BIOENERGETICS AND THERMOREGULATION IN THE ROCK HYRAX, *PROCAVIA CAPENSIS* (PALLAS).

by

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ABSTRACT

1.Hyrax, *Procavia capensis*, were found to have a lower than predicted resting metabolic rate (RMR) and conductance (C). The thermoneutral zone was found to be from 20° to 30°C in adults and from 25° to 30°C in juveniles. The body temperature (Tb) was highly labile in adults, ΔTb = 4,0°C, but less so in juveniles, ΔTb = 1,5°C. Acclimation to lower ambient temperatures caused an overall lower Tb to be maintained.

2.There was a positive linear relationship between heart rate (HR) and RMR, supporting the hypothesis VO_2 = f.HR . There was also a positive relationship between HR and the degree of activity.

3.Average daily metabolic rate calculated from HR, RMR and activity at the outdoor holding facility, was similar to values based on direct calorimetry.

4.Infra-red radiation was implicated in the increase of Tb shown in hyrax otherwise exposed to constant ambient temperatures.

5.No clear relationship between the thyroid data and environmental conditions could be discerned.

6.The difference between adult and juvenile thermoregulation seems to be that where adults show no change in conductance but exhibit considerable thermolability when exposed to low ambient temperatures, juveniles limit their degree of thermolability and exhibit a decrease in conductance when acclimated to low ($10^{o}C$) ambient temperatures. It is suggested that the considerable thermolability shown by adults is of decided value in energy conservation in that it allows the adults to limit the metabolic rate increase to an extent, lower than would otherwise have occured when exposed to low ambient temperatures with the concomitant limited food supplies.

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-LIST OF ABBREVIATIONS-

ADMR - Average daily metabolic rate ($kJ(g.24h)^{-1}$)

ANOVA - Analysis of variance

A-V O_2 diff - Arterio-venous oxygen difference

BMR - Basal metabolic rate

C - Conductance

HE - Haematoxylin-eosin

HR - Heart rate (beat/min)

IR - Infra-red

ME - Metabolizable energy ($kJ(g.24h)^{-1}$)

NST - Non-shivering thermogenesis

RIA - Radio-immuno assay

RMR - Resting metabolic rate

SV - Stroke volume

Ta - Ambient temperature (^{o}C)

Tb - Body temperature (^{o}C)

Tlc - Lower critical temperature (^{o}C)

TMr - Total metabolic requirement

TNZ - Thermoneutral zone

Tr - Radiant temperature (^{o}C)

Trec - Rectal temperature (^{o}C)

TSH - Thyroid stimulating hormone

Tuc - Upper critical temperature (^{o}C)

T3 - Triiodo-L-thryonine

T4 - L-thyroxine

VO_2 - Oxygen consumption (ml $O_2(g.h)^{-1}$)

W - Mass (g)

CHAPTER ONE : INTRODUCTION

The Hyracoidea are a successful order, considered both in terms of evolution and distribution, and occupy a wide range of habitats in Africa and the Middle East. These range from sea level to the alpine zone, and from semi-desert to rain forest (Coe 1962, Hanse 1962, Sale 1965, Lensing 1975).

Phylogenetically the Hyracoidea are the most primitive living ungulates and are grouped, along with the Proboscidea and the Sirenia, in the superorder Paenungulata. Within the order Hyracoidea there is only one family, namely Procaviidae. The three genera contained herein are Procavia (the rock hyrax), Heterohyrax (the bush hyrax) and Dendrohyrax (the tree hyrax). They represent a total of 11 species (Thomas 1892, Hahn 1934, Roberts 1951, Sale 1960, Bothma 1964,1971, Hoeck 1975). More recently, however, Roche (1972) published a reclassification of the order that differs considerably from the previous approach.

Procavia and Heterohyrax are gregarious and are usually found in rocky or eroded areas, utilising essentially the same resources. Where they are allopatric they occupy similar niches, whilst when they are sympatric the separation seems to be on the basis of diet (Sale 1966,1970a, Hoeck 1975, Deniro & Epstein 1978, Walker, Hoeck & Perez 1978). When sympatric in distribution very little interspecific aggression has been noted and the two species are sometimes found together sharing a rocky outcrop while basking (Turner & Watson 1965, Hoeck 1975).

Procavia, the larger and more aggressive genus is distributed throughout Africa (Roberts 1951) and the Middle East (Meltzer 1973). Procavia capensis

(Pallas) 1766 is regarded by Bothma (1964) as monotypic and its range in southern Africa extends from Cape Agulhas in the south to Damaraland in South West Africa/Namibia and the Chimanimani mountains of Zimbabwe. It appears to be found in isolated groups in Mozambique (Smithers & Tello 1976).

Past research on the southern African Hyracoidea has, besides taxonomic studies, been concerned with palaeontological, morphological and anatomical studies on especially Procavia capensis. For example, Wells (1936), Whitworth (1954), Churcher (1956) and Kitching (1966) described fossil hyracoids from southern Africa and postulated their relationship with older fossils from northern, central and eastern Africa. While the early detailed anatomical studies of Owen (1832) and Hahn (1934) have been followed more recently by the publications of Millar (1970), Sale (1970b), Swart (1970) and Coetzee (1976) who described various anatomical features of P. capensis.

On the other hand, very little published information is available on the ecology and behaviour of Procavia capensis. Lensing (1975,1979) studied their ecology in SWA, while their nutritional requirements have been described in captivity (Fairall & Millar 1977). In addition, the digestion has been examined by Leon (1980) and Eloff (1981) and growth rates and concomitant age determination criteria delineated by Fairall (1980).

Physiological studies of P. capensis have been concerned mainly with reproduction, serological relationships and the role of hyraxes in transmitting diseases or hosting parasites. The only studies carried out on environmental physiology or related aspects of P. capensis have been done by Louw (1969), Louw (1971) and Louw, Louw & Retief (1973) who reported on renal function and aspects of thermoregulation. Booth (1975) examined the regulation of body temperature in this hyrax while McNairn & Fairall (1979)

carried out a preliminary study into the relationship between heart rate and metabolic rate.

The wide distribution of P. capensis, and the hyracoids in general, poses questions which cannot be adequately answered from published research. For example:- how does the animal cope with high ambient temperatures combined with aridity on the one hand, and low ambient temperatures associated with a relatively limited food supply on the other? A reasonable explanation for the first aspect can be found in behavioural avoidance of high ambient temperatures by remaining within the cool microclimate of the rocky crevices that hyrax utilise. This is combined with an adequate intake of water with the food, as well as the production of metabolic water to make the animal independant of free water (Sale 1965,1966, Louw, et al. 1973, Meltzer 1976, Rubsamen, Heller, Lawrenz & Engelhardt 1979). It will, however, still drink water should this be available (Meltzer 1976, McNairn, I.S. unpublished data).

The second question has, on the other hand, been investigated on the basis of energy metabolism and the first to do this were Taylor and Sale (1969), who suggested that the metabolism of the hyrax may have evolved to conserve energy, possibly utilising an external solar energy source to override a natural hypothermia. Bartholomew & Rainy (1971) in a far more detailed study on Heterohyrax brucei, also indicated that hyrax conserve energy by maintaining a low metabolic rate and a labile body temperature. They reinforced the hypothesis put forward by Taylor & Sale (1969). Rubsamen, et al. (1979) using the relationship between water turnover and metabolic rate, showed P. habessinica to have a lower metabolic rate than predicted on a basis of body mass. To follow up these ideas, McNairn and Fairall (1979) compared the hyrax (P. capensis) to a mammal similar in size, conformation and feeding habits, the guinea pig (Cavia porcellus).

This again confirmed that P. capensis has a lower than predicted metabolic rate and indicated a labile body temperature.

The question now posed by the presence of these stratagems is; in what manner does the highly labile body temperature influence the metabolic rate, especially when the animals are acclimatised or acclimated to lower ambient temperatures?

However, before postulating any more questions, it is necessary to recap and examine the validity of wanting to measure the specific physiological parameters that have been decided upon.These parameters are: metabolic rate, heart rate, body temperature, activity and thyroid gland function.

Metabolic rate, as indicated by either oxygen consumption or metabolised energy, is the simplest method of judging how much it has "cost" the animal to live under the specific conditions to be examined (Kleiber 1947, Schmidt-Nielsen 1979).

Heart rate as an indirect monitor of metabolic rate, has been quite extensively used in a number of different species. Rodents (Morhardt and Morhardt 1971), blue-winged teal (Owen 1969,1970), calves (Holmes, Steven & Toner 1976), sheep (Webster 1967), black duck (Wooley & Owen 1977) and P. capensis in a pilot study (McNairn 1978). The intention is to utilise heart rate measurement in free ranging animals to give an indication of metabolic rate in the field.

The measurement of body temperature was prompted by all the studies showing hyrax to have a labile body temperature (Taylor & Sale 1969, Bartholomew & Rainy 1971, Louw, et al. 1973, Booth 1975, McNairn 1978). The question already stated, is how does this affect the other physiological

parameters to be investigated?

The intention of studying free-ranging animals brings in the requirement to examine the activity patterns of hyrax in the wild, or at least under semi- natural conditions, and to attempt to allocate energetic requirements to the different activities.

In studying the hyrax under varying environmental conditions, it becomes interesting to see how acclimatisation and acclimation affect them and in this way to see what role, if any, the thyroid plays in maintaining homeostasis, both in the laboratory and in the wild. For this reason both thyroid histology and thyroid hormone assays are included.

Finally before attempting to tie up all the loose ends, an inclusion of field data is of vital importance as it helps to put the laboratory data into perspective. The data examined here included age, sex, mass, body temperature, condition and activity on a superficial level.

All these above aspects are illustrated in the form of a flow diagram (Figure 1).

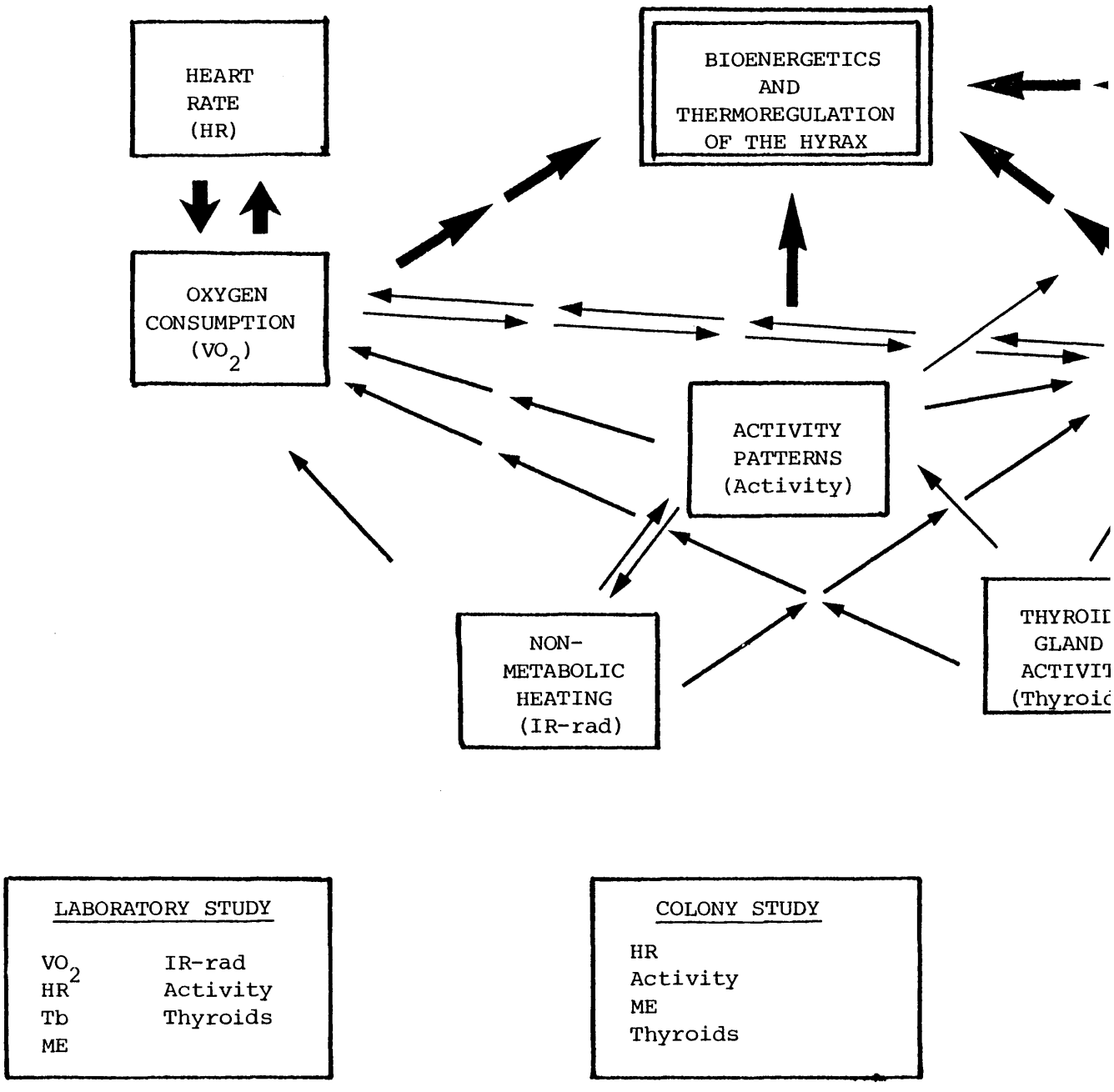

Figure 1: Flow-diagram of research lay-out

STATEMENT OF INTENT

Knowing that the basal metabolic rate (BMR) is lower than predicted and that the hyrax possesses a labile body temperature, it was decided to examine the body temperature in greater detail. At the same time it was intended to measure metabolic rate (both by oxygen consumption and metabolised energy), heart rate, radiant energy utilisation, activity patterns and, where possible thyroid hormones and thyroid histology. During the course of the research, the following questions presented themselves.

