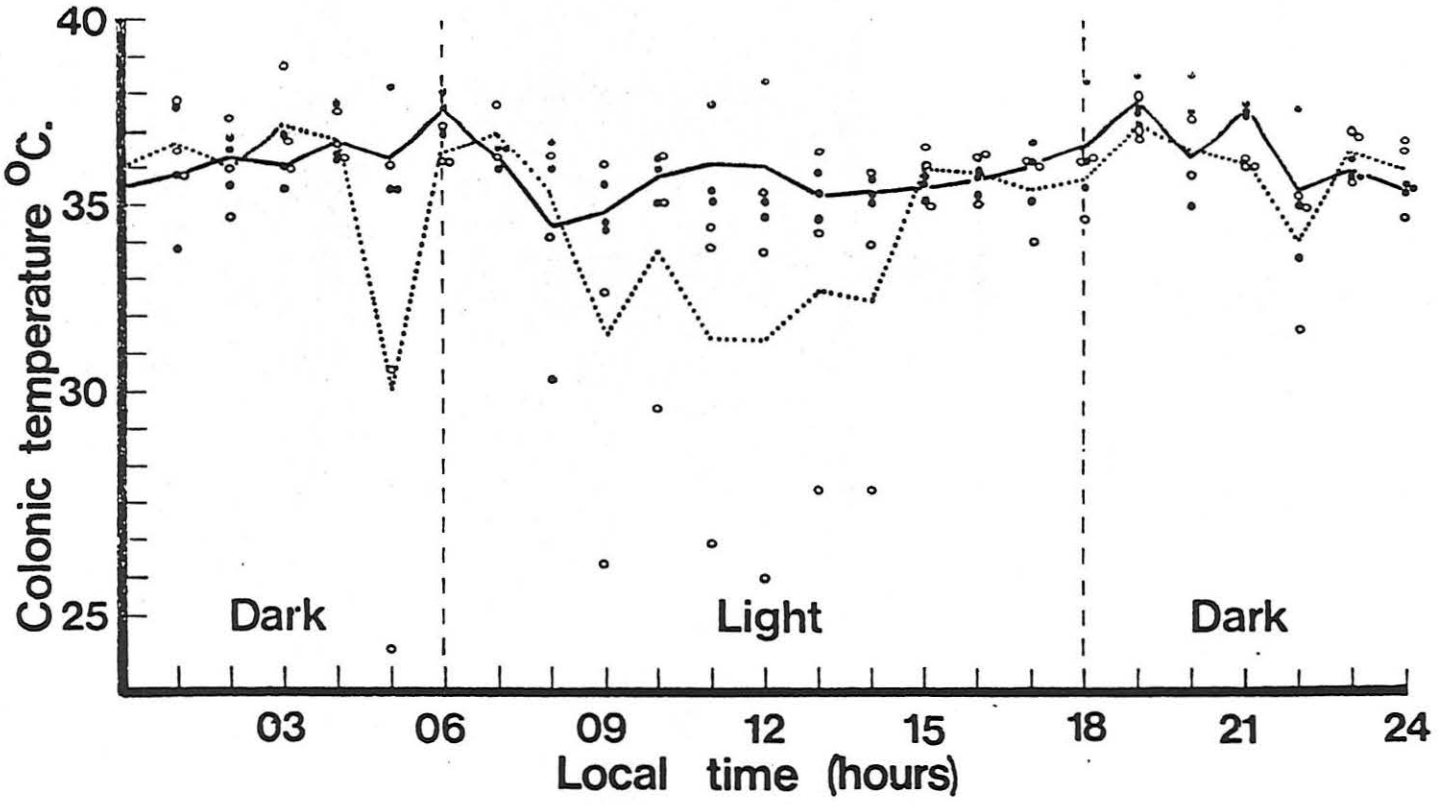

Colonic temperature °C.
40
35
30
25
Dark
Light
Dark
03
06
09
12
15
18
21
24
Local time (hours)

Fig 7.2 Rectal temperatures of three male and three female chuditches at 15°C (T_a) measured in autumn in a 12/12 hour light/dark regime. Hourly mean temperatures for males and for females are connected by trend lines.

Symbols: as for Fig 7.1.

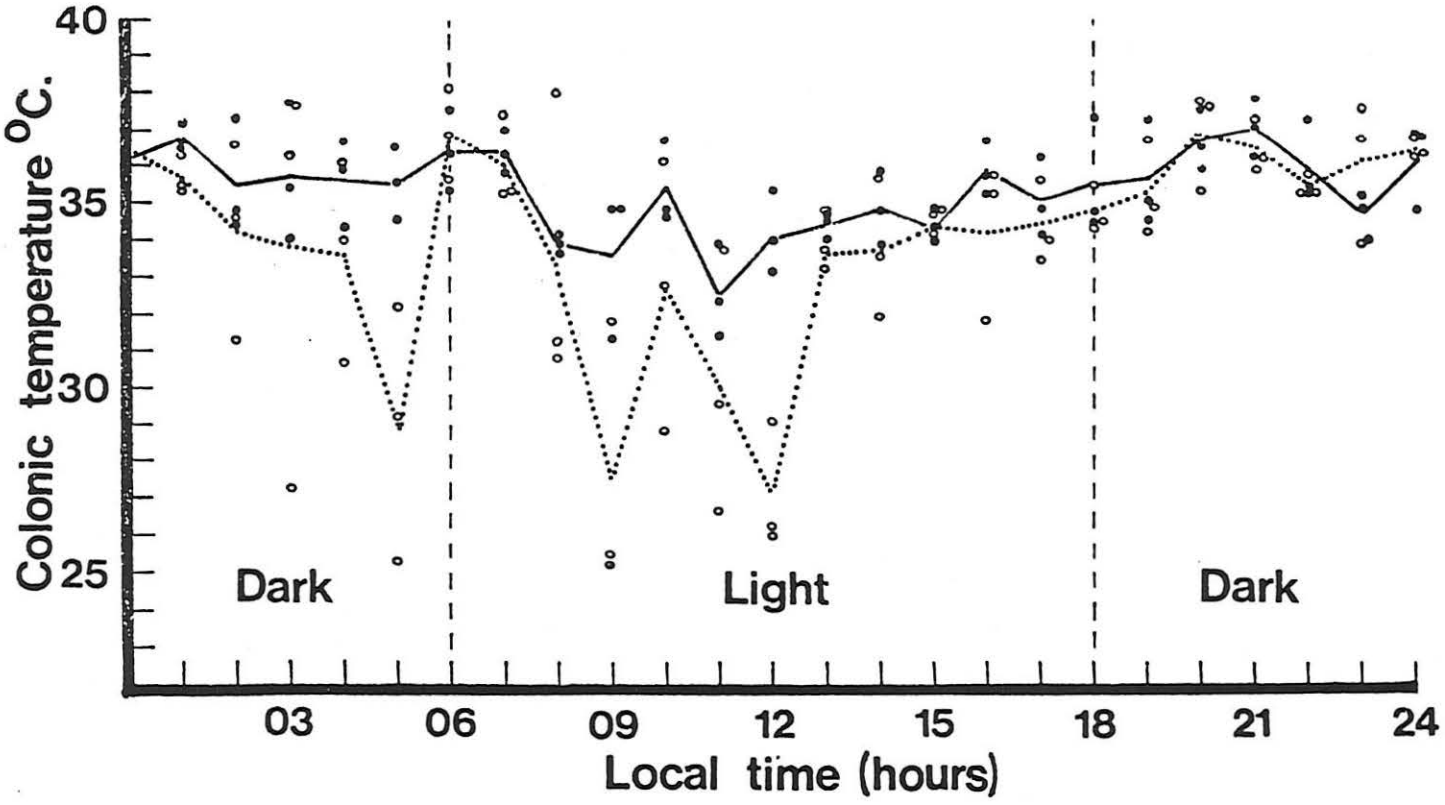
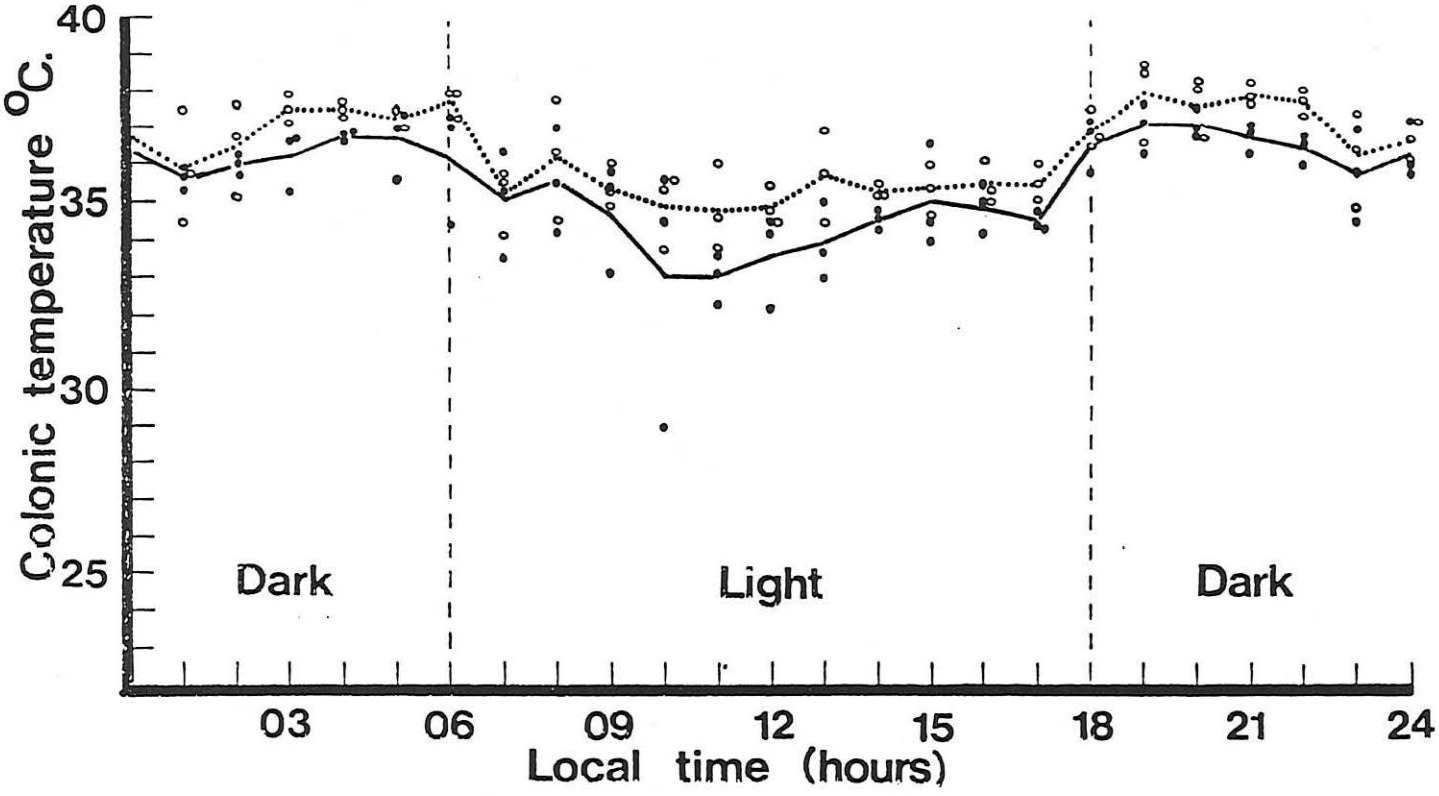

Colonic temperature °C.
40
35
30
25
Dark
Light
Dark
03
06
09
12
15
18
21
24
Local time (hours)

Fig. 7.3 Rectal temperatures of three male and three female chuditches at 15°C (T_a) measured in spring in a 12/12 hour light/dark regime. Hourly mean temperatures for males and for females are connected by trend lines.

Symbols: as for Fig 7.1.


Colonic temperature °C.
40
35
30
25
Dark
Light
Dark
03
06
09
12
15
18
21
24
Local time (hours)

temperatures declined towards midnight.

Colonic temperatures were measured for the 24-hour period at 15.5°C in two separate trials. The first was carried out in autumn between April 20, 1968, and May 10, 1968 (Fig 7.2) and the second, in spring, between September 26 1968 and November 13 1968 (Fig 7.3). Considerable differences were observed in the results obtained for the two trials. During the autumn trial all three females were found in a torpid condition, with body temperatures below 30°C, on several occasions (see Table 7.4). As in the trial at 11°C, no male was ever observed in torpor; the lowest body temperature to be recorded for a male was 31.3°C at 0900 hours. Hourly mean body temperatures rose from 1300 hours to peak at 2000-2100 hours. Other peaks occurred at midnight to 0100 hours and at the beginning of the light period. This latter peak may have been artificially produced by the sudden change from darkness to light at this time.

During the spring trial at 15.5°C only one body temperature of less than 30°C was recorded; 29.0°C in a male. In contrast to the autumn trial, hourly mean body temperatures of the three females were consistently higher than those for the males. Body temperatures during the light period were lower and more variable than those recorded during the dark period. Highest temperatures were recorded from 2000-2200 hours and from 0300-0600

hours. The latter peak cannot, in this case, be attributed to a sudden change from darkness to light.

Fig 7.4 shows individual body temperatures and hourly mean values for the 24-hour period when air temperature was maintained at 20.5°C. The cycle observed at this temperature was similar to those described for the lower environmental temperatures. One of the three females was found to have a body temperature of less than 30°C on six occasions (see Table 7.4). Neither of the other females was observed in torpor although body temperatures below 33°C were recorded for both animals on several occasions. In one of the females unusually high body temperatures, in excess of 37°C, were recorded at five different times during the light period. This animal subsequently showed a marked loss of body weight and died. The lowest body temperatures recorded for males were 30.6° at 1100 hours and 30.7°C at 0900 hours for the same animal. The highest hourly mean values for both males and females occurred at 2200 hours, four hours after the onset of darkness. This peak occurred as the climax of a general rise in hourly mean values commencing at 1300-1400 hours. Several other peaks occurred: as midnight, and in the hour preceding and the hour following the beginning of the light period.

Colonic temperatures of individuals and hourly means for males and females measured when the air temperature was maintained at 30°C are shown on Fig 7.5. The

Fig 7.4 Rectal temperatures of three male and three female chuditches at 20°C (T_a) in a 12/12 hour light/dark regime. Hourly mean temperatures for males and for females are connected by trend lines.

Symbols: as for Fig 7.1.

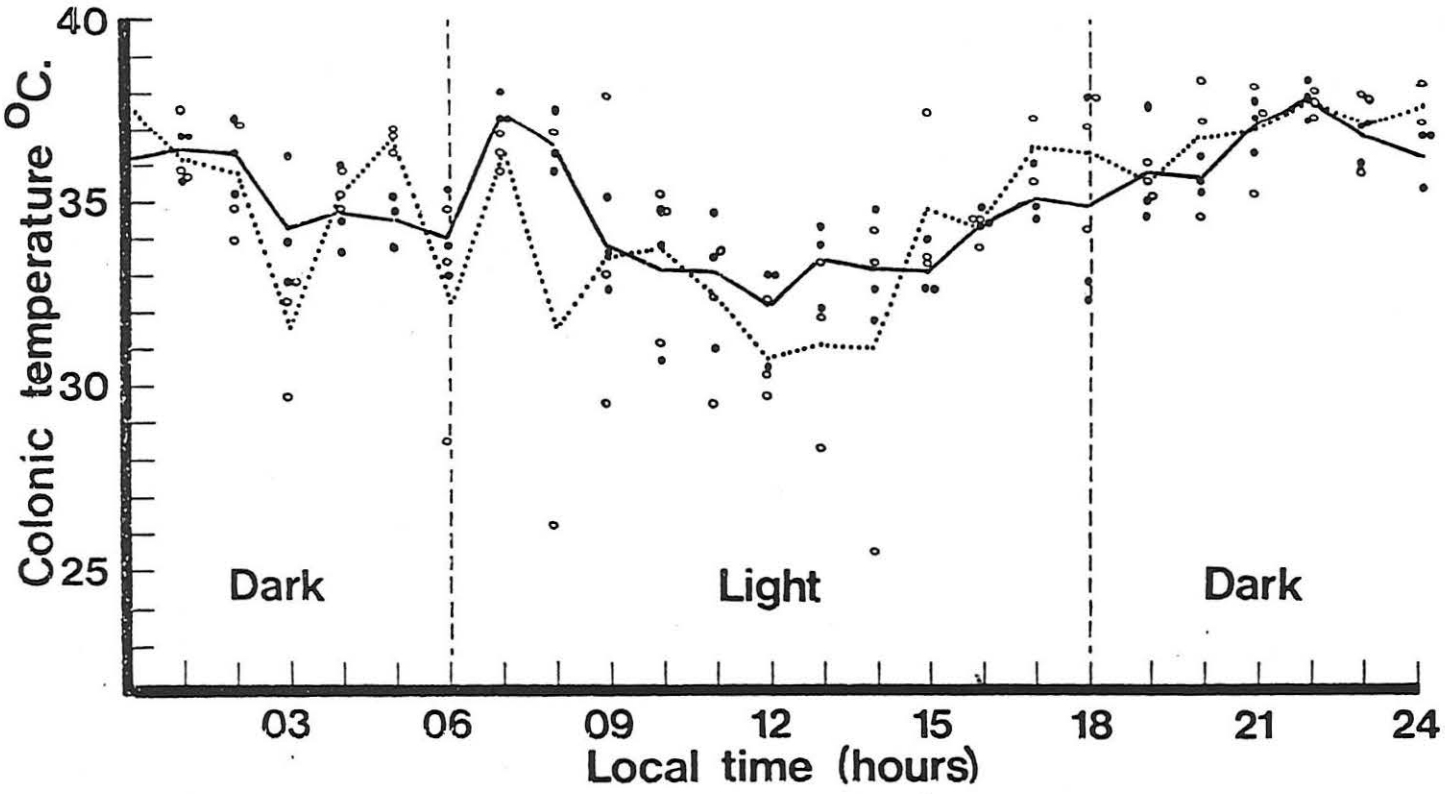

Colonic temperature °C.
40
35
30
25
Dark
Light
Dark
03
06
09
12
15
18
21
24
Local time (hours)

Fig 7.5 Rectal temperatures of three male and three female chuditches at 30°C (T_a) in a 12/12 hour light/dark regime. Hourly mean temperatures for males and for females are connected by trend lines.

Symbols: as for Fig 7.1.

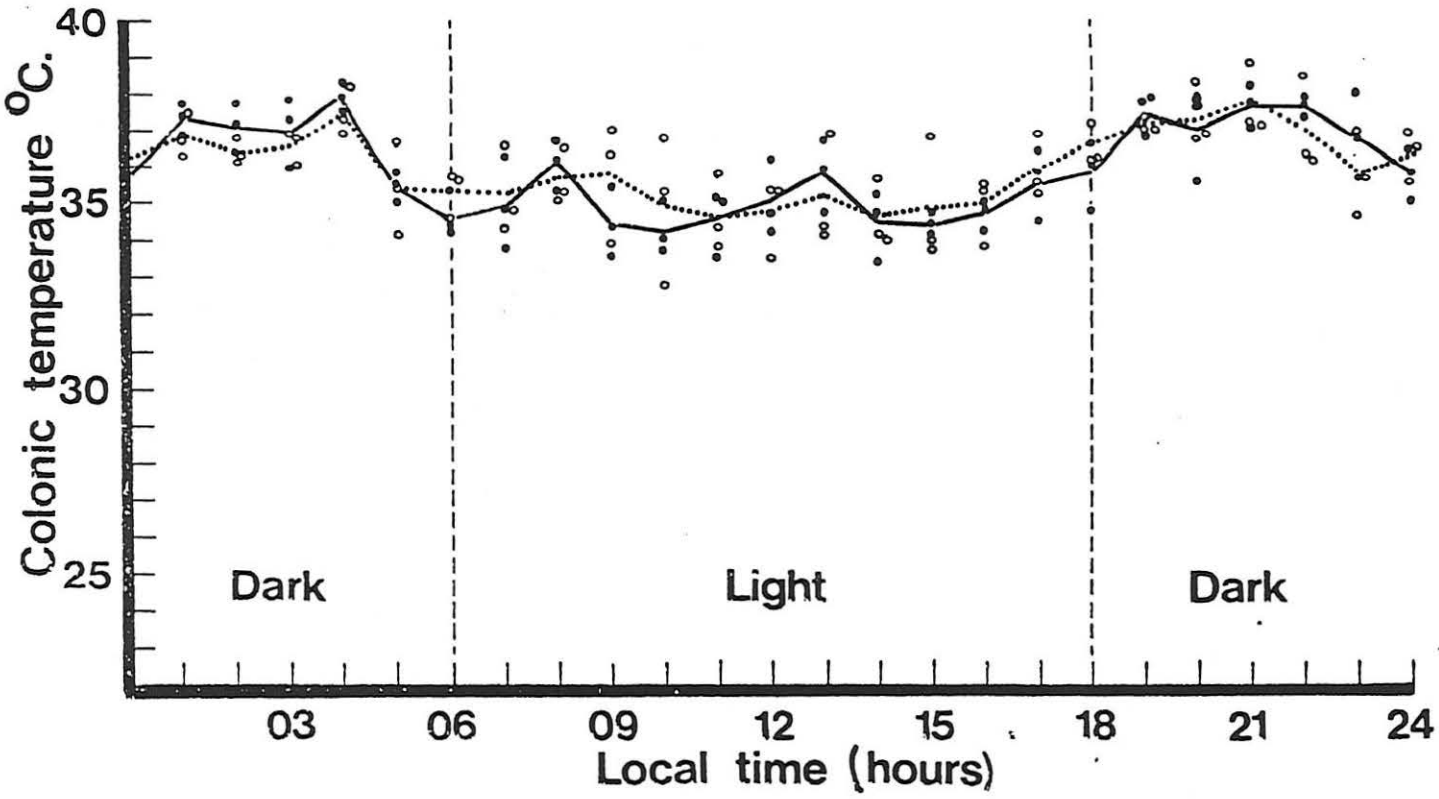
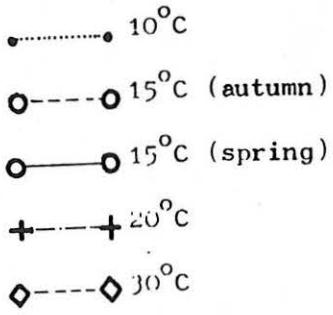
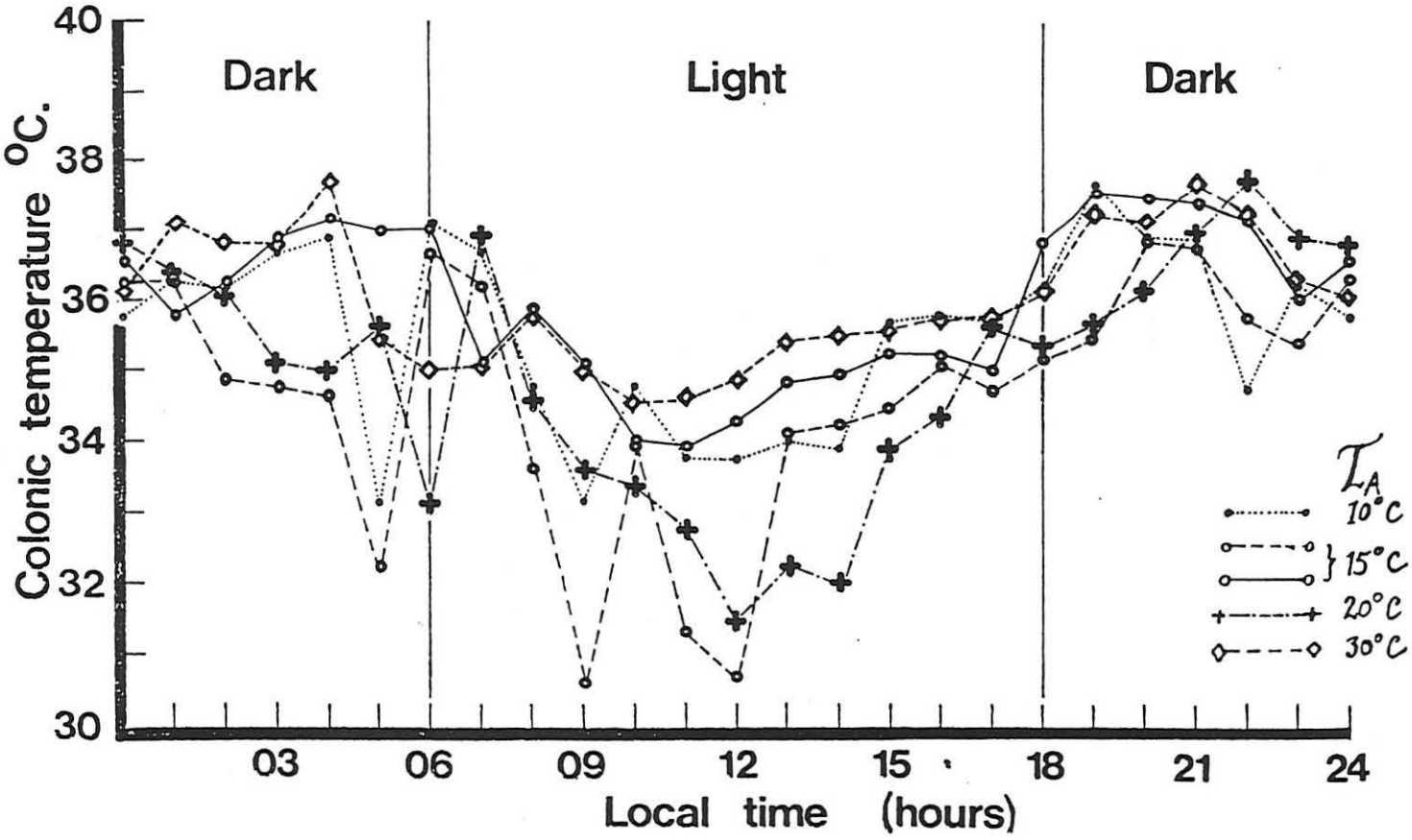

Colonic temperature °C.
40
35
30
25
Dark
Light
Dark
03
06
09
12
15
18
21
24
Local time (hours)

Fig 7.6 Hourly mean rectal temperatures for groups of six (three male, three female) chuditches at constant ambient temperatures and in a 12/12 hour light/dark regime.




Dark
Light
Dark
Colonic temperature °C.
40
38
36
34
32
30
03
06
09
12
15
18
21
24
Local time (hours)
T_A
10°C
15°C
20°C
30°C

7.20

thermal neutral zone, when oxygen consumption rates are at a minimum, extends from 27-33°C (Chapter VIII). Thus colonic temperatures measured in this trial should represent the body temperature cycle occurring when heat production is minimal. Compared with the body temperatures measured at lower environmental temperatures, the results from this trial showed less variation. The lowest body temperatures were recorded during the light period and were 32.7°C for a female and 33.4°C for a male. Hourly mean body temperatures rose from 1400-1500 hours to peaks at 2100 hours, three hours after the onset of darkness. A second peak occurred at 0400 hours, two hours before the lights were turned on.

Fig 7.6 shows the mean body temperatures of animals (both males and females) for each hour of the 24-hour period in the five trials described above. During the light period body temperatures are generally lower than during the dark period. The main features of the body temperature cycles observed at constant environmental temperatures below and within the thermal neutral zone are shown in Table 7.2.

The amplitudes of the circadian cycles in body temperature for females ranged from 3.2° and 3.3°C in the spring trial at 15.5°C and at 30°C respectively to 9.8°C in the autumn trial at 15.5°C. Amplitudes in the cycles for males were least at 11°C and 30°C (3.6° and 3.9°) and greatest at 20°C (5.2°C).

Table 7.2

Mean maximum and mean minimum colonic temperatures of six chuditches (3 males, 3 females) and the times at which maxima and minima occurred at constant T_a below and within the thermal neutral zone

Environmental Temperature °C	Mean Max. Rectal Temp. °C				Mean Min. Rectal Temp. °C				Amplitude of cycles °C	
	Males		Females		Males		Females			
	Time	Temp.	Time	Temp.	Time	Temp.	Time	Temp.	Males	Females
11 ± 1	1900	38.0	1900	37.3	0800	34.4	0900 0500	31.4 29.9	3.6	6.3
15.5 ± 0.5 (1) (autumn)	2100	37.0	0600 2000	36.9 36.9	1100	32.6	1200	27.1	4.4	9.8
15.5 ± 0.5 (2) (spring)	1900-2000	37.1	1900	38.0	1100	33.0	1100	34.8	4.1	3.2
20.5 ± 0.5	2200	37.8	2200	37.7	1200	32.6	1300	31.1	5.2	6.6
30 ± 2	2100-2200 0400	38.0 37.9	2100	38.0	1000	34.1	1100	34.7	3.9	3.3

Body Temperature during Active and Inactive Periods of the Daily Cycle

It is apparent from Figs 7.1-7.5 that colonic temperatures in each of the constant temperature trials were more variable during the light period than during the dark period. Observations of the animals in the constant temperature room showed that, during the light period from 0800-1400 hours, animals were generally quiet, usually sleeping and easy to handle. During the first three or four hours of the dark period however, they were usually active and were frequently aggressive.

In order to assess the difference between body temperatures of animals when they were judged to show least activity and in the periods when they were judged to be showing the greatest activity, mean body temperatures during 'active' and 'inactive' periods were calculated for the five trials conducted at environmental temperatures below and within the thermal neutral zone. These means, together with standard errors and Pearson's coefficient of variability, are shown in Table 7.3.

The change in mean body temperature between 'active' and 'inactive' periods at the one environmental temperature ranged from 2.2-3.9^{o}C and no consistent difference between mean body temperatures for males and females was apparent. Males did not exhibit a decrease in mean colonic temperature with decrease in environmental temperature. Females

Table 7.3

Colonic temperature (arithmetic means, standard errors of means, and coefficients of variation) for male and female chuditches measured at four ambient temperatures in inactive periods (0800-1600 hours inclusive) and periods of greatest activity (1900, 2000, 2100 hours inc. at 10° and 15°C; 2000, 2100, 2200 hours inc. at 20° and 30°C). The figures within brackets indicate numbers of determinations (left) and numbers of animals (right). V = Pearson's coefficient of variation.

			Ambient Temperature (°C)			
			10 - 12°	15 - 16°	20 - 21°	28 - 32°
MALES	Inactive	$\bar{x}$	35.4° ± 0.26 (27/3)	34.3° ± 0.19 (57/6)	33.4° ± 0.22 (45/3)	34.8° ± 0.22 (27/3)
		V	3.9	4.1	4.5	3.2
	Active	$\bar{x}$	37.6° ± 0.35 (9/3)	36.8° ± 0.18 (18/6)	37.2° ± 0.24 (9/3)	37.4° ± 0.26 (9/3)
		V	2.8	2.1	1.9	2.1
FEMALES	Inactive	$\bar{x}$	33.3° ± 0.76 (26/3)	33.5° ± 0.42 (59/6)	33.4° ± 0.45 (42/3)	35.0° ± 0.22 (27/3)
		V	11.6	9.6	8.8	3.2
	Active	$\bar{x}$	36.7° ± 0.27 (8/3)	37.1° ± 0.29 (18/6)	37.2° ± 0.35 (9/3)	37.3° ± 0.32 (9/3)
		V	2.0	3.3	2.8	2.6

(Table from Arnold and Shield, 1970).

did, however, show a slight decrease in colonic temperature when mean body temperature of active and inactive periods in the thermal neutral zone were compared with values for lower environmental temperatures. Variations were greater for both males and females in the inactive periods than in the active periods, the females showing greater variation than the males at 10°, 15° and 20°C but about the same amount of variation at 30°C.

Torpor

Females were occasionally found torpid, with body temperatures below 30°C, in the yards during the mornings in the months of May and June, and one female which was kept in a cage outside the laboratory in a corridor also went into torpor. But torpor was only observed on weekends when traffic through the yards or along the corridor was minimal. Only one male was ever found in the yards to have a body temperature below 30°C.

During three constant temperature room trials carried out during the months of March through June to determine circadian variation in body temperature at environmental temperatures below the thermal neutral zone, the females were occasionally found to be in a state of torpor. Thirty such observations were made on three animals (Table 7.4). Torpor was most frequently observed between 0900 and 1400 hours. When in the torpid condition

normally aggressive animals were incapable of biting or of giving the throaty threatening hiss with which they normally greeted the handler. Body temperatures were less than 30°C and the animals were stiff and incapable of co-ordinated movement. Torpor was observed only between 0200 and 1400 hours and most frequently between 1000 and 1300 hours. In a trial carried out in October-November at 15.5°C environmental temperature, none of the females was ever observed in torpor but a single male was found to be torpid, with a body temperature of 29.0°C on one occasion (1000 hours).

For an animal confined within the metabolism chamber the lowest temperature to be recorded by means of a thermistor probe inserted into the colon was 31.4°C. This and other low body temperatures recorded in the metabolism chamber are shown in Table 7.5. The relationship between body temperature and oxygen consumption will be discussed in Chapter VIII. At this point it can be noted that in the metabolism chamber:

(i) low body temperatures were recorded for both males and females,

(ii) low body temperatures occurred most frequently before 1400 hours,

(iii) body temperatures less than 34°C were, with two exceptions, recorded at ambient temperatures of 18-21°C.

Table 7.4

Colonic temperatures of torpid animals and the local times at which the temperatures were measured at the specified T_a.

Local Time											
0300	0400	0500	0600	0700	0800	0900	1000	1100	1200	1300	1400
T_a 11°C											
–	–	23.1	–	–	–	25.4	29.6	25.9	25.0	27.4	27.4
T_a 15°C											
–	–	29.2	–	–	–	25.2	28.9	29.6	26.3	26.8	–
–	–	–	–	–	–	25.5	–	29.7	29.1	26.3	–
–	–	–	–	–	–	–	–	26.0	–	–	–
T_a 20°C											
29.7	–	26.3	28.5	–	26.2	29.5	–	29.5	29.7	28.3	25.5
–	–	–	–	–	–	–	–	–	–	26.8	–
–	–	–	–	–	–	–	–	–	–	29.4	–

Table 7.5

Lowest body temperatures measured by colonic probes for animals in the metabolism chamber; and local times when measurements were made.

Run No.	Temperature (°C)		Time
	Ambient	Body	
Delan 35 (F)*	19.7	31.4	1250
	19.7-20.6	32.0 (or less)	1110-1338
Dehyd 19 (F)	18.4	33.4	1309
Dehyd 24 (F)	19.8	33.8	1718
Dehyd 25 (M)	0.0	33.0	1034
Dehyd 26 (M)	19.7-22.5	31.8-32.2	0949-1137
Dehyd 28 (F)	20-21	33.7-33.8	1320-1334
Dehyd 31 (F)	24.9	31.8	1237-1303
Dehyd 32 (M)	18.8	32.9	0955-1000

* F = Female; M = Male.

In an attempt to determine whether torpor resulted from food deprivation, three males and three females were starved for seven days in the constant temperature room when the environmental temperature was maintained at 20.5°C. During this period water was provided ad lib. The average loss in body weight for the six animals was 25.8 g/kg. day. The percentage loss of body weight during the seven days of starvation ranged from 10.7 per cent for one male to 22.9 per cent for one female (mean weight loss 16.62 per cent of body weight). One female died several days after feeding was recommenced having lost 19.3 per cent of its body weight during the period of starvation (changes in body weight which occurred during starvation are tabulated in Appendix D). In spite of this severe starvation no animal was found in torpor during the seven-day period and thus there is no evidence of a relationship between food deprivation and entry into torpor.

When torpid animals were disturbed they responded by shivering violently. Shivering was accompanied by a rapid rise in body temperature. For three animals, body temperature was measured at intervals after the initial observation of torpor to determine the rate at which temperature was raised to normal levels. During arousal from torpor violent shivering occurred continuously. Movements became more co-ordinated as body temperature rose and, as temperature approached normal levels, the animals

showed threatening behaviour and regained their usual aggressive responses.

One animal increased its body temperature from 23.1°C to 37.3°C in 36 minutes, at an average rate of 0.4° per minute. Three other observations of arousal for this same animal showed the following changes in body temperature: 28.8° - 37.7°C in 23.5 minutes; 27.6° - 37.6°C in 29.5 minutes; 27.2° - 35.9°C in 26 minutes. The average rates of warming were 0.3°-0.4° per minute. Two other animals showed slower rates of arousal with body temperature rising at about 0.1° per minute. Fig 7.7 shows T_b vs. lapse time during arousal from torpor in these six cases.

Body Temperature measured in the Metabolism Chamber

Fig 7.8 shows mean body temperatures measured by thermistor probes in the colons to depths of 6-8 cm when animals were in the metabolism chamber during determinations of oxygen consumption and evaporative water loss. Means were calculated by grouping body temperatures measured for individual animals at one degree intervals of ambient temperature. The daily means (from Table 7.1) of colonic temperature recorded during the trials at constant temperatures of 11°, 15.5°, 20.5° and 30°C (described above, p. 7.5-21), together with the standard errors and ranges, are shown for comparison.

In the ambient temperature range 0°-29.9°C most mean

Fig 7.7 Changes in T_b vs. lapse time during arousal from torpor for three female chuditches.

Symbols: ●——● 1, 2, 3.

1 adult female on 3 different occasions

1. T_a 25°C

2 & 3. T_a 20°C

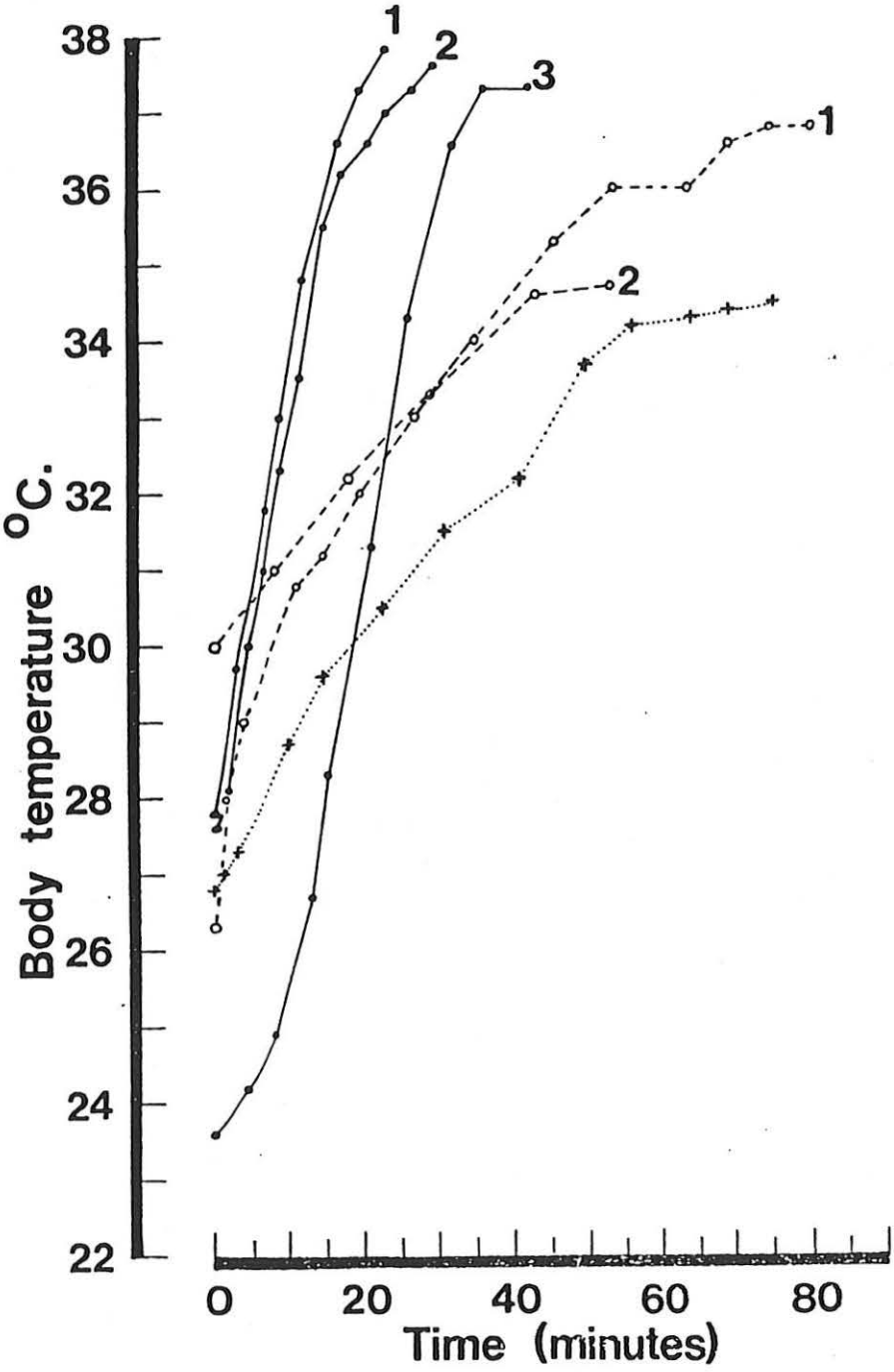
○----○ 1, 2.

1 adult female on 2 different occasions

1. T_a 15°C

2. T_a 20°C.

+·····+ 1 adult female at T_a 15°C.


38
36
34
32
30
28
26
24
22
Body temperature °C.
1
2
3
1
2
0
20
40
60
80
Time (minutes)

colonic temperatures measured in the metabolism chamber ranged between 33.5-36.5°C. The daily means from the constant temperature trials were 34.5-35.9°C although the ranges of extreme values were considerably wider. Animals did not drop their body temperatures to the low levels recorded in the constant temperature room trials, no doubt because of the cramped conditions within the chamber and because of the noise emanating from associated pumps and refrigerator. Although body temperature at ambient temperatures below 30°C was variable no distinct trend relative to ambient temperature could be detected.

Body temperatures below 30°C were never recorded in the metabolism chamber, but a close relationship between body temperature and rate of oxygen consumption was observed. At ambient temperatures well below the thermal neutral zone oxygen consumption would frequently fall to levels equal to basal rates for periods of a few minutes to several hours. During such periods body temperature would also fall rapidly. Cycles of low and high rates of oxygen consumption associated with falling and rising body temperature lasted from a few minutes to several hours. This phenomenon will be further discussed in Chapter VIII.

At ambient temperatures above 30°C the body temperature rose so that the temperature difference between deep body and air temperatures was diminished from about 5° at an ambient temperature of 30°C to zero at 38-39°C. At air

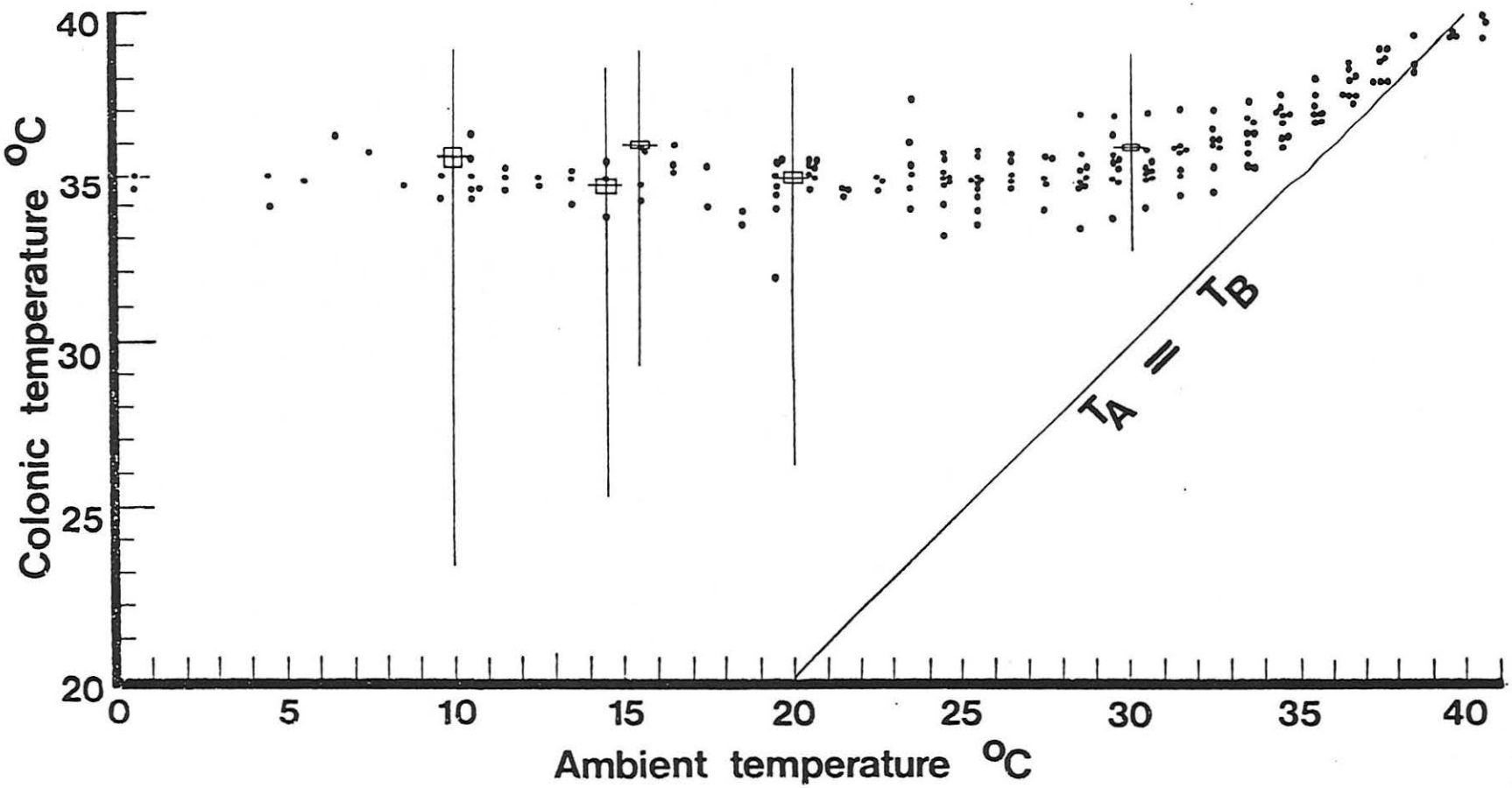
Fig 7.8 T_b of chuditches in the metabolism chamber at T_a 0-41°C and means, standard errors and ranges of body temperatures of animals maintained in small cages at constant ambient temperatures of 11°C, 15°C, 20°C and 30°C.

Symbols: ● mean body temperatures of individual animals.

Short horizontal lines:
mean T_b for 24 hour period at constant T_a.

Vertical lines:
ranges of T_b measured in 24 hour period.

Boxes:
$\pm$ 1 standard error of mean of T_b for 24 hour period at constant T_a.


Colonic temperature °C
40
35
30
25
20
0
5
10
15
20
25
30
35
40
Ambient temperature °C
TA = TB

temperatures higher than about 39°C, the body temperature could be maintained below ambient for at least periods of one to two hours (Chapter X).

Discussion

The mean body temperature of the chuditch, over a 24-hour period at environmental temperatures within and below the thermal neutral zone, ranged from 34.6° (at T_a 15°C) to 35.9°C (at T_a 30°C). No clear relationship between environmental temperature and mean body temperature could be demonstrated.

MacMillen and Nelson (1969) recorded body temperatures of 12 species of the Dasyuridae. Body temperatures in the thermal neutral zone reported for the two species most closely related to the chuditch, D. viverrinus and D. hallucatus, were 36.7° and 38.1°C respectively. "Representative mean body temperature" below the thermal neutral zone for D. hallucatus was 35.8°C, which is higher than mean T_b for D. geoffroii at T_a 11° and 20°C, and about the same as at T_a 28°-32°C, in the thermal neutral zone (Table 7.1). As body temperatures were measured by MacMillen and Nelson at the end of one hour in a respirometer the high values may be attributed to some disturbance of the animals as they were removed from the chamber.

The chuditch exhibits a circadian cycle in body temperature. The cycle is characterised by low and variable

body temperatures during the light period and high, relatively less variable, body temperatures during one or more periods of activity during hours of darkness.

Bligh and Johnson (1973) defined homeothermy as 'the pattern of temperature regulation in a tachymetabolic species in which the cyclic variation in core temperature, either nychthemerally or seasonally, is maintained within arbitrarily defined limits ($\pm$ 2^{o}C) despite much larger variations in ambient temperature'. Species which display greater cyclic variations in body temperature are termed 'heterotherms'. In accordance with this definition the chuditch must be regarded as a heterothermic species.

Despite the large cyclic variations in body temperature, the chuditch is able to regulate its body temperature effectively at ambient temperatures at least as low as 0^{o}C and can maintain body temperature below ambient temperatures around 40^{o}C for one to two hours (see Chapter X). It is therefore an efficient thermoregulator. The animals heterothermy, therefore, does not arise from inadequacies in its physiological capacities.

It has been clearly established by many workers that marsupials are good thermal regulators and that their abilities to contend with moderately low and moderately high environmental temperatures are equal to those of most eutherian mammals (Higginbotham and Koon, 1955; Bartholomew, 1956; Robinson and Morrison, 1957; Bentley, 1960;

Morrison, 1962, 1965; W. Dawson and Bennett, 1970; T. Dawson, 1973; Hulbert and T. Dawson, 1974b). These studies have disposed of the proposals, attributed to Martin (1903) and subsequently often repeated, that marsupials are less effective thermoregulators than placental mammals and, with the monotremes, represent an intermediate evolutionary stage in the development of homeothermy.

Morrison (1965) measured body temperatures of seven species of the family Dasyuridae, with body weights ranging from 11-6700 g. Body temperatures were measured in holding cages at ambient temperatures of 25-30°C to obtain information about the daily cycles of body temperature. Body temperatures were also measured at low (5°-10°) and high (35°-40°C) ambient temperatures to determine the responses of the animals to moderate temperature stress.

Morrison observed a uniform response in all of the dasyurid species he studied. He found that they displayed daily cycles in body temperature with amplitudes of 0.8°-4.0°C. During active periods mean body temperatures ranged from 37.4°-38.8°C. Some species exhibited a "daily aestivation" during which the body temperature approached ambient levels. All species could maintain their body temperature at low ambient temperatures and their ability to contend with high ambient temperatures was related to body size, smaller species being less effective in this

regard than larger ones.

The circadian cycle in body temperature of the chuditch and its response to low and high ambient temperatures is similar to those described by Morrison for other dasyurid species. When the daily body temperature cycle is compared with that observed by Morrison in the closely related Dasyurus hallucatus it appears that both species exhibit cycles with an amplitude of 4°C (at ambient temperature 25-30°C for D. hallucatus; 30°C for D. geoffroii) although D. geoffroii is less regular.

Godfrey (1968) confirmed the occurrence of daily temperature cycles in Sminthopsis crassicaudata and S. froggatti (larapinta) with mean amplitudes of 0.79°C and 4.24°C respectively.

Female chuditches were shown to go into a state of torpor during the period when the lights were on in the constant temperature room, most frequently in the three hours at the middle of the light period. The tendency to enter torpor appeared to be limited to the females and there is a suggestion that it may be a seasonal phenomenon as it was not observed during spring, but only in autumn and early winter. From limited evidence torpor does not appear to be induced by food deprivation. Torpor in other dasyurid marsupials has, on the other hand, been shown to be related to lack of food. Sminthopsis froggatti (larapinta) was found to go into torpor in response both to low

environmental temperatures and to food deprivation while S. crassicaudata become torpid only in response to food shortage (Crowcroft and Godfrey, 1968; Godfrey, 1966, 1968).

Morrison (1965) described "daily aestivation" in some of the dasyurids, particularly in Dasycercus. Arousal from daily aestivation in Dasycercus appears to be similar to arousal from what I have termed torpor in D. geoffroii (p. 7.25), although Dasycercus is able to raise body temperature at a faster rate during arousal. Recently Wallis (1976) has described torpor in Antechinus stuartii which appears to be a starvation-induced winter phenomenon. In some respects the torpor in Antechinus resembles torpor in the chuditch:

1. Wallis found it to occur only in animals captured in the winter; chuditches also were found torpid only during the winter months.
2. T_b never fell below 21°C in Antechinus which aroused from torpor; the lowest T_b observed for a chuditch was 23.1°C. However some otherwise unexplained deaths of captive animals may have been due to failure to arouse from torpor.
3. Torpor appears to occur at similar air temperatures in the two species. Wallis shows oxygen consumption rates for Antechinus with T_b less than 32°C at T_a 15°, 20° and 25°C (Fig 2). Chuditches were most frequently found torpid at T_a 15° and 20°C (see also Chapter VIII).

On the other hand Wallis was able to demonstrate a clear relationship between starvation and entry into torpor in Antechinus whereas I was unable to do so with the chuditch. Furthermore there is a marked difference in body weight between the two species. Antechinus at 25-30 g body weight is of a comparable size to many eutherian species exhibiting daily torpor or hibernation, whereas the chuditch at 700-2000 g is well outside the size range in which torpor occurs. Bartholomew (1972) has pointed out that what he terms 'adaptive hypothermia' (defined as a pattern of dormancy which occurs under a variety of conditions in a number of taxa of birds and mammals) with a daily periodicity is known to occur only in birds and mammals weighing less than 100 g. The rate warm-up from torpor has been shown to be inversely related to body weight (Heinrich and Bartholomew, 1971) according to the predictive equation for birds and mammals:

$$\text{Rate of warm-up } (^{\circ}C/\text{min}) = 2.03W^{-0.40}$$

where W = body weight in grams. From this equation the rate of warm-up of 700 g and 1000 g animals would be respectively 0.15°C/minute and 0.13°C/minute, too slow according to Bartholomew to fit easily into a daily periodicity, whereas the rate of warm-up for a 30 g animal would be 0.52°C/minute. One chuditch warmed-up during arousal from torpor at 0.3-0.4°C/minute, a rate considerably faster than that predicted by the equation of Heinrich and

Bartholomew. Two other animals showed a rate of warm-up close to that predicted. Wallis, however, found that Antechinus warmed-up more slowly than would be expected from the predictive equation.

The phenomenon of torpor is not restricted to the dasyurid marsupials. Bartholomew and Hudson (1962) found that the pigmy possum Cercartetus nanus exhibits torpor. Captive south-western pigmy possums, Cercartetus concinnus, and honey possums, Tarsipes spenserae, also are occasionally found in a torpid state on cold mornings (Heather Vose, personal communication).

Arousal from torpor in eutherian mammals which display adaptive hypothermia is facilitated by thermogenesis in brown adipose tissue. Estimates of the size of its contribution to heat production during arousal vary from species to species from 10 per cent to 60 per cent of the total heat expenditure (review: Smith and Horwitz, 1969).

In Chapter VI I suggested that brown adipose tissue is probably not present in marsupial pouch-young. This is supported directly by the work of Jones (1970) on the effects of exogenous catecholamines on the quokka joey; indirectly by the observation that the ability to shiver develops in pouch-young of the opossum and the chuditch before they are able to maintain T_b above T_a and that the ability to thermoregulate appears to depend upon shivering and fur insulation. If brown adipose tissue is absent from the

pouch-young it is implicit that it is also absent from the adults. If this is the case then the warm-up during arousal from torpor must involve heat production by shivering thermogenesis alone.

Good agreement was obtained between body temperatures measured by means of mercury-in-glass thermometers inserted into the colon immediately after the animal had been removed from the metabolism chamber, and by measurements made by thermistor probes in the colon during long-term confinement within the metabolism chamber. Body temperatures measured in the metabolism chamber by thermistor probes were, on the average, slightly lower than daily means for the 24-hour period obtained with mercury-in-glass thermometers. The differences no doubt are due to two factors:

1. the animals were normally confined in the metabolism chamber during the daytime when their activity levels were low, and
2. animals in the metabolism chamber had previously been starved and were in a post-absorptive state.

The body temperature of the chuditch rises at ambient temperatures of 30°C or higher. As a result, body temperature remains higher than air temperature so that heat may be lost by other than evaporative means until $T_a = T_b$ at about 39°C. At higher ambient temperatures, body temperature is maintained below ambient by high rates of evaporative heat loss (Chapter X).

A number of investigators have drawn attention to the tendency of marsupials to become hyperthermic at ambient temperatures above the thermal neutral zone. W. Dawson and Bennett (1970) observed moderate hyperthermia in Lagorchestes conspicillatus at ambient temperatures of 35-42.8°C. T. Dawson (1973) found that body temperatures of the two large kangaroos, Macropus robustus and Megaleia rufa tended to rise at air temperatures above 22°C. Hulbert and Dawson (1974b) found that three bandicoot species, Perameles nasuta, Isoodon macrourus and Macrotis lagotis, showed an increase in body temperature above ambient temperatures of 30°C; only Perameles and Macrotis could maintain their body temperatures below ambient at 40°C.

The chuditch can be characterized as a heterotherm in that it has a labile body temperature with a circadian cycle of 4°C or more in amplitude. Its mean body temperature is comparable to that of other marsupials and somewhat lower that that of most eutherian mammals. The body temperature during activity peaks is, however, at 36.9°-38.0°C and similar to that of eutherians. Like other marsupials, except the very small species, the chuditch regulates its body temperature efficiently over a wide range of ambient temperatures.

Current views on the evolution of homeothermy, as stated by Bligh (1973), contend that neural mechanisms for

temperature monitoring, necessary for homeothermy, preceded the ability to maintain a high metabolic rate and a low thermal conductance, which are necessary for the maintenance of high, stable body temperatures. The present view is that these neural mechanisms possibly existed in the reptilian ancestors of both birds and mammals before the divergence of these groups and that endothermic homeothermy arose in the birds and mammals as a result of improved insulation and elevated metabolic rates. Bligh suggests that thermal lability, as it occurs in a number of placental mammals as well as in marsupials, probably represents an adaptation to particular kinds of environments and may have arisen separately in different groups. If it is true that the neural patterns underlying homeothermy are ancient and are shared by such widely divergent taxa as birds and eutherian mammals, it seems improbable that marsupials differ basically in their homeothermic controls.

CHAPTER VIII

ENERGY METABOLISM

Preamble

This study of the energy metabolism of Dasyurus geoffroii was begun at a time when there was growing evidence that marsupials have lower energy requirements than most eutherian mammals. Martin (1903) demonstrated a low rate of metabolism for several species of Australian marsupials and suggested that this indicated a phylogenetic difference, the marsupials being more primitive than placental mammals. Bartholomew and Hudson (1962) showed Cercartetus nanus to have a relatively low resting oxygen consumption but attributed this to obesity of the captive animals they used. Other correlates of metabolism indicated low rates of energy usage in some marsupials which were shown to have low nitrogen requirements and low rates of nitrogen excretion (Macropus robustus Brown and Main, 1967) and low water requirements (Macropus eugenii Kinnear, Purohit and Main, 1968). Brown and Kinnear (1967) showed that resting heart rates of 17 species of Australian marsupials are low in comparison with eutherian mammals, implying a low level of energy metabolism in marsupials.

Meanwhile, direct studies of the energy usage of a large number of species appeared (MacMillen and Nelson, 1969; Dawson and Hulbert, 1969, 1970) showing that

Australian marsupials have standard rates of metabolism some 30 per cent lower than expected on the basis of body weight from the interspecific predictive equation for metabolic rate of eutherian mammals:

$$M(kcal/day) = 70\ W^{0.75}$$

where W = body weight in kg (Kleiber, 1961). Further studies (e.g. Dawson and Bennett, 1970; Dawson, 1973; Hulbert and Dawson, 1974a; Kinnear and Shield, 1975) have confirmed that Australian marsupials generally have metabolic rates significantly lower than most eutherian mammals. In spite of the relatively low metabolic level marsupials have been found to be effective thermal regulators (see discussion, Chapter VII).

A study of the pattern of energy usage of the chuditch was carried out, in conjunction with an investigation of its ability to regulate body temperature, in order to determine:

1. the rate/temperature curve of oxygen consumption vs. ambient temperature and, thus, the thermal neutral zone;

2. the resting metabolic level in a thermal neutral environment;

3. the rate of energy usage necessary to maintain stable body temperature at ambient temperatures below the thermal neutral zone;

4. the metabolic cost of maintaining body temperature at ambient temperatures above the thermal neutral zone.

The lability of the body temperature of the chuditch (Chapter VIII) was found to influence all aspects of the energy metabolism so that both T_a and T_b had to be taken into account in the analysis of the results. It was expected that the relationship between T_b and O_2 consumption would provide insight into the metabolic cost of controlling T_b within narrow limits vs. relaxation of control of T_b. Furthermore it was expected that the circadian cycle in T_b would be reflected in a circadian cycle in resting rates of O_2 consumption.

A number of aspects of energy metabolism in the chuditch reported in this thesis have already been published elsewhere (Arnold and Shield, 1970).

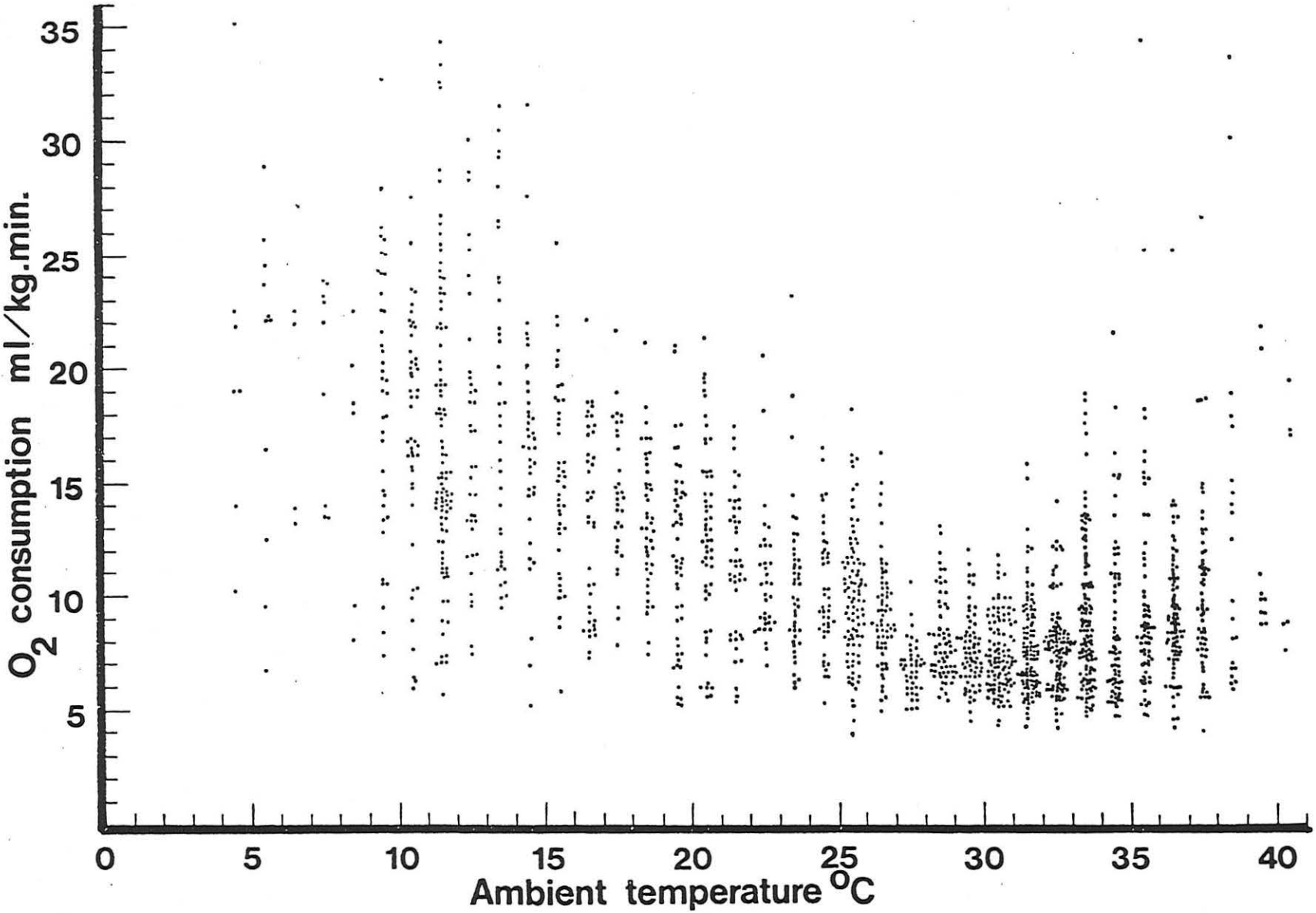
. Results

Oxygen Consumption Rates in the Ambient Temperature Range 4° to $41^{\circ}C$

O_2 consumption rates of 26 animals measured in the ambient temperature range 4.0° to $40.9^{\circ}C$ are shown in the scatter diagram, Fig 8.1. The O_2 consumption rates were measured while T_a within the metabolism chamber was slowly raised over a period of eight to twelve hours. Some animals were subjected to the full range of ambient temperatures, others to the lower part of the range from about 10° to $25^{\circ}C$, and others to temperatures above $29^{\circ}C$.

The wide scatter of measured rates of O_2 consumption

Fig 8.1 Scatter diagram of O_2 consumption (ml/kg. min.) vs. T_a for chuditches; values measured as T_a gradually increased.


35
30
25
20
15
10
5
O_2 consumption ml/kg.min.
0
5
10
15
20
25
30
35
40
Ambient temperature °C

shown in Fig 8.1 is due largely to variation displayed by individual animals rather than to between-animal differences. This variation will be considered in this section and in a later section in relation to body temperature.

Mean rates of O_2 consumption at one degree intervals of ambient temperature for the 26 animals are shown in Fig 8.2 together with the variance of each $1^{\circ}C$ set of values used to calculate the means (Data tabulated in Appendix E). The lowest mean rates of O_2 consumption, 6.7-7.7 ml/kg. min., occurred in the range of T_a 27° to $33^{\circ}C$. Mean O_2 consumption rates increased at ambient temperatures below $27^{\circ}C$ to 20.5 ml/kg. min. at $4^{\circ}C$, and increased above $33^{\circ}C$ to 11 ml/kg. min. at $40^{\circ}C$. The thermal neutral zone, if defined as the range of ambient temperatures in which O_2 consumption is minimal, bounded on each side by rising rates (Mount, 1974), extends from 27° to $33^{\circ}C$ and is centred on $30^{\circ}C$. The variation in the O_2 consumption rate, as indicated by the variance, is lowest within the thermal neutral zone and increases at higher and lower temperatures.

The time course of the variation in O_2 consumption rate displayed by individual animals is illustrated by examples in Fig 8.3, A-D. These four graphs, in which the O_2 consumption rates are plotted against local time, show portions of records obtained from four different animals for which O_2 consumption was measured while T_a

was maintained constant at 10°, 15°, 19° and 20°C respectively. All four animals remained quiet for the periods shown. Variation is therefore revealed as resulting from definite short term trends rather than being produced by randomly scattered values. Mean rates of O_2 consumption at 10°, 15°, 19° and 20°C, from Fig 8.2, are shown as dashed lines on graphs A, B, C, and D respectively.

The following terminology will be used in consideration of the figures:

"average rates" = the mean O_2 consumption for each degree of ambient temperature as measured in a gradient of increasing T_a and shown on Fig 8.2.

"minimum rates" = rates of O_2 consumption of 4-7 ml/kg. min. (equal to or slightly lower than the standard metabolic rate in the thermal neutral zone) which occur over the full range 4° to 38°C T_a.