1: Is there any difference between adult and juvenile metabolic rates and conductance? If so, what could the reason(s) be for this?

2: How is metabolic rate affected by acclimation to different ambient temperatures and how is the relationship between VO_2 and HR affected?

3: Is it feasible to predict BMR or resting metabolic rate (RMR) from metabolizable energy (ME)?

4: Does VO_2 = fHR (Johnson and Gessaman 1973, McNairn 1978) remain valid for juveniles and adults, and is there any difference between the two groups?

5: How well can average daily metabolic rate (ADMR) be predicted from using VO_2 = fHR when taking activity into account?

6: What advantage, selective or otherwise, does the labile body temperature confer on the hyrax? Is there any difference between adults and juveniles?

7: Is there any relationship between body size and body temperature, or between body size and body temperature fluctuations?

8: Are hypotheses formulated in the laboratory supported by data from fieldwork?

9: Does the thyroid gland, histologically or hormonally, reflect any changes that occur in any other of the parameters studied? Is there any difference in the thyroid status of field animals and laboratory animals?

10: How do any physiological stratagems that may be shown by P. capensis, fit in with the known behavioural stratagems of the hyrax when seen on an holistic level, with regards to the animal and its environment?

11: Is it possible, on the strength of the data that have been collected in this study, to set up a bioenergetic model for P. capensis in southern Africa?

CHAPTER TWO : STUDY AREA

FIELD STUDY AREA

Wolwekraal (25°35'S : 27°44'E) near Brits is an agricultural area that is bisected by parallel mountain ranges, the continuation of the Magaliesberg. The actual area where the hyrax were collected was the north facing slope of a range of low mountains running east to west (altitude: 1100m to 1400m). The habitat was dense bush and trees, maximum canopy height approximately 3m, interspersed with barren rocky outcrops. The vegetation type, according to Acocks (1975), is Sour Bushveld which is found overlying the Bushveld Coagulation Complex. The climatic data is indicated in Figure 2.

CAPTIVE COLONY FACILITY

A colony was set up at the Experimental Farm of the University of Pretoria which is situated some 12km east of the city centre. The climatic conditions of this area are summarized in Figure 3 and in an area slightly cooler than the Wolwekraal study area. It is also slightly dryer, although the number of days on which rain falls is more than at Wolwekraal.

The colony was set up in July 1979 and comprised 40 hyrax from a captive colony obtained from Senekal OFS, five hyrax originally from the Problem Animal Control Research Farm Vrolijkheid, at Robertson, Cape Province, and

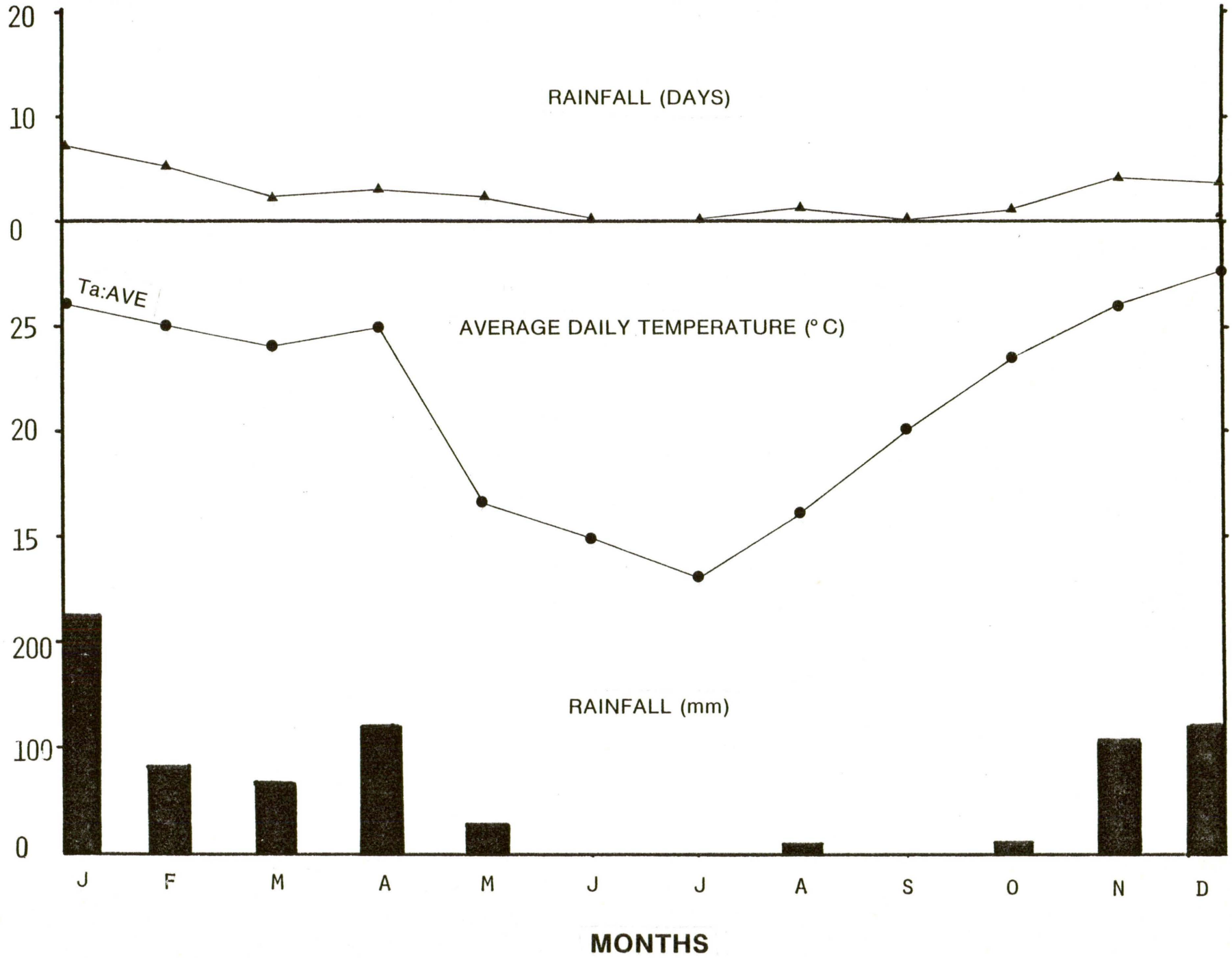

Figure 2: Climatic data for Wolwekraal

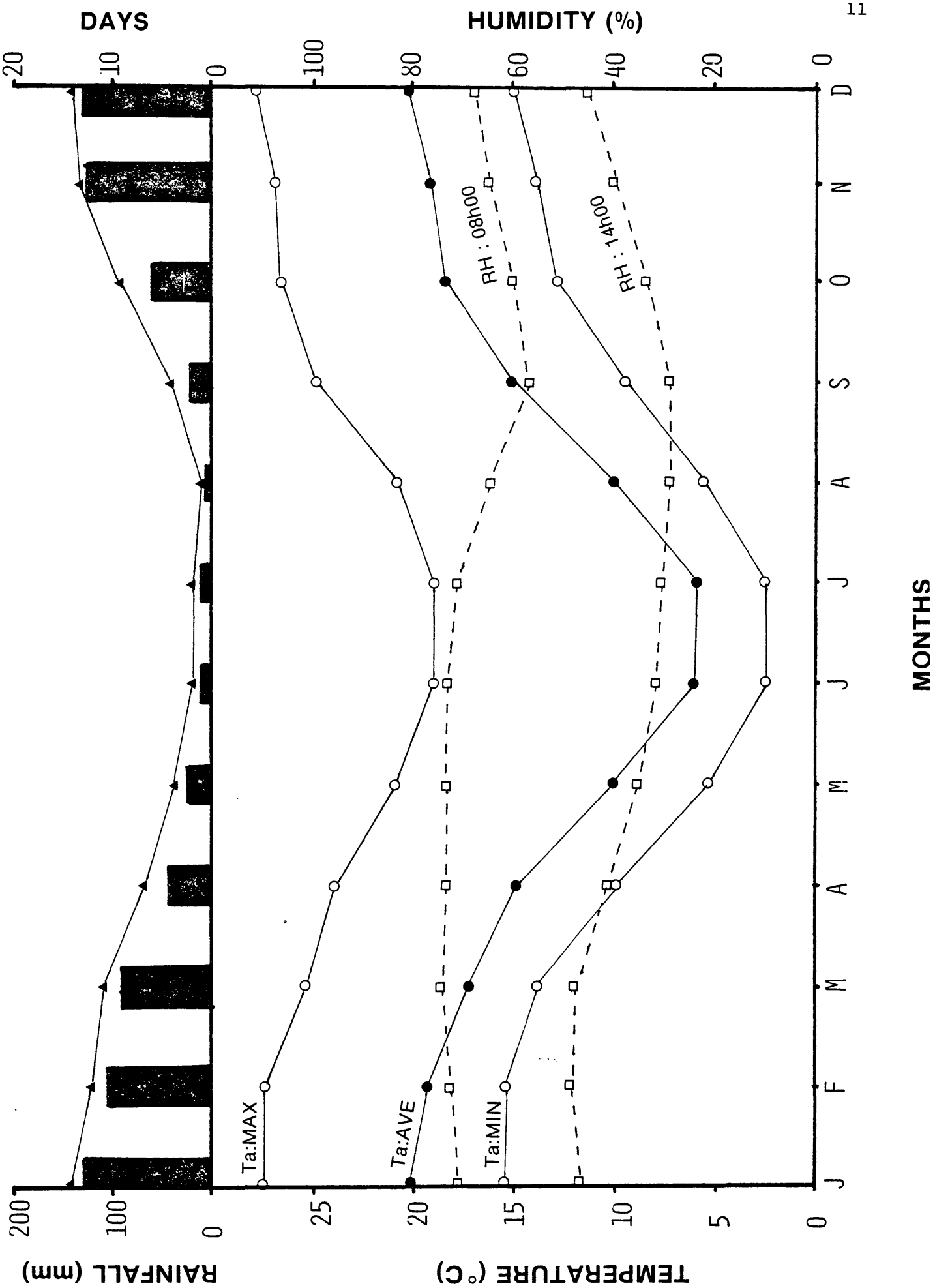

Figure 3: Climatic data for Pretoria (Lynnwood)

one juvenile hyrax caught near Hofmeyr,in the Eastern Cape Province. The hyrax were kept at the University Experimental Farm in an enclosure that measured 7,5 x 6,75 x 3 m, covered in wire mesh (diamond mesh for strength, but later chicken wire to prevent neonates from escaping). The plan of the enclosure and details within it, can be seen in Figure 4. This particular arrangement allowed the hyrax to be either exposed to the sun, or in the shade. Due to the internal half- walls and roof-beams, there were plenty of perches on different levels allowing sufficient spatial separation of the hyrax to help alleviate stress caused by social interaction. The sleeping boxes were placed in an under-cover section of the enclosure to prevent them from being soaked by the rain; which, it was also hoped, might reduce the high infant mortality. The other covered section was used exclusively for feeding, the pelleted food having to be kept dry. The whole enclosure was strewn with large logs (2 to 3 m long), partially to give the hyrax access to the half- walls and ledges but primarily to supply more three- dimensionality to the enclosure, to increase the possibility of spatial separation for the animals.