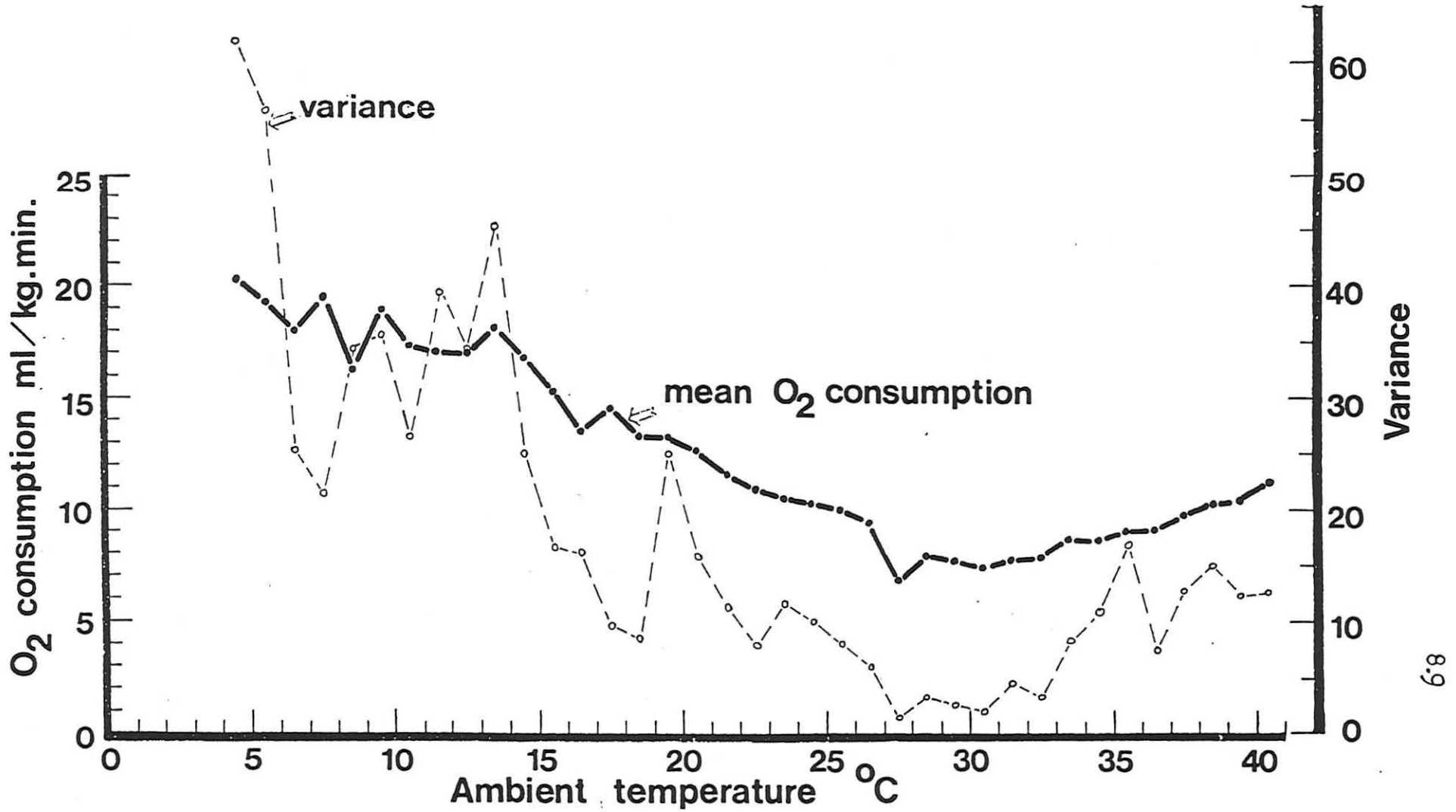
1. Fig 8.3 A; T_a 10° to 11°C

The trend-line shows two periods, each of more than three-quarters of an hour, during which O_2 consumption fell below the average rate for 10°C and approached minimum rates. During these periods the animal remained quiet, was apparently sleeping, and showed no evidence of muscle tremor or shivering. It would then begin to shiver (indicated on the graph by hatched bars) either intermittently or

Fig 8.2 Mean rates of O_2 consumption vs. T_a and variance of the rates; data from Fig 8.2 grouped at 1°C intervals of ambient temperature.

Symbols: ●——● mean O_2 consumption rates linked by trend-lines

o----o variance of O_2 consumption rates used to calculate mean values, linked by trend-lines


variance
mean O_2 consumption
O_2 consumption ml/kg.min.
Variance
Ambient temperature °C
0
5
10
15
20
25
30
35
40
0
5
10
15
20
25
30
40
50
60

continuously for up to 30 minutes. With no other apparent change in activity, shivering could raise the rate of O_2 consumption to four times the minimum rate.

2. Fig 8.3 B; T_a 15°C

This animal was apparently awake for the four-hour period represented on the graph. The cycles of high and low rates of O_2 consumption were shorter than those described above, with only brief periods when O_2 consumption approached minimum rates. The arrows indicate shivering and they coincide with rising or high rates of O_2 consumption.

3. Fig 8.3 C; T_a 19°C

The animal remained awake for the three-hour period shown. Its mean O_2 consumption rate during this time was 14.2 ml/kg. min. compared with the average rate at T_a 19°C of 13.2 ml/kg. min. The characteristic cycles from high to low rates of O_2 consumption were short and minimum rates were attained only for very brief intervals.

4. Fig 8.3 D; T_a 20°C

This animal was apparently asleep for about half of the four-hour period shown. During wakeful periods, when it nevertheless remained quiet, O_2 consumption rose to the average rate or above it. During sleep, the rate of O_2 consumption fell to the minimum rate and remained at about 5 ml/kg. min. for one period of 40 minutes. Two periods when the animal was asleep, but shivering, were marked by

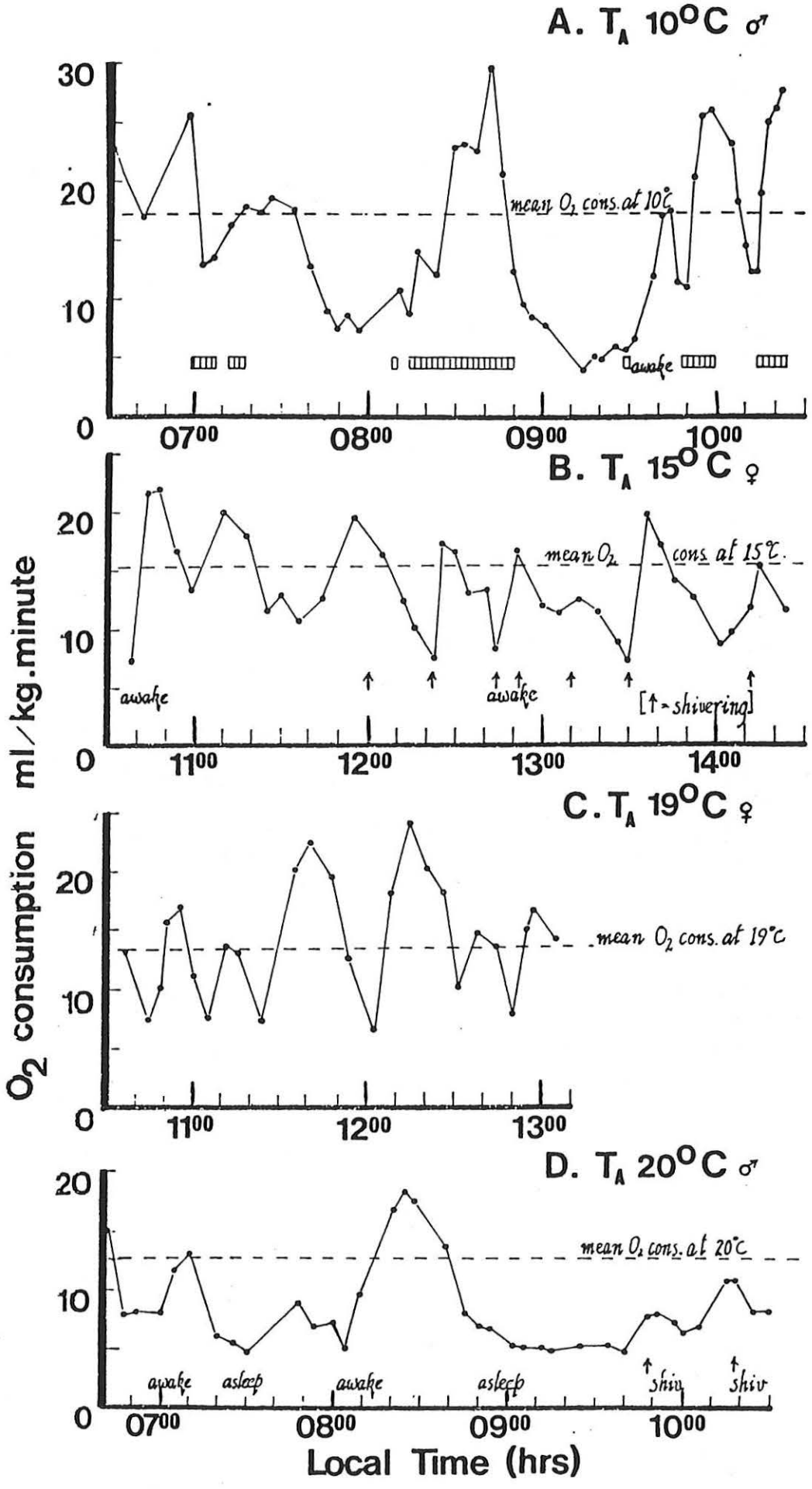
Fig 8.3 Portions of records from four runs at different constant ambient temperatures showing short-term trends in rates of O_2 consumption; O_2 consumption rates are plotted against local time and linked by trend-lines.

8.3A - T_a 10°C.

8.3B - T_a 15°C.

8.3C - T_a 19°C.

8.3D - T_a 20°C.


A. T_A 10°C ♂
mean O_2 cons. at 10°C
awake
B. T_A 15°C ♀
mean O_2 cons. at 15°C
awake
awake
[↑ = shivering]
C. T_A 19°C ♀
mean O_2 cons. at 19°C
D. T_A 20°C ♂
mean O_2 cons. at 20°C
awake
asleep
awake
asleep
shiv
shiv
O_2 consumption ml/kg.minute
Local Time (hrs)

an increase in the O_2 consumption rate above the minimum rate but to less than the average rate.

Trends in O_2 consumption rates, as illustrated above, were correlated with differences in the level of arousal of the animals and whether or not they were shivering. Subsequently, when body temperature was measured simultaneously with O_2 consumption rates the overall variation could be related to lability in body temperature (see p. 8.22).

Standard Metabolic Rate (SMR) and Metabolic Level

Means were calculated for each of 41 separate sets of measurements of O_2 consumption made on 29 different animals resting in the range T_a 30.0° to 30.9°C, taken to be the centre of the thermal neutral zone. The mean rates for all 29 animals (some determined more than once) and for the 14 males and 15 females separately are shown in Table 8.1, together with mean body weights and standard errors of means for O_2 consumption and body weight.

The mean of each separate set of O_2 consumption rates in the thermal neutral zone was compared with the value predicted from the interspecific regression of weight-relative O_2 consumption for dasyurid marsupials (MacMillen and Nelson, 1969):

$$O_2 \text{ consumption (ml/g. hr)} = 2.45W^{-0.261}$$

where W = body weight in grams. Values calculated from

this expression were converted to ml/kg. min. The means of these calculated values for all animals and for males and females separately, together with observed mean values expressed as percentages of predicted values, are shown in Table 8.1. The overall mean of the 41 values was 6.84 ml/kg. min. which is slightly lower (93.2 per cent) than the mean rate of 7.34 ml/kg. min. determined for animals in rising temperature gradients (Fig 8.2). The lower values are attributed to the prolonged periods of equilibration allowed in the determinations of SMR. The observed rates of O_2 consumption for males were about six per cent higher than predicted values, while observed rates for females agreed precisely with those predicted. Mean rates and predicted rates for each separate case are tabulated in Appendix F.

The standard metabolic rate (kcal/day) was calculated for each of the 41 mean O_2 consumption rates at T_a 30°-30.9°C assuming 4.8 kcal/litre O_2. This permitted comparison of the standard metabolic rates of individual chuditches with the metabolic level established by Dawson and Hulbert (1969, 1970) for Australian marsupials:

$$\text{SMR (kcal/day)} = 48.6\ W^{0.75}$$

when W = body in kg. Fig 8.4 shows the 41 separate metabolic rates for chuditches vs. body weight (log scale) together with the predictive regressions for marsupials (Dawson and Hulbert) and for eutherian mammals (Kleiber,

Table 8.1

Means and standard errors of means of body weights and weight-relative O_2 consumption rates for chuditches at 30-30.9°C (T_a) together with predicted O_2 consumption rates calculated from the interspecific expression for dasyurid marsupials (McMillen and Nelson, 1969) and observed O_2 consumption rates expressed as percentages of predicted rates. (Rates and predicted values for individual animals are tabulated in Appendix F).

	Number of animals*	Mean body weight (kg)	Mean O_2 consumption (ml/kg.min)	Predicted O_2 consumption (ml/kg.min)	Observed O_2 cons. / Predicted O_2 cons. (per cent)
Males & Females	29/41	1.105±0.051	6.84 ± 0.27	6.56	103.0 ± 3.84
Males	14/20	1.308±0.079	6.75 ± 0.41	6.28	105.9 ± 5.77
Females	15/21	0.910±0.025	6.93 ± 0.36	6.90	100.2 ± 5.15

* As some animals were used more than once, the value to the left of the slant indicates the number of different animals; the number to the right of the slant indicates the number of separate determinations.

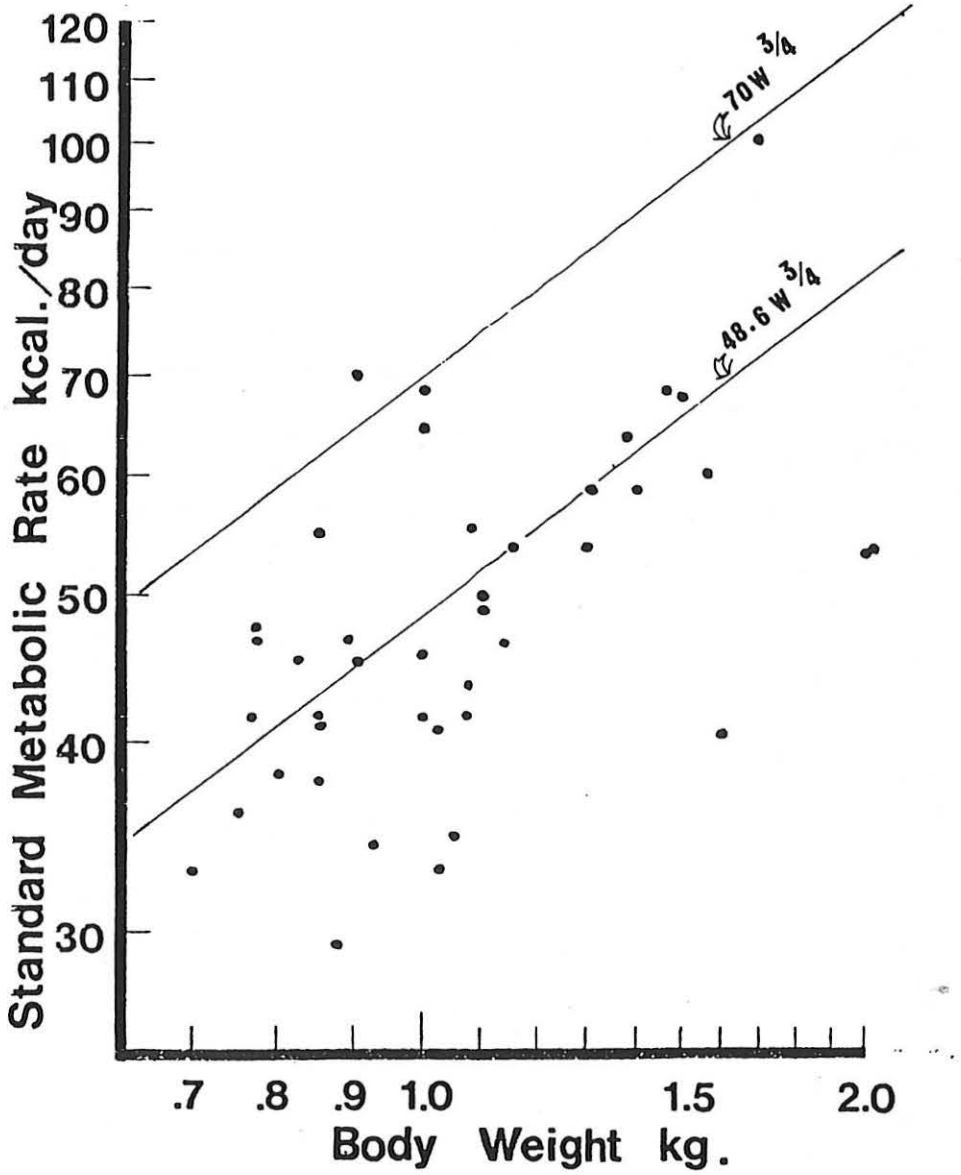
1961). The values for the chuditches show a wide scatter, four values falling close to the eutherian metabolic level and many being considerably lower than the marsupial level. The mean metabolic rate for the chuditch, calculated from the 41 values, is 49.9 kcal/day (mean body weight 1.105 kg). This mean is 95 per cent of the marsupial metabolic level of 52.4 kcal/day for animals of 1.105 kg and 66 per cent of the eutherian metabolic level for animals of equivalent body weight as predicted from the Kleiber equation.

Circadian Cycle in the Rate of O_2 Consumption

It might be expected that the chuditch would show a circadian cycle in O_2 consumption rate related to the cycle in body temperature (Chapter VII). Two animals, one male and one female, were maintained at constant ambient temperature within the metabolism chamber for 24 hours or more (at 10° and 30°C for the male and at 15° and 30° for the female). O_2 consumption rates were measured at frequent intervals during these periods. Fig 8.5 shows the mean O_2 consumption rates calculated for each hour of these four long runs (Data tabulated in Appendix G).

The female showed clear evidence of a cycle in O_2 consumption rate at both 15° and 30°C. At 15°C hourly mean O_2 consumption rates were low and steady at 11.5-13 ml/kg. min. from about 1200-1700 hours, local time.

Fig 8.4 Standard metabolic rates (kcal/day) vs. body weight (kg) on logarithmic axes; the inter-specific regressions of metabolic rate of eutherians, $70W^{\frac{3}{4}}$ (Kleiber, 1961) and of marsupials, $48.6W^{\frac{3}{4}}$ (Dawson and Hulbert, 1969) are also shown.


120
110
100
90
80
70
60
50
40
30
Standard Metabolic Rate kcal./day
70W 3/4
48.6 W 3/4
.7
.8
.9
1.0
1.5
2.0
Body Weight kg.

Hourly mean rates during the night were generally higher and more variable with the highest means occurring at 1800-2000 hours, 0300-0400 hours and 0500-0600 hours. At 30°C, hourly mean O_2 consumption rates of this animal showed a similar cycle, O_2 consumption between 0900-1700 hours being lower than in the remaining hours. The mean of the hourly means for the last 24 hours of these runs are 16.15 ml/kg. min. at T_a 15°C and 6.90 ml/kg. min. at T_a 30°C. Both of these values are within a few per cent of average rates at 15°C and 30°C respectively.

Less evidence of a daily cycle in O_2 consumption was obtained from the male at 10° and 30°C. At 10°C the lowest hourly mean rates occurred between 0700-1000 hours but low hourly mean rates occurring at other times of the day were interspersed with hours when the mean rates were high. However there was a general trend towards higher hourly mean values between 1800 hours and midnight and between 0300-0700 hours. After the first seven hours at T_a 30°C this animal maintained its O_2 consumption rate at a low and very constant level throughout the entire run with a slight elevation of the mean hourly rate between 1800-2200 hours and between 0400-0500 hours. In the case of the male the mean of the hourly means for the last 24 hours of the runs are 19.55 ml/kg. min. at 10°C and 6.00 ml/kg. min. at 30°C. At the lower temperature this represents 113 per cent of the average rate whereas the

Fig 8.5 Hourly mean O_2 consumption vs. local time during periods in excess of 24 hours for one male at T_a 10° and 30°C and for one female at T_a 15° and 30°C.

Symbols:

●——● male at 10°C

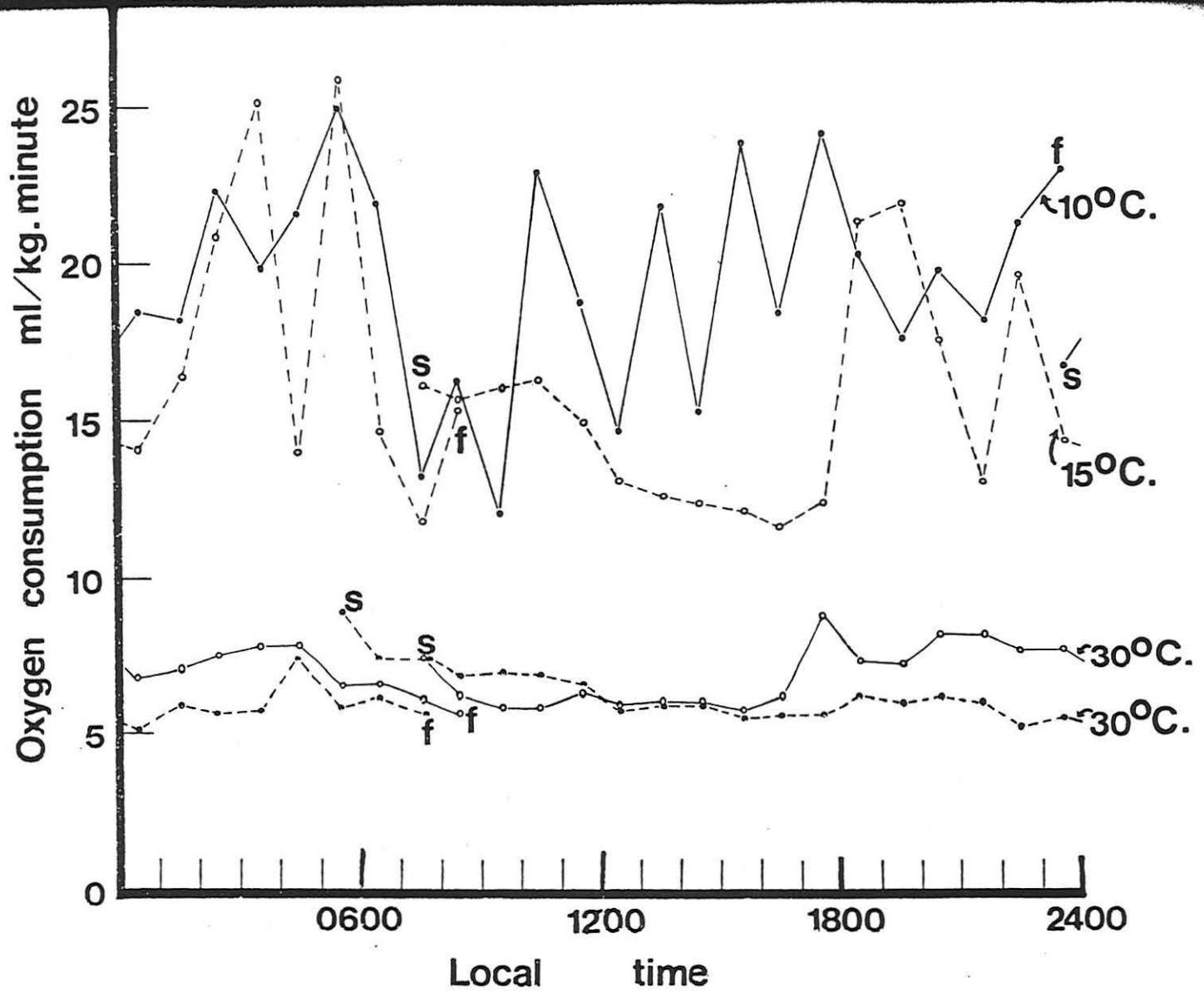
●- - -● male at 30°C

○- - -○ female at 15°C

○——○ female at 30°C

s = start of run

f = finish of run


Oxygen consumption ml/kg. minute
25
20
15
10
5
0
0600
1200
1800
2400
Local time
s
f
10°C.
15°C.
30°C.
30°C.

value for the higher temperature represents only 87 per cent of the average rate.

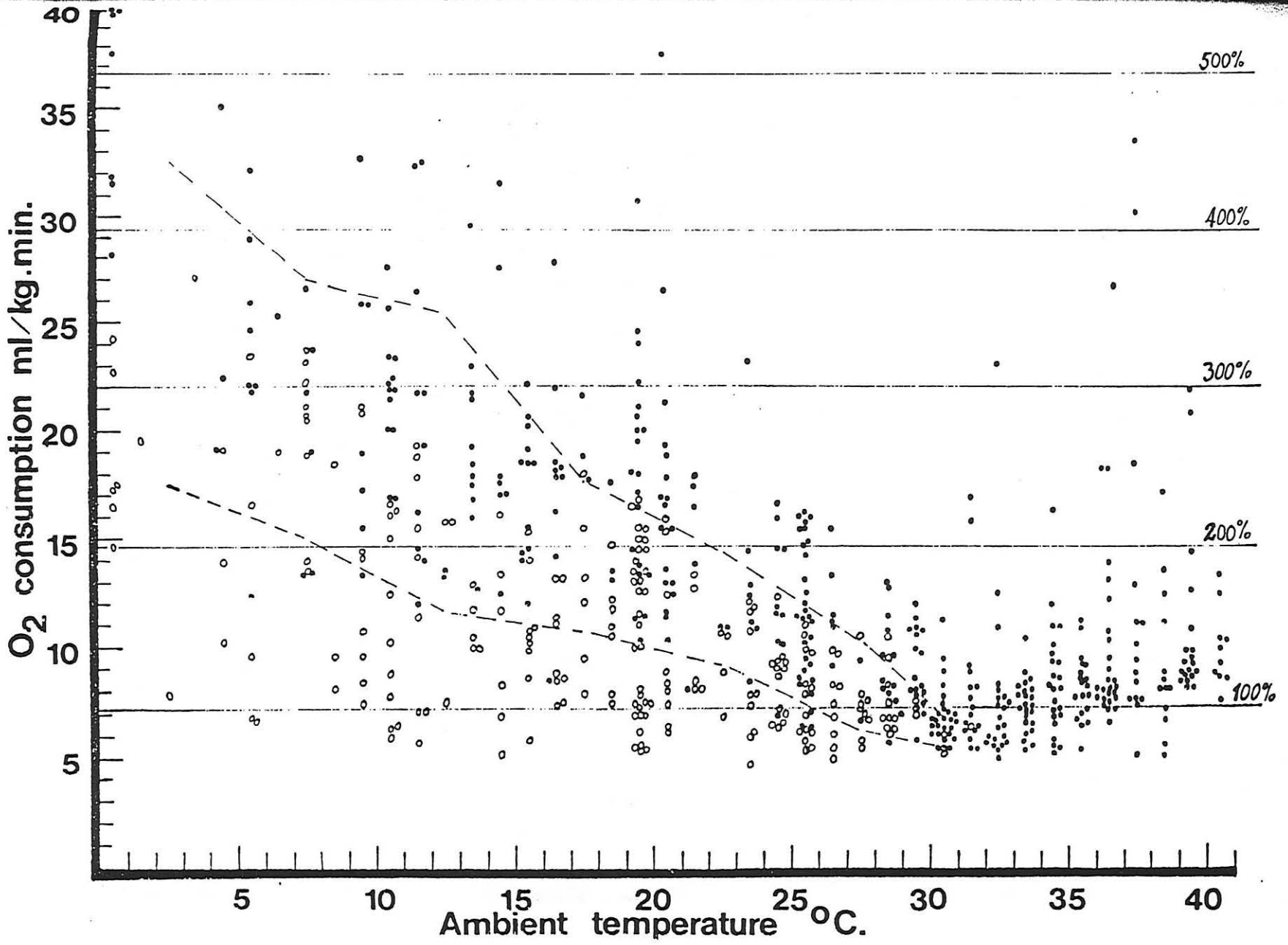
The times when the O_2 consumption rates were lowest generally coincided with the times when the animals have been found to have low body temperatures and to be inactive (Chapter VII). The higher rates of O_2 consumption occurred after 1700 hours and after 0300 hours, at times when the body temperature has been shown to be high and the animals active.

The Relationship between O_2 Consumption Rate and Body Temperature

1. Below the thermal neutral zone.

The individual variations in O_2 consumption rates at T_a below the thermal neutral zone have already been noted (p. 8.13). When O_2 consumption and T_b were measured simultaneously, rising and falling O_2 consumption rates could be related to large and rapid changes in T_b. Fig 8.6 shows O_2 consumption rates vs. T_a for eight animals for which T_b was measured at the same time as O_2 consumption. O_2 consumption rates measured while T_b was decreasing or stable following a decrease are shown by hollow circles and O_2 consumption rates measured while T_b was increasing or stable following an increase are shown by solid circles. Generally, low O_2 consumption rates were associated with decreasing T_b or stable T_b following a decrease and high

Fig 8.6 Scatter diagram of O_2 consumption (ml/kg. min.) vs. T_a for eight animals for which T_b was measured at the same time as O_2 consumption; showing rates of O_2 consumption measured when T_b was increasing or stable following as increase (●) and rates measured when T_b was decreasing or stable following a decrease (o). The broken lines indicate average trends in O_2 consumption rates when T_b increasing (upper line) and when T_b decreasing (lower line) calculated by grouping O_2 consumption rates at 5^oC intervals (0-4.9, 5-9.9, 10-14.9, 15-19.9, 20-24.9, 25-29.9^oC). The horizontal lines indicate multiples of the average O_2 consumption rate at 30^oC (from Fig 8.2).


40
35
30
25
20
15
10
5
O_2 consumption ml/kg.min.
500%
400%
300%
200%
100%
5
10
15
20
25
30
35
40
Ambient temperature °C.

8.24

rates were associated with increasing T_b or stable T_b following an increase. Above 31°C (T_a) T_b always remained stable or increased. The upper and lower trend lines show estimates of mean O_2 consumption rates measured when T_b was increasing and decreasing respectively. The trends were obtained by grouping rates at intervals of 5°C. Low O_2 consumption rates of 4-7.5 ml/kg. min. occurred throughout the T_a range 5° to 38°C. Such minimum rates were equal to low rates observed in the thermal neutral zone in the absence of thermal stress. Below about 24°C these occurrences were invariably associated with T_b decreasing or stable following a decrease.

Fig 8.6 also shows the highest O_2 consumption rates observed for the chuditch. One animal, shivering violently but otherwise inactive, consumed O_2 at the rate of 40 ml/kg. min. for a short period at 0°C (T_a). This represents 5.8 times SMR. This animal raised T_b from 33.0° to 34.8°C during 26 minutes while mean O_2 consumption was 32.5 ml/kg. min. (4.8 x SMR). A second animal was kept at 0°-1°C for 10½ hours during which its T_b ranged from 33.8° to 35.8°C (35.3°C at the end of run). During this time its mean O_2 consumption was 22.0 ml/kg. min. or 3.2 x SMR.

The close relationship between O_2 consumption and T_b is further illustrated in Fig 8.7 A-E. The graphs are portions of records obtained from five different animals in the metabolism chamber with thermistor probes permitting

constant monitoring of colonic temperature. In each graph the average O_2 consumption rate at the appropriate T_a and at 30°C (from Fig 8.2) are shown for comparison with the measured rates. It is assumed that at these average O_2 consumption rates normal T_b would be maintained.

Fig 8.7 A; T_a 10°C

T_b followed a falling trend for the first 1½ hours when O_2 consumption rate was below average for most of the time. For the last 30 minutes of the period shown O_2 consumption was mostly above average and T_b rose to 36.2°C, about 0.7°C above mean T_b at 10°C (Table 7.1).

Fig 8.7 B; T_a 16°C

During a two-hour period body temperature fell from 36° to 35°C in 20 minutes while O_2 consumption was less than half the average rate. A subsequent rise in O_2 consumption above the minimum rate but below the average rate coincided with the T_b stabilizing at 34.0-34.2°C. This is below the mean T_b at 15° whether autumn or spring values are considered (Table 7.1).

Fig 8.7 C; T_a 20°C

The rate of O_2 consumption was maintained at between 5 and 7.5 ml/kg. min. for six hours, during which time T_b fell 4.9° from 36.3° to 31.4°C. At the end of six hours, when O_2 consumption rose above 8 ml/kg. min., T_b rose by 1.4° to 32.8°C in 84 minutes; even so, the rate of O_2

consumption as T_b was rising was lower than the average rate of O_2 consumption at 20°C. The mean T_b at 20°C is 34.9°C (Table 7.1) and the mean value for inactive females is 33.4°C (Table 7.3).

Fig 8.7 D and 8.7 E should more appropriately be considered in later sections but they are included here to indicate the lability of T_b when O_2 consumption is at minimum rates.

Fig 8.7 D; T_a 30°C

A fall in T_b of 0.9° to 35.2°C occurred during two hours when O_2 consumption was almost continuously below the average rate at 30°C. The mean T_b at 28-32°C was 35.9°C (Table 7.1), while mean T_b of animals during the inactive period of their circadian cycle was 34.8° to 35.0°C (Table 7.3).

Fig 8.7 E; T_a 32°C

For $2\frac{1}{2}$ hours O_2 consumption was below the average rate while T_b increased from 35.0° to 36.0°C. This is a typical case: at the upper end of the thermal neutral zone the animals may tolerate a rise in body temperature which is not accompanied by increased rates of O_2 consumption (see p. 8.49).

The observation that animals reduce the rate of O_2 consumption to levels equal to or lower than the standard rate at ambient temperatures outside the thermal neutral zone, and that such low rates are associated with decreasing

body temperature when T_a is below the thermal neutral zone, suggests an explanation for the low body temperatures, associated with torpor, which have been observed for some animals (Chapter VII p.7.27). To return to Fig 8.7 C, which shows a period of 5¾ hours when T_b fell from 36.3° to 31.4°C while O_2 consumption was maintained at minimal levels: it is possible to calculate the rate of further cooling at T_a 20°C. Assuming the decrease in T_b follows an exponential trend, then the following relation should hold:

$$^{o}C_x = {}^{o}C_o \; e^{-rt}$$

when $^{o}C_o$ is the body temperature measured initially, $^{o}C_x$ is the body temperature measured at time t (in hours) after the initial value, and r = the cooling constant.

Substituting values from Fig 8.7 C and calculating r:

$$31.4 = 36.3 \; e^{-5.75r}$$

$$r = 0.0252$$

Consequently if the animal maintained the same rate of O_2 consumption for 10 hours or 12 hours and maintained a similar cooling constant (r), T_b would be 28.2° or 26.8°C respectively. Such rectal temperatures have been measured in animals which were torpid under conditions described in Chapter VII (p. 7.25).

Table 8.2 shows data relating to six cases in which animals had prolonged periods of low O_2 consumption accompanied by decreasing T_b. Only periods exceeding one

Fig 8.7 Portions of records from five runs at different constant T_a showing separate measurements of O_2 consumption and T_b vs. time (hours).
Individual values are linked by trend-lines.