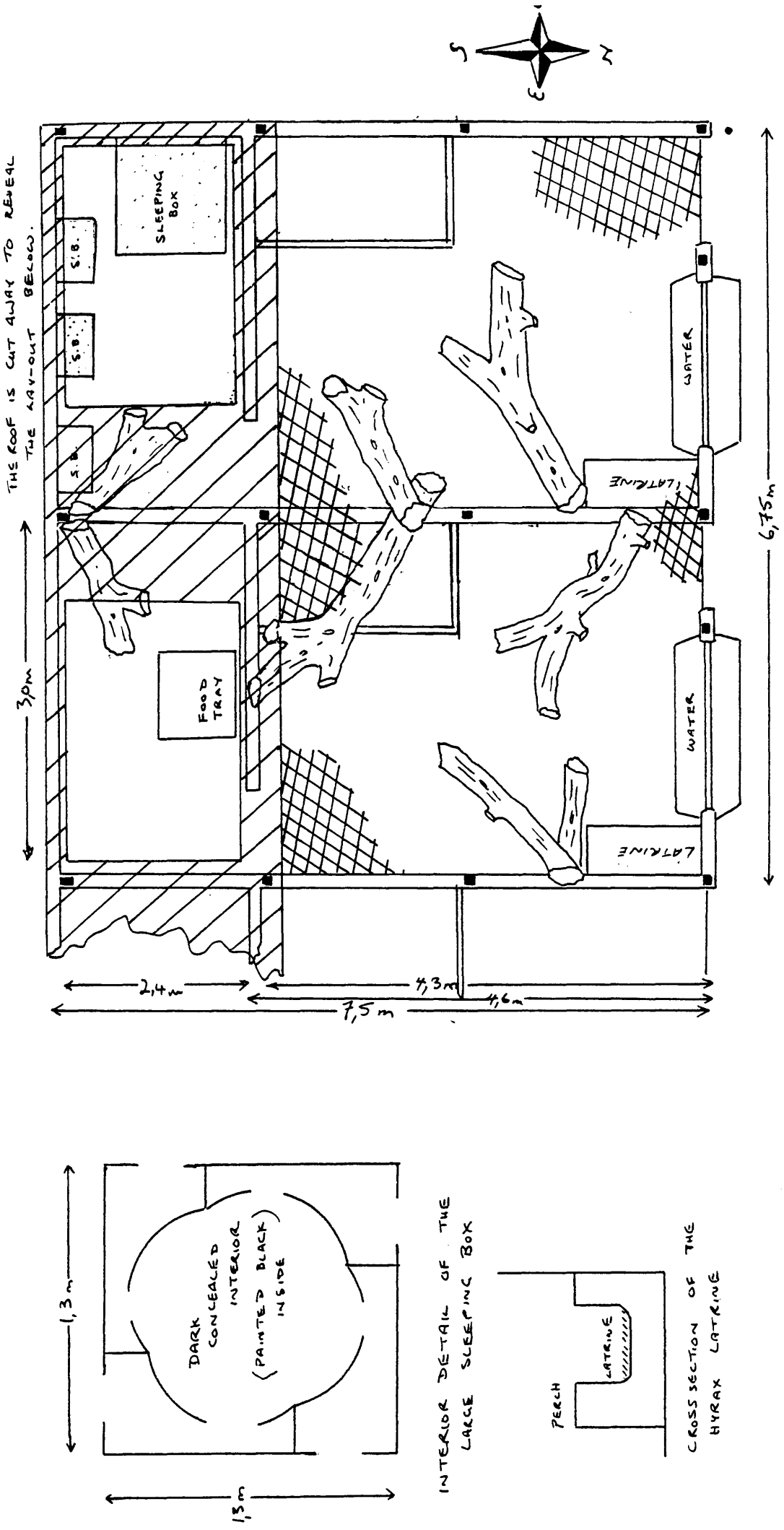

Figure 4: Plan of the hyrax enclosure

CHAPTER THREE : MATERIALS AND METHODS.

MAINTENANCE

The feasibility of using the hyrax as a laboratory study animal has been undertaken in a number of studies (Griner 1968). In addition, maintenance of colonies for study purposes (Thomson 1970) and the requirements for keeping hyrax successfully in captivity (Eismann 1897, Hanse 1962), have also been examined. These have all concluded that hyrax adapt well to captivity.

It was felt that the 153m^3 enclosure with all its logs, half-walls and beams supplied sufficient opportunity for spatial separation or distancing, to presumably reduce agonistic interactions considerably.

The hyrax were fed commercial rabbit pellets (19% protein) (Epol, Vereeniging Consolidated Mills, Johannesburg) on an ad lib. basis, and with the addition of fresh food at intervals during the week. The fresh food included apples, pumpkins, cucumbers, radishes, lettuce, celery, tomatoes, pawpaws, oranges, beans, carrots and fronds. Thomson (1970) stated that 200 - 300g of lucerne per head per day provided a satisfactory ration, while Hanse (1962) found hyrax to consume an average of 616g fresh lucerne or 675g green garden plants per day. Due to this great difference in suggested requirements, it was decided to base the choice of food on Fairall & Millar's (1977) suggestion of approximately 1088 kJ per day, for hyrax with a mass of 2 kg and containing a minimum protein content of 10% on a dry basis. The ad lib. feeding of the commercial diet does supply all this as it has a minimum of 19% protein (on a dry basis) and contains the vitamins

and minerals normally required by most mammals.

Hyrax have highly efficient kidneys and can produce urine hyperosmotic to that of the camel (Louw, et al. 1973) and, combined with their selection of succulent vegetation (Hanse 1962, Hoeck 1975, Fairall & Millar 1977), this allows them to survive without drinking water. Eismann as long ago as 1897 made the same observation and stated "Sie trinken nur wenig, doch sorge ich dufür , dass frishers Wasser nie fehit". On the other hand the hyrax were observed to drink regularly when water was available, and fresh water was therefore always provided. The dry commercial rabbit pellets would also result in their requiring drinking water.

Both Coe (1962) and Kingdon (1971) observed wild hyrax urinating and defaecating in a communal or latrines. This is also true for captive animals and an effort was made to localise their latrines at two specific localities (Figure 4).

Animals in the colony were captured by placing a box (50 x 35 x 35 cm) with a sliding door at one end up against the sleeping box entrance and removing the sleeping box lid slightly, forcing the hyrax to retreat into the catching box. Once inside this smaller box the hyrax was either squeezed up against the far end of the box and injected with anaesthetic, or caught by a noose, at the end of a pole, behind the head and held quietly while the animal was gripped firmly by hand behind the head, and the noose removed.

FIELD-DATA COLLECTION

Hyrax were collected in the field by shooting. A number of different calibers were used in the course of the study. A .22 Hornet was found to be the best caliber to use, as it resulted in the least number of wounded animals, while not causing too much unnecessary tissue damage.

Rectal temperature of shot hyrax was measured immediately on retrieval, and in some cases this temperature was measured again over the following 10 to 20 min to gain an indication of post mortem temperature changes. The temperature was measured rectally using a clinical mercury thermometer inserted to a depth of 5 to 6 cm.

Immediately following the first temperature reading, blood was collected (if the heart was still intact) by direct cardiac puncture with an 18 gauge needle on a 20 ml syringe . As much as 10 ml could be collected from a hyrax after being shot. The blood was stored, unheparinised, in vacutainers and allowed to coagulate. This coagulated blood was delivered within 6 h to the Pathology laboratory (H.F.Verwoerd Hospital, Pretoria) where the radioimmuno assay for thyroid hormones was carried out on the serum. [T3 - Abbott, RIA-diagnostic; % T3 retention - Abbott, Triabsorb; T4 - Abbott, RIA-diagnostic; TSH - Abbott, RIA-diagnostic & free T4 - Clinical assay, Gamma-coat].

The thyroid glands were removed and immediately fixed, intact, in AFA (Acetic Formol Alcohol). The solution was made up of 1000ml H_2O, 200ml conc. acetic acid, 200ml conc. formalin and 600ml 96% ethanol.

Measurements were taken of mass, body length, cranial length, ear length,

girth, hind foot length, and subjective factors namely, conditions of pelage, subcutaneous fat; and sex was noted. These data were not of direct importance to the field study but it was felt that the data may be of use to other researchers, even at a later date.

Blood (for thyroid hormone assay) and thyroid glands were also collected from animals at the colony which were killed during the course of A. Eloff's study of the digestion of hyrax. Blood was also collected from live anaesthetised hyrax by means of cardiac puncture.

MEASUREMENTS

It was decided to group hyrax into three size or mass classes following Fairall (1980) and to extrapolate age from mass as follows

Class I : up to and including 1,5kg;
Class II : from 1,5kg to below 3,0kg;
Class III : from (and including) 3,0kg upwards.

According to Fairall's (1980) Von Bertalanfy growth curves for hyrax, animals of 1,5kg would be in the region of 12 - 14 months old which coincides with the definition used here of juveniles.

The colony animals used in the laboratory studies were grouped into two groups:

Juveniles : with a mass in the region of 1,1kg.

Adults : with a mass in the region of 3,2kg.

As can be seen Class I and Juveniles are virtually synonymous, while Class II and Class III can be grouped as adults.

DRUGS

Hyrax were anaesthetised for surgical implantation of transmitters and to facilitate blood sampling by cardiac puncture.

10 mg/kg Ketamine (Bayer, Leverkusen Germany) and 5 mg/kg Xylazine (Bayer) were given by intramuscular injection in a total injectable volume of 0,5 ml/kg. Surgical anaesthesia was obtained in 5 min and recovery began after 40 min. Complete recovery took between 2 to 6 h.

Pharmacologically Xylazine is classified as an analgesic and sedative (but not a neuroleptic, tranquilizer or anaesthetic)(Meyer-Jones, Booth and McDonald 1977). Ketamine seems to be an analgesic, mild anaesthetic, a B-blocker, but may cause cataleptoid anaesthesia when administered in dosages of 22 - 44 mg/kg intramuscularly (Meyer-Jones, et al. 1977).

A total of 35 animals were anaesthetised in this manner. There were two fatalities possibly ascribable to the anaesthetic. The hyrax anaesthetised varied in mass from 0,9 to 4,5 kg. All the dosages were calculated from a dose of 10 mg Ketamine and 5 mg Xylazine/kg.

ACCLIMATISATION AND ACCLIMATION

Acclimatisation is the change in temperature tolerance, habituation or the adaptation in reaction of the animal to environmental conditions. Acclimation is where similar effects are simulated in the laboratory by keeping the animals for some time at specific temperatures (Schmidt-Nielsen 1979). This connotation was used in the present study.

Animals collected in the field were also grouped according to Summer, Winter or Spring/Autumn. Summer was defined as being from November to March, Winter as May to September, Autumn as April and Spring as October.

Five juvenile hyrax (2 males, 3 females) with a mean body mass of 1016 g (increasing to 1210 g by the end of the study) and 10 adult hyrax (5 males, 5 females) with a mean mass of 3457 g, were temporarily housed in wire-mesh cages (50 x 45 x 30 cm) while being kept in the climatic room.

The captive animals were housed in the laboratory in a climatic room where they were acclimated for three weeks to Summer, Spring/Autumn and Winter equivalent temperatures of 26°, 15° and 10°C, before any of the experiments commenced. The Mean Summer temperatures for the area where the colony was kept was 26°C and this was therefore the temperature applied in the laboratory. 15°C was used to represent Spring/Autumn and 10°C applied for Winter. The light regime was 12 h light : 12 h dark, with the light period commencing at 08h00.

Acclimation was followed by a seven day measurement of food intake and faeces production, after which the metabolic rate, body temperature and heart rate measurements at each temperature regime were carried out.

RESTING METABOLIC RATE (RMR)

Metabolic rate was measured as oxygen consumption (VO_2) in ml O_2 $(g.h)^{-1}$ (standard temperature and pressure, dry) in an open flow metabolic chamber based on the system described by Depocas and Hart (1957). This 40 x 20 x 20 cm perspex chamber was equipped with ports for incoming and outgoing air, and the air flowing both in and out was dried by self- indicating silica gel. In addition the floor of the chamber was covered in a layer of silica gel under a removable footplate. The air-tight metabolic chamber was immersed in a water bath where the temperature could be maintained between 5°C and 30°C ($\pm$ 0,5°C). The incurrent air, after having been dried, passed through a submerged coil of copper piping, 150 cm long with a bore of 0,75 cm, to allow the air to equilibrate to the same temperature as the chamber and surrounding water. The temperatures in the chamber and surrounding water were monitored by chromel-alumel thermocouples connected to a Kane-May KM 2012 portable digital thermometer. Measurements were made from 30°C to 5°C at five degree intervals.