Symbols: o-----o body temperature

●——● O_2 consumption

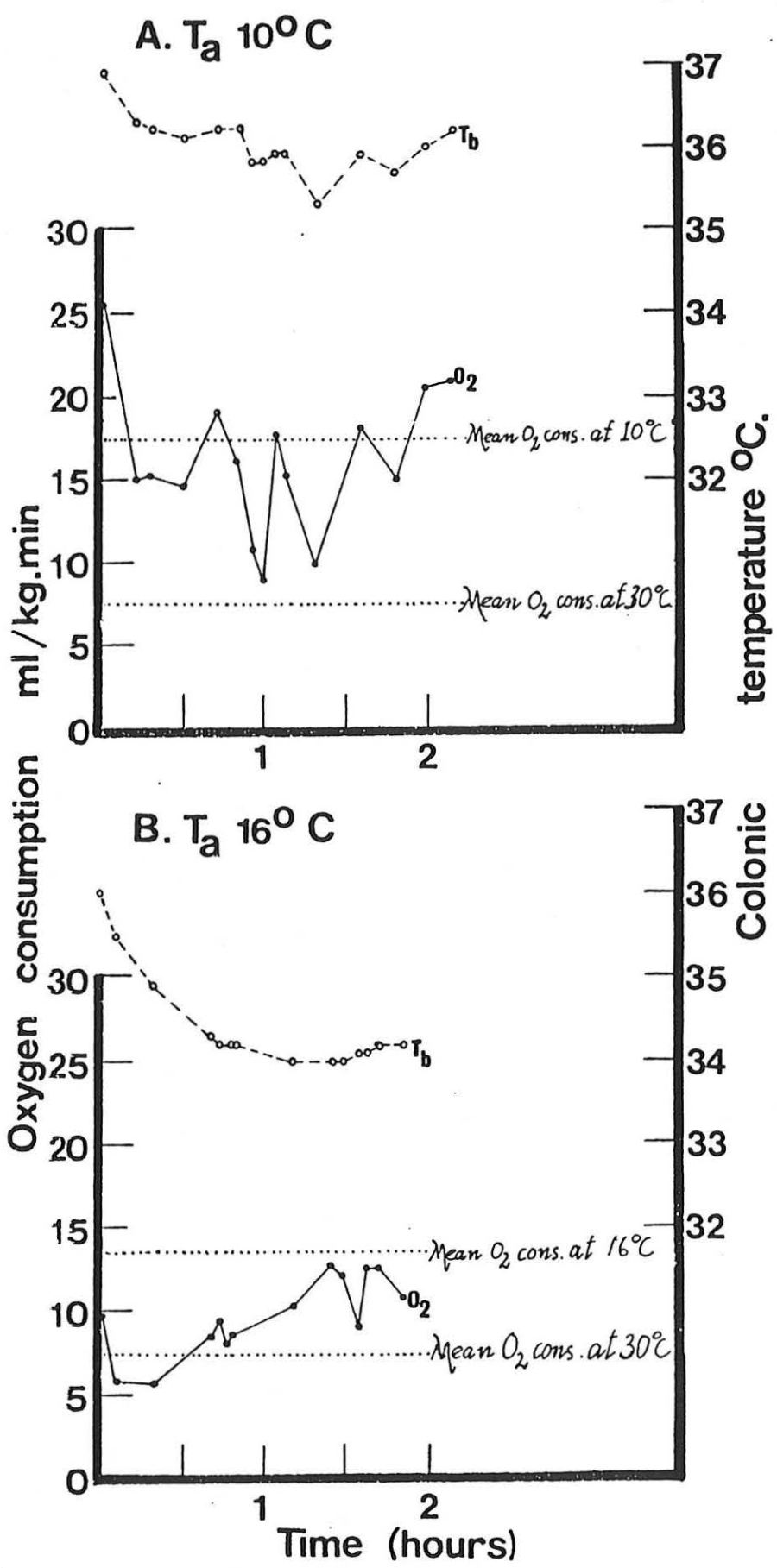
A: T_a 10°C

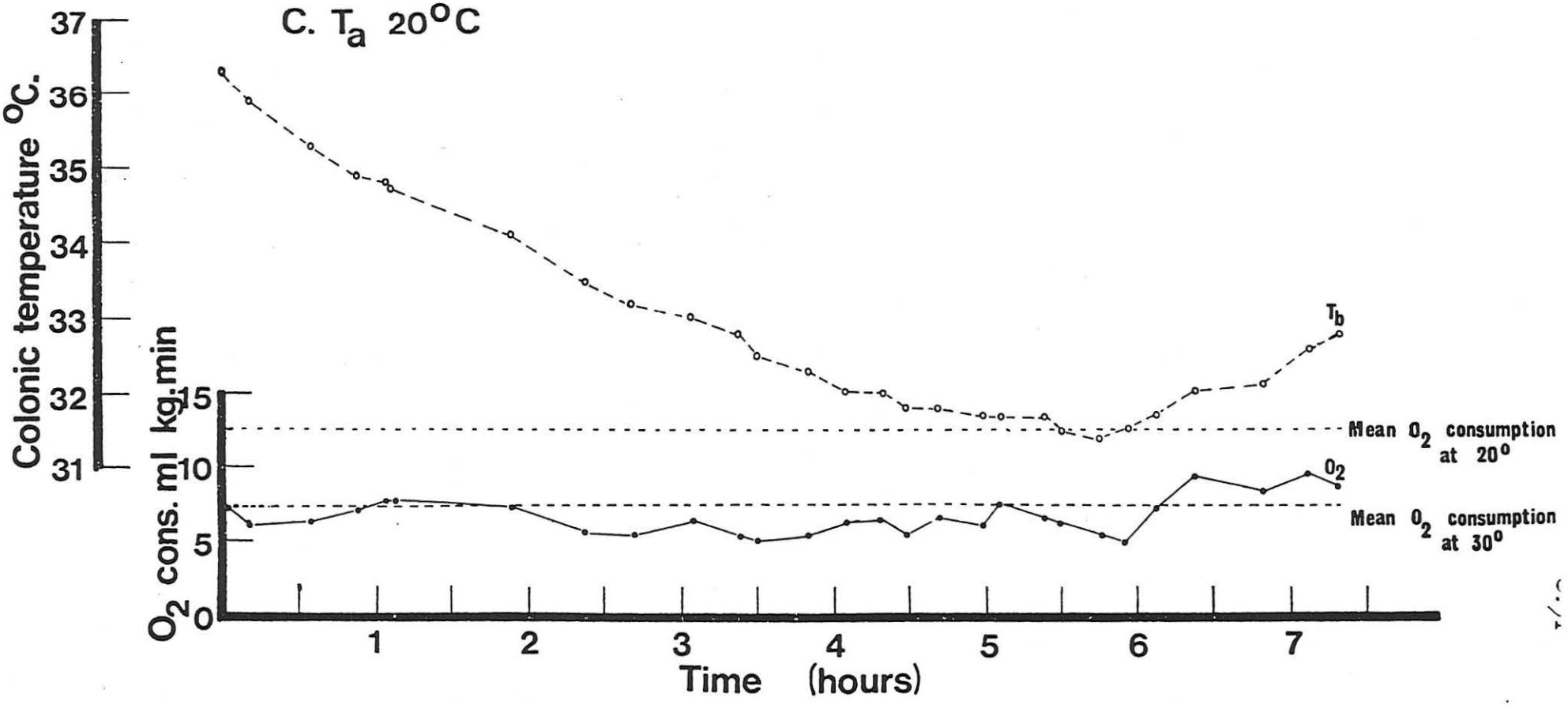
B: T_a 16°C

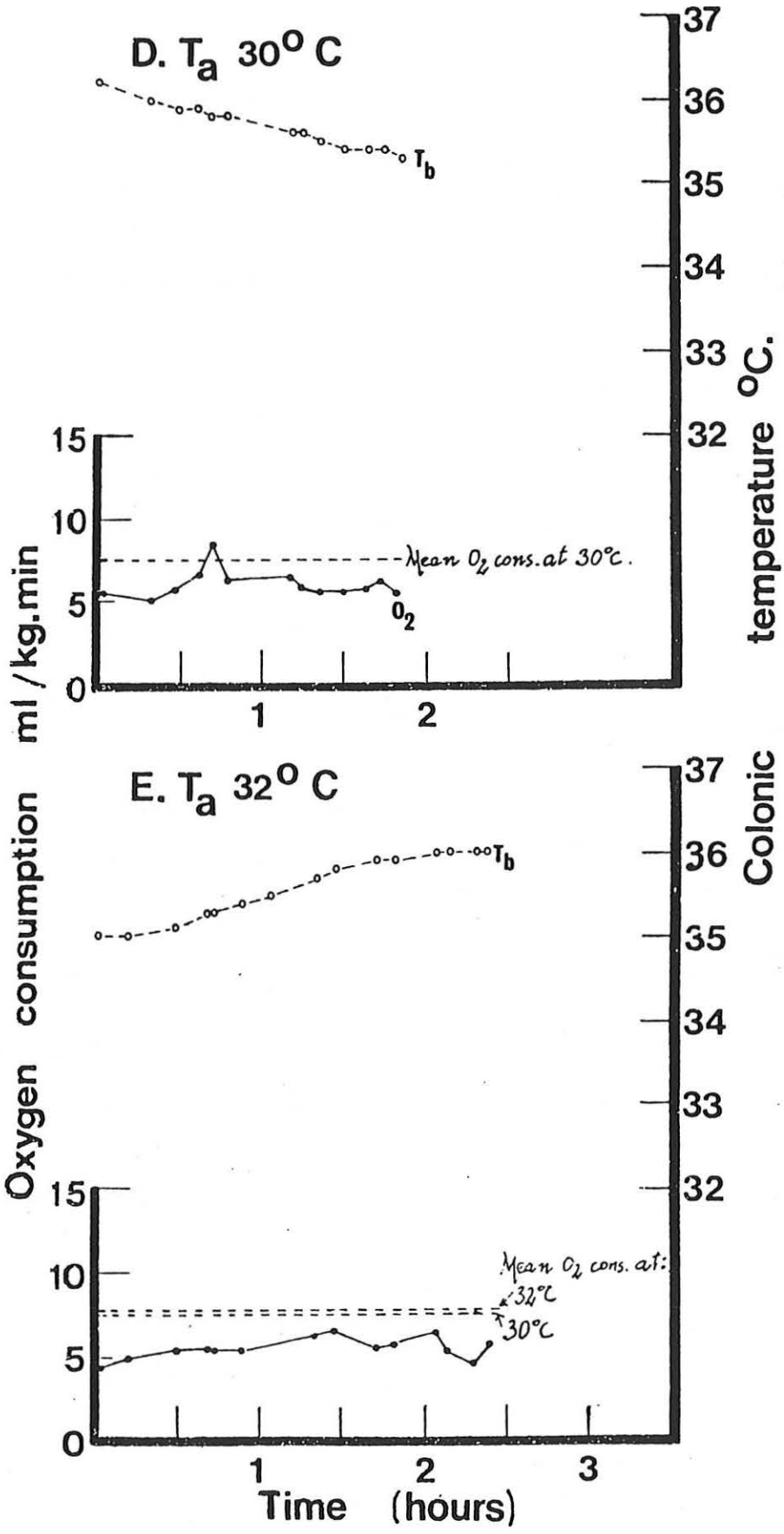
C: T_a 20°C

D: T_a 30°C

E: T_a 32°C


A. T_a 10° C
T_b
O_2
Mean O_2 cons. at 10°C
Mean O_2 cons. at 30°C
B. T_a 16° C
T_b
O_2
Mean O_2 cons. at 16°C
Mean O_2 cons. at 30°C
Oxygen consumption ml/kg.min
Colonic temperature °C.
Time (hours)
0
5
10
15
20
25
30
32
33
34
35
36
37
1
2


C. T_a 20°C
Colonic temperature °C.
37
36
35
34
33
32
31
T_b
O_2 cons. ml kg.min
15
10
5
0
O_2
Mean O_2 consumption at 20°
Mean O_2 consumption at 30°
1
2
3
4
5
6
7
Time (hours)


D. T_a 30° C
T_b
37
36
35
34
33
32
temperature °C.
15
10
5
0
Mean O_2 cons. at 30°C.
O_2
1
2
Oxygen consumption ml / kg.min
E. T_a 32° C
T_b
Colonic
Mean O_2 cons. at:
32°C
30°C
1
2
3
Time (hours)

hour were considered. I was not able to obtain a suitably long period of concurrent O_2 consumption and T_b measurements for animals held at T_a below 20°C. The examples shown in Table 8.2 include the one at T_a 20°C considered in detail above and five others at higher T_a. Even at T_a 30°C substantial decreases in T_b occurred when O_2 consumption rate was reduced to minimum levels.

2. In the thermal neutral zone.

Two apparently conflicting pictures emerge when considering the relationship between body temperature and the rate of O_2 consumption in the thermal neutral zone, specifically at T_a 30°C. On one hand is the situation illustrated in Fig 8.7 D in which T_b drifts downward for several hours while the O_2 consumption rate is maintained at the minimum level. On the other there is an apparent tight relationship between T_b and the rate of O_2 consumption.

A significant positive correlation between O_2 consumption rate and body temperature was found in data from eight animals for which colonic temperatures were measured at the same time as O_2 consumption at 30°C (T_a). Values obtained after the animals had been held in the metabolism chamber for two hours to attain a resting state are shown in Table 8.3. The table includes sex of the animals, body weight, mean T_b and mean O_2 consumption expressed in ml/kg. min. and ml/$kg^{0.75}$. min. for periods

Table 8.2

Cooling constants for periods when O_2 consumption was at or below the standard level, together with sex, body weight and mean O_2 consumption during the period of cooling, for animals which showed a pronounced fall in T_b during confinement in the metabolism chamber; T_b at the beginning (^oC_o) and at the end of the period (^oC_x), the duration of the period (t) and the cooling constant (r), together with calculated T_b for durations of 2, 5 and 10 hours (r calculated from the formula $^oC_{tx} = {}^oC_{to}\ e^{-rt}$.

Run	Sex	Body Wt. (kg)	T_a (^oC)	mean O_2 cons. ml/kg.min	$^oC_{to}$	$^oC_{tx}$	t (hrs)	r	Calculated T_b after:		
									2 hrs	5 hrs	10 hrs
Delan 35*	F	1.200	20	6.4	36.3	31.4	5.75	0.0252	34.5 -1.8	32.0 -4.3	28.2 -8.1
Dehyd 31	F	0.750	24-25	6.1	35.5	31.8	3.55	0.0310	33.4 -2.1	30.4 -5.1	26.0 -9.5
Delan 23B	M	2.000	30	4.9	36.8	35.2	2.35	0.0189	35.4 -1.4	33.5 -3.3	30.5 -6.3
Delan 29A*	F	1.025	30	6.0	36.2	35.3	1.83	0.0138	35.2 -1.0	33.8 -2.4	31.5 -4.7
Delan 33A	M	1.565	30	6.2	37.2	35.4	5.72	0.0087	36.6 -0.6	35.6 -1.6	34.1 -3.1
Dehyd 21	F	0.875	30	5.1	36.4	35.2	4.95	0.0068	35.9 -0.5	35.2 -1.2	34.0 -2.4

* same animal

ranging from 1 hour 20 minutes to more than six hours after the initial equilibrium period while the animals remained quiet. The correlation co-efficient for eight pairs of values of T_b and O_2 consumption rate was +0.87 ($p < .01$). When O_2 consumption was expressed in terms of metabolic body weight the significance of the correlation was increased ($r = +0.95$, $p < .001$). Fig 8.8 shows the linear regression fitted to the eight bivariate values by the method of least squares:

$$y = 2.603x - 86.817$$

where y = O_2 consumption (ml/kg$^{0.75}$. min.) and x = T_b (^{o}C). A conversion of the interspecific predictive expression of weight-relative metabolic rate of eutherian mammals (Kleiber, 1961) to ml O_2/kg$^{0.75}$. min., assuming 4.8 kcal/litre O_2, gives the value 10.12 ml O_2/kg$^{0.75}$. min. Extrapolation of the regression line shows that on the basis of the trend shown, the rate of O_2 consumption should reach 100 per cent of the eutherian metabolic level at T_b 37.25^{o}C. A similar conversion of the Dawson and Hulbert interspecific equation for marsupials gives a value of 7.04 ml/kg$^{0.75}$. min. at T_b 36.07^{o}C.

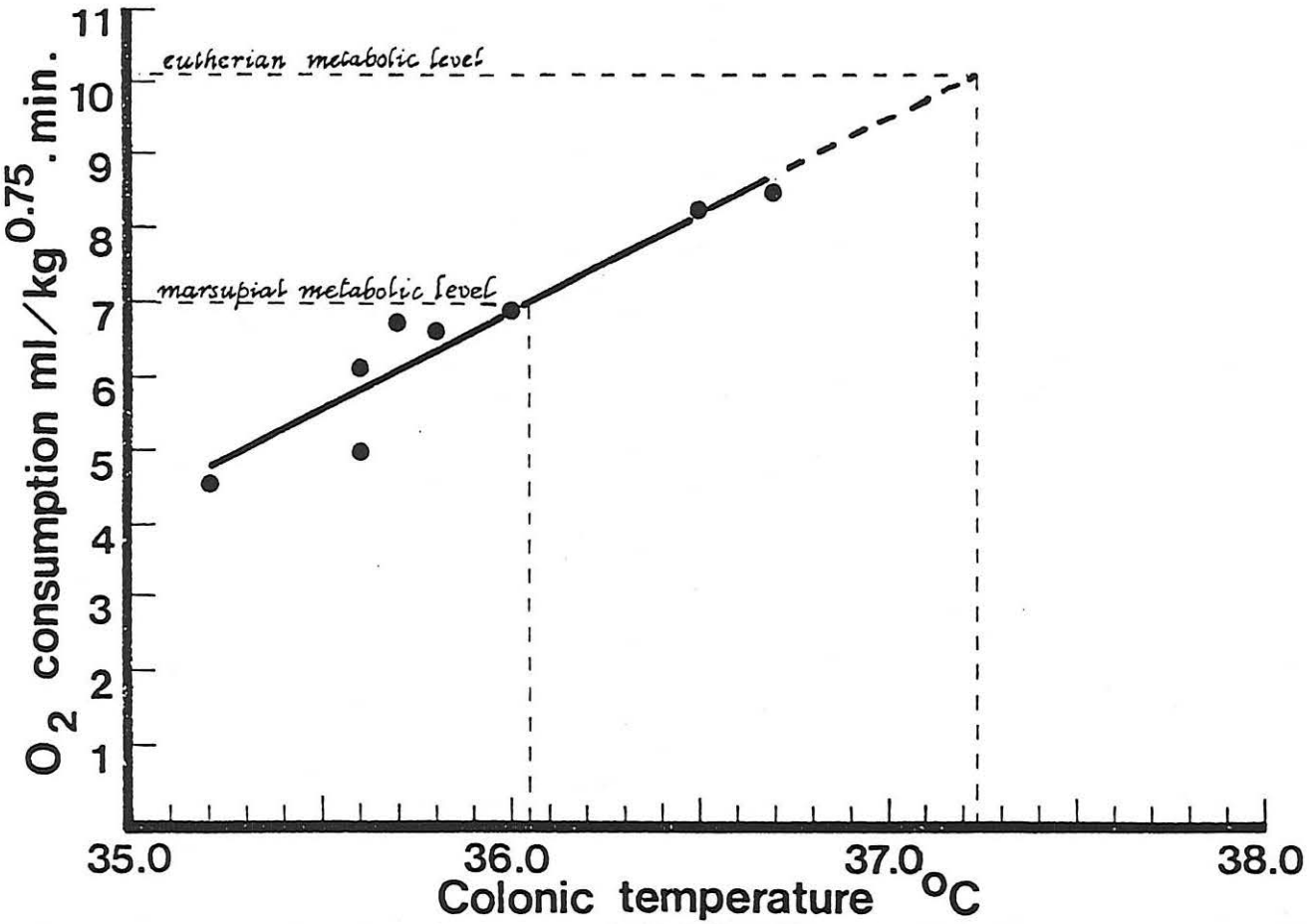
The rate of O_2 consumption almost doubled over the range of body temperature observed (35.2^{o} to 36.7^{o}C). Such an increase is too great to be accounted for by a Q_{10} effect resulting from an increase in body temperature. The increased O_2 consumption possibly results from

Table 8.3

Mean O_2 consumption rates and body temperatures of eight animals at T_a 30°C; O_2 consumption rates are expressed as ml/kg. min. and as ml/$kg^{0.75}$ min.

Run	Sex	Body wt. (kg)	T_b (°C)	O_2 Cons. rate	
				ml/kg. min.	ml/$kg^{0.75}$ min.
Dehyd 21	F	0.875	35.2	4.75	4.60
Delan 23B	M	2.000	35.6	4.21	5.01
Delan 29A	F	1.025	35.6	6.11	6.14
Delan 30A	F	0.700	35.7	7.38	6.76
Delan 33A	M	1.565	35.8	5.92	6.62
Delan 25	M	1.465	36.0	6.26	6.88
Delan 31A	M	0.775	36.5	8.81	8.26
Delan 32A	M	0.775	36.7	9.03	8.47

Fig 8.8 Mean rates of O_2 consumption, expressed in relation to metabolic body weight ($W^{0.75}$) vs. T_b for eight animals at T_a 30.0°-30.9°C. The regression ($y = 2.603x - 86.817$) is extrapolated to a value equivalent to $10.12W^{0.75}$ (eutherian metabolic level); the marsupial metabolic level = $7.04W^{0.75}$.


eutherian metabolic level
marsupial metabolic level
O_2 consumption ml/kg$^{0.75}$.min.
11
10
9
8
7
6
5
4
3
2
1
35.0
36.0
37.0
38.0
Colonic temperature °C

differences in the level of arousal of the animals reflected in an increase in body temperature.

3. Above the thermal neutral zone.

T_b rose at high ambient temperatures so that $T_b = T_a$ at about 39°C (see Chapter VII). The rate of O_2 consumption also rose above the thermal neutral zone. Fig 8.9 A shows O_2 consumption vs. T_b for three animals at 33° to 41°C (T_a). A linear regression fitted by the method of least squares to the 26 pairs of values is described by the expression:

$$y = 0.8726x - 24.109 \quad (r = +0.55, p \quad 0.02)$$

where y = O_2 consumption (ml/kg. min.) and x = T_b (°C).

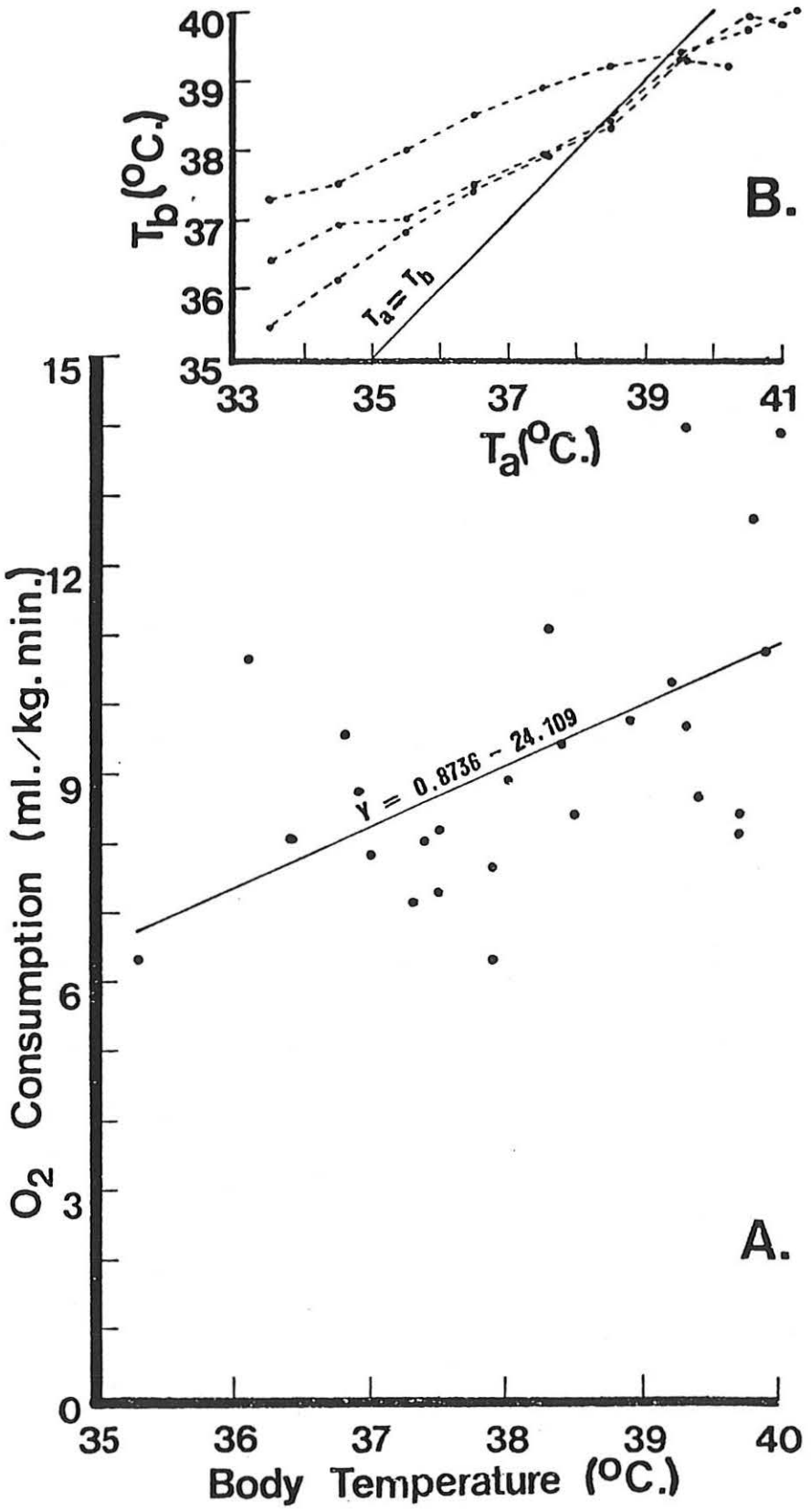
The Q_{10} value calculated from intercepts of the regression at T_b 36.5° and 39.5°C is 2.6, indicating that this rise in O_2 consumption rate can be attributed largely to the accompanying rise in body temperature. This suggests that accelerated breathing rates which occur at high ambient temperatures (Chapter IX) require relatively little energy. The inset, Fig 8.9 B, shows T_b vs. T_a for the same three animals as O_2 consumption rates were measured.

Thermal Conductance

A measure of the coefficient of heat transfer, or thermal conductance, can be obtained either from the slope of the linear relationship between O_2 consumption rate and ambient temperature (Method 1) or from the formula:

Fig 8.9 A: O_2 consumption (ml/kg. min.) vs. T_b for three animals at T_a 33°-41°C and the linear regression fitted to the 26 bivariate values.

8.9 B: T_b vs. T_a for three animals, measured at the same time as the O_2 consumption rates shown in Fig 8.9 A.


40
39
38
37
36
35
T_b (°C.)
B.
$T_a = T_b$
33
35
37
39
41
T_a (°C.)
15
12
9
6
3
0
O_2 Consumption (ml./kg. min.)
Y = 0.8736 - 24.109
A.
35
36
37
38
39
40
Body Temperature (°C.)

$$\text{Thermal Conductance (C)} = \frac{\text{Metabolic Rate}}{T_b - T_a} \text{ (M)} \quad \text{(Method 2)}$$

Both methods of calculation should give the same result if the straight-line relationship of metabolic rate vs. T_a below the thermal neutral zone extrapolates to zero metabolism when $T_b = T_a$. If however the regression line extrapolates to zero metabolism at T_a higher than the mean resting body temperature then the thermal conductance estimated by the first method will be lower than that estimated by the second method.

Method 1.

The linear relationship between O_2 consumption and T_a was determined by fitting a least squares regression line to mean rates of O_2 consumption at 1^oC intervals in the temperature range 4^o to 28^oC (Fig 8.2; Appendix E). The slope of the regression line provides a measure of the coefficient of heat transfer, or thermal conductance, from the body below the thermal neutral zone. Means rather than individual rates of O_2 consumption were used because the number of values varied greatly from one temperature to another and the resulting regression would have been biased accordingly. The regression of mean O_2 consumption vs. T_a is:

$$O_2 \text{ consumption (ml/kg. min.)} = 22.7506 - (0.513)(T_a{}^oC)$$

The 95 per cent confidence intervals being

22.7506 ± 1.068 for the intercept on the y axis and

-0.513 ± 0.061 for the slope of the line.

The thermal conductance determined from the slope of the regression line then is 0.513 ml O_2/kg/min/^oC. Assuming 4.8 cal/ml O_2 this represents 0.148 cal/g/hr/^oC. The regression line extrapolates to zero O_2 consumption at T_a 44^oC, some 9.0^o to 9.5^oC higher than mean resting body temperatures below the thermal neutral zone. The thermal conductance obtained from the slope of the mean O_2 consumption vs. T_a represents a composite of values obtained from animals weighing 0.7-1.7 kg. It also represents an average of rates measured when T_b was stable, or rising, or falling.

Method 2.

Weight-specific thermal conductance was calculated for five animals, whose O_2 consumption rates and body temperatures were measured over a range of ambient temperatures below the thermal neutral. The formula used was:

$$\text{Thermal conductance (C)} = \frac{M(O_2 \text{ consumption/kg. min.})}{T_a - T_b}$$

C was expressed as cal/g/hr/^oC, assuming 4.8 cal/ml O_2. Fig 8.10 shows the thermal conductance so calculated vs. T_a together with the least squares regressions fitted to the values (solid circles, solid lines and regressions indicated by a). For three of the five animals, significant correlations could be demonstrated between thermal conductance and T_a; there was no significant difference between the regression coefficients in these three cases. In all but one case, thermal conductance increased with increasing

T_a, indicating that total heat loss is increased at higher ambient temperatures.

It is necessary to pre-empt results from Chapter X (Evaporative Water Loss) to complete the examination of thermal conductance. The values plotted as solid circles in Fig 8.10 represent total conductance and include evaporative heat loss. Total conductance is the value normally given as evaporative heat loss represents a rather small proportion of heat loss from the body below the thermal neutral zone. However the proportion of heat lost by evaporation may increase as ambient temperature rises towards the lower critical temperature. In order to demonstrate the contribution of insensible heat loss to thermal conductance at temperatures below the thermal neutral zone, the caloric equivalents of insensible water loss were subtracted from the calculated total thermal conductance values. These values are shown in Fig 8.10 as hollow circles. They represent heat loss by non-evaporative means only i.e. 'dry' conductance. The least squares regressions fitted to 'dry' conductance for the five cases illustrated in Fig 8.10 are shown by dashed lines and as the equations (b). In two cases, as for total conductance, the correlation coefficients for 'dry' conductance vs. T_a are non-significant. In the other three, although the levels of significance are reduced when compared with those for total thermal conductance,

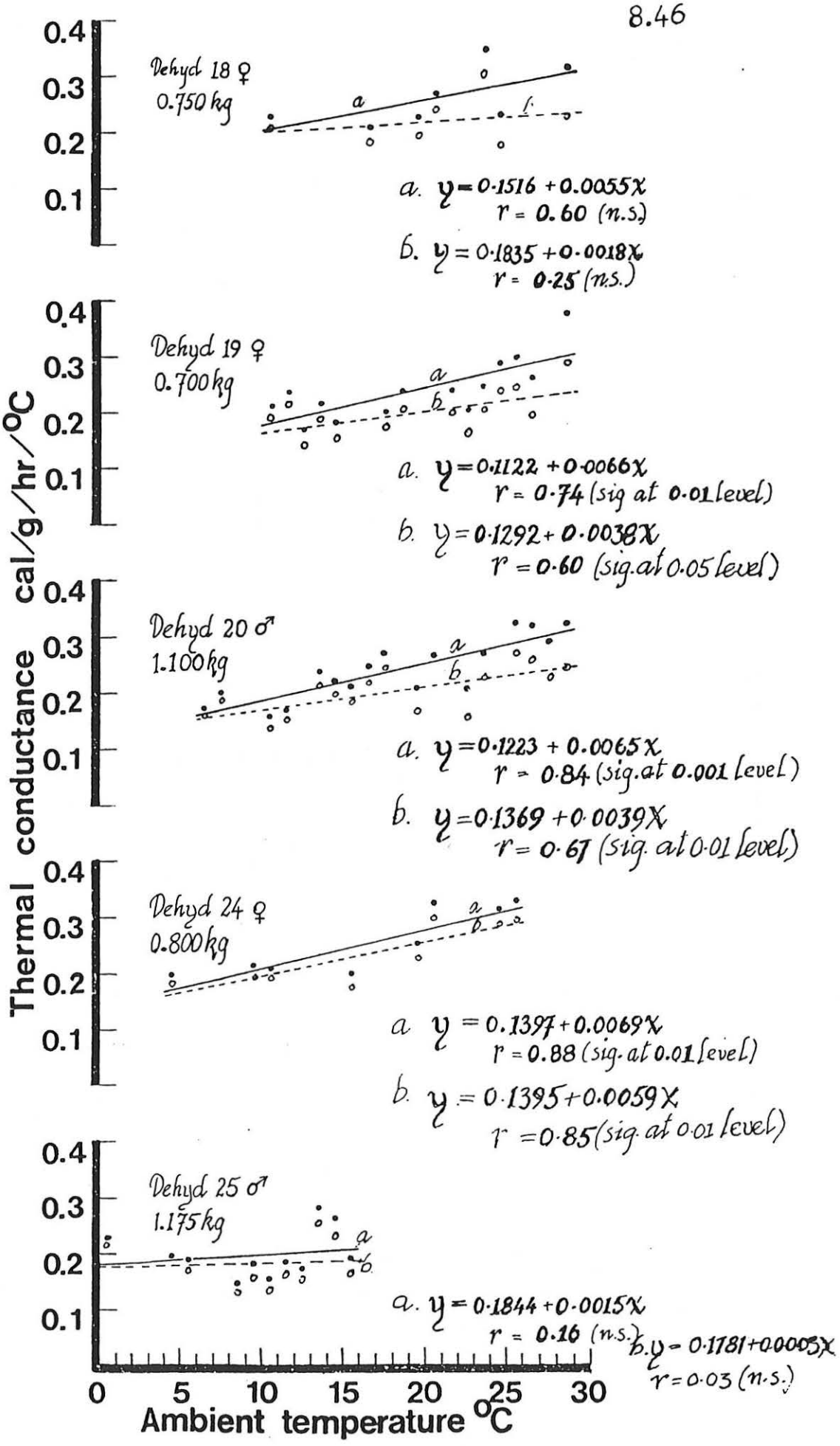
Fig 8.10 Weight-specific thermal conductance vs. T_a for five animals as total thermal conductance and as total conductance minus evaporative heat loss ('dry' conductance).