The outgoing air, after being dried, flowed through a Beckman OM 14 polarigraphic oxygen analyser (digital readout and linear chart recorder) where the oxygen content (O_2 percentage) was measured. The incurrent airflow was maintained at 1000 ml/min and utilising the oxygen content that was measured for incurrent and excurrent air, VO_2 was determined by the difference. This whole system is a modification of the method described by McNairn & Fairall (1979).

Hyrax were allowed to adjust to each temperature for one hour before measurement was commenced. The mean of five stable consecutive determinations taken every two minutes in a 15 min period, was taken as the

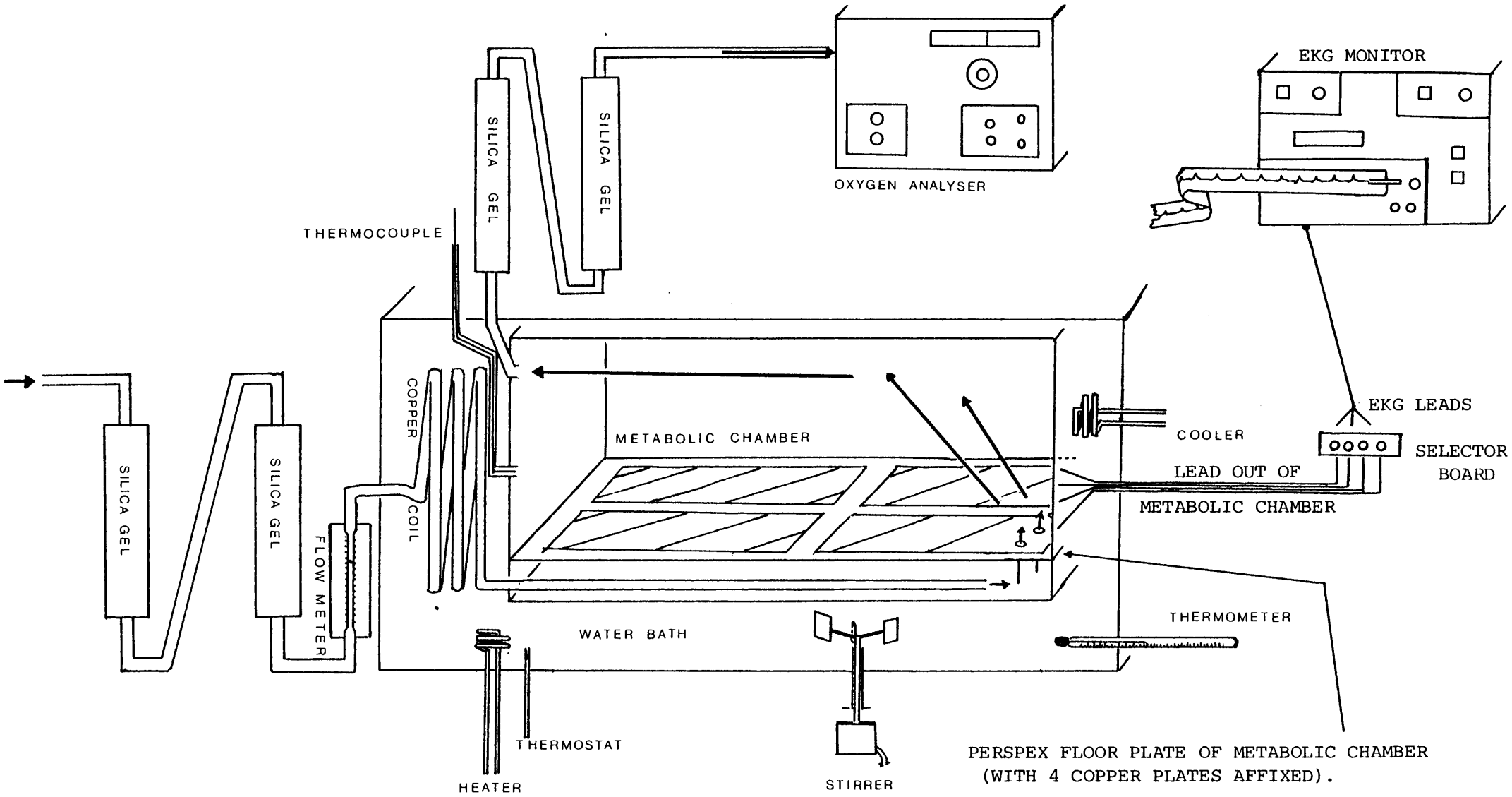

Figure 5: Diagram of the open flow system used in this study incorporating the heart rate monitoring system.

oxygen consumption at that temperature. Runs were commenced at 09h00 each day and were terminated after 6 to 8 h in the chamber. The system used for VO_2 and heart rate determination is illustrated in Figure 5.

HEART RATE (HR)

Heart rate has been measured externally by "hardwire" leads to surface electrodes (Webster 1967) but, as was shown in the pilot study by McNairn (1978), an in-line system is not feasible with P. capensis. To quote Johnson & Gessamen (1973) : "The only feasible method of measuring heart rate of a free-living animal is (by) radiotelemetry". For this reason the captive colony portion of the heart rate study was carried out by means of a radio transmitter. The laboratory study of heart rate and metabolic rate was carried out using the method described by McNairn & Fairall (1979).

Copper rods were affixed to the removable footplate of the metabolic chamber and these were connected by wire leads to a Washington model 400 MD2C recording oscillograph. The rods were 1 cm wide and were spaced 1,5 cm apart with the intention that the hyrax would have to stand on separate rods and would be able to straddle no more than two rods with one foot. The assumption was that the hyrax would stand with at least two front feet or one front foot and one back foot on separate rods, so enabling an ECG to be picked up by the Washington system. Due to the number of rods present on the footplate, a selector board was necessary to connect the correct rod (with a foot resting on it) to the ECG leads of the Washington. The copper rods were periodically sanded clean and were dampened lightly with electrolyte gel prior to each run. In this way it was possible to measure the heart rate of the hyrax while measuring its oxygen consumption during exposure to specific ambient temperatures.

Heart rates were the means of five random one minute readings taken during the 15 min continuous measuring period at each temperature.

The intention to use transmitters to measure heart rate of hyrax at the experimental farm was modified by four considerations :

1. The range of effective transmission,
2. the total mass of the transmitter, and
3. where to affix the transmitter to the animal, and
4. the availability of a working transmitter.

HR TRANSMITTER #1

A small ECG transmitter was imported from the United Kingdom. The SNR 102 F (Dynamic Electronics, London, U.K.) was modified to use Duracell MN9100 1,5V batteries to increase the operating lifetime to a predicted 11 days. In actual usage the best lifespan obtained was 9,5 days. This transmitter had a range of approximately 4 m. The total mass of transmitter, batteries and harness was 48,01 g which, when fitted on a 3 kg hyrax, was less than 2% of body mass. Webster and Brooks (1980) in their study into the effects of radiotransmitters on the meadow vole, Microtus pennsylvanicus, used 10% of body mass as the upper limit of transmitter mass. It was decided, due to the shortness of the transmitter lifetime, not to encapsulate and implant the transmitter, but rather to affix it to a harness around the hyrax neck and shoulders (Figure 6).

The ECG electrodes from the transmitter were connected to external cardiac pacemaker leads (Cordis Corporation, Miami, Fla.) that were subcutaneously inserted on either side of the chest, posterior to the fore-legs. These stainless steel leads were then sutured in place.

This transmitter was used to collect continuous 24 h heart rate data in the laboratory, where its limited range would not be a hindrance. The monitoring was carried out at 25° and 15°C on a Class III male hyrax over three days. Due to the occasional non-reception of the signal, as a result of the limited transmission range, a complete set of readings for the three days was not obtained.

HR TRANSMITTER #2

The requirement of wanting to monitor heart rate of a free moving hyrax at the Experimental Farm necessitated the acquisition of a transmitter that had a range of at least 10 m. Mr C. Smith (CSIR, Pretora) designed and built a larger (than the SNR 102 F) FM ECG transmitter that was easily received up to 20 m. This transmitter (#2), using three penlight batteries, transmitted for 25 days, (predicted lifetime 30 days). Due to the increased size, transmitter #2 also had to be fitted externally and it was done in exactly the same manner as with transmitter #1 (Figure 6). The mass of this transmitter (with batteries and harness) was 135g and, when fitted to a 4,5 kg hyrax, was 3% of total body mass (still a long way under the suggested 10% limit). As well as being used on a colony hyrax at the experimental farm, this transmitter was used to monitor heart rate of a hyrax while it was being made to run on a treadmill, to gain an idea of exercise related heart rate. A single male Class III hyrax wearing HR transmitter #2 was placed on a treadmill and allowed to walk around until relaxed. The treadmill was then switched on to a speed of 4km/h for 30 sec. After the hyrax had rested for 5 min the treadmill was switched on again for 30 sec. The animal was allowed to recover again. During all these procedures the heart rate was being monitored and recorded on tape.

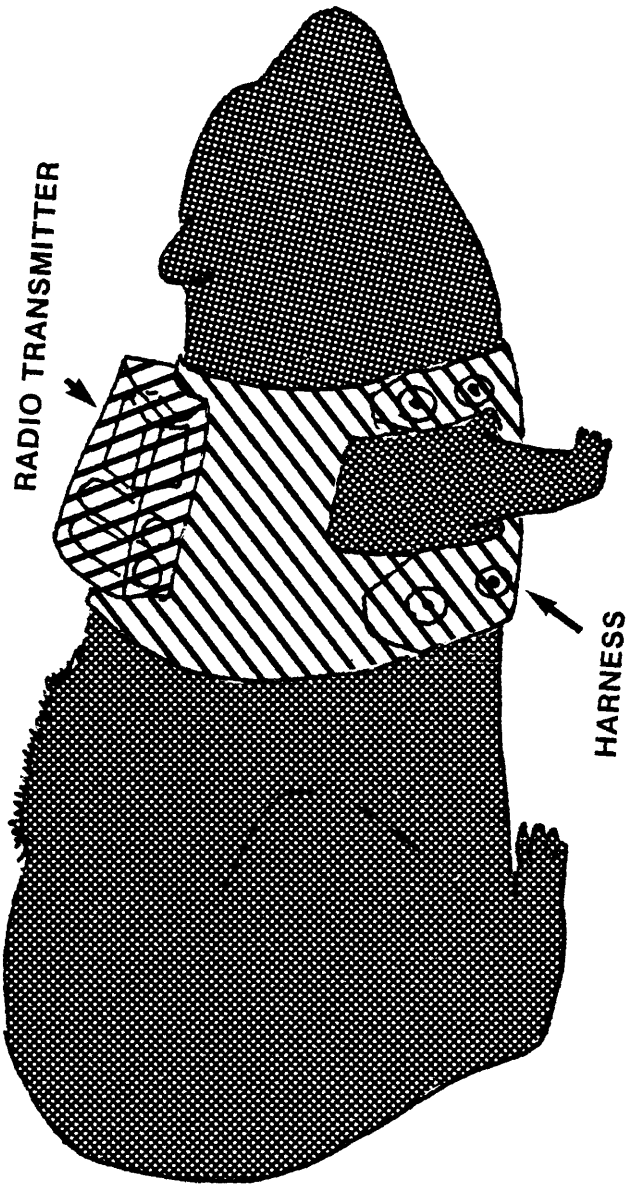

Figure 6: Diagram of the ECG-transmitter package attached to the harness on hyrax

During the course of reading the literature, fear bradycardia was noticed to be of importance in species that make use of cover and hiding in predator avoidance. This aspect was examined by means of stressing a hyrax and monitoring its heart rate.

BODY TEMPERATURE (Tb)

Laboratory Tb

Each of the five juvenile hyrax and five of the adult hyrax had a small (2,3g) temperature sensitive transmitter (Model L, Mini-Mitter Co. Indianapolis) implanted in their peritoneal cavity just posterior to the diaphragm. The 2,9g transmitter (2,3g before encapsulation) weighed less than 0,08% of an adult hyrax and less than 0,3% of a juvenile hyrax. Smith (1981) examined the effect of intraperitoneal transmitters on Peromyscus leucopus in terms of juvenile growth rate, reproductive performance in the wild and survival in the wild. His transmitters were a maximum of 10% of body mass and he found no significant difference between animals with and without transmitters. Based on this, it was felt that it was unlikely that the small transmitters used in this study would have any noticeable effect on the physiology of these hyrax.

These animals were anaesthetised using Ketamine and Xylazine in the manner previously described. Sterile instruments were used. The surgery was clean but not sterile; the hair was clipped and then totally removed with a depilatory cream (Nair, Carter Wallace OS, Pietermaritzburg). The incision was about 3 cm long, parallel with the midline and just off to one

side. The encapsulated transmitter was placed in an antiseptic solution (Savlon, ICI laboratories Johannesburg) before being inserted.

The peritoneum and muscle were closed with two to three sutures and the skin with a further four sutures. The suture material was No. 0 surgical catgut with a swedged-on needle (Ethicon, Ethnor laboratories Johannesburg).

The animal was then injected (intramuscularly) with a $2cm^3$ of depo-penicillin (Compropen : Glaxo, Johannesburg). The animals were left to recuperate for a minimum of seven days before any readings were taken.

It was decided that the transmitters would have to be encapsulated as they would be exposed to a warm, corrosive, aqueous solution with continued movement in the surrounding tissue (Donaldson 1981). Due to the relatively short time of being operative (approximately two months), it was felt that a wax coating might be sufficient. Fryer (1970) stated that wax seals well against moisture, so it was considered safe to attempt it's use. The wax was very successful and only one transmitter, on removal, showed any signs of moisture having penetrated. The radiocapsule transmitted a pulsed signal which was received on a commercial FM/AM receiver.

The pulse frequency was a function of the temperature of the transmitter, and by inference, the temperature of its surrounds, the hyrax. The pulse frequency of each transmitter was calibrated, after encapsulation, in a water bath where the water could be controlled to within $0,5^{o}C$. The calibration curves for each of the transmitters are shown in Figure 7.

In this manner body temperature was measured in both the climatic room to obtain 24 h body temperature profiles at constant ambient temperatures, and in the metabolic chamber during oxygen consumption measurements, to obtain body temperature as affected by varying ambient temperatures. The

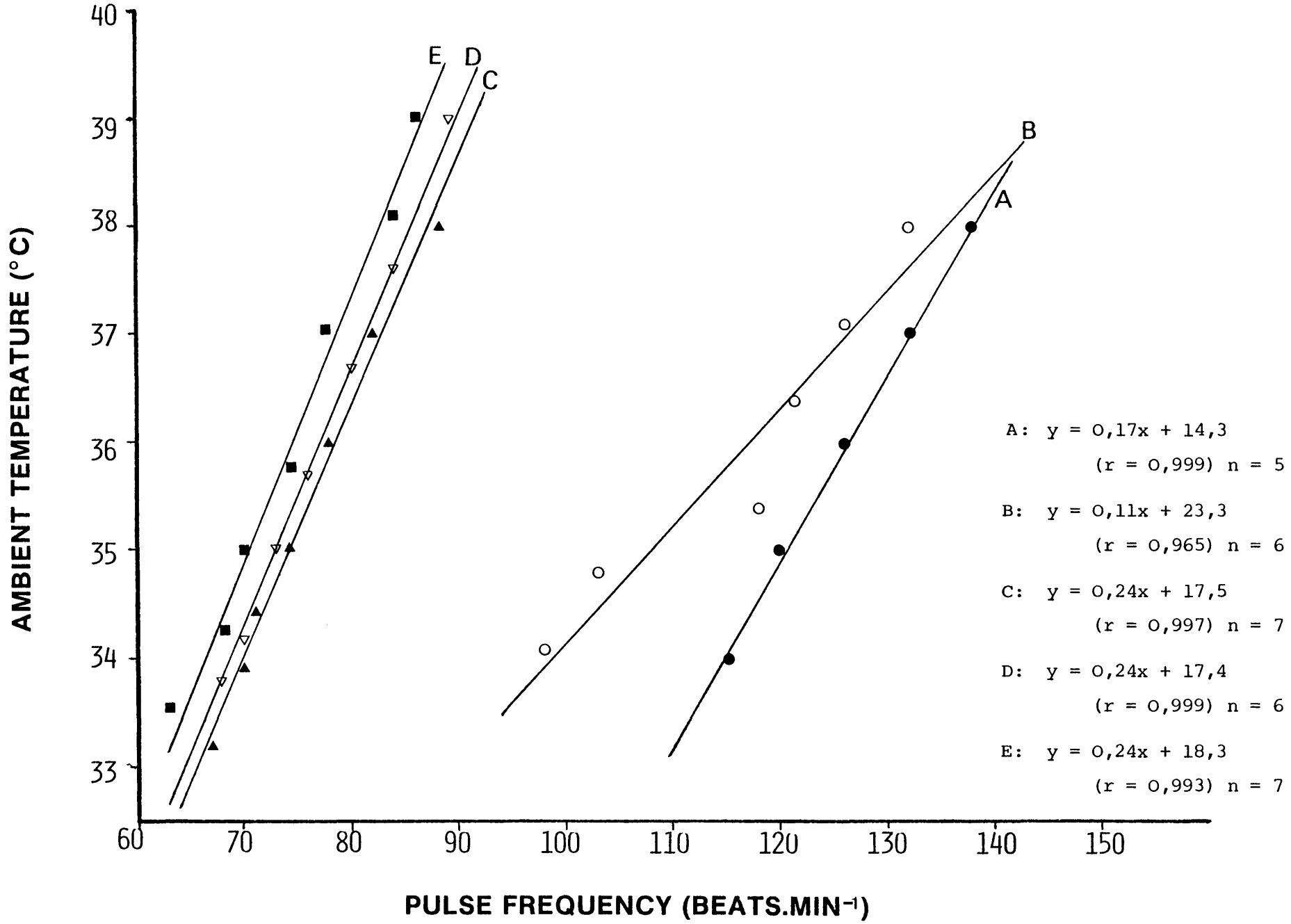

Figure 7: Calibration lines for the temperature sensitive transmitters

body temperature in the metabolic chamber was measured directly. The 24 h body temperature was stored on a magnetic tape. The tape recorder and the radio receiving the body temperature transmissions were switched on every hour for five minutes by a custom built mechanical/electronic timer. C-90 compact cassettes with 45 min recording on each side were used and were turned over every 8 h, which allowed for continuous recording.

Field Tb

This was only measured in shot hyrax. The problem associated with post mortem body temperature measurement is the risk of cooling, which is compounded by low environmental temperatures and the length of time between shooting and actually measuring rectal temperature. As a result it was decided to measure decrease in body temperature over time after shooting. These so called profiles would give an indication of a safe limit in maximum delay before measuring body temperature. It was decided to utilise only those temperatures that were collected within the first 10 min post mortem as these were felt to be acceptably close to actual body temperature. This therefore limited the sample size to 60 (excluding one 40,2°C individual).

METABOLIZABLE ENERGY (ME)

During the seven days that this parameter was investigated, the animals maintained at the acclimated temperature each received a measured amount of food and water ad lib. All the faeces and remaining food were removed daily, dried to a constant mass at 75°C and weighed. Subsamples of food and faeces for each day were bombed in a ballistic bomb calorimeter

(Gallenkamp). The means of three measurements of each subsample were used for each determination. Comparisons were made on the basis of $kJ(g.h)^{-1}$ (Blaxter 1966, Gessamen 1973). This is based on the relationship A = I - E (A = assimilated energy, I = ingested energy and E = egested energy). A is better known as metabolizable energy (ME) where ME = I - E (urine, methane and faeces). The contribution of urine and methane was ignored in this study, which would mean that ME measured here may be fractionally higher than the expected ME when urine and methane production (Eloff 1981) are taken into account.

The adult mass remained constant throughout the duration of the study. The juveniles, however, increased in mass during the course of the experiment which meant that the ME values obtained at 26°, 15° and 8°C could not be compared directly with one another. It was decided was to correct the ME values by the percentage that the body mass increased. It was felt, however, that the percentage increase should be calculated by comparing the metabolic mass ($W^{0,75}$ [Kleiber 1961]) at the three temperatures, as the difference in metabolic rate is directly related to metabolic mass. From this it could be seen that the juvenile metabolic mass had increased by 8,3% between the time that they were at 26°C to when at 15°C. The increase between when at 26°C and at 8°C was 14%. Utilising these percentage increases, the ME value at 15°C was increased by 8,3% and the ME value at 8°C was increased by 14%. Thus all the values were standardised for a mass of 1016g (the mass of the juveniles at the beginning of the study at 26°C), as though the juveniles had maintained a constant mass during the study and had not grown. This would hopefully counteract the decreased metabolic rate caused by an increase in body mass and thus allow for changes in ME due to ambient temperature to be more visible. The data obtained in this study are also compared to that of Eloff (1981) where urine and methane are considered in the calculation.

RADIATED HEAT (Radiant temperature Tr)

At each acclimation temperature in the climatic room the heat radiated by the juvenile hyrax through its pelage was measured with a radiation thermometer (IRCON 700 AC) assuming a pelt emmiscivity of 0,98 (Moen 1973). Unfortunately, this instrument was functioning at the lower extreme of its scale and as a result its accuracy is open to question. Radiant temperatures below 20°C could not be measured. However, the trend observed is of particular importance even if the magnitude of the differences is treated with hesitance.

NON-METABOLIC HEATING

At each acclimation temperature the juvenile hyrax were allowed to heat up for 1 h in front of a bank of six 250 W infrared lamps (placed 1,5 m in the front of the cages). Body temperature was monitored every 15 min and at the end of each period the heat radiated by each animal was measured.

[Unfortunately, due to the limited availability of the IRCON 700 AC radiation thermometer, it was not possible to repeat the previous two sections on adult hyrax as was intended].

ACTIVITY PATTERNS

The approach here was to examine the activity of hyrax at the colony and it was carried out in two ways. Initially the number of animals visible at any one time relative to the total population was measured every half hour

for 24 h for four days, in July 1981 for the Winter period and three days in December 1981 for the Summer period.

The other approach was to observe a focal animal for as long as it was sufficiently light to clearly make out what the animal was doing. At the same time this hyrax, with a heart rate transmitter fitted, was having its heart rate monitored for each activity. The heart rate was monitored by using a stop watch and counting the number of heart beats per unit time (usually one minute). If the activity was of very short duration, there was only time for one such reading. However, if the activity carried on for a long period, up to 10 readings were taken. After two days all the heart rates for similar activities were grouped together and the means and standard deviations were calculated. The percentage of time spent on each activity was based on the number of hours spent in total on each activity, expressed relative to the number of hours spent observing the animals. In this way the percentage of time (in daylight hours) spent carrying out each activity, coupled to the heart rate caused by this activity, could be plotted for a single animal. This was carried out for both the Summer and Winter, but the heart rate aspect was only measured in Summer as the transmitter only became available at the end of the study.

THYROID GLANDS AND HORMONES

From 14 field hyrax and seven of the colony hyrax, thyroid glands were collected and fixed. Blood was also collected from 16 hyrax with a view to examining the thyroid hormones present in the serum.

Histological study

The fixed thyroid glands were embedded in paraplast and then were sectioned (5 µm thick) on a microtome, mounted and stained with hematoxylin-eosin (HE). The thyroid activity was gauged from the relationship d/n (Lever 1948) where d = inner diameter of the follicle and n = the number of epithelial cells surrounding that follicle. Ten random follicles were measured in this manner in each thyroid gland preparation. The means and S.D.'s were calculated. The lower the d/n value, the more active the follicle is supposed to be, which is as a result of the smaller follicle diameter and/or the greater number of cells per unit size of the follicle.

Hormonal study

The radioimmuno assay (RIA) carried out on the serum, gave values for the following fractions; T_3, T_4, Free T_4, TSH and free thyroxin index.

These data were compared between colony and field animals and between acclimated and acclimatised conditions. An attempt was made to relate the hormone values to histological data where applicable.

STATISTICAL ANALYSIS

All data, where more than one sample is utilised, are presented as means ($\bar{x}$) with Standard Deviations (S.D.). Pearson correlation coeffient's (r) are given for those sets of paired data where a linear relationship is suspected and is tested for by means of a least-squares linear regression.