Symbols:

a. total conductance and least squares regressions fitted to these values

b. 'dry' conductance and least squares regressions fitted to these values

r = correlation coefficient



a. $y = 0.1516 + 0.0055x$
$r = 0.60$ (n.s.)

b. $y = 0.1835 + 0.0018x$
$r = 0.25$ (n.s.)

a. $y = 0.1122 + 0.0066x$
$r = 0.74$ (sig at 0.01 level)

b. $y = 0.1292 + 0.0038x$
$r = 0.60$ (sig. at 0.05 level)

a. $y = 0.1223 + 0.0065x$
$r = 0.84$ (sig. at 0.001 level)

b. $y = 0.1369 + 0.0039x$
$r = 0.67$ (sig. at 0.01 level)

a $y = 0.1397 + 0.0069x$
$r = 0.88$ (sig. at 0.01 level)

b. $y = 0.1395 + 0.0059x$
$r = 0.85$ (sig. at 0.01 level)

a. $y = 0.1844 + 0.0015x$
$r = 0.16$ (n.s.)

b. $y = 0.1781 + 0.0005x$
$r = 0.03$ (n.s.)

they do remain significant. In all cases the evaporative component is increased as T_a approaches the lower critical. Nevertheless 'dry' conductance is lower at T_a 10°C than at 25°C. Table 8.4 shows the total thermal conductance and 'dry' conductance calculated from the linear regressions (Fig 8.10) for each of the three animals for which significant correlations between thermal conductance and T_a could be demonstrated. For comparison the table also shows thermal conductance calculated from the weight-specific regression for eutherians (Herreid and Kessel, 1967) and for dasyurid marsupials (MacMillen and Nelson, 1969):

$$C\ (cal/g/hr/^oC) = 4.91W^{-0.505} \quad \text{and}$$

$$C\ (ml\ O_2/g/hr/^oC) = 0.914W^{-0.463} \quad \text{respectively.}$$

W = body weight in grams in each case. Values calculated from the equation of MacMillen and Nelson are expressed as cal/g/hr/°C by multiplying by 4.8.

Discussion

For the chuditch the lowest mean rates of O_2 consumption, for resting non-torpid animals, occur at 27° to 33°C (T_a). In this temperature range the variation in O_2 consumption rate is also lower than that observed at higher and lower temperatures. The low rates, together with reduced variation, indicate that the animal approaches equilibrium with its environment with least metabolic effort in this temperature range.

Table 8.4

Thermal conductance for three animals at 10°C and 25°C (T_a) together with thermal conductance for animals of equivalent body weight as predicted by the weight-specific regressions for dasyurid marsupials (MacMillen and Nelson, 1969) and for eutherian mammals (Herreid and Kessel, 1967)

Body Wt. (g)		Calculated thermal cond. cal/g/hr/°C		Predicted conductance cal/g/hr/°C	
		T_a 10°C	T_a 25°C	MacM. & N.	H. & K.
Dehyd 19 / 700	total	0.178	0.277	0.205	0.173
	'dry'	0.167	0.224		
Dehyd 20 / 1100	total	0.187	0.285	0.171	0.143
	'dry'	0.176	0.234		
Dehyd 24 / 800	total	0.209	0.312	0.199	0.168
	'dry'	0.199	0.287		

The concept of thermal neutrality is open to various interpretations (Mount, 1974):

"1. Minimal metabolism, bounded on each side by rising metabolic rate, ...

2. Least thermoregulatory effort, coinciding with minimal material demand, bounded at the colder limit by rising metabolic rate and at the warmer limit by increased evaporative loss, ...

3. Zones defined for particular purposes: e.g. comfort zones, zones of optimal productivity etc."

All of these interpretations assume that the animal under consideration maintains its body temperature within narrow limits. Such is not the case with the chuditch which, at any given ambient temperature, may vary its body temperature by several degrees. Variations in T_b are associated with variations in the rate of metabolism. With this proviso though, definitions (1) and (2) above are satisfied for the chuditch if the zone of thermal neutrality is designated as the range of ambient temperature extending from 27° to 33°C. The body temperature rises slightly at the warmer end of the range without a marked increase in O_2 consumption or evaporative water loss (Chapter X). Considerations of 'comfort' and productivity could not be taken into account in this study.

The mean resting rate of O_2 consumption for chuditches

at 30°C (T_a), in the centre of the thermal neutral zone, was 6.84 ml/kg. min. This value agrees closely with the Standard Metabolic Rate of other dasyurid marsupials (MacMillen and Nelson, 1969) and of other Australian marsupials (Dawson and Hulbert, 1969, 1970).

The rate at which O_2 is consumed by the chuditch is highly variable, particularly at ambient temperatures below the thermal neutral zone. This variation is reflected directly in variations in the body temperature. The O_2 consumption rate falls to levels equal to or lower than the standard rate in the thermal neutral zone at ambient temperatures as low as 5°C. Decreases in body temperature occur during periods when the O_2 consumption rate approaches these low levels, and the size of the decrease in T_b can be related to the length of the period of reduced O_2 consumption. Below 20°C (T_a) animals in the metabolism chamber showed only short-term drops in O_2 consumption but at 20°C and above, several animals maintained minimal rates of O_2 consumption for one hour or more (Table 8.2). The rates of cooling displayed by these animals are sufficient to account for significant decreases in T_b if O_2 consumption is reduced to minimal levels for several hours during the 'inactive' period of the animals' circadian cycle. On this basis it is possible to account for the phenomenon of torpor without postulating a further reduction in O_2 consumption rate. Torpor was observed only during the early

morning (in the night-time 'inactive period') or during the mid-morning (daytime inactive period). If the calculated cooling constant for one animal over a 5¾ hour period at 20°C (T_a) applied for a 12 to 14 hour period when the animal was sleeping with O_2 consumption at the minimal level, then T_b would fall to 28.2° or 26.8°C. The lowest recorded body temperature at 20°C (T_a) was 25.5°C (Table 7.4) but in seven of the ten observations of torpor made at 20°C, animals had body temperatures of 28.3-29.7°C. Most of these observations were made between 0900 and 1400 hours, 13-18 hours after the early evening activity peak (Chapter VII) and could have resulted from the animals sleeping through the early morning activity period. At T_a 15°C (Fig 8.7 B) T_b decreased by one degree in 20 minutes while O_2 consumption was at the minimal level. Thus when ambient temperature is below 20°C, body temperature probably falls more rapidly than in the example discussed above. As relatively low ambient temperatures prevail during the early morning hours in the wild, even if the animals displayed a pre-dawn activity peak, sleep accompanied by low rates of O_2 consumption, could result in rapid cooling to body temperatures approaching those measured for torpid animals.

It must be noted that the lowest rates of O_2 consumption observed below the thermal neutral zone:-

1. reached a similar level irrespective of ambient temperature (see low values on Figs 8.1 and 8.6),

2. appeared to occur only when the animals ceased to shiver; visible muscle tremor would immediately restore O_2 consumption to levels equal to or greater than average rates (Fig 8.3 A and B),
3. reached a similar level irrespective of body temperature (see Fig 8.7 C in which O_2 consumption was maintained at 5-6 ml/kg. min. during a period when T_b fell from 36.3 to 31.4°C),
4. were never appreciably lower than the Standard Metabolic Rate in contrast to hibernators in which the metabolic rate is reduced by 20 to 100 times (Prosser, 1973).

These observations imply that the minimum rate of O_2 consumption is, in some way, independent of temperature and that the hypothalamic control of heat production may, under some circumstances, be suspended. Such a suspension of control for quiet periods of the animals circadian cycle would result in economies of energy usage which would not be possible if the body temperature was kept constant at 35°-36°C.

The extent of the economies may be illustrated in the following simple budget: For example, suppose O_2 consumption falls to minimal levels for five or ten hours each day when T_a is 20°C, i.e. from an 'average rate' of about 12.5 ml/kg. min. to about 6 ml/kg. min.:

1. O_2 requirement (ml/kg. day)

   @ 12.5 ml/kg. min. for 24 hours .... 18,000 ml = 100%

2. O_2 requirement (ml/kg. day)

   19 hrs @ 12.5 ml/kg. min. ..... 14,250 ml

   5 hrs @ 6.0 ml/kg. min. ..... 1,800 ml

   16,050 ml = 89%

3. O_2 requirement (ml/kg. day)

   14 hrs @ 12.5 ml/kg. min. ..... 10,500 ml

   10 hrs @ 6.0 ml/kg. min. ..... 3,600 ml

   14,100 ml = 78%

i.e. somewhere between 11-22 per cent reduction in energy requirements.

Similar budgets for 10°C and 25°C suggest savings of 14 and 28 per cent and 8 and 17 per cent respectively. However the budgets do not take into account that during the evening and early morning activity peaks the chuditch raises its body temperature to 37° to 38°C. By extrapolation from the relationship between T_b and O_2 consumption in the thermal neutral zone (Fig 8.8) the metabolic level approaches that of strictly homeothermic eutherians when body temperature exceeds 37°C.

A circadian cycle of metabolic rate has been demonstrated for a number of species of rodents (e.g. Chew et al, 1965 for Perognathus; Heusner et al, 1971 for Peromyscus), and Kinnear and Shield (1975) showed circadian cycles in O_2 consumption in three marsupials, Setonix, Macrotis and

Pseudocheirus, which in each case were correlated with circadian cycles in body temperature.

The circadian cycle in O_2 consumption displayed by one female chuditch at 15°C (T_a) (Fig 8.5) showed a six hour period when hourly mean O_2 consumption was reduced to about 80% of the average rate at 15°C. The same animal also had three shorter periods when hourly mean O_2 consumption was 140-160 per cent of the average rate. These occurred at times in the circadian cycle when the animal would be active. At 30°C (T_a) this animal had a period of 10 hours when O_2 consumption was around 10 per cent below the average rate (from 0800 hrs to 1700 hrs) followed by eight hours from 1700 hrs when hourly mean O_2 consumption was up to 15 per cent above the average rate.

If low rates of O_2 consumption during inactive periods of the circadian cycle result in a reduction of the total daily O_2 requirement below that indicated by the 'average rate' for a given ambient temperature (as shown in Fig 8.2 and Appendix E), the mean O_2 consumption rate for a 24-hour period should be lower than the average rate. This assumes that the average rate at a particular temperature represents the O_2 requirement necessary to maintain 'normal' body temperature.

This reasoning is not supported by data obtained from a male and a female chuditch kept in the metabolism chamber for more than 24 hours at 10° and 15°C respectively

(Fig 8.5 and p. 8.16). The 24-hour grand means (calculated from the mean rates of O_2 consumption for each of the last 24 hours of the runs) were 113 per cent and 106 per cent of the 'average rate' at 10° and 15°C respectively. This certainly doesn't represent a reduction in the requirement for O_2 below the average rate.

However what I have been calling average rates are means of all rates measured at a particular temperature whether body temperature was rising, stable, or falling. If, instead, the upper trend line in Fig 8.6 is taken as a measure of the average O_2 consumption necessary to maintain or raise T_b, then average rates at 10° and 15°C are 26.5 ml/kg. min. and 22 ml/kg. min. respectively and the 24-hour means represent slightly more than 70 per cent of the average rates at both 10° and 15°C.

Such hypothetical budgets of course can in no way present a realistic picture of the energy requirements of the animals. They do suggest that, compared with a mammal which strictly controls its body temperature, the chuditch may economise on its energy requirements in two ways:

1. in the over-all reduction of metabolic level by about 30 per cent compared with Kleiber's inter-specific predictive equation for eutherian mammals, and
2. a further reduction in the metabolic 'cost' of maintaining stable body temperature below the

thermal neutral zone by assuming low rates of oxygen consumption and allowing body temperature to fall during periods when the animals are not active.

In the thermal neutral zone in which, by definition, the animal should not be subject to thermal stress and should maintain normal body temperature by heat production from basal metabolic activities, two contradictory relationships between O_2 consumption and T_b were observed:

1. when O_2 consumption was minimal and steady at 5-6 ml/kg. min. T_b fell several degrees (see Fig 8.7 D; Table 8.2), and
2. when a high correlation between O_2 consumption rate and T_b could be demonstrated (see Fig 8.8 and Table 8.3).

The conflict between these two observations may be more apparent than real if, in the first case, T_b is equilibrating following a fall in O_2 consumption rate during an inactive period and, in the second case, different levels in arousal towards the active period in the circadian cycle are reflected in the direct relationship between O_2 consumption and T_b.

A significant relationship between O_2 consumption rate and T_b can be demonstrated for the chuditch at ambient temperatures above the thermal neutral zone (Fig 8.9). The Q_{10} value calculated for the three degree rise in T_b from

36.5° to 39.5°C is 2.6 which is not much higher than would be expected from the acceleratory effect of a rise in temperature on the rate of metabolic processes. Hulbert and Dawson (1974b) reported a Q_{10} of 2.2 for Macrotis lagotis which, unlike the chuditch, fails to show an evaporative response to heat. The relatively low Q_{10} determined for the chuditch at ambient temperatures at which breathing rates are increased (Chapter IX) suggests that the metabolic cost of panting is low. Hales and Brown (1974) have shown that the total heat production in sheep with mean respiratory frequencies of up to 270 breaths/min. is not significantly higher than that in a thermo-neutral environment, another case where panting does not have a high metabolic cost.

Thermal conductance, as estimated by the average slope of O_2 consumption vs. T_a below the lower critical temperature and expressed in terms of heat loss (cal), is about 0.148 cal/g/hr/°C. This approximates the predicted thermal conductance for an 1100 g animal (approx. mean weight of chuditches used, both male and female together) from the weight-specific regression for eutherian mammals (Herreid and Kessel, 1967) (0.143 cal/g/hr/°C) and is lower than the equivalent value from the regression for dasyurid marsupials (0.171 cal/g/hr/°C) (MacMillen and Nelson, 1969).

Higher values of thermal conductance are obtained

when calculated from the formula $C = \frac{M(O_2 \text{ cons})}{T_b - T_a}$

Thermal conductance so calculated for three animals at T_a 10°C agrees closely with weight-specific values predicted by the regression of MacMillen and Nelson (this predictive regression was obtained using data obtained between 9.4° and 12°C (T_a)), but is considerably higher at T_a 25°C. Part of the increase in total thermal conductance as T_a approaches the lower critical temperature can be accounted for by increased evaporative heat loss. Other factors which could contribute to the change in the thermal conductance are:

1. T_b tends to be slightly higher at T_a 10°C than at T_a 20° (Chapter VII), and thus the value $T_b - T_a$ is magnified at 10°C.
2. the animals undergo postural changes at lower T_a, curling up and covering nose and ears with the rather bushy tail; these changes in posture would tend to reduce heat loss.
3. although not investigated, it is probable that vaso-constriction, and thus reduced skin temperature, would contribute to increased insulation at lower T_a.

The weight-relative standard metabolic rate of Australian marsupials is, with two exceptions, consistently 30-35 per cent below the SMR of homeothermic, as opposed to heterothermic, eutherian mammals (references cited in Preamble, p. 8.1). The exceptions are Phalanger maculatus

(Dawson and Degabriele, 1973) and Macrotis (Hulbert and Dawson, 1974a; Kinnear and Shield, 1975) which have standard metabolic rates of 50-60 per cent of the standard eutherian levels. The relatively low standard metabolic level of marsupials has been taken to indicate a phylogenetic difference between the marsupials and the 'advanced' eutherian mammals (for example, Dawson, 1972).

Scholander et al (1950) stated that 'the basal metabolic rate of terrestrial mammals from tropics to arctic is fundamentally determined by a size relation ... and is phylogenetically non-adaptive to external temperature conditions'. According to this point of view, phylogenetic adaptation to cold or hot climates can take place only through factors which regulate heat dissipation.

However reduction of the level of energy metabolism is a common response of eutherian mammals to arid environments (e.g. Dawson, 1955; Bartholomew and McMillen, 1961; McNab and Morrison, 1963) and it has been shown to occur, among others, in fossorial rodents (McNab, 1966) and in Australian desert rodents (McMillen and Lee, 1970). Brown and Main (1967), when reporting the low nitrogen requirements of Macropus robustus, noted the possibility that the reduced need reflected an adaptation to aridity.

It is apparent then that metabolic level is adaptive when certain ecological constraints are imposed. Kinnear and Shield (1975) have discussed the diversity in the level

of energy metabolicm in homeotherms with reference to marsupials and eutherians. They regard basal metabolism as adaptive to the environment rather than as a physiological baseline for interspecific comparison or as a phylogenetic characteristic.

I do not propose to enter this debate because the data presented here on the chuditch provides no further evidence one way or the other. What does emerge is that the standard metabolic level, determined during the inactive period of the animals circadian cycle, provides only a fragmentary picture of the energy requirements of the chuditch. The energy requirements during 'active' periods, when T_b is raised to 37-38°C, are greatly increased, even for animals in the metabolism chamber.

However, the low O_2 requirements associated with low body temperature, during the day are no doubt of ecological importance to the species, not only with regard to the direct energy requirements but also to the water requirements for evaporative cooling. The characteristics of the chuditch's pattern of energy usage do appear to fit it for an arid environment with a rather wide range of environmental temperatures. These characteristics are:

1. The ability to maintain body temperature within normal limits at environmental temperatures at least as low as 0°C.
2. The ability to reduce the metabolic rate to low

levels over a wide range of environmental temperatures and, at the same time, undergo a reduction in body temperature. The low metabolic rate in the thermal neutral zone and at higher temperatures reduces the production of heat so that the combined effect of endogenous heat plus environmental heat on body temperature is reduced.

3. The ability to tolerate hyperthermia.

4. Points 2 and 3 above probably contribute to limitation of water lost by evaporation.

CHAPTER IX

BREATHING RATES

Preamble

The rate of breathing is a parameter of metabolic activity which is readily measured and which can be related to metabolic rate. The breathing rate is typically at a minimum in the thermal neutral zone and is increased at environmental temperatures both below and above this zone. The increase in breathing rate at low ambient temperatures reflects a greater demand for O_2 while that at high ambient temperatures indicates the capacity of a particular species for increased evaporative water loss from the respiratory surfaces and hence its capacity for evaporative cooling.

Breathing rates were routinely measured for chuditches confined in the metabolism chamber at the same time as measurements were made of O_2 consumption rate, body temperature and evaporative water loss. Besides reflecting a general response to the temperature prevailing in the chamber, breathing rates also provided an index of the animals' immediate condition. Steady rates occurred when the animals were resting whereas high, or irregular, rates indicated stress or restlessness.

Results

Table 9.1 and Fig 9.1 show means, standard errors of means, and ranges of breathing rates measured in the ambient temperature range 0-40°C while the animals were confined within the metabolism chamber. Below 30°C means and standard errors were calculated from values for individual animals grouped at 5° intervals of ambient temperature. At 30°C and above, values were grouped at 1° intervals. These mean values are displayed in Fig 9.1, together with standard errors of means at the 5° and 1°C intervals.

The mean minimum breathing rate was 21 breaths/minute at 30°C. Below 30° the mean rate of breathing increased slightly as ambient temperature decreased so that, at 0°-4.9°C, it was 33 breaths/minute. Rates of less than 20 breaths/minute, indicated by the lower limits of the ranges, occurred over the range 0° to 36°C. Such low breathing rates occurred below the thermal neutral zone when O_2 consumption rates were low and body temperature was falling. No periods of apnoea were observed. High breathing rates below the thermal neutral zone occurred during brief intermittent periods of activity, usually when the animals were grooming.

Mean breathing rates within the thermal neutral zone were 21-23 breaths/minute. Minimum rates as low as 9 breaths/minute were, however, observed within this temperature range.

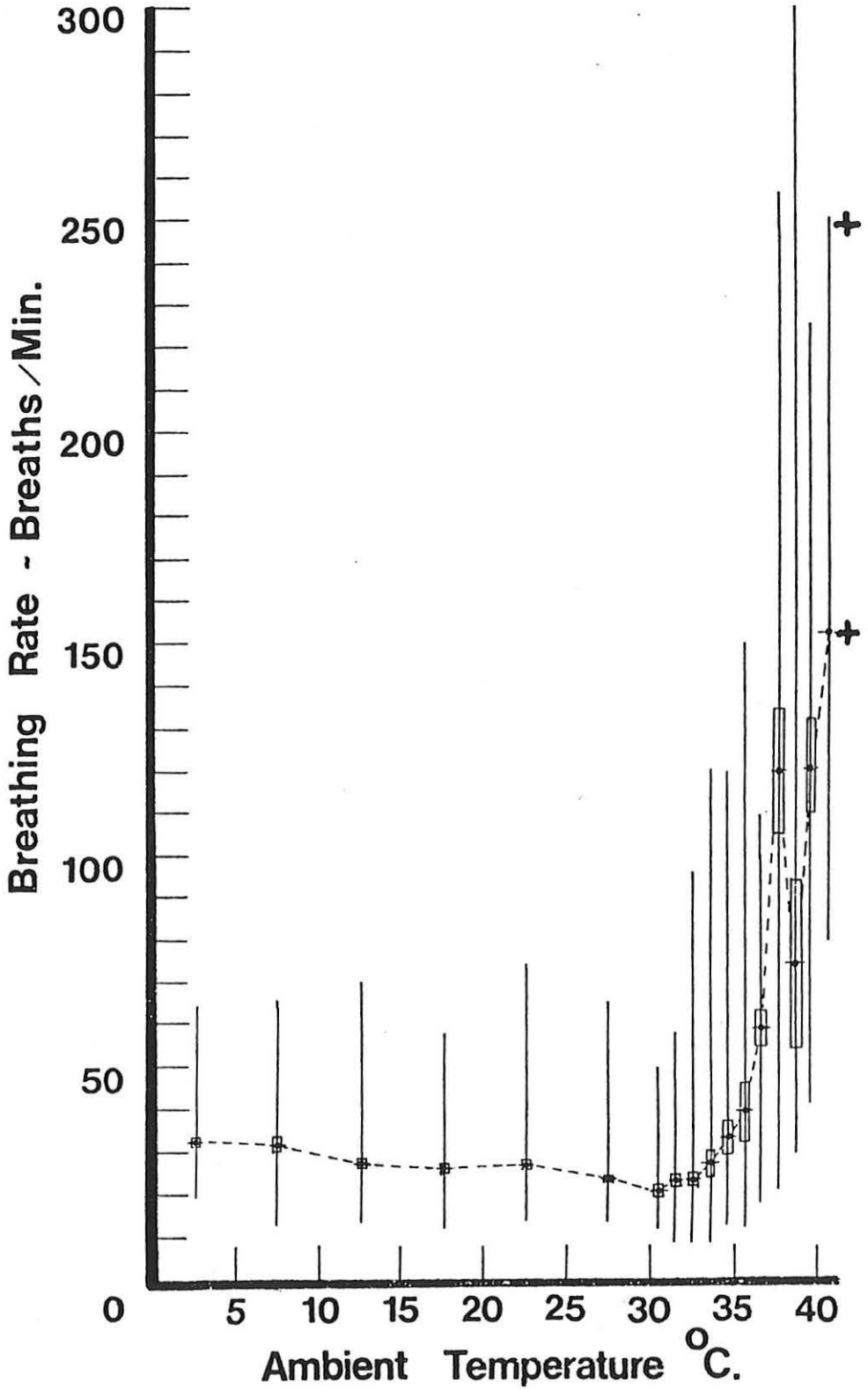
Table 9.1

Means, standard errors of means, and ranges of breathing rates measured for animals in the metabolism chamber at the specified ambient temperatures.

T_a °C	No. values/ No. animals	Mean breathing rate ± 1 s.e. breaths/min.	Range
0 - 4.9	83/2	33.0± 0.98	19 - 65
5.0 - 9.9	35/3	32.1± 1.65	13 - 66
10.0 - 14.9	81/6	27.8± 0.92	14 - 70
15.0 - 19.9	115/11	26.7± 0.85	12 - 58
20.0 - 24.9	171/14	27.1± 0.87	14 - 74
25.0 - 29.9	197/18	23.3± 0.55	14 - 68
30.0 - 30.9	101/17	20.9± 0.78	12 - 50
31.0 - 31.9	67/15	23.2± 1.21	9 - 58
32.0 - 32.9	61/15	23.4± 2.05	9 - 96
33.0 - 33.9	54/17	27.2± 3.27	9 - 120
34.0 - 34.9	45/15	33.4± 3.67	13 - 120
35.0 - 35.9	32/10	39.5± 6.81	12 - 150
36.0 - 36.9	55/10	59.2± 3.95	18 - 110
37.0 - 37.9	31/8	120.0±14.66	21 - 256
38.0 - 38.9	14/3	74.4±19.89	30 - 300
39.0 - 39.9	17/3	121.5±11.22	42 - 225
40.0 - 40.9	9/2	152+ *	80 - 250+*

*+ indicates that mean and upper limit of range are underestimates.

Fig 9.1 Breathing rates vs. T_a measured in the metabolism chamber. Mean rates are shown by horizontal lines, $\pm$ 1 s.e. of mean by boxes and ranges by vertical lines. Mean values are connected by trend lines (+ mean and upper limit of range are underestimates).


300
250
200
150
100
50
0
Breathing Rate - Breaths/Min.
5
10
15
20
25
30
35
40
Ambient Temperature °C.

A few animals had breathing rates in excess of 100 breaths/minute for short periods when the ambient temperature was 33° to 35°C, but mean rates did not reach 60 breaths/minute until the air temperature exceeded 36°C. At 39°C prolonged periods of rapid breathing occurred at rates in excess of 60 breaths/minute and up to 300 breaths/minute. These periods of rapid breathing could be related to body temperatures in excess of 37.5°C. At T_a 40°C, when T_b was 39°C or more, open-mouthed panting was observed. No statistically significant correlation between body temperature and breathing rate could be established at ambient temperatures below 35°C although observations suggested such a relationship.

The relationship between breathing and evaporative water loss will be considered in Chapter X.

Discussion

When T_a is increased from 0° to 30°C the mean breathing rate is reduced by 36 per cent. This reduction is associated with a reduction of 66 per cent in O_2 consumption rate. This observation suggests that tidal volume is higher at ambient temperatures below the thermal neutral zone. The mean breathing rate shows a seven-fold to eight-fold increase when ambient temperature is further raised from 30° to 40°C, the most rapid rise occurring above 35°C. That this increase is not paralleled by a

comparable rise in O_2 consumption (Chapter VIII, p. 8.39) indicates that ventilation becomes more shallow at high temperatures.

The mean minimum breathing rate of the chuditch in the thermal neutral zone is low compared with expected rates for eutherian mammals of equivalent body weight. Guyton (1947) found that tidal air, respiratory minute volume and respiratory rate/minute were related to body weight in seven species of laboratory mammals and man. Guyton's data were obtained from quiet animals breathing normal air from a mask, under conditions which were considered to avoid problems of breathing against a resistance, or of increased dead space. The environmental temperature at which rates were measured was not specified but was presumably at room temperature in the range 20° to 25°C. Guyton derived the equation:

$$\text{Rate of breathing/minute} = 295\ W^{-\frac{1}{4}}$$

where W = body weight in grams.

Stahl (1967) also derived a number of power law prediction parameters for respiratory variables for mammals. Among these was a predictive equation for breathing rate which is very close to that of Guyton's:

$$\text{Breathing rate/minute} = 53.5\ W^{-0.26}$$

Where W = body weight in kg.

(When W is expressed in grams Stahl's equation becomes:

$$\text{Breathing rate/minute} = 322.4\ W^{-0.26}).$$

Predictions of breathing rate calculated from Stahl's equation are higher than those from Guyton's equation by 6 per cent (body weight 10g) to 3 per cent (body weight 100 kg).

Minimum breathing rates of Australian marsupials are low compared with those predicted from the above interspecific equations for eutherian mammals. Table 9.2 shows observed minimum breathing rates of 12 species of Australian marsupials, together with the rates predicted from Guyton's equation. The data were obtained from the sources cited in the table. Breathing rates for the marsupials are 45-86 per cent of those predicted. A regression fitted to the twelve pairs of log breathing rates and log body weights is described by the equation:

$$\text{Breathing rate/minute} = 109.3\ W^{-0.193}$$

where W = body weight in grams. This regression is shown in Fig 9.2 with minimum breathing rate/minute vs. body weight on log axes for the 12 marsupial species. The regression line described by Guyton's predictive equation for eutherian mammals is shown for comparison. Breathing rates predicted from the marsupial equation range from 42 per cent of those predicted by Guyton's equation for body weight 10 g to 67 per cent at body weight 30 kg.

All the minimum breathing rates for marsupials were extracted from studies in which the thermal neutral zone was established and in which breathing rates represent

Table 9.2

Mean body weights and mean minimum breathing rates of 12 species of marsupials compared with predictions of breathing rates based on the interspecific equation for breathing rates of eutherians of Guyton (1947).

Species	Source†	Body wt. (g)	Observed Breathing rate (Breaths/min)	Predicted Breathing rate (Breaths/min)	Observed rate / Predicted rate (per cent)
Tarsipes spenserae	8	11	86	162	53
Cercartetus nanus	1	70	50	102	49
Perameles nasuta	6	645	ca 40*	59	68
Macrotis lagotis	6	1,011	ca 20*	52	38
Dasyurus geoffroii	9	1,082	21	51	41
Isoodon macrourus	6	1,551	ca 25*	47	53
Trichosurus vulpecula	2	1,980	20	44	45
Lagorchestes conspicillatus	4	2,660	25	41	61
Setonix brachyurus	7	3,100	20	40	50
Macropus eugenii	3	4,960	28	35	80
Megaleia rufa	5	25,000	17	23	74
Macropus robustus	5	30,000	19	22	86

* estimated from published figure.

† Sources: (1) Bartholomew & Hudson, 1962; (2) T. Dawson, 1969a; (3) T. Dawson, 1969b; (4) W. Dawson & Bennett, 1970; (5) T. Dawson, 1973; (6) Hulbert & Dawson, 1974a & b; (7) Kinnear & Shield, 1975; (8) Kinnear & Arnold, unpublished; (9) Arnold, this study.

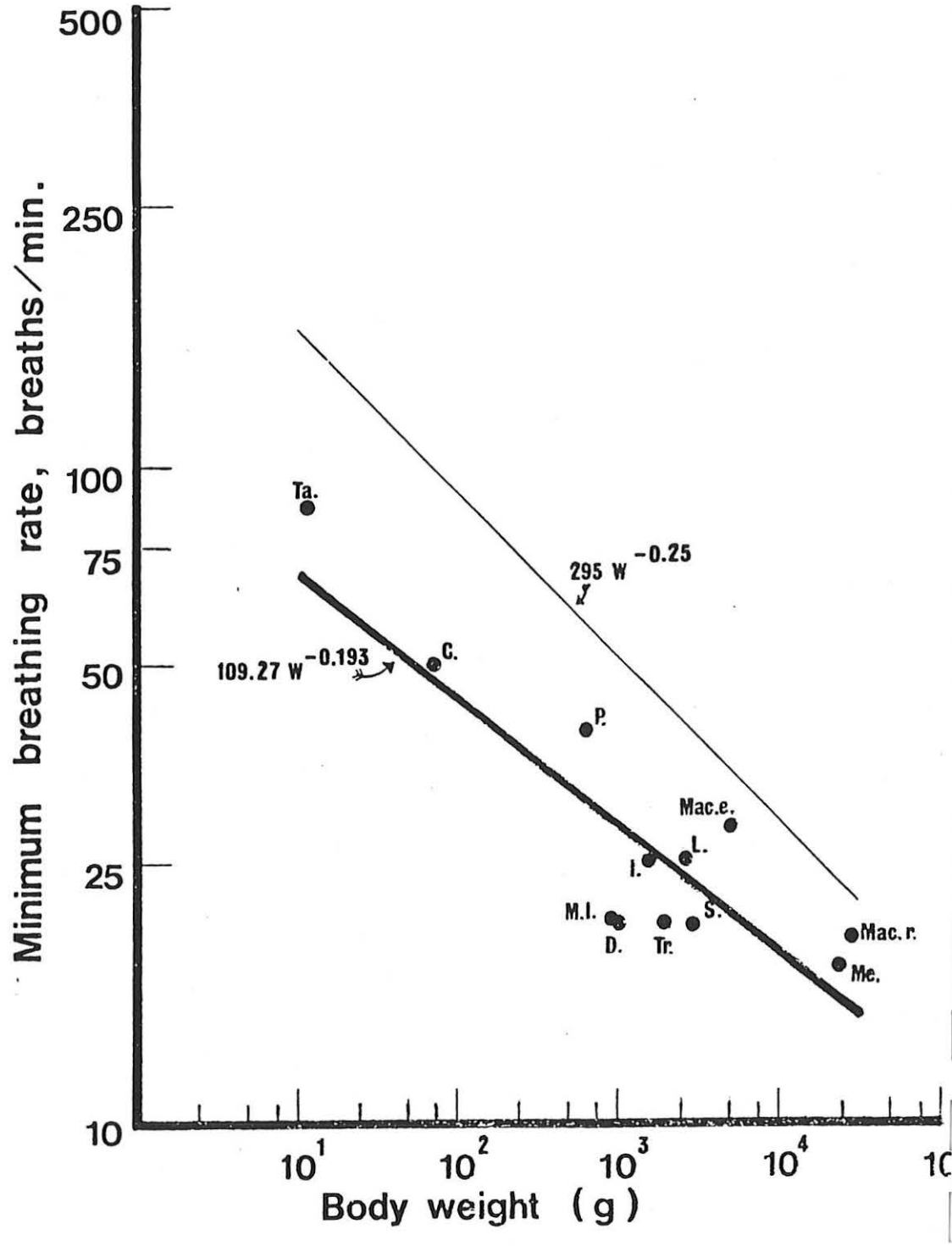
mean minimum values. The rates for the smaller eutherian mammals on which Guyton's relationship was based may possibly have been determined below the thermal neutral zone and consequently may not represent true minimum rates. This could account for the slight difference in slope between the two regressions shown in Fig 9.2.

A relationship between low metabolic rate and low breathing rate therefore holds for Australian marsupials. A similar relationship has also been demonstrated for some eutherian mammals. Hudson and Deavers (1973) calculated expected breathing rates of six species of ground squirrels (Spermophilus) which had metabolic rates about 30 per cent lower than expected on the basis of body weight. All but two species were found to have breathing rates of about half the predicted rates calculated from the equation of Stahl (1967).

Robinson and Morrison (1957) reported respiratory rates for 25 species of marsupials in a study of their responses to hot atmospheres. Control values were obtained before the animals were placed in the hot room and thereafter at half-hourly intervals during exposure to high environmental temperatures (35°, 37.5° and 40°C). The control values appear extraordinarily high for some species compared with resting breathing rates reported subsequently. For instance:

Trichosurus vulpecula	55-78, cf. 20 (Dawson, 1969)
Megaleia	92, cf. 17 (Dawson, 1973)
Setonix	100, cf. 20 (Kinnear and Shield, 1975).

Fig 9.2 Minimum breathing rates of 12 species of Australian marsupials vs. body weight (log axes). The regression $109.27W^{-0.193}$ was logarithmically fitted to the 12 values and is compared with the weight-relative regression for eutherian minimum breathing rates (Guyton, 1947). Initial code for species: Ta = Tarsipes; C = Cercatetus; P = Perameles nasuta; M.l. = Macrotis lagotis; D = Dasyurus geoffroii; I = Isoodon macrourus; Tr = Trichosurus vulpecula; L = Lagorchestes conspicillatus; S = Setonix brachyurus; Mac. e. = Macropus eugenii; Me = Megaleia rufa; Mac. r. = Macropus robustus. References as for Table 8.2.


Minimum breathing rate, breaths/min.
500
250
100
75
50
25
10
Ta.
295 W -0.25
109.27 W -0.193
C.
P.
Mac.e.
L.
I.
M.I.
S.
D.
Tr.
Mac.r.
Me.
10 1
10 2
10 3
10 4
Body weight (g)

It appears that, for these species at least, control respiratory rates determined by Robinson and Morrison do not represent resting rates.

All of the marsupial species included in the study of Robinson and Morrison, with the exception of Macrotis, Sarcophilus and Petaurus, showed a marked increase in breathing rate at 40°C, compared with control values. The authors concluded that respiratory activity constitutes a most important method of heat regulation for most of the species studied. Hulbert and Rose (1962) have since shown that Sarcophilus also exhibits a marked increase in breathing rate at high temperatures, the breathing rate increasing sevenfold from 20° to 40°C (see Chapter X). The absence of an increase in breathing rate for Macrotis at high ambient temperatures has been confirmed (Hulbert and Dawson, 1974b).

The chuditch, like other Australian marsupials, has a low breathing rate in the thermal neutral zone compared with mammals with average weight-relative metabolic rates. The seven- to eight-fold increase in breathing rate which occurs at between 30°-40°C points to respiratory water loss as an important factor in temperature regulation when this species is subjected to an environmental heat load.

CHAPTER X

EVAPORATIVE WATER LOSS

Preamble

Water lost to the environment by evaporation from the skin and respiratory surfaces represents both a drain on the water reserves of the body and a significant means of disposing of heat. The maintenance of a balance between water intake and water output is therefore critical to animals which live in hot environments where free water is likely to be in short supply. An animal which can limit its evaporative water loss by physiological or behavioural means is well-adapted to aridity. On the other hand, although severe water loss may result, the ability to lose heat by effective evaporation from the skin and respiratory surfaces must be an advantage to an animal which is, even occasionally, exposed to extreme heat.

Although no definitive and comprehensive study has yet been made it seems reasonable to expect that species with relatively low body temperatures and low metabolic rates would also have low rates of evaporative water loss in comparison with species which maintain high and stable body temperatures at relatively high metabolic cost.

Thermal lability may also permit economies in energy usage at both low and high environmental temperatures. A relatively low body temperature at environmental temperatures

below the thermal neutral zone would reduce the amount of water lost in saturated air leaving the respiratory passages. At high air temperatures a tolerance to hyperthermia would maintain a gradient down which heat could be lost from the body by radiation and conduction. It would also raise temperature threshold above which evaporation is the only effective means of dissipating heat.

Carnivorous mammals, like the chuditch, are at an advantage compared with herbivores in arid conditions. Their prey provides appreciable quantities of water whereas seeds and dry herbage have very low water contents. However, evaporative cooling remains very important for temperature regulation at high environmental temperatures irrespective of diet.

Behaviour is also a factor. Animals which are active at night are able to avoid high temperatures and their needs for evaporative cooling are reduced. Shelter in burrows or other refuges by day also prevents exposure to high air temperatures and low humidities.

The tendency of the chuditch to assume low body temperatures at moderate environmental temperatures, and to tolerate a rise in body temperature of several degrees at temperatures above the thermal neutral zone, suggests two likelihoods:

i. that the insensible water loss below the thermal

neutral zone would be low; and

ii. that high rates of evaporative cooling would not be necessary during short-term exposure to high ambient temperatures.

Further economies could also be expected from its carnivorous diet and its nocturnal activity pattern.

Rates of evaporative water loss of the chuditch from the combined skin and respiratory surfaces were measures in order:

1. to determine the amount of water dissipated by the animals over the ambient temperature range 0^{o} to $40^{o}C$;

2. to determine the capacity of the animals for evaporative cooling at high ambient temperatures and the relationship between heat production, body temperature and evaporative heat loss;

3. to permit comparison of rates of evaporative water loss in this species with those of other mammals; and

4. in an experiment not directly related to evaporative aspects of water balance two animals were deprived of water for over one week to determine their ability to survive on a diet of uncooked meat and fat.

Results

Evaporative Water Loss in the Ambient Temperature Range 0^{o} to $41^{o}C$

Fig 10.1 shows means, standard errors of means and ranges of evaporative water loss (mg/kg. min.) measured over

the ambient temperature range 0° to 40°C. Below 30°C values represent data grouped at intervals of five degrees and plotted at the mid-point of the intervals. At 30°C and above the data are grouped at intervals of one degree. The values are tabulated in Table 10.1 which also shows mean evaporative water loss converted to heat loss (cal/kg. min.) and evaporative heat loss expressed as percentage of heat production over the same temperature range.

Mean rates of evaporative water loss (EWL) of 7 to 9 mg/kg. min. were obtained below 10°C (T_a). From 10° to 30°C mean rates of EWL were rather constant at 11.2-12.5 mg/kg. min. Above 30°C there was a rise in EWL so that, at 35°C it was double that at 30°C (26.5 mg/kg. min.). EWL rose steeply above 35°C to reach rates in excess of 80 mg/kg. min. at 39° to 41°C. Expressed in different terms; for a 1 kg animal, water lost by evaporation below 31°C amounted to 750 mg/hr or less; at 35°C EWL was 1590 mg/hr, and at 39°C EWL was in excess of 5500 mg/hr. This represents more than a seven-fold increase in EWL from 30° to 39°C.

The Relationship between EWL and other Correlates of Metabolism

The ratio mg H_2O expended per ml O_2 utilized increased with rising T_a, for example:

T_a (°C)	mg H_2O/ml O_2
0-5	0.3
20-25	1.2
25-30	1.7
32	2.2
40	7.8

Fig 10.1 Evaporative water loss (mg/kg. min.) in the T_a range $0°$-$40°C$. Means are indicated by horizontal lines; ± 1 s.e. by boxes and ranges by vertical lines. Mean values are connected by a trend-line.

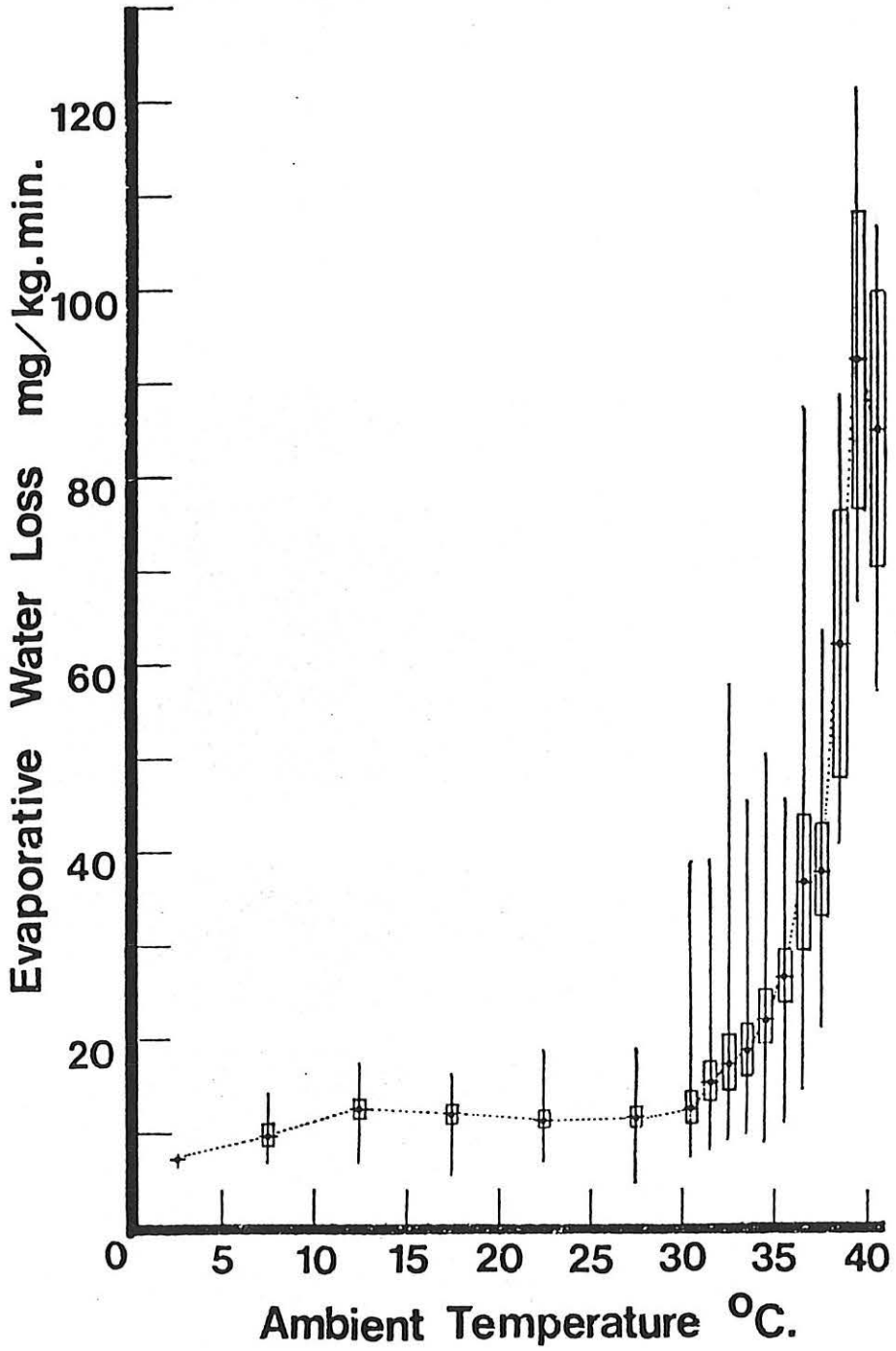

Evaporative Water Loss mg/kg.min.
120
100
80
60
40
20
0
5
10
15
20
25
30
35
40
Ambient Temperature °C.

Table 10.1

Means, standard errors of means and ranges of evaporative water loss measured at the specified ambient temperatures together with mean EWL expressed as evaporative heat loss (EHL) and EHL as a percentage of heat production (HP).

T_a (°C)	No. animals* /no. determinations	E.W.L. mg/kg. min. (mean ± s.e.; range)	E.H.L. cal/kg. min. (mean)	$\frac{E.H.L.}{H.P.}$ %
0 - 4.9	3/3	7.2; 6.5- 7.5	4.2	4
5.0- 9.9	3/6	9.7±1.11; 6.9-14.1	5.6	7
10.0-14.9	5/17	12.5±0.67; 6.6-17.3	7.2	10
15.0-19.9	6/13	11.8±0.84; 5.7-16.3	6.8	11
20.0-24.9	8/23	11.2±0.78; 6.8-18.8	6.5	13
25.0-29.9	8/23	11.7±0.82; 4.7-19.1	6.8	17
30.0-30.9	18/18	12.5±1.67; 7.6-39.1	7.2	20
31.0-31.9	15/15	15.3±2.04; 8.1-39.2	8.9	24
32.0-32.9	15/15	17.1±3.03; 9.4-58.0	9.9	27
33.0-33.9	16/16	18.6±2.68; 10.0-45.5	10.8	26
34.0-34.9	16/16	22.0±2.85; 9.0-50.5	12.8	31
35.0-35.9	13/13	26.5±2.71; 11.3-45.8	15.4	36
36.0-36.9	9/9	36.7±7.28; 15.0-87.6	21.3	49
37.0-37.9	8/8	37.8±4.76; 21.6-63.8	21.9	47
38.0-38.9	3/3	62.1±14.12; 40.8-88.8	36.0	73
39.0-39.9	3/3	92.3±15.95; 66.7-121.6	53.5	107
40.0-40.9	3/3	85.1±14.66; 57.2-106.9	49.4	94

* number to left of slant = no. of animals
number to right of slant = no. of measurements.

When evaporative water loss was related to O_2 consumption by expressing both in terms of their caloric equivalents (1 mg H_2O = 0.58 cal.; 1 ml O_2 = 4.8 cal.) and expressing evaporative heat loss (EHL) as a percentage of heat production, the caloric equivalent of water lost by evaporation below 5°C represented 4 per cent of heat production. EHL increased from 11 per cent at T_a 10°C to 17 per cent at T_a 29°C. At 30°C EHL represented 20 per cent of heat production. Above 30°C the amount of heat production dissipated by evaporation rose to 36 per cent at 35°C and to more than 100 per cent at 39°C. Some animals were capable, at least for short periods, of dissipating more than 100 per cent of heat production by means of evaporation at ambient temperatures around 40°C.

As the chuditch has a variable body temperature below the lower critical temperature (Chapter VII), a relationship between the rate of EWL and body temperature could be expected because of the effect of temperature on the amount of water vapour in saturated air (e.g. at 33°C, 35.7 mg/l; 37°C, 44.0 mg/l; i.e. saturated air at 33° contains 81 per cent of the water contained in saturated air at 37°C). A positive correlation was indeed found ($r = +0.46$; $p < 0.001$) and a linear regression fitted to 76 pairs of values for colonic temperature and EWL measured below 30° (T_a) is described by the equation:

$$y = 2.096x - 61.207$$

where y = EWL (mg/kg. min.) and x = colonic temperature (°C).

Predictions of evaporative water loss from this equation give expected evaporative water losses at 33° and 37°C (T_b) of 8.0 and 16.3 mg/kg. min. respectively, representing a doubling of EWL for a 4° rise in body temperature. This is more than would be expected from the differences in the amounts of water contained in saturated air at the different temperatures alone. No doubt insensible water loss from the skin is increased at elevated T_b and this contributes to the overall increase in EWL.

No significant correlation could be demonstrated between breathing rate and EWL at ambient temperatures below the lower critical temperature. However, an increase in EWL above the thermal neutral zone was associated with an increased breathing rate. High rates of EWL above 38°C were invariably associated with panting, in some cases at rates exceeding 200 breaths/min.

The response to high ambient temperatures varied between individual animals (Fig 10.2). Some animals showed only moderate increase in EWL (to 20-30 mg/kg. min.) until T_a exceeded 35°C while a few would pant and increase EWL at T_a 32° to 33°C. This was puzzling at first. It was thought that the differences may have reflected acclimatization to seasonal conditions. However the simple answer appears to relate to the size of the metabolism chamber. The small females tolerated increased T_a well. They would lie stretched out on their backs and presumably were able

to facilitate heat loss by exposing the belly and feet. The larger males were, however, rather cramped and had to remain partially curled up. It was invariably the males that became distressed at relatively low T_a.

Fig 10.3A shows evaporative heat loss (EHL) as a percentage of heat production (HP) vs. body temperature for three animals at 33° to 41°C (T_a). The regression fitted by the method of least squares to the 26 bivariate values is described by the equation:

$$y = 22.2826x - 780.1899$$

where $x = T_b$ and y = EHL/HP per cent. ($r = 0.81$; $p < 0.001$)

Fig 10.3B shows body temperature vs. ambient temperature for the same three animals during the time when evaporative water loss was measured. From the regression, EHL/HP = 100 per cent when $T_b = 39.5°C$. It can be seen from Fig 10.3B that T_a exceeds T_b above 38°C for two animals, and above 39°C for one animal. The need to dissipate the full complement of heat production by evaporative means does not occur until T_b has risen above 38°C, three or four degrees above the resting T_b within and below the thermal neutral zone. If T_b were rigidly maintained at 34° to 35°C, high rates of EWL would be necessary at air temperatures some four or five degrees lower than indicated above.

Evaporative Water Loss during Adjustment to Chamber Conditions

Fig 10.4 shows evaporative water loss, oxygen consumption, body temperatures and breathing rate of one

Fig 10.2 Trends in rates of evaporative water loss (mg/kg. min.) vs. T_a for 16 animals as T_a was slowly increased above $30^{\circ}C$.

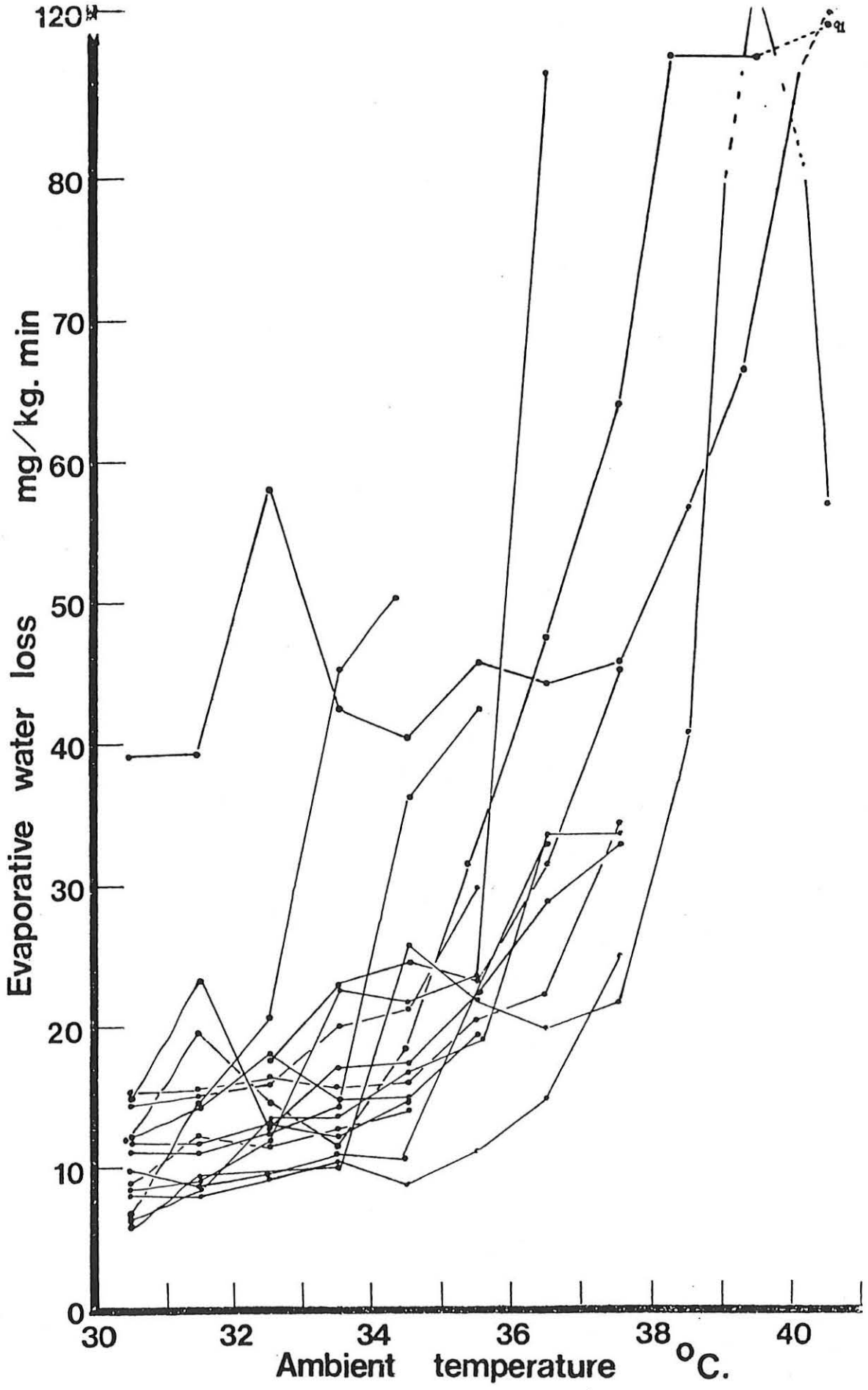
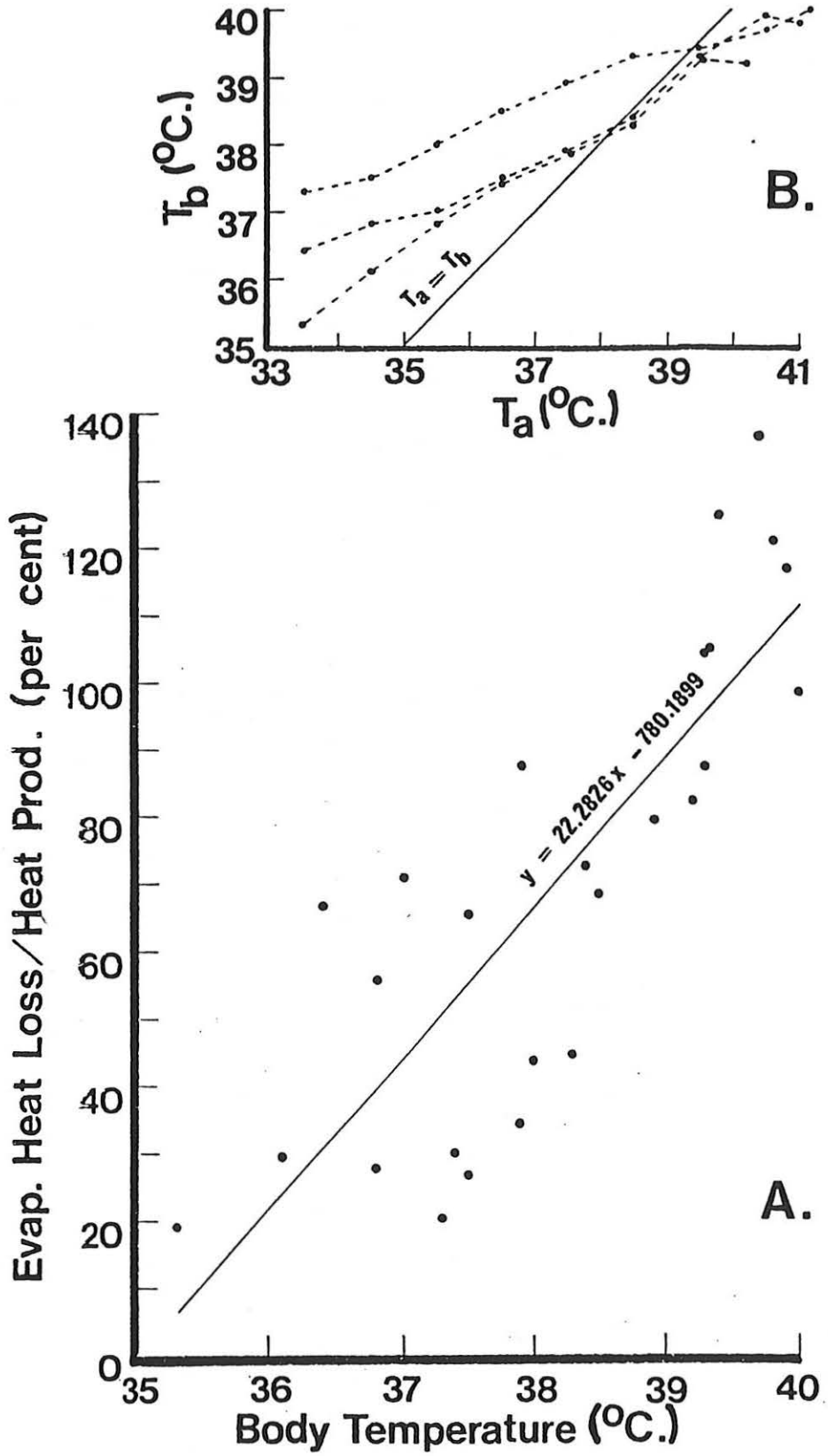

120
80
70
60
50
40
30
20
10
0
Evaporative water loss mg/kg. min
30
32
34
36
38
40
Ambient temperature °C.

Fig 10.3A Evaporative heat loss (EHL) / heat production (HP), expressed as percentages vs. T_b (^oC) for three animals in the T_a range 33^o-41^oC and the linear regression fitted to these 26 bivariate values.

10.3B T_b vs. T_a for the same three animals, measured at the same time as the data shown in Fig 10.3A.


40
39
38
37
36
35
T_b (°C.)
$T_a = T_b$
B.
33
35
37
39
41
T_a (°C.)
140
120
100
80
60
40
20
0
Evap. Heat Loss/Heat Prod. (per cent)
y = 22.2826x - 780.1899
A.
35
36
37
38
39
40
Body Temperature (°C.)

female chuditch at T_a 0°-1°C and 30°-31°C. The trend shows the effect of duration of confinement within the metabolism chamber on EWL.

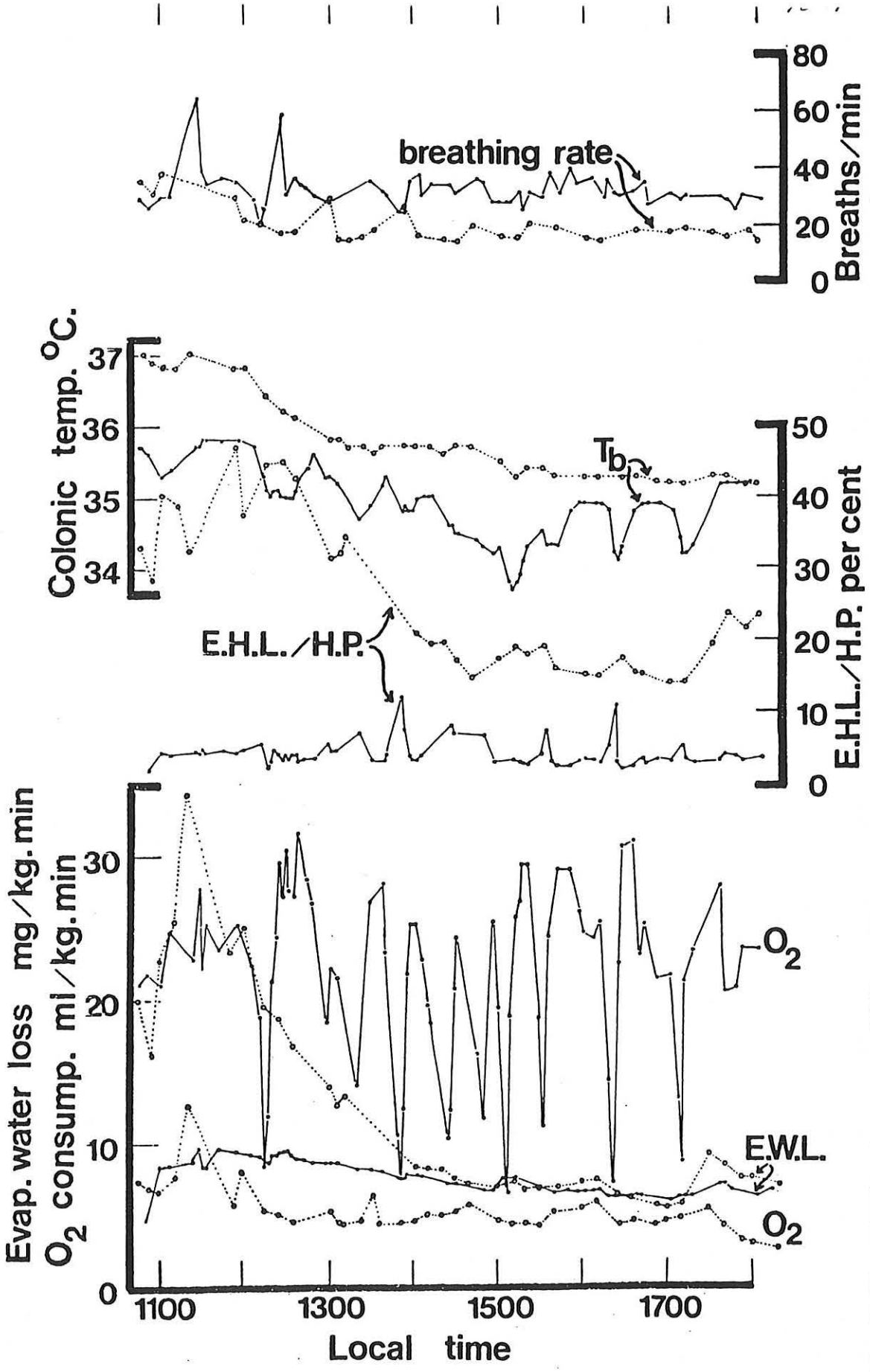
During the first two hours of confinement at 30°C rates of EWL were high but at the end of three hours EWL stabilized. T_b fell from 37°C at the beginning of the run to stabilize around 35.3°C after three hours in the chamber. Breathing rates were higher during the first hour than in the latter part of the run. Evaporative heat loss as a percentage of total heat production was about 40 per cent initially, falling to 15-20 per cent after three hours. The rate of O_2 consumption, which was high during the first $1\frac{1}{2}$ hours, fell to steady levels thereafter.

The period of adjustment to chamber conditions necessary to achieve fairly stable values at 0°-1°C also appears to be about three hours but the trend is not so clear because of the great short-term variations in rates of O_2 consumption. EWL fell from about 10 mg/kg. min. at first to 6-7 mg/kg. min. after about $2\frac{1}{2}$ hours. O_2 consumption, however, showed the cyclic variation from high to low rates which typically occurred at low T_a (see Chapter VIII, p. 8.6). It is likely that the animal was shivering during the periods when O_2 consumption was high (as illustrated in Fig 8.3A and 8.3B) but as I wished to avoid disturbing it I did not observe it during this time. Variation in T_b and breathing rate can be related to the

Fig 10.4 Trends in O_2 consumption, evaporative water loss, evaporative heat loss, breathing rate and body temperature for one animal during exposure to T_a 0°-1°C and 30°-31°C for longer than seven hours.

Symbols: ●——● T_a = 0°-1°C

○·····○ T_a = 30°-31°C


breathing rate
Breaths/min
80
60
40
20
0
Colonic temp. °C.
37
36
35
34
Tb
E.H.L./H.P.
E.H.L./H.P. per cent
50
40
30
20
10
0
Evap. water loss mg/kg.min
O2 consump. ml/kg.min
30
20
10
0
O2
E.W.L.
O2
1100
1300
1500
1700
Local time

cycles in O_2 consumption rate. However both T_b and breathing rate were lower after three hours than they were at first, whereas no similar reduction in O_2 consumption was apparent.

Response to Water Deprivation

Body weight changes and mean rates of food intake for two animals, at first when no free water was provided and later with free access to water, are shown in Table 10.2. Both animals gained weight slightly during nine days of water deprivation in the absence of thermal stress (T_a 14.5°-22°C). No consistent difference in the rate of food intake was observed, whether or not water was available, although intake varied from day to day both in the presence and absence of drinking water. It is concluded that, at least for short periods, the chuditch can maintain food intake and body weight when deprived of drinking water.

Discussion

Evaporative water loss in the chuditch, in the absence of thermal stress, may be compared with rates of loss of other marsupials and of eutherian mammals. The interspecific relationship between insensible water loss (I.W.) and body weight, as expressed by Chew (1965), is used as a basis for comparison. In this expression:

$$I.W. = 2.58\ B_o^{0.826}$$

B_o = body weight in kg, and I.W., in g/hr, includes water

Table 10.2

Body weight and food intake for two animals during a nine-day period when drinking water was unavailable, and a six-day period when drinking water was freely available.

Animal	Body Weight (g)				Food intake/day (g)			
	Mean	Start	End	Change (%)	Lean	Fat	Total	g/kg
No water available								
Male	1564	1500	1588	+5.9	88.4	20.4	108.8	72.5
Female	731	725	730	+0.7	67.8	16.5	84.3	116.0
Free access to water								
Male	1559	1588	1588	0	96.0	7.2	103.2	64.9
Female	737	730	738	+1.1	77.5	16.8	94.3	129.2

lost by diffusion through the skin and from the respiratory surfaces. Chew derived this relationship using data from 49 species on their insensible water loss for the ambient temperature range 18° to 29°C, below the panting or sweating thresholds for all species. Only one marsupial (Setonix brachyurus, Bentley, 1955) was included among the 49 species. The relationship therefore relates particularly to eutherian mammals.

I will use the abbreviation I.W. in subsequent discussion to refer to insensible water loss in the sense that Chew used it, i.e. in the absence of thermal stress. Evaporative Water Loss (EWL) has been used in the Results to include pulmocutaneous water loss, whether insensible loss at temperatures below the thermal neutral zone or with evaporation facilitated by increased breathing rates at higher temperatures.

Table 10.3 shows rates of insensible water loss for 13 species of marsupials (references cited in the table) at T_a 20° to 25°C compared with I.W. for mammals of equivalent body weight calculated from Chew's equation. The observed I.W. for Perameles, Macrotis, Isoodon and Lagorchestes are approximations from small published figures. The values for Sminthopsis, Dasycercus and Dasyuroides are observed rates uncorrected to zero relative humidity (Haines et al, 1974). Body weights for Sminthopsis and Dasycercus were obtained from Macfarlane et al (1971).

Table 10.3

Rates of insensible water loss below the thermal neutral zone for thirteen species of marsupials compared with rates predicted by the interspecific equation I.W. = 2.58 W $(kg)^{0.826}$ (Chew, 1965).

Species	Reference	T_a (°C)	Body weight (kg)	Insensible Water Loss (mg/g.hr)	Predicted I.W. (mg/g.hr)	Observed I.W. / Predicted I.W. (per cent)
Sminthopsis crassicaudata	5,9	25	0.02*	10.10*	5.2	193
Dasycercus cristicauda	5,9	25	0.09*	2.94*	3.9	74
Dasyuroides byrnei	5,9	25	0.13*	2.29*	3.7	62
Perameles nasuta**	7,8	20	0.6	2.1	2.8	75
Dasyurus geoffroii	10	20-25	1.0	0.67	2.58	26
Macrotis lagotis**	7,8	20	1.01	1.2	2.6	46
Isoodon macrourus**	7,8	20	1.6	0.9	2.4	37
Trichosurus vulpecula**	3	25	1.98	0.7	2.2	30
Lagorchestes conspicillatus**	4	25	2.66	0.6	2.24	27
Setonix brachyurus	1	21	3.55	1.55	2.07	75
Macropus eugenii	2	24	4.96	0.55	1.95	28
Megaleia rufa	6	22.1	25.00	0.45	1.47	30
Macropus robustus	6	22.1	30.00	0.34	1.43	24

References: 1. Bentley, 1955; 2. Dawson, Denny & Hulbert, 1969; 3. Dawson, 1969; 4. W. Dawson & Bennett, 1970; 5. MacFarlane et al, 1971; 6. T. Dawson, 1973; 7. Hulbert & Dawson, 1974a; 8. Hulbert and Dawson, 1974b; 9. Haines et al, 1974; 10. This study.