Differences between such sets are determined by a paired t-test with significance being set at P = 0,05. Where the means of several distributions are compared, a one-way analysis of variance (ANOVA) is carried out with P = 0.05 (Zar 1974, Strike 1981).

CHAPTER FOUR : RESULTS

RESTING METABOLIC RATE (RMR)

The relationship between VO_2 and ambient temperature (Ta) in adult and juvenile hyrax is shown in Figure 8. The correlation between VO_2 and Ta below thermoneutrality for hyrax is well described by the equations derived by simple linear regression. In the adult hyrax (mean mass 3150g) the thermoneutral zone (TNZ) seems to be from just above 20°C to just below 30°C. The VO_2 in this range is 0,49 mlO_2 $(g.h)^{-1}$ for the adults acclimated to 26°C. A linear regression of observations below thermoneutrality for the adults acclimated to 26°C, is described by the equation VO^2 = 1,0736 - 0,0265 Ta (the r averaged 0,997). The line described for adults acclimated to 15°C, was VO_2 = 1,0997 - 0,0241 Ta (r = 0,983), while for adults acclimated to 10°C, it was VO_2 = 1,0895 - 0,0286 Ta (r = 0,995). No significant difference could be shown for VO_2 values between 26° 15° or 10°C. Nor was there any significant difference between the slopes of the lines.

In the juvenile hyrax (mean mass 1016 g) the TNZ seems to be from approximately 25 °C to in the region of 30°C, as the VO_2 at 30°C is still lower than at 25°C. The $VO_2$for juveniles acclimated to 26°C was 0,48 mlO_2 $(g.h)^{-1}$. The linear regression below thermoneutrality is described by the equation VO_2 = 1,616 - 0,0529 Ta (The r averaged 0,992). The line for juveniles acclimated to 15°C, was VO_2 = 1,698 - 0,0371 Ta (r = 0,991) while that for juveniles at 10°C, was VO_2 =1,473 - 0,0285 Ta (r

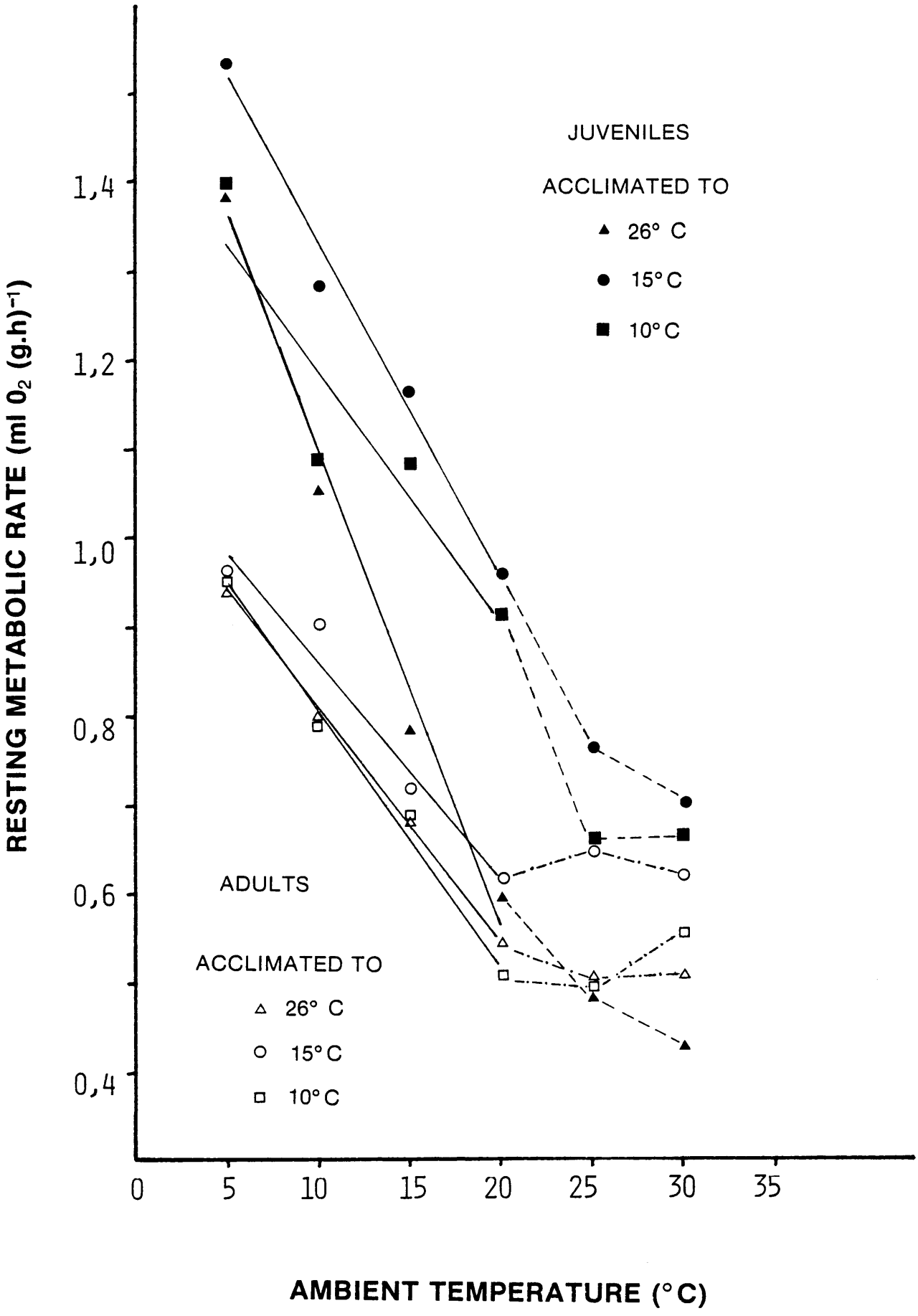

Figure 8: Resting metabolic rate (RMR) of adult and juvenile hyrax at various ambient temperatures.

= 0,932). VO_2 values between 26°C and 15°C were significantly different (P = 0,05, paired t - test, n = 5), as were values between 15°C and 10°C (p = 0,05). No significant difference could be shown between the VO_2 values at 26°C and 10°C as was also the case for the slopes of the calculated lines. The means and S.D.'s of the adult and juvenile data are included in table form in the Appendix.

HEART RATE (HR)

The relationship between HR and ambient temperature in adult and juvenile hyrax is shown in Figure 9. The heart rates for both adults and juveniles were minimal at 25°C to 30°C irrespective of acclimation temperatures, and there was no significant difference between adults and juveniles within the TNZ. The heart rates varied from 108 beats/min to 131 beats/min within the TNZ.

Below thermoneutrality heart rate increased linearly in both adults and juveniles. There was a significant difference (p = 0,05) between adult and juvenile heart rate reactions to a decrease in ambient temperature. The equation of the line expressing the juvenile heart rate increase, was HR = 194 - 3,404 Ta (r^2 = 0,896) while the adult equation was HR = 156,5 -1,913 Ta (r = 0,842). As can be seen, the difference between the two lines coincides with the apparent difference of VO_2 in adults and juveniles at the same temperatures.

Using the CSIR transmitter, it was possible to evaluate the heart rates of hyrax at the Experimental Farm while they carried out certain activities. These activities were (with the mean heart rate in beats/min in parentheses):

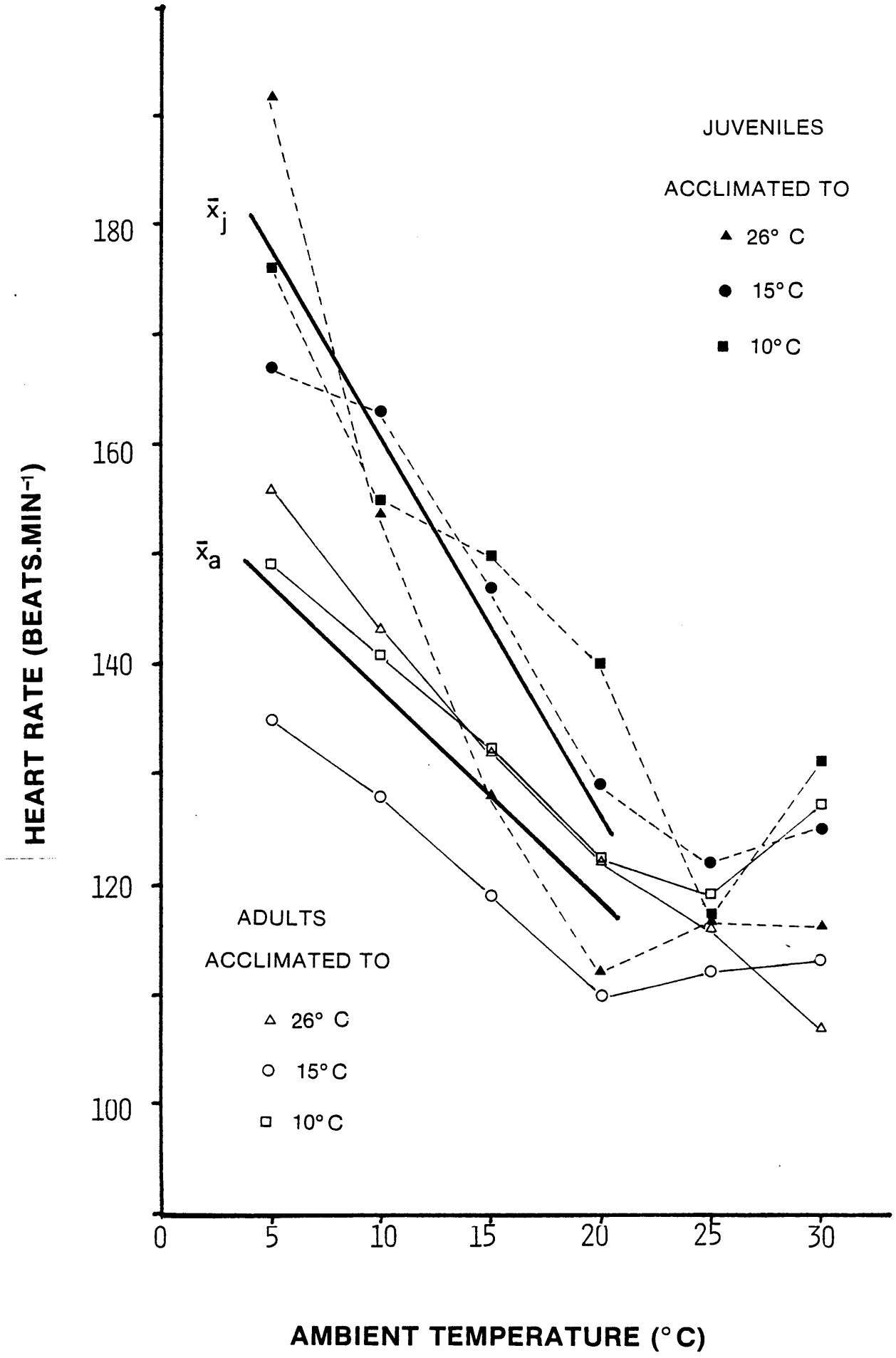

Figure 9: Heart rate of adult and juvenile hyrax at various ambient temperatures

N.V. : Not visible, inside sleeping box (109 ± 10)

L : Lying in shade or sunlight (119 ± 7)

S : sitting in shade or sunlight (123 ± 6)

S.C. : sitting grooming and changing posture (131 ± 9)

F : feeding and drinking (133 ± 9)

MOV : Standing/walking/running/jumping (143 ± 7)

I.I. : Intraspecific interactions (142,5 ± 13)

These can be seen along with S.D.'s in Figure 10. The measurements were made on one Class III male hyrax in summer over a period of three days.

The heart rate pattern over a 24 h period can be seen in Figures 11 and 12. There is a great variability of heart rate, as can be seen from the graphs, but there does seem to be a trend towards an increase in heart rate from around 10h00 until 20h00 - 22h00 at both 26°C and 15°C. This would coincide with daylight and early evening and could possibly be ascribed to increased activity.

Figure 13 shows the heart rate profile obtained from the same male hyrax (when frightened by the close proximity of the researcher), and it is clearly a case of tachycardia. It was felt that these data might not be a true reflection of the situation, so a second method of testing the reactions to fear was applied where the animal was suddenly exposed to a loud noise (Figure 14). Fear bradycardia can clearly be seen to occur.