* body weights from (5), I.W. from (9).

** Rates of evaporative water loss estimated from published figures of evaporative heat loss; amounts of water were calculated by assuming 1 mg H_2O = 0.58 cal.

All of the marsupials, except Sminthopsis, have weight-relative rates of insensible water loss appreciably lower than those predicted by Chew's equation. Except for Setonix all of the species weighing more than one kilogram have I.W. at least 50 per cent below that predicted. (A personal communication from Bentley and Shield suggests that a recent study of Setonix now shows its I.W. to be about one-quarter of Bentley's (1955) estimate).

The species included in Table 10.3 all have standard metabolic rates about 30 per cent lower than average weight-relative eutherian rates; the body temperature is two or three degrees lower than average eutherian body temperatures; and as shown in Chapter IX, marsupial breathing rates are about 40 per cent of average breathing rates for eutherians. All of these factors would contribute to reducing water loss from the respiratory surfaces.

Insensible water loss for the chuditch is comparable to I.W. of Trichosurus, the large kangaroos, Lagorchestes and Macropus eugenii. It is considerably lower than that of the small desert dasyurids and the bandicoots.

There is some evidence that mammals from arid environments have relatively low rates of I.W. Chew (1965) noted that a number of small, desert-adapted species have lower I.W. than predicted by his interspecific equation. I.W., expressed as a function of O_2 consumption, is also lower for some desert species than for species from less arid

environments. This was demonstrated by Schmidt-Nielsen and Schmidt-Nielsen (1950). They found that for Dipodomys merriami, as well as for hamsters and wild mice, the total evaporation was around 0.5 mg H_2O/ml O_2 utilized, presumably at T_a 25°C. Total evaporation in white rats and mice under similar conditions was about 0.9 mg H_2O/ml O_2. Hudson and Rummel (1966) found somewhat higher ratios of H_2O/O_2 for two other small rodents, Liomys salvani which can maintain body weight on dry seed without drinking water, and L. irroratus which loses weight under similar conditions. Total evaporation for both species at T_a 28°C was between 0.9 and 1.03 mg H_2O/ml O_2. Hudson and Rummel's values were more comparable to those of the Schmidt-Nielsens for rodents not from arid environments than for the desert-adapted Dipodomys.

The ratio of mg H_2O evaporated/ml O_2 consumed for the chuditch is higher than ratios reported for rodents either from deserts or from non-arid environments. The ratio for the chuditch is 1.2 at T_a 20°-25°C rising to 1.7 in the thermal neutral zone. Haines et al (1974) reported higher ratios for small desert-living dasyurids: 3.1 for Sminthopsis and 1.9-2.0 for Dasycercus and Dasyuroides at T_a 25°C. These high ratios have, however, been corrected to zero relative humidity. The uncorrected ratios of 2.4 for Sminthopsis and 1.3 for Dasycercus and Dasyuroides are more comparable with ratios reported here for the chuditch for which no adjustment for relative humidity has

been made. Nevertheless the uncorrected ratios for the marsupials are higher than those found for desert rodents from the New World. Haines et al reported lower rates of evaporative water loss for five murid rodents from arid environments in Australia than for the dasyurids. The uncorrected ratios given for Leporillus, and two species each of Pseudomys and Notomys are 1.0-1.5, comparable with results from Liomys reported by Hudson and Rummel (1966) but higher than the Schmidt-Nielsen's ratios for Dipodomys.

Two factors contribute to increased evaporative water loss in the chuditch above T_a 30°C. These are the rise in body temperature associated with increased ambient temperature (Chapter VII) and increased breathing rate (Chapter IX). Panting appears to be the major avenue of heat loss at ambient temperatures above the thermal neutral zone. Rapid increase in EWL is related to the onset of panting. However I suspect that experimental conditions under-estimate the capacities of the chuditch to cope with high ambient temperatures. Large males which were cramped in the metabolism chamber invariably became distressed and began to pant at lower ambient temperatures than smaller females which presumably were able to rely on non-evaporative means of heat loss until T_a reached T_b at 38° to 39°C.

Chuditches were not observed to spread saliva on the fur at high T_a as do the macropodids and Trichosurus. However animals which became distressed in the metabolism

chamber at high T_a were found to have wet fur on removal from the chamber whereas animals which remained quiet in the chamber, even though panting rapidly, emerged dry except for the pads of the feet. Dawson (1973) found that sweating did not occur in resting kangaroos in response to environmental heat load although obvious sweating was observed when the animals struggled at high T_a. Dawson also found that saliva-spreading or 'licking' was not of major importance for temperature regulation in the red kangaroo and euro. Panting appeared to be the most important form of evaporative heat loss in Trichosurus and active sweating was not an important thermoregulatory response (Dawson, 1969). Bentley (1960) showed that temperature regulation at high T_a in Setonix was not affected by saliva-spreading and that regulation was impaired by dehydration, indicating that evaporative water loss was of primary importance. A similar picture emerges for the tammar (Dawson et al, 1969) and for Lagorchestes (Dawson and Bennett, 1970). Although sweating was implicated in the effective thermal regulation of Sarcophilus at high T_a (Robinson and Morrison, 1957), Hulbert and Rose (1972) consider that the 50 per cent increase in cutaneous water loss from 20° to $40^{\circ}C$ (T_a) is insignificant compared with accelerated EWL possible from a sevenfold increase in breathing rate over the same temperature range. Guiler and Heddle (1974) however, found that Sarcophilus did not pant at T_a 35° to $39^{\circ}C$.

Rates of EWL remained high for some time after chuditches were placed in the metabolism chamber and did not reach minimum levels until they had been in the chamber for about three hours (Fig 10.4). O_2 consumption rates, breathing rates and T_b stabilized somewhat sooner. The relatively high rates of EWL observed initially were probably the result of disturbance to the animals as they were placed in the chamber. Dawson (1973) demonstrated an increased cutaneous water loss in Megaleia during and after a bout of struggling although, as noted earlier in this discussion, active sweating did not occur in resting animals in response to an environmental heat load. He suggested an 'adrenomedullary involvement' in this response. The high EWL observed for the chuditch during the first few hours in the metabolism chamber may have a similar cause. The observation points to the need to allow animals enough time to settle down if minimum rates are to be measured.

Water deprivation, in the absence of thermal stress, for a period of nine days, had no significant effect either on body weight or on food intake for a male and a female chuditch. Other flesh-eating mammals can survive for long periods when deprived of water if they have access to fresh flesh or fish. Prentiss et al (1959) found that cats provided with food but no water maintained body weight for up to 142 days, although weight loss resulted when partly dessicated food was provided. Dogs can survive for weeks

in the absence of water if provided with fresh fish (Danowski et al, 1944). Schmidt-Nielsen (1964) and Chew (1965) noted that the carnivorous desert rodent Onychomys torridus survives for long periods without water if provided with fresh mouse carcasses or raw pork liver. Among the marsupials the desert dasyurid Dasycercus cristicauda can maintain water balance if fed freshly killed mice or minced meat at T_a 25° to 30°C with no access to water (Schmidt-Nielsen and Newsome, 1962). So too can Dasycercus, whereas Sminthopsis is unable to do so (Kennedy and Macfarlane, 1971).

It is notable that the breeding season of the chuditch is restricted to the winter months when temperatures are low and free water is more likely to be available. Thus the requirement for water for the formation of milk in lactating females would not occur at the same time as heavy demands for evaporative cooling at high ambient temperatures. The nocturnal activity pattern of the chuditch would also reduce demands for evaporative cooling. Body temperature is highest at night (Chapter VII) and, during the day, chuditches probably seek refuge in burrows or hollow trees. Although little is known of the behaviour of this species, captive animals have been seen to dig burrows and one wild chuditch was known to occupy a hole in the ground, formed when a large tree-root was burnt out in a bush-fire. These observations suggest that they seek sheltered resting places.

The chuditch then, having a low rate of evaporative water loss at T_a below the thermal neutral zone, and a diet which would provide it with a certain amount of water, appears to be provided with the means of occupying rather arid environments. Its tolerance of hyperthermia and ability to dissipate heat by evaporative means up to about 40°C also appears to fit it to tolerate high ambient temperatures, at least for short periods. However its pattern of behaviour most likely ensures that it avoids extremely high air temperatures.

A capacity to survive in a hot dry environment may not appear to be very relevant to a species which is presently apparently restricted to south-western Australia, with its reliable rainfall and rather few days when T_a exceeds 37.8°C (100°F). It does serve to explain, however, how the species in the recent past was able to range across the arid inland of the continent.

CHAPTER XI

HEART RATES

Preamble

Heart, or pulse, rate can be used to provide an index of metabolic rate. Brody (1945) cited Clark (1927) who had compiled and analysed pulse rate data obtaining the pulse-rate-weight equation for eutherian mammals:

$$f = 217W^{-0.27}$$

where f = pulse rate and W = body weight in kg.

Seventeen species of Australian marsupials were found to have a heart-rate - body weight equation

$$f = 106W^{-0.27}$$

(Brown and Kinnear, 1967) indicating that marsupial heart rates are slightly less than half those of eutherians of equivalent body weight.

It was planned to measure heart rates of Dasyurus geoffroii at the same time as oxygen consumption rates and body temperatures as an additional correlate of metabolic rate. In order to obtain heart rates the animals had to be restrained to prevent them from biting off electrocardiogram electrodes. The animals did not respond well to such restraint. Body temperatures generally remained high, as did oxygen consumption rates. Data were obtained from only three animals and these are reported below.

Results

Table 11.1 shows heart rate, oxygen consumption and body temperature for three animals at T_a 10° to 14°C and 28° to 30°C (thermal neutral zone). Weight-relative heart rates calculated from the equations

$$f = 217W^{-0.27}$$

and

$$f = 106W^{-0.27}$$

are shown for comparison with rates recorded in the thermal neutral zone.

The values for animal 1 are mean rates for $2\frac{1}{2}$ hour periods when, in both temperature ranges, it remained relatively quiet. Rates for animals 2 and 3 are minimum observed rates recorded during brief periods of rest.

There were large differences between rates recorded for different animals at T_a 28° to 30°C. The differences are too large to be accounted for as simple Q_{10} effects resulting from differences in body temperature in the thermal neutral zone. Heart rates recorded at T_a 10° to 14°C are less variable.

It was not possible to obtain data about cardiac output. However "oxygen pulse":-

$$\frac{O_2 \text{ consumption/min}}{\text{heart rate/min}}$$

indicates the amount of oxygen delivered to the tissues by each heart beat. Oxygen pulse as a ratio of body weight was also calculated. These values are shown in Table 11.2.

Table 11.1

Heart rate, body weight, O_2 consumption rate and T_b for three chuditches at 10° to 14°C and 28° to 30°C (T_a)

Animal	Observed Heart Rates beats/min.	Predicted min. heart rates		O_2 consumption		T_b (°C)
		Marsupial*	Eutherian†	ccs/min	ccs/kg, min	
10-14°C						
1. female 0.8 kg	251	—	—	19.90	24.87	37.4
2. male 1.275 kg	218	—	—	26.33	20.65	34.0
3. male 1.25 kg	284	—	—	21.42	17.14	36.2
28-30°C						
1. female 0.8 kg	154	112	230	5.62	7.02	35.9
2. male 1.275 kg	85	99	203	11.62	9.11	35.2
3. male 1.25 kg	234	100	204	10.95	8.76	37.1

* $f = 106W^{-0.27}$ (Brown & Kinnear, 1967)

† $f = 217W^{-0.27}$ (Brody, 1945: citing Clark, 1927)

Table 11.2

Oxygen pulse for three chuditches at T_a 10° to 14°C and 28° to 30°C, and oxygen pulse as a ratio of body weight in the thermal neutral zone.

Animal	Oxygen Pulse ccs O_2/heart beat		Oxygen Pulse/body wt. (kg) in thermal neutral zone
	10°-14°C	28°-30°C	28°-30°C
1. female 0.800 kg	0.079	0.036	0.045
2. male 1.275 kg	0.121	0.137	0.107
3. male 1.250 kg	0.075	0.047	0.038

Discussion

Brown and Kinnear (1967) reported a minimum heart rate of 89 beats/min. for one chuditch. This value agrees closely with the value obtained for one animal (No. 2) of 85 beats per minute. The higher rates obtained here for two other animals are considered to reflect non-resting levels rather than significantly higher resting rates. The body temperature of animal No. 2 was consistent with resting body temperature of animals in the thermal neutral zone although its rate of oxygen consumption was considerably higher than the standard level. Heart rates for the three animals predicted from Brown and Kinnear's equation are close to the low value recorded for one animal. Heart rates at T_a 10° to 14° were 2-2½ times the predicted rates in the thermal neutral zone. Oxygen pulse at the lower ambient temperatures were also considerably higher than that in the thermal neutral zone. In other words, at the lower ambient temperature the amount of O_2 delivered by each heart beat is increased over that in the thermal neutral.

Brody (1945) showed that the oxygen pulse is directly related to body weight in eutherian mammals

$$\frac{\text{oxygen pulse}}{\text{weight (kg)}} = 0.05$$

When the weight relative equations for standard metabolic rate of Australian marsupials (Dawson and Hulbert, 1969)

and heart rate (Brown and Kinnear, 1967) are used to calculate oxygen pulse of marsupials a value of 0.06 ccs O_2/heart beat is obtained. This is slightly higher than that for eutherians, as a consequence of metabolic levels of approximately 70 per cent of eutherians while heart rates are slightly less than half eutherian rates. Thus, in the marsupials each heart beat is expected to deliver slightly more oxygen to the tissues than in eutherians.

The ratios O_2 pulse/body weight for the three chuditches in the thermal neutral zone differ from the expected value of 0.06, two animals having somewhat lower values and one being considerably higher. Thus the expectations are not born out by the results, probably because the animals did not achieve resting states when they were restrained.

CHAPTER XII

BLOOD VOLUME

Preamble

It has been suggested that marsupials with low metabolic rates may have low blood volumes compared with eutherian mammals. The volume of blood normally represents 7-10 per cent of body weight in eutherian mammals (Prosser, 1973). Two marsupials, the American opossum (Burke, 1954) and the Australian brush-tailed possum, Trichosurus vulpecula (Dawson and Denny, 1967) apparently have relatively low blood volumes. On the other hand, Setonix brachyurus has a blood volume within the normal eutherian range (Shield, 1971).

The blood volume of the chuditch was determined in order to see whether the low standard metabolic rate of this species was associated with a blood volume significantly lower than reported values for eutherian mammals.

Results

Table 12.1 shows the relative red cell volume, plasma volume and total blood volume (ml/kg) for each of ten animals as determined simultaneously by separate and distinct methods (see Chapter II, Material and Methods, p. 2.24). Blood volumes estimated from I^{125} labelled albumin and haematocrit were slightly higher than those estimated from

Table 12.1

Relative red cell volumes, plasma volumes and total blood volumes (ml/kg) for ten chuditches: volumes estimated from Fe^{59} labelled red cells and I^{125} labelled albumin, and from haematocrit (Hcrt) and I^{125} labelled albumin.

Expt. No.	Sex	Hcrt (% red cells)	Red cell volume (ml/kg)		Plasma volume (ml/kg)		Total blood volume (ml/kg)		F_{cells}
			Fe^{59}	Hcrt.*	I^{125} in whole blood	I^{125} + Hcrt	Fe^{59} + I^{125}	I^{125} + Hcrt	
1.	M	36.0	19.0	20.7	40.8	40.0	59.8	60.6	0.88
2.	F	43.5	27.0	31.5	44.9	44.5	71.9	76.1	0.86
3.	M	48.0	28.7	31.0	36.3	36.2	65.0	67.2	0.92
4.	F	51.2	28.0	35.3	36.4	37.0	64.5	72.3	0.85
5.	F	36.5	23.9	29.7	55.2	56.2	79.1	85.9	0.83
6.	F	51.8	32.3	34.2	33.6	34.6	65.9	68.8	0.95
7.	F	45.0	39.8	32.6	41.9	43.4	81.7	76.0	1.08
8.	M	46.8	33.5	34.9	42.1	43.2	75.6	78.1	0.95
9.	F	50.0	39.7	34.8	36.1	37.9	75.8	72.6	1.05
10.	F	51.5	33.5	33.5	33.2	34.3	66.7	67.8	0.98
	Mean	46.0	30.5	31.8	40.1	40.7	70.6	72.5	0.93
	Standard error of mean	1.85	2.08	1.37	2.09	2.07	2.29	2.22	0.027

* corrected for 10 per cent trapped plasma

Fe^{59} labelled red cells and radioiodinated albumin in all but two cases (2.7 per cent higher on the average). The differences between volumes determined by the two methods were not statistically significant (Student's t test). The mean red cell volume of 30-32 ml/kg represents about 43 per cent of the mean total blood volume of 71-73 ml/kg.

The difference between the two estimates may be explained by the fact that the cells in large vessels (from which the haematocrit samples were taken) are normally more concentrated than in the circulation as a whole, as expressed in the F_{cells} value (Reeve et al, 1953). The normal F_{cells} value for man is in the range 0.89-0.94 (Lawson, 1962). The F_{cells} for the 10 chuditches ranged from 0.83-1.08, but the mean value of 0.93 falls within the range displayed by man.

Table 12.2 shows microhaematocrit values for the same group of animals determined at various intervals during a period of one year. The table includes the mean haematocrit of the animals when tranquilised for blood volume measurements. The reduction in the sample size was due to the death of one male and two females and to the omission of one female which was suckling a litter (24/8/71). Only small differences were observed between values whether determined at well separated times, or at different times on the same day.

Table 12.2

Microhaematocrit values (per cent packed red cells) for a group of chuditches for which the blood volume was measured.

Date:	30.9.70	1.12.70	1.2.71	1.2.71	24.8.71	11.9.71	13.9.71
Time:	afternoon	*	afternoon	night	night	morning	night
No. animals:	9 2M;7F†	10 3M;7F	9 3M;6F	9 3M;6F	6 2M;4F	7 2M;5F	7 2M;5F
Mean Haematocrit: (% red cells)	48.3	46.0	44.8	46.3	44.5	48.2	47.1
Standard error:	1.47	1.88	0.81	1.08	1.70	1.31	1.58
Range:	41.0-52.0	36.0-51.8	41.0-47.5	40.0-50.0	38.5-48.5	43.0-51.2	42.0-52.7

*Haematocrits determined as part of blood volume measurements; animals tranquilised with Diazepam 5 mg/kg.

†M = male; F = female.

Discussion

The use of the tranquiliser, Diazepam, to facilitate handling the chuditches may open the results to criticism, as it may have had the effect of pooling blood in the spleen. The tranquiliser Chlorpromazine has been shown to bring about engorgement of the spleen (Turner and Hodgetts, 1960) and the drug has been used to investigate the influence of the spleen on blood volume of Trichosurus (Dawson and Denny, 1967). Microhaematocrit values for the same group of chuditches when untranquilised, as determined over a period of almost one year, did not differ significantly from values determined in conjunction with the blood volume determinations when the animals were tranquilised. This suggests that the use of Diazepam did not materially affect the distribution of red cells in the circulation.

Although the blood volume of eutherian mammals normally represents 7-10 per cent of the body weight (Prosser, 1973), values ranging from about 55 ml/kg (Felis, Macaca, Oryctolagus, Bos) to 143 ml/kg (Phocoenoides) have been measured (Altman and Dittmer, 1971).

The relative blood volumes for the marsupials Didelphis and Trichosurus, of 58 ml/kg (Burke, 1954) and 57 ml/kg (Dawson and Denny, 1967) respectively, are near the lower limit of the range of eutherian blood volumes but not outside it. Blood volumes have been

measured for several other marsupials. Maxwell et al (1964) obtained a value of 87.5 ml/kg for a mixed sample of kangaroos, including reds, greys and a euro, and 93.5 ml/kg for the tammar. Shield (1971) found that the mean blood volume of captive Setonix was 70 ml/kg. min. The blood volumes of Megaleia and Macropus robustus were found to represent respectively 8.4 and 6.3 per cent of body weight by Denny and Dawson (1975).

The relative blood volume of the captive chuditch of 71 ml/kg is comparable with that of well-fed captive quokkas (Shield, 1971) and is within the normal range for eutherian mammals. There is therefore no evidence for a relatively low blood volume associated with the measured low metabolic rate of the chuditch.

It is apparent then that the suggestion of a relationship between low metabolic rate and low relative blood volume in marsupials cannot be sustained. This is not surprising in that similar relative blood volumes to those of mammals have been measured for representatives of most of the other major vertebrate groups (Prosser, 1973).

CHAPTER XIII

GENERAL DISCUSSION

A number of aspects of the biology of the chuditch have been examined in this study. These include: its breeding pattern, the growth and development of its pouch young, its capacity to regulate its body temperature in the temperature range it is likely to encounter in the wild, and its resting requirements for O_2 and evaporative water in the same range of environmental temperatures.

Discussion of the separate aspects of the study has followed presentation of the results in the foregoing chapters. In this final chapter the growth and energetics sections of the study will be considered in an attempt to interrelate the various chapters, specifically:

1. breeding season, growth and development (Chapters IV, V and VI), and
2. the interrelations of the various metabolic parameters; body temperature, energy metabolism, breathing rates and evaporative water loss (Chapters VII, VIII, IX and X).

1. Breeding, Growth and Development

The limitation of the time of conception to a brief period in late autumn or early winter seems to fit the species to the climatic conditions in which it presently

occurs, namely a climate with a reliable winter rainfall, and with a moderate range of temperature, the extremes of which include rather few frosts in the wet winter months and relatively few extreme high temperatures in the dry summer months (Chapter III). The restricted breeding season:

(i) ensures that the young animals emerge from the pouch in the spring when temperatures are moderate and food and water are likely to be abundant;

(ii) ensures that the females will not have to cope with high ambient temperatures and water shortage when they are lactating and carrying pouch litters; and

(iii) fixes the age at which animals become reproductively mature at either the first or second breeding season after birth, when they are either one or two years of age.

The sequence of developmental events in the pouch-young reflects the demands of pouch life. These differ greatly from the priorities of development in eutherian young. Adolph (1968) showed that the rat and the opossum have very different priorities in the establishment of certain developmental 'stagemarks' and remarked that the "programs by which regulations develop differ widely between rodents and marsupials".

Within the marsupialia the birth weight, the number of pouch young and the pouch environment differ from one group to another. The differences are particularly apparent between the dasyurids, with their large litters and rather open pouches, and the macropodids with single joeys and with large forward-opening pouches. The didelphids, which carry large litters, could be expected, on the other hand, to be similar to the dasyurids in their pouch development. A comparison of the sequence of development of pouch-young from different marsupial groups was attempted to see if any differences could be detected.

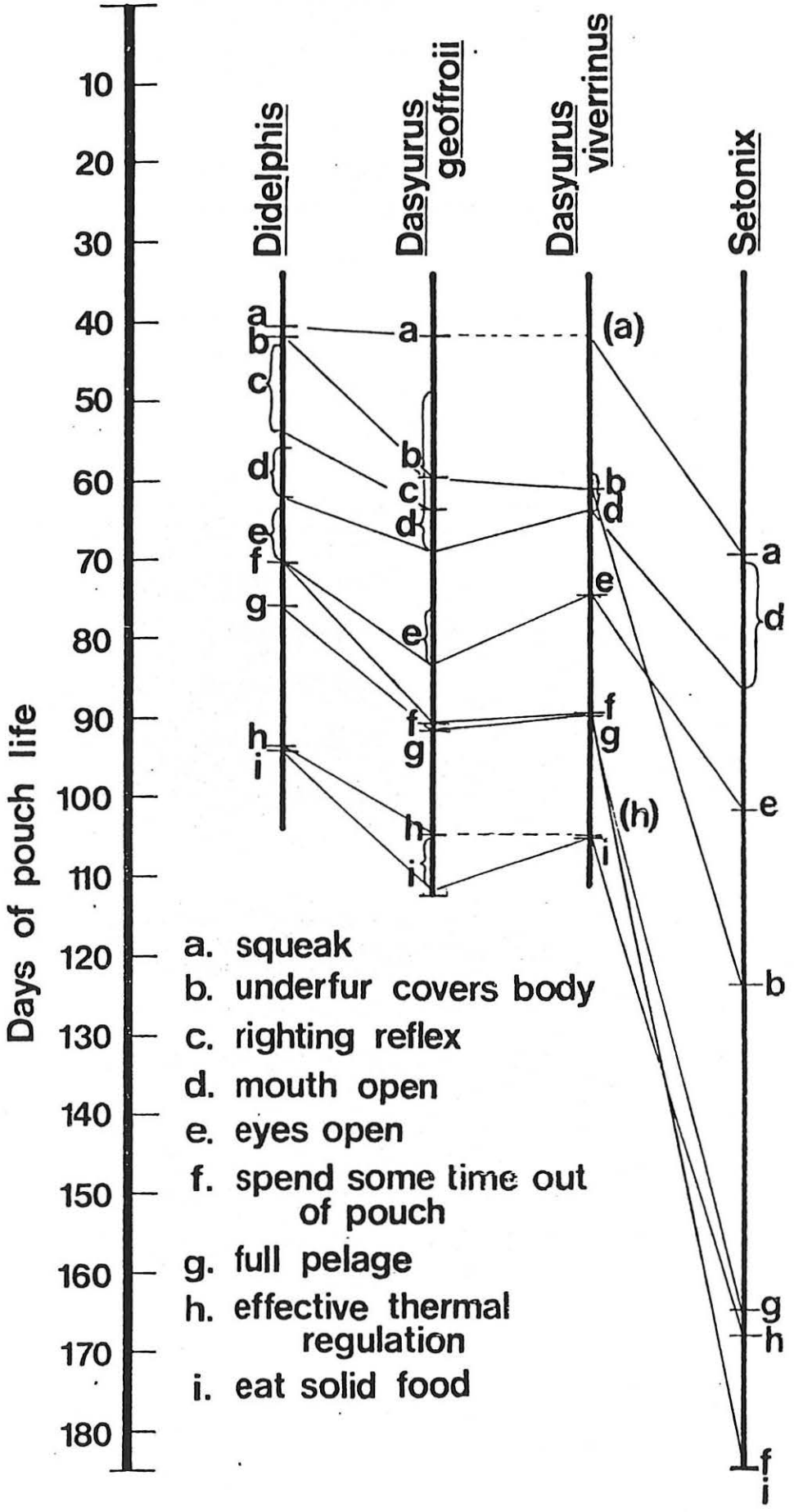
Fig 13.1 shows a comparison between the developmental sequences of four marsupials, Didelphis virginiana, Dasyurus geoffroii, D. viverrinus and Setonix brachyurus. This permits comparison between the chuditch and its close relative, and between the dasyurids and representatives of two other marsupial groups, the Didelphidae and the Macropodidae. Didelphis is polytocous and has a rather open pouch but has a birth weight (130 mg, Hartman 1928) which is much greater than that of Dasyurus viverrinus and D. geoffroii (12.5 and 15.0 mg respectively). Setonix has single young, a relatively large birth weight (340 mg) and a pouch which appears to provide a much more stable environment for the pouch-young than do the pouches of the other three species. The source references are: Didelphis - Langworthy (1925), Hartman (1928) and Reynolds

(1952): Dasyurus viverrinus - Hill and Hill (1955); Setonix - Shield (1961); D. geoffroii - this study.

Comparison of the developmental sequence of the specified stagemarks in Didelphis and the chuditch shows that the events occur in a similar sequence but that Didelphis is one to two weeks in advance of the chuditch. The chuditch and the closely related Dasyurus viverrinus resemble each other closely throughout their pouch life, reaching equivalent stages at almost the same ages throughout. Some of the apparent differences between these two species may have arisen because observations were made only weekly or less frequently.

When the development of the chuditch is compared with that of the quokka some differences in the sequence of events can be seen. Not only does the quokka have a much longer pouch life with equivalent stages being reached more slowly than in the other three species, but the sequence in which the developmental events occurs is slightly different. The development of the underfur is retarded and the quokka joey leaves the pouch later in the sequence than do the other three species. In the opossum and the chuditch the ability to regulate T_b at adult levels occurs sometime after the animals begin to spend time outside the pouch as the combined size and weight of several pouch-young becomes too great to accommodate in the pouch before they are fully furred. In the case of the quokka,

Fig 13.1 Stagemarks in development during pouch life for four species of marsupials.


Days of pouch life
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
Didelphis
Dasyurus geoffroii
Dasyurus viverrinus
Setonix
a. squeak
b. underfur covers body
c. righting reflex
d. mouth open
e. eyes open
f. spend some time out of pouch
g. full pelage
h. effective thermal regulation
i. eat solid food

Shield (1966) has speculated that the high pouch temperature and the limitation on evaporative cooling may stimulate the homeothermic joey to make its first brief sorties out of the pouch.

2. Interrelations of Metabolic Parameters

Whereas the breeding pattern of the chuditch appears to be neatly adapted to the climatic conditions of the region in which the species now occurs, i.e. to reliable winter rainfall ensuring ready availability of food and water during pouch life and at emergence from the pouch, some aspects of its energetics appear to fit it to live in a more arid and variable environment. These aspects are:

(i) low resting levels of metabolism;

(ii) effective temperature regulation at air temperatures likely to be encountered on frosty nights;

(iii) a labile body temperature at moderate environmental temperatures and a tendency to become torpid;

(iv) a tolerance of hyperthermia at high environmental temperatures so that evaporative water loss is relatively low until other avenues of heat loss are cut off at about 39°C.

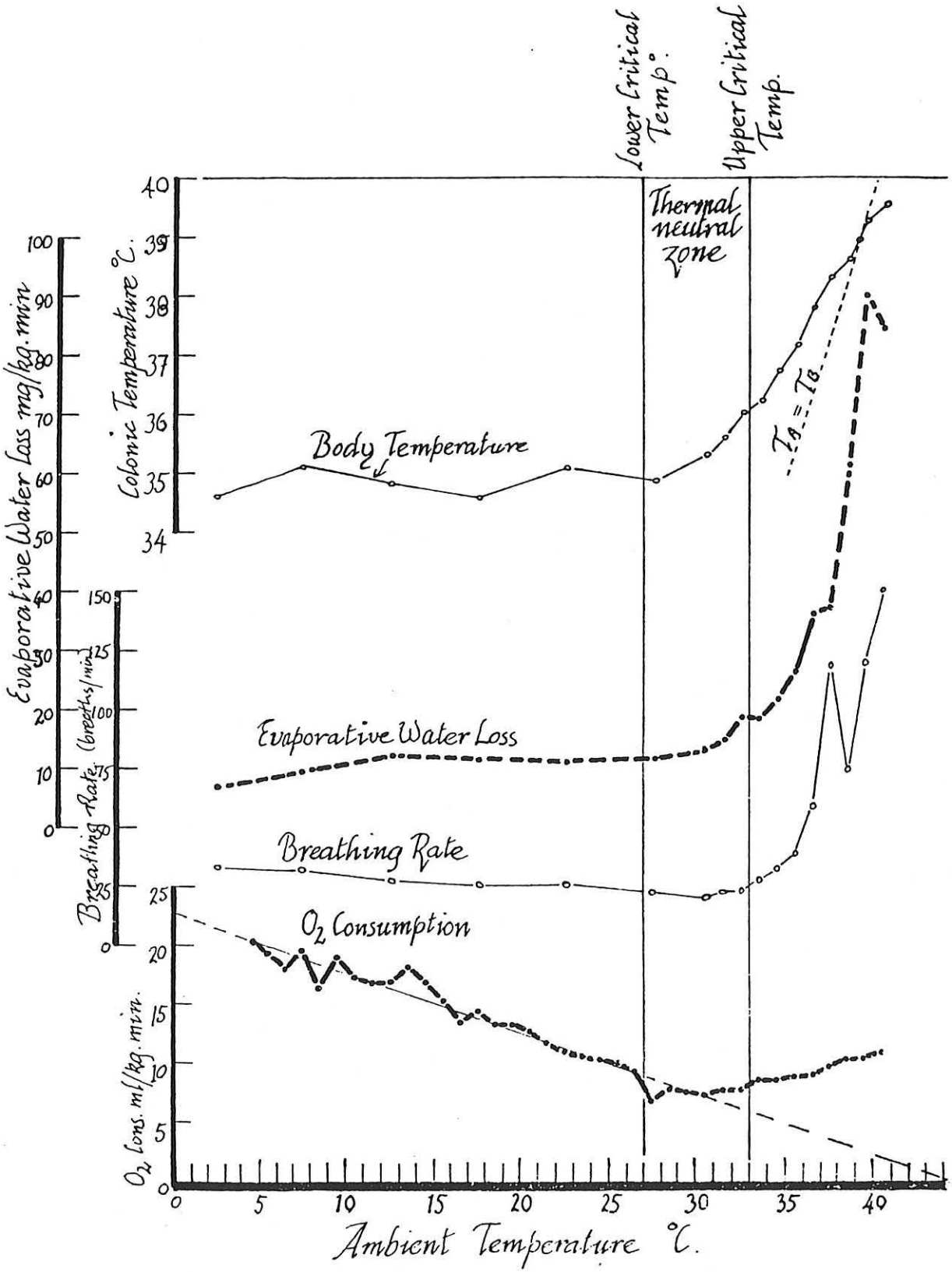
Figs 13.2 and 13.3 summarise the response of the chuditch to ambient temperatures from 0° to 41°C. Fig 13.2 shows mean T_b and mean rates of O_2 consumption, breathing

and evaporative water loss (EWL). The lower (27°C) and upper (33°C) critical temperatures bound an ill-defined thermal neutral zone, extending over six degrees, within which O_2 consumption and breathing rates are minimal despite an average increase in T_b from about 35° to 36°C. Mean rates of EWL rise from 11 mg/kg. min. to 19 mg/kg. min. through the thermal neutral zone (by about 70 per cent) but this rise is not accompanied by an increase in breathing rate. It must be due therefore partly to the increased amount of water in saturated air leaving the lungs (at an increased T_b) and partly to increased insensible water loss from the skin.

Below the lower critical temperature average T_b of resting animals varies between 34.6° and 35.2°C. At the lower limit of the ambient temperature range (near 0°C) EWL is lower than at the lower critical temperature while O_2 consumption shows a three-fold increase and breathing rate is increased by about 50 per cent.

Above the upper critical temperature T_b increases so that T_b equals T_a at 39°C and is maintained slightly below T_a at higher temperatures. Under these conditions EWL is 600 to 700 per cent of the rate at the lower critical temperature and the heat equivalent of EWL is equal to heat production. A marked increase in the breathing rate accompanies the rise in EWL at high T_a, indicating that evaporation from the respiratory surfaces

Fig 13.2 Summary graph showing four parameters of metabolism of the chuditch vs. ambient temperature.


Lower Critical Temp.
Upper Critical Temp.
Thermal neutral zone
Body Temperature
$T_A = T_B$
Evaporative Water Loss
Breathing Rate
O_2 Consumption
Evaporative Water Loss mg/kg.min
Colonic Temperature °C.
Breathing Rate (breaths/min)
O_2 Cons. ml/kg.min.
Ambient Temperature °C.

is of prime importance in dissipating body heat. The increase in O_2 consumption which occurs above the upper critical temperature can be attributed largely to the Q_{10} effect resulting from increased T_b (Q_{10} = 2.6). This suggests that the amount of energy utilized for panting is not large.

The metabolic parameters of O_2 consumption and EWL in the range 0^o-41^oC (T_a) are expressed in terms of heat production and heat loss (cal/g/hr) in Fig 13.3. Mean body temperature is again shown. The amount of heat lost by evaporation varies only slightly over the range 4^o to 30^oC although, as heat production is reduced the closer the lower critical is approached, it represents an increasing proportion of heat production (about 5 per cent at 4^oC; 20 per cent at 30^oC). Evaporative heat loss (EHL) does not represent a significantly greater proportion of heat production until 36^oC (T_a) when EHL equals about 50 per cent of heat production. At 39^o EHL represents slightly more than 100 per cent of heat production. The most rapid increase in EHL naturally coincides with the closing of other avenues of heat loss as T_a approaches T_b. The animals become hyperthermic at temperatures above the lower critical temperature so that T_b is greater than T_a until 39^oC, some four degrees above resting T_b at the lower critical temperature. This hyperthermia maintains a positive thermal gradient from the body to the environment. The

shaded area (A) on Fig 13.3 represents the portion of heat production at 27° to 39°C which is either stored in the body, causing an increase in T_b, or which can be dissipated to the environment by radiation, convection and conduction. It also represents the amount of heat which would need to be lost by evaporative means if T_b were rigidly maintained at 35°C. The area within (A) can be expressed as cal/g/hr/°C or as mg H_2O/g/hr/°C to approximate the size of this saving (Table 13.1).

According to this representation then, when T_a is 39°C, there is a total of 10.7 cal/g/hr which has not been dissipated by evaporation. This should be sufficient to raise T_b by more than 10°C. In fact T_b rises by about 4°C. Thus not all of the heat represented by (A) has been stored. Some then must be lost by non-evaporative means. That this suggestion is correct is supported by an observation noted in Chapter X, p. 10.9. Here it was noted that the smaller females, which could stretch out in the metabolism chamber, tolerated high T_a better than the larger males which were cramped and presumably could expose a smaller proportion of their body surfaces.

The cost of dissipating (A) by evaporation of water is high compared with the measured evaporative water loss at T_a 27°-39°C. Measured EWL (from Table 10.1 but expressed as mg H_2O/g/hr) is compared with the calculated amount of water that would have to be evaporated to dissipate the

Fig 13.3 Summary graph showing heat production, evaporative heat loss and body temperature of the chuditch vs. ambient temperature.

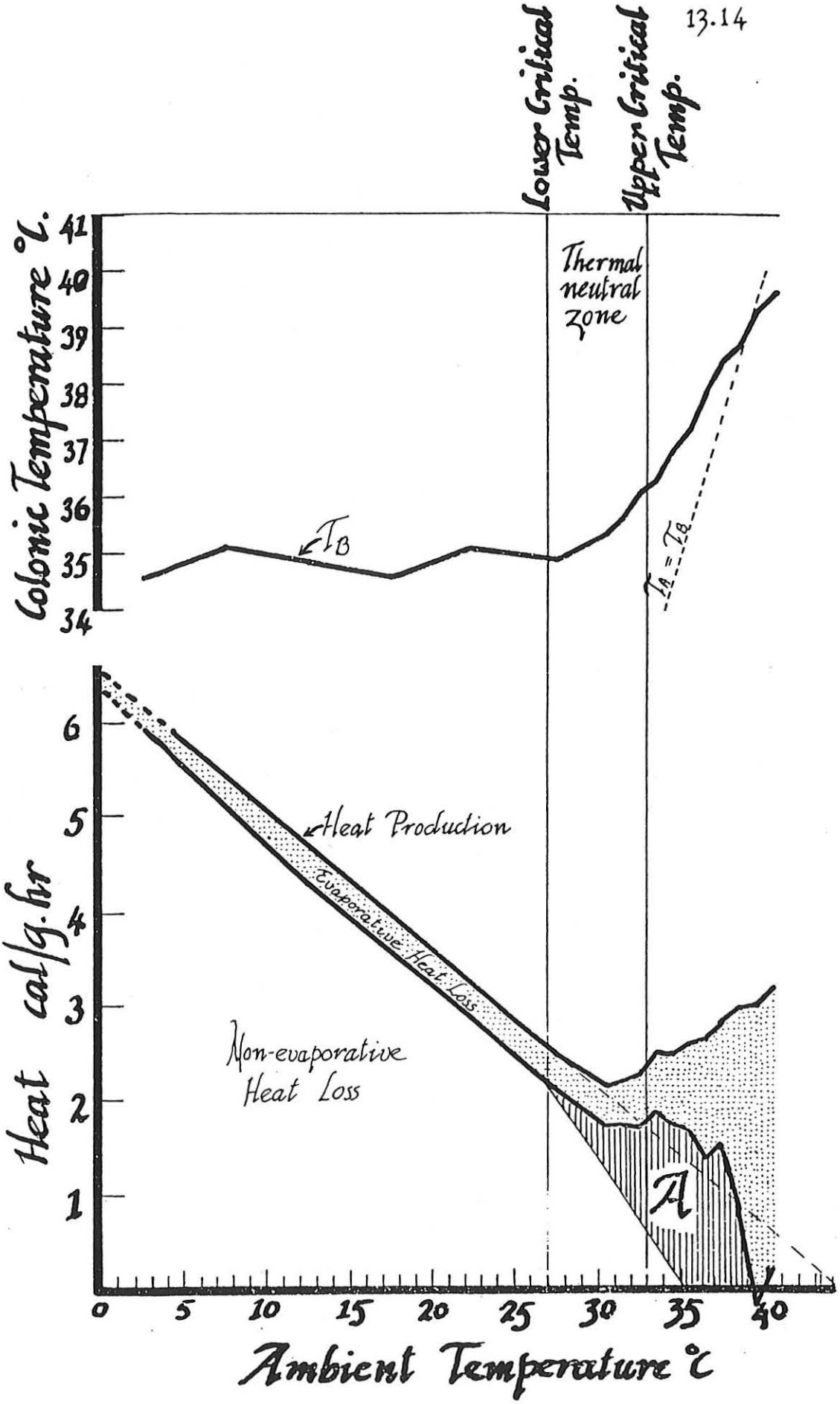

Lower Critical Temp.
Upper Critical Temp.
Thermal neutral zone
Colonic Temperature °C.
41
40
39
38
37
36
35
34
T_B
$T_A = T_B$
Heat cal/g.hr
6
5
4
3
2
1
Heat Production
Evaporative Heat Loss
Non-evaporative Heat Loss
A
0
5
10
15
20
25
30
35
40
Ambient Temperature °C

Table 13.1

Area (A) from Fig 13.3 expressed as cal/g/hr/°C, and mg H_2O/g/hr/°C compared with measured evaporative water loss (from Table 10.1, p.10.7) expressed in the same units.

T_a (°C)	Area (A)		Measured EWL
	cal/g/hr/°C	mg H_2O/g/hr/°C	mg H_2O/g/hr
27 - 28	0.06	0.1	0.7
28 - 29	0.18	0.3	
29 - 30	0.30	0.5	
30 - 31	0.48	0.8	0.7
31 - 32	0.72	1.2	0.9
32 - 33	0.96	1.7	1.0
33 - 34	1.38	2.4	1.1
34 - 35	1.56	2.7	1.3
35 - 36	1.62	2.8	1.6
36 - 37	1.38	2.4	2.2
37 - 38	1.38	2.4	2.3
38 - 39	0.72	1.2	3.7

portion of (A) for each degree interval in Table 13.1. It is clear that until T_a exceeds 38°C, measured EWL is much lower than it would be if T_b were to be maintained at 35°C by evaporative heat loss.

A classical precept of mammalian thermoregulation is that body temperature is maintained constant at ambient temperatures above the thermal neutral zone, at the cost of high evaporative water loss, and that hyperthermia occurs only when evaporative cooling fails to dissipate the environmental heat load plus the metabolic heat load. At this stage body temperature rises and so, as a consequence, does metabolic rate. The result is an impasse in which body temperature rapidly rises to lethal limits unless the heat load is removed. In other words hyperthermia occurs only at the limits of an animal's capacity to deal with high ambient temperatures. There are many exceptions to this pattern in which hyperthermia occurs before the onset of high rates of evaporative cooling. By tolerating a rise in body temperature a positive gradient is maintained from the body to the environment, allowing heat to be lost by radiation and other non-evaporative means.

Hart (1971) cited many cases in which rodents become hyperthermic above 30°C (T_a) and noted that some desert rodents appear to show a remarkable ability to elevate T_b without an accompanying elevation of O_2 consumption. MacMillen and Lee (1970) found that two Australian desert

rodents, Notomys cervinus and N. alexis, become markedly hyperthermic at T_a 37°C. Hyperthermia at high ambient temperatures occurs in a number of large ungulates, notably the camel (Schmidt-Nielsen et al, 1957) and in Grant's gazelle and the oryx (Taylor, 1970).

A number of marsupials show an increase in T_b when T_a is above thermal neutrality. Morrison (1946) investigated the response to low and high T_a of three central American mammals, a rodent, Proechimys, and two didelphids, Didelphis marsupialis and Metacheirus nudicaudatus. All maintained rather constant T_b from about 15°-28°C (T_a) but T_b rose sharply above 30°C (T_a). Bentley (1960) found little evidence of hyperthermia in Setonix exposed for three hours to 40°C, temperature of normally hydrated animals rising 0.48°C above resting T_b compared with 1.88°C for dehydrated animals. However Kinnear and Shield (1975) found that Setonix, as well as Pseudocheirus and Macrotis, shows increased T_b at high ambient temperatures. Several other marsupials show a marked rise in T_b at high T_a. Body temperature of Trichosurus vulpecula rises gradually from 35.9°C at 22°-26.5°C (T_a) to approximately 37°C at 30°C (T_a) and to 39.1°C at 38.5°-41.5°C (T_a) (Dawson, 1969). Lagorchestes conspicillatus becomes moderately hyperthermic between 35° and 42.8°C (T_a) (Dawson and Bennett, 1970). The large kangaroos, Megaleia and Macropus robustus, show a rise in body temperature from a minimum of 35.7° and 35.5°C

respectively at 22°C (T_a) to 37.8° and 37.6°C respectively at 45°C (T_a). In the bandicoots Isoodon macrourus, Macrotis lagotis, and Perameles nasuta, an increase in body temperature occurs above 30°C (T_a) (Hulbert and Dawson, 1974b).

The hyperthermia displayed by the chuditch as T_a rises above about 30°C is typical of the response of many mammals to high environmental temperatures. It should not be regarded as a consequence of imperfect thermal regulation. Rather it appears to be, even in small mammals, a stratagem to avoid high rates of water loss when there is moderate thermal stress.

In its breeding and development the chuditch is similar to the closely related Dasyurus viverrinus. The breeding season and the duration and sequence of pouch development are similar in the two species.

The basal energy requirements of the chuditch are lower than those of many eutherian mammals. In this it resembles other Australian marsupials on one hand and a number of small eutherian mammals from arid environments on the other.

The chuditch is known to have occurred in the inland of Australia where rainfall is unreliable, free surface water is limited and extremes of temperature occur,

although it is now apparently restricted to the more temperate south-western part of the continent. It is therefore not surprising that, within the limits of its small body size, it is physiologically equipped to tolerate a wide range of environmental temperatures. Its thermal regulation is effective at temperatures close to freezing; its labile body temperature at moderate environmental temperatures appears to reflect a mechanism to reduce energy usage during the portion of the daily cycle when it is inactive; a tolerance of hyperthermia reduces the need for evaporative water loss during short-term exposure to high temperatures. The reasons for the contraction in its range of distribution since European settlement must therefore be sought in its ecological relationships rather than in its physiology.

APPENDICES

APPENDIX A

Schedule of mean body weights and head and pes lengths for known-age chuditches from birth to 21 weeks of age, together with tooth eruption stages and certain features which become established at the specified ages.

Age (weeks)	Body Weight (g)	Head Length (mm)	Pes Length (mm)	Tooth Eruption stage	Other Features
0	0.015				
2	0.38	7.8*	2.5		eye rudiment visible; ankle joints and digits visible
4	1.02	10.8*	3.4		underfur on head; permanent claws present
6	3.30	17.6*	5.5		pinnae pigmented
7	4.74	17.3**	8.1		
8	10.75	25.3	10.4		underfur all over body; can progress
9	17.83	28.6	13.3		righting reflex
10	26.9	34.6	17.2		lips free; shiver

* 1 animal

** 2 animals, not including *.

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APPENDIX A (concluded)

Age (weeks)	Body Weight (g)	Head Length (mm)	Pes Length (mm)	Tooth Eruption stage	Other Features
				incisors visible through oral membrane	
11	46.6	40.0	21.3		eyes open; ears erect
12	61.6	43.4	24.2		stand erect
13	84.5	46.8	26.7	I $\frac{1}{3}$	
					movements well co-ordinated; body fully furred
14	115.2	50.5	31.2	I $\frac{2}{3}$;C $\frac{0}{1}$	
15	144.0	54.2	34.0	I $\frac{2 - 3}{3}$;C $\frac{1}{1}$;M	full coat; eat meat
16	171.7	56.8	37.8		
17	210.6	60.5	40.9	I $\frac{3}{3}$;C $\frac{1}{1}$;M	cusps well erupted
19	310.3	67.5	48.0	I $\frac{4}{3}$	
21	406.4	73.3	52.9		

APPENDIX B

Body temperature of known-age pouch young on removal from the pouch and at 10 minute intervals thereafter for one hour; body weight and prevailing ambient temperature are also given.

Age (wks)	Body wt.* (g)	T_a (°C)	Body Temperature after specified time of exposure (°C)≠						
			Initial	10 min.	20 min.	30 min.	40 min.	50 min.	60 min.
10 (n=5)	25.7± 0.51	19.3	30.4±0.27 29.7-31.2	26.7±0.33 25.9-27.5	24.2±0.26 23.4-24.7	23.4±0.14 23.1-23.8	23.1±0.18 22.5-23.5	23.3±0.29 22.7-24.6	23.4±0.26 22.7-24.3
11 (n=8)	46.6± 2.24	18.4-19.3	29.9±0.85 27.4-34.8	26.3±0.78 24.5-29.8	24.9±0.47 23.5-27.6	24.7±0.41 23.4-27.3	24.4±0.41 23.2-26.9	23.9±0.64 22.5-26.9	23.1±0.57 21.9-26.9
12 (n=8)	63.7± 5.44	18.7-19.4	30.4±0.46 28.5-32.2	27.4±0.62 24.7-30.4	25.8±0.54 24.0-28.3	24.4±0.47 23.5-26.9	23.8±0.54 22.8-26.8	23.2±0.51 22.1-26.5	22.8±0.46 21.6-25.6
13 (n=8)	84.5± 7.25	17.4-19.2	28.6±1.30 25.3-32.0	27.3±0.90 24.9-31.1	26.7±0.84 24.2-30.1	26.6±0.76 24.3-30.0	26.0±0.74 23.9-29.2	25.9±0.86 23.4-29.8	25.7±0.94 23.1-29.9
14 (n=8)	115.2± 8.63	17.9-21.8	31.7±0.45 29.7-33.6	31.9±0.64 29.0-34.6	31.8±0.72 28.6-34.1	32.3±0.92 28.5-35.7	32.3±1.00 28.4-35.8	32.5±1.05 28.3-36.1	32.5±1.03 28.2-35.6

* mean ± 1 s.e.

≠ mean ± 1 s.e. and range

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APPENDIX B (concluded)

Age (wks)	Body wt.* (g)	T_a (°C)	Body Temperature after time of exposure (°C)≠						
			Initial	10 min.	20 min.	30 min.	40 min.	50 min.	60 min.
15 (n=8)	144± 14.1	17.9- 20.8	34.4±0.95 30.1-36.8	35.0±0.78 30.2-37.5	34.9±0.73 30.3-37.6	35.1±0.70 30.6-37.6	35.1±0.70 30.6-37.7	35.1±0.65 31.0-37.6	35.1±0.72 30.6-37.8
16 (n=	172± 16.5	18.0- 20.8	35.5±0.29 35.0-36.0 (3)	35.7±0.48 34.4-37.4 (7)	36.2±0.32 35.3-37.8 (7)	36.6±0.29 35.6-37.9 (8)	37.5±0.25 37.0-37.8 (3)	36.6±0.30 35.6-38.0 (8)	36.3±0.31 35.4-37.6 (8)
17 (n=8)	211± 18.4	17.5- 18.3	—	32.3±0.94 28.7-36.2	34.6±0.75 31.4-37.8	35.7±0.50 33.4-37.6	36.3±0.37 34.5-37.9	36.5±0.33 35.0-37.9	36.5±0.30 35.1-37.6
18 (n=	307± 33.2	17.5- 18.5	—	36.8 36.1-37.5 (2)	—	38.1±0.17 37.8-38.4 (3)	37.8 37.8 (2)	37.9±0.09 37.8-38.1 (3)	37.8±0.20 37.6-38.2 (3)

* mean ± 1 s.e.

≠ mean ± 1 s.e. and range

APPENDIX C

(Data plotted on Fig 6.2)

Diurnal variation in body temperature for six juveniles, and four adults measured at the environmental temperature prevailing in 'home' cages.

Local time (hrs)	Mean Environmental Temperature (°C)	Juveniles			Adults		
		No. values	Mean Body Temp. °C. ± 1 s.e.	Range	No. values	Mean Body Temp. °C. ± 1 s.e.	Range
0600	16.3	18	34.01 ± 0.195	33.0-35.4	12	35.07 ± 0.455	33.4 - 37.8
0900	20.8	18	33.74 ± 0.239	31.5-35.4	12	34.65 ± 0.476	32.0 - 36.9
1200	22.9	18	34.02 ± 0.159	33.1-35.3	12	34.98 ± 0.412	33.0 - 37.8
1500	22.5	18	34.41 ± 0.165	33.2-35.6	12	34.35 ± 0.336	32.1 - 36.2
1800	20.3	18	34.30 ± 0.155	33.6-36.1	12	34.64 ± 0.456	32.2 - 36.8
2400	17.8	24	35.15 ± 0.182	33.0-36.6	7	36.83 ± 0.172	36.5 - 37.8
Overall		114	34.32 ± 0.087	31.5-36.6	67	34.96 ± 0.187	32.0 - 37.8

APPENDIX D

Weight losses of six animals maintained singly in small cages at an ambient temperature of 20°C during a period of seven days starvation.

Animal No.	Age in months	Sex	Weight (gm) 1 day after feeding	Wt.(gm) 7 days after feeding	Wt. loss grams	Wt. loss per cent	Mean loss /day grams	Mean loss grams/kg.
8	9	female	930	750	180	19.3	30.0	32.3
14	Adult	female	700	540	160	22.9	22.9	32.7
6	21	female	800	675	125	15.6	20.8	26.0
9	9	male	1420	1150	270	19.0	45.0	31.7
4	21	male	1225	1075	150	12.2	25.0	20.4
3	21	male	1175	1050	125	10.7	20.8	17.7

APPENDIX E

O_2 consumption rates at one degree intervals of ambient temperature, for animals in the metabolism chamber while T_a was gradually increased.

T_a (°C)	O_2 consumption (ml/kg.min)			Variance	No. Values
	Mean	s.e.	Range		
4.0- 4.9	20.25	2.975	10.28-35.19	62.0	7
5.0- 5.9	19.28	2.361	6.85-28.96	55.8	10
6.0- 6.9	17.94	2.515	13.28-22.60	25.3	4
7.0- 7.9	19.49	1.538	13.44-23.86	21.3	9
8.0- 8.9	16.15	2.391	8.10-22.42	34.3	6
9.0- 9.9	18.89	0.956	7.47-32.70	35.6	39
10.0-10.9	17.28	0.753	6.01-27.65	26.6	47
11.0-11.9	16.94	0.639	5.76-34.35	39.6	97
12.0-12.9	16.82	0.951	7.48-30.02	34.3	38
13.0-13.9	18.12	1.108	9.45-31.36	45.4	37
14.0-14.9	16.71	0.810	5.21-31.51	24.9	38
15.0-15.9	15.24	0.621	5.86-25.64	16.6	43
16.0-16.9	13.41	0.633	7.42-22.09	16.0	40
17.0-17.9	14.42	0.549	7.89-21.62	9.7	32
18.0-18.9	13.24	0.447	7.42-21.10	8.6	43
19.0-19.9	13.19	0.536	5.33-32.67	25.0	87
20.0-20.9	12.64	0.508	5.71-21.37	15.7	61
21.0-21.9	11.54	0.479	5.43-17.97	11.2	49
22.0-22.9	10.80	0.460	6.92-20.62	7.8	37
23.0-23.9	10.40	0.488	4.74-23.21	11.4	48
24.0-24.9	10.19	0.454	5.36-20.42	9.9	48
25.0-25.9	9.97	0.285	3.93-18.21	7.9	97
26.0-26.9	9.34	0.297	5.02-16.33	5.9	67
27.0-27.9	6.78	0.165	5.11-10.67	1.3	47
28.0-28.9	7.85	0.217	5.21-13.08	3.3	70
29.0-29.9	7.68	0.189	4.64-12.07	2.7	75

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APPENDIX E (concluded)

T_a (°C)	O_2 consumption (ml/kg.min)			Variance	No. Values
	Mean	s.e.	Range		
30.0-30.9	7.34	0.113	4.34-11.60	1.9	152
31.0-31.9	7.71	0.180	4.34-16.90	4.6	141
32.0-32.9	7.76	0.159	4.25-14.22	3.3	129
33.0-33.9	8.68	0.260	4.81-18.82	8.3	122
34.0-34.9	8.57	0.296	4.78-21.47	10.1	115
35.0-35.9	8.96	0.413	3.41-34.20	16.7	98
36.0-36.9	9.09	0.261	4.26-25.21	7.2	106
37.0-37.9	9.77	0.385	4.09-26.70	12.3	83
38.0-38.9	10.22	0.674	5.22-18.85	15.0	33
39.0-39.9	10.38	0.690	8.20-21.85	12.4	26
40.0-40.9	10.93	0.950	7.67-19.39	12.6	14

APPENDIX F

Weight-relative O_2 consumption, predicted O_2 consumption from the interspecific regression for dasyurids (MacMillen and Nelson, 1969) and observed/predicted O_2 consumption (per cent) for 41 determinations carried out on 29 animals in the ambient temperature range 30°-30.9°C. Experiment numbers bracketed together are for the same animal carried out at different times.

Exp. No.	Sex	Body Wt. (kg)	O_2 consumption (ml/kg.min)		Observed O_2 / Predicted O_2 (%)
			Observed	Predicted	
Delan 1	M	1.075	5.64	6.60	85.5
13		1.140	5.93	6.50	91.2
27A		1.600	3.68	5.95	61.8
33A		1.565	5.59	5.99	93.3
Delan 2	M	1.300	6.03	6.29	95.9
28A		1.500	6.58	6.05	108.8
Delan 3	M	1.300	6.57	6.29	104.5
Delan 4	F	1.000	9.93	6.73	147.5
29A		1.025	5.80	6.69	86.7
Delan 17	M	1.400	6.09	6.16	98.9
25		1.465	6.77	6.09	111.7
Delan 23A	M	2.000	3.88	5.62	69.0
23B		2.000	3.88	5.62	69.0
Delan 19	F	1.030	4.64	6.68	69.5
Delan 21	F	0.850	9.36	7.02	133.3
Delan 20	F	0.890	7.61	6.94	109.7
Delan 18	F	0.900	11.22	6.92	162.1
Delan 16	F	0.855	6.98	7.01	99.6
26A		1.000	6.04	6.73	89.7
7		1.075	5.87	6.60	88.9
Delan 24	M	0.900	7.27	6.92	105.1
Delan 30A	F	0.770	7.81	7.20	108.5
Delan 32A	M	0.775	8.75	7.19	121.7
Delan 31A	M	0.775	8.90	7.19	123.8
Delan 6	F	0.850	7.09	7.02	101.0
Delan 22	M	1.375	6.72	6.19	108.6
Dehyd 21	F	0.875	4.89	6.96	70.3
23		0.850	6.44	7.02	91.7

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APPENDIX F (concluded)

Exp. No.	Sex	Body Wt. (kg)	O_2 consumption (ml/kg.min)		Observed O_2 / Predicted O_2 (%)
			Observed	Predicted	
Dehyd 11	F	0.800	6.93	7.13	97.2
19		0.700	6.81	7.39	92.2
Dehyd 3	F	0.925	5.39	6.87	78.5
27		1.050	4.80	6.64	72.3
Dehyd 7	M	1.000	9.38	6.73	144.6
Dehyd 8	F	0.825	7.96	7.08	112.4
Dehyd 9	M	1.675	9.10	5.88	154.8
Dehyd 10	M	1.075	7.50	6.60	113.6
Dehyd 12	F	1.100	6.45	6.57	98.2
Dehyd 14	F	1.000	6.61	6.73	98.2
Dehyd 18	F	0.750	6.96	7.25	96.0
Dehyd 20	M	1.100	6.59	6.57	100.3
Dehyd 26	M	1.150	10.09	6.49	155.5

APPENDIX G

Mean Hourly Oxygen Consumption Rates measured during prolonged exposure to Constant Ambient Temperature. (Data plotted on Fig 8.5).

Hour	No. values	O_2 consumption (ml/kg.min)		
		Mean	Standard Error	Range
a) Lab.No.2, male-Body Wt. 1.4 kg. 25 hr run at 10°C (T_a)				
0000 - 0059	28	18.50	0.82	11.96 - 26.71
0100 - 0159	13	18.23	0.96	11.60 - 24.55
0200 - 0259	10	22.37	0.65	18.19 - 25.36
0300 - 0359	9	19.79	1.28	14.86 - 25.03
0400 - 0459	13	21.54	1.11	13.72 - 28.77
0500 - 0559	9	24.95	0.44	23.24 - 27.04
0600 - 0659	4	21.91	1.82	16.98 - 25.76
0700 - 0759	12	13.22	1.25	7.29 - 18.55
0800 - 0859	12	16.21	2.07	8.40 - 29.81
0900 - 0959	15	12.01	1.95	3.82 - 26.01
1000 - 1059	26	22.93	1.14	12.11 - 29.92
1100 - 1159	26	18.73	0.97	9.04 - 26.55
1200 - 1259	18	14.58	0.87	9.51 - 20.44
1300 - 1359	12	21.84	1.37	13.19 - 28.09
1400 - 1459	10	15.34	1.69	8.24 - 23.57
1500 - 1559	16	23.97	1.21	12.28 - 29.66
1600 - 1659	11	18.48	1.07	12.42 - 22.70
1700 - 1759	12	24.20	1.77	9.74 - 31.27
1800 - 1859	11	20.36	1.73	10.29 - 26.60
1900 - 1959	8	17.66	1.28	13.99 - 23.06
2000 - 2059	9	19.73	0.94	14.79 - 24.21
2100 - 2159	12	18.27	1.02	10.04 - 22.29
2200 - 2259	13	21.47	0.62	18.03 - 25.39
2300 - 2359				
Start		16.72	0.75	10.88 - 26.26
Finish		23.02	1.20	20.63 - 24.35
Mean of means for last 24 hours of run	24	19.55	0.71	

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APPENDIX G (contd.)

Hour	No. values	O_2 consumption (ml/kg.min)		
		Mean	Standard Error	Range
b) Lab.No.15, female-Body Wt. 0.9 kg. 26 hr run at 15°C (T_a)				
0000 - 0059	5	14.03	1.16	10.86 - 17.23
0100 - 0159	7	16.47	1.17	12.58 - 21.89
0200 - 0259	7	20.89	2.31	15.06 - 31.86
0300 - 0359	8	25.07	2.25	13.22 - 31.54
0400 - 0459	7	14.00	0.37	12.02 - 14.94
0500 - 0559	6	25.89	3.30	15.72 - 36.36
0600 - 0659	10	14.68	1.23	8.28 - 21.93
0700 - 0759				
Start	8	16.05	0.55	13.23 - 17.81
Finish	9	11.83	0.74	8.10 - 14.57
0800 - 0859				
Start	6	15.71	1.59	11.11 - 21.73
Finish	11	15.27	0.93	8.16 - 18.39
0900 - 0959	10	16.12	0.90	12.32 - 22.88
1000 - 1059	8	16.22	1.70	7.44 - 21.83
1100 - 1159	7	14.99	1.51	10.54 - 19.92
1200 - 1259	10	13.06	1.17	7.27 - 17.30
1300 - 1359	10	12.60	1.17	7.21 - 19.86
1400 - 1459	8	12.34	0.90	8.46 - 15.37
1500 - 1559	8	12.03	0.77	8.29 - 14.84
1600 - 1659	8	11.62	0.68	8.91 - 13.79
1700 - 1759	8	12.39	0.86	8.80 - 15.87
1800 - 1859	12	21.47	1.56	12.93 - 30.70
1900 - 1959	9	21.96	3.52	11.38 - 39.32
2000 - 2059	7	17.54	1.02	13.97 - 21.73
2100 - 2159	6	13.10	1.18	10.34 - 17.59
2200 - 2259	4	19.65	4.43	12.24 - 31.88
2300 - 2359	7	14.47	2.11	6.03 - 22.55
Mean of means for last 24 hours of run	24	16.15	0.86	

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Hour	No. values	O_2 consumption (ml/kg.min)		
		Mean	Standard Error	Range
c) Lab.No.2, male - Body Wt. 1.4 kg. 27 hr run at 30°C (T_a)				
0000 - 0059	3	5.06	0.15	4.76 - 5.21
0100 - 0159	6	5.95	0.29	5.21 - 6.83
0200 - 0259	5	5.68	0.22	4.94 - 6.29
0300 - 0359	5	5.75	0.08	5.57 - 5.94
0400 - 0459	5	7.47	1.01	5.58 -11.25
0500 - 0559				
Start	6	8.95	0.40	7.79 -10.55
Finish	6	5.83	0.16	5.33 - 6.15
0600 - 0659				
Start	5	7.42	0.48	4.54 - 7.42
Finish	5	6.11	0.28	5.50 - 6.78
0700 - 0759				
Start	5	7.44	0.35	6.93 - 8.66
Finish	6	5.59	0.37	4.88 - 7.39
0800 - 0859	4	6.82	0.21	6.20 - 7.12
0900 - 0959	4	6.96	0.30	6.11 - 7.42
1000 - 1059	7	6.92	0.21	6.51 - 7.78
1100 - 1159	7	6.59	0.15	6.30 - 7.47
1200 - 1259	5	5.70	0.20	5.39 - 6.38
1300 - 1359	4	5.91	0.54	4.75 - 7.35
1400 - 1459	3	5.98	0.30	5.38 - 6.28
1500 - 1559	7	5.50	0.17	5.02 - 6.17
1600 - 1659	4	5.58	0.04	5.54 - 5.72
1700 - 1759	5	5.55	0.02	5.47 - 5.65
1800 - 1859	7	6.18	0.16	5.83 - 6.90
1900 - 1959	7	6.00	0.29	5.02 - 7.17
2000 - 2059	5	6.16	0.17	6.18 - 7.17
2100 - 2159	5	6.08	0.35	5.02 - 7.17
2200 - 2259	5	5.19	0.11	4.86 - 5.40
2300 - 2359	4	5.53	0.08	5.40 - 5.75
Mean of means for last 24 hours of run	24	6.00	0.12	

(concluded on next page)

APPENDIX G (concluded)

Hour	No. values	O_2 consumption (ml/kg.min)		
		Mean	Standard Error	Range
d) Lab.No.15, female-Body Wt. 0.86 kg. 26 hr run at 30°C (T_a)				
0000 - 0059	7	6.73	0.22	5.85 - 7.42
0100 - 0159	5	7.07	0.29	6.14 - 7.79
0200 - 0259	6	7.50	0.49	6.33 - 9.16
0300 - 0359	6	7.91	0.40	6.34 - 8.96
0400 - 0459	5	7.99	0.34	7.11 - 8.87
0500 - 0559	5	6.50	0.37	5.85 - 8.08
0600 - 0659	4	6.55	0.26	6.14 - 7.20
0700 - 0759				
Start	7	7.46	0.42	6.21 - 9.61
Finish	4	6.11	0.12	5.85 - 6.43
0800 - 0859				
Start	7	6.17	0.21	5.53 - 6.89
Finish	5	5.65	0.11	5.36 - 6.04
0900 - 0959	8	5.81	0.14	5.35 - 6.41
1000 - 1059	6	5.83	0.10	5.53 - 6.04
1100 - 1159	8	6.29	0.16	5.81 - 6.89
1200 - 1259	6	5.98	0.27	5.33 - 7.17
1300 - 1359	6	6.06	0.32	5.04 - 6.78
1400 - 1459	7	6.00	0.45	5.13 - 8.62
1500 - 1559	6	5.70	0.06	5.52 - 5.81
1600 - 1659	8	6.18	0.10	6.00 - 6.68
1700 - 1759	7	8.85	1.09	5.26 -13.27
1800 - 1859	8	7.37	0.28	6.51 - 8.60
1900 - 1959	8	7.27	0.31	5.86 - 8.80
2000 - 2059	7	8.27	0.45	6.35 - 9.87
2100 - 2159	9	8.28	0.79	6.85 -14.29
2200 - 2259	8	7.80	0.37	6.16 - 9.24
2300 - 2359	8	7.81	0.35	6.39 - 9.24
Mean of means for last 24 hours of run	24	6.90	0.20	

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