The male hyrax placed on the treadmill and allowed to rest before running had a HR that peaked at 180 beats/min and then dropped to 136 (figure 15). After running for 30 sec the HR peaked at 196 beats/min which was probably as much due to stress as exercise, as the treadmill would force the

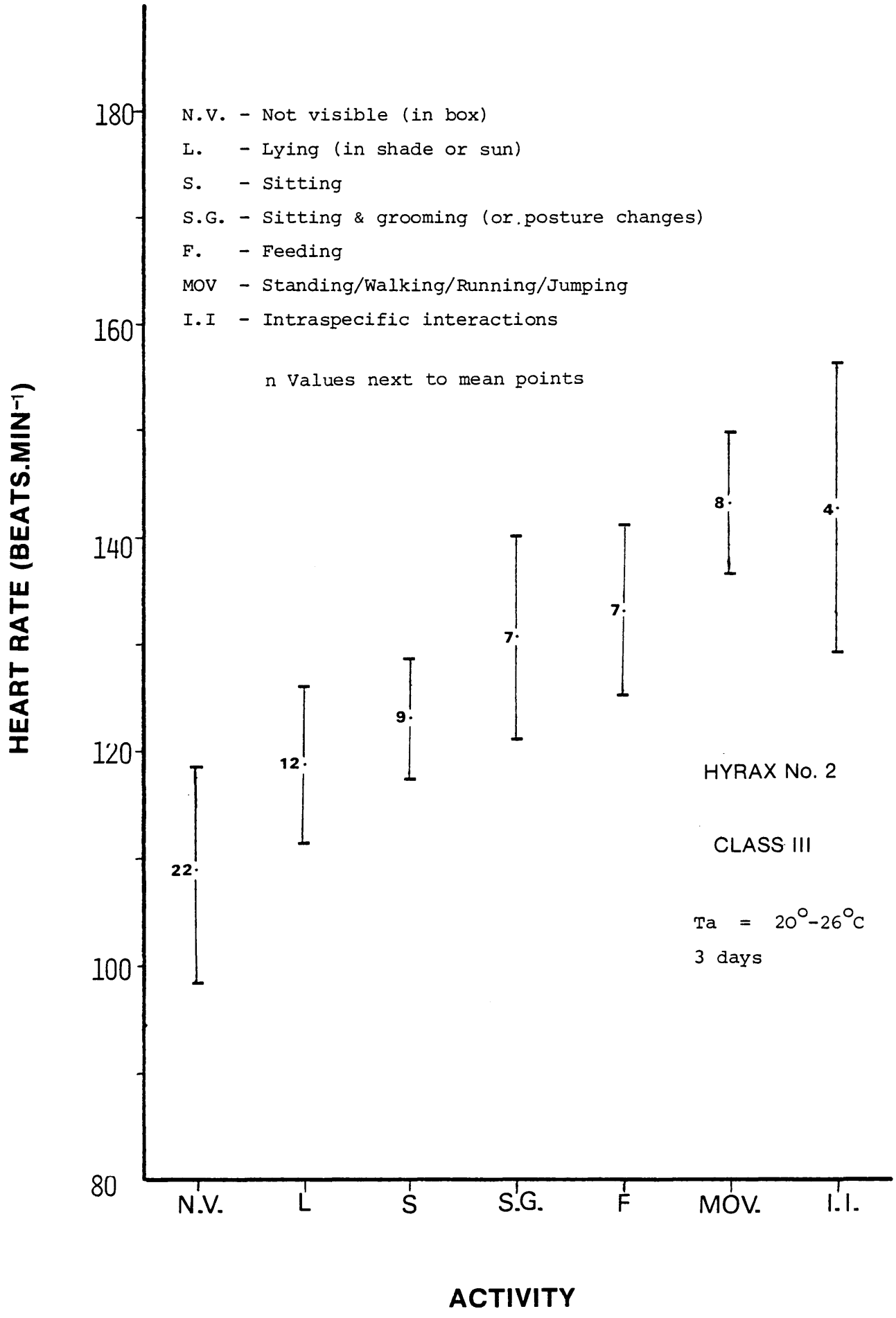

Figure 10: Mean heart rates of hyrax #2 while performing various activities

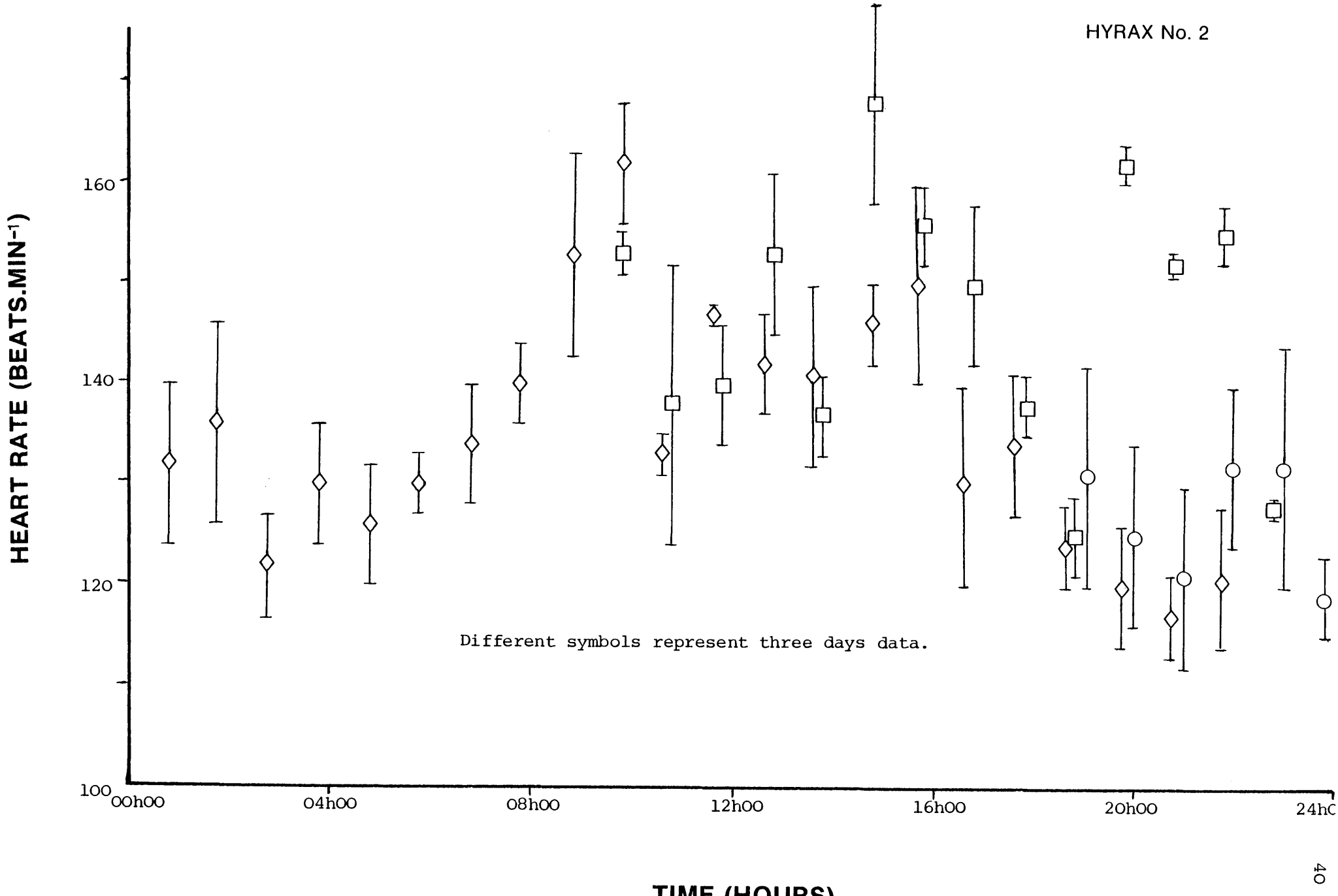

Figure 11: 24h heart rate profiles at 26°C

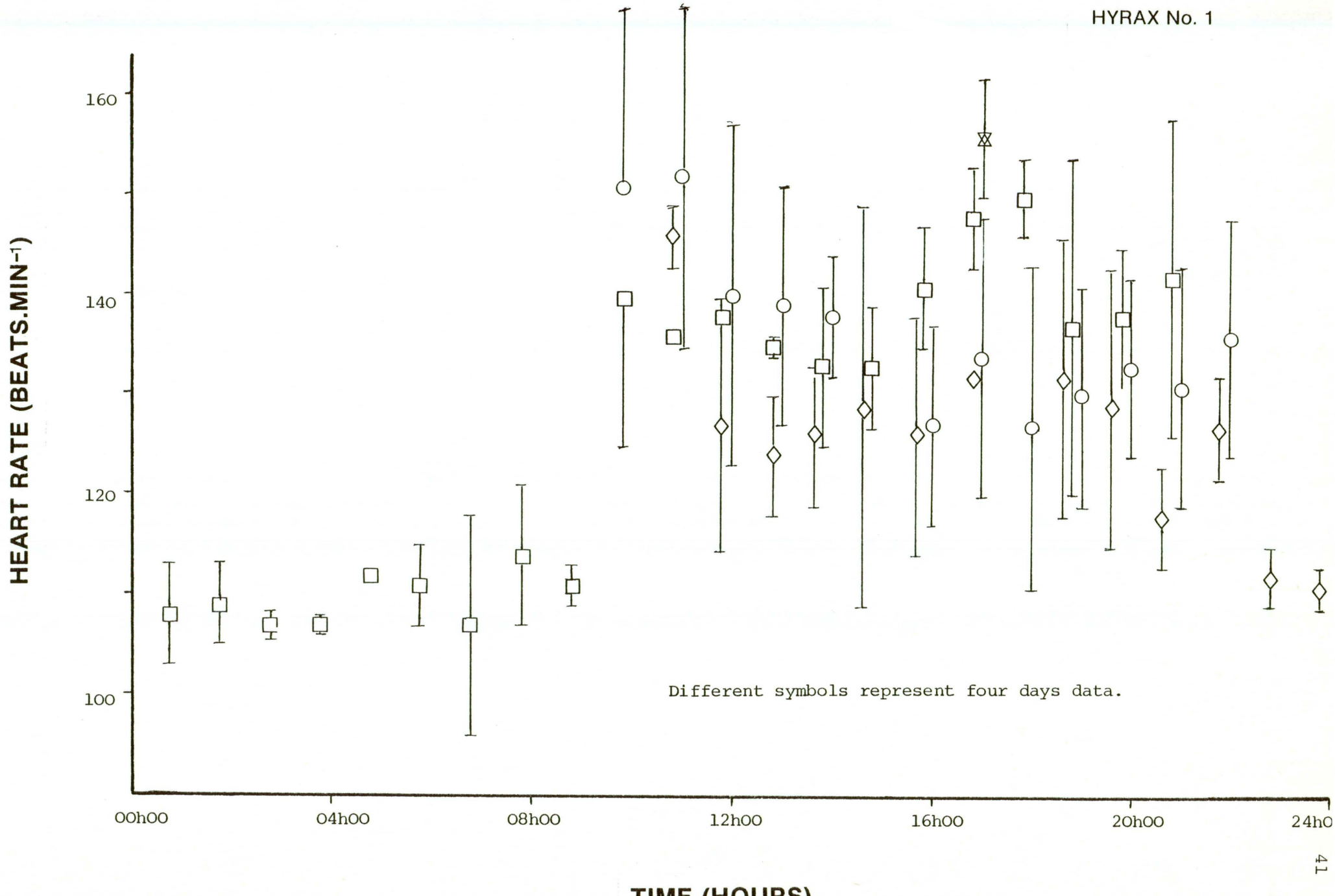

Figure 12: 24h heart rate profiles at 15°C

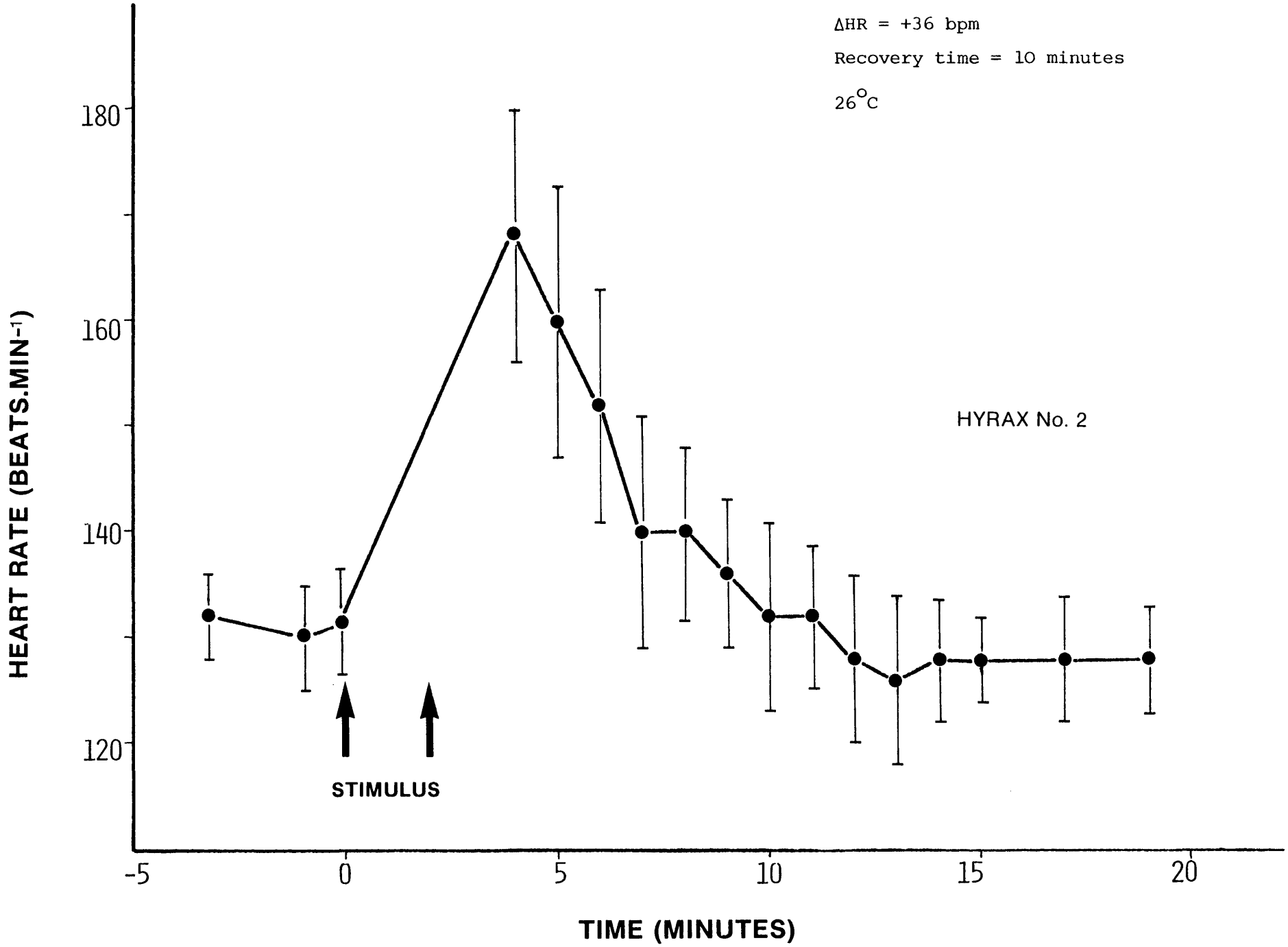

Figure 13: Fear tachycardia and recovery profile

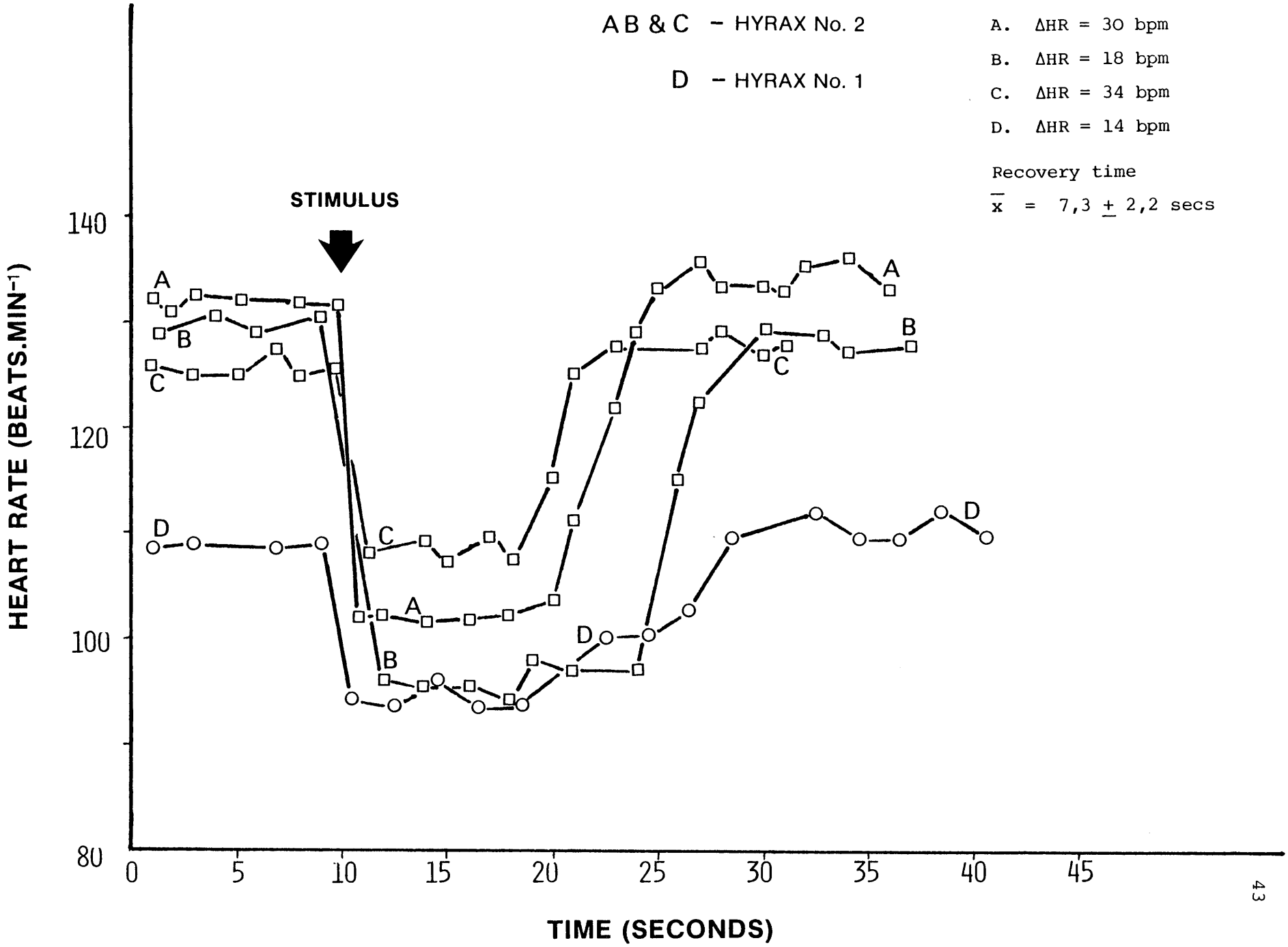

Figure 14: Fear bradycardia and recovery profile

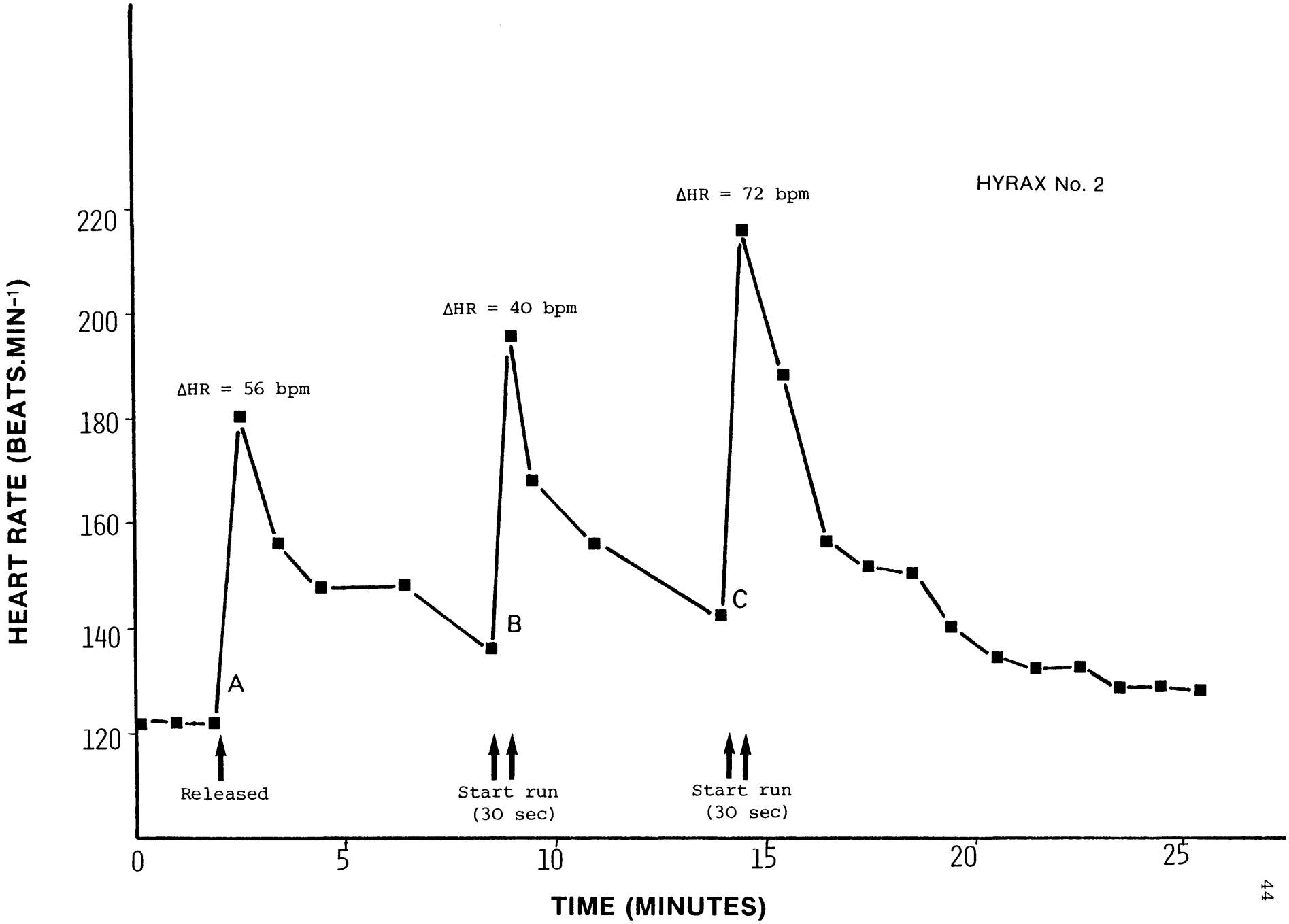

Figure 15: Heart rate when under stress and when exercised

hyrax to one end, the hyrax would then turn around, run back to the beginning and then get carried to the top again. (This happened 4 times during the 30 sec run). After 5 min resting, the heart rate had dropped to 142 beats/min and the next 30 sec run was commenced, resulting in a maximum HR of 216 beats/min. After approximately 9 min recovering time the HR had dropped to 128 beats/min and looked as if it had levelled off. This recovery profile is very similar in time and shape to the one following after "fear" tachycardia in Figure 13.

BODY TEMPERATURE (Tb)

Sixty one hyrax were shot between January 1979 and December 1981 whose body temperature (rectal temperature) were measured, post mortem. These temperatures ranged from 34,5°C to 40,2°C. When plotted in the form of an histogram (Figure 16), they show the distribution about a mean of 37,09 $\pm$ 0,91°C. As can be seen the single measurement of 40,2°C is outside the range of the majority of temperatures measured, in fact, it is further than three standard deviations from the mean, and as a result it has been decided to discard this figure as unreliable. The mean of 60 body temperatures (excluding 40,2°C) is 37,04 $\pm$ 0,82°C.

Figure 17 shows Class I hyrax temperature profiles. The maximum S.D. here is 0,81°C, which is in a 1,15kg hyrax exposed to an environmental temperature of 16°C over 22 min. In Figure 18 can be seen Class II hyrax where the maximum S.D. was 0,58°C (1,8kg hyrax exposed to 21°C) over 24 min. The largest animals (Figure 19) show a maximum S.D. of 0,28°C (3,0kg, 21°C, 15 min). Besides a few animals in Class I and II, the majority of hyrax did not have body temperatures that varied much over the period of time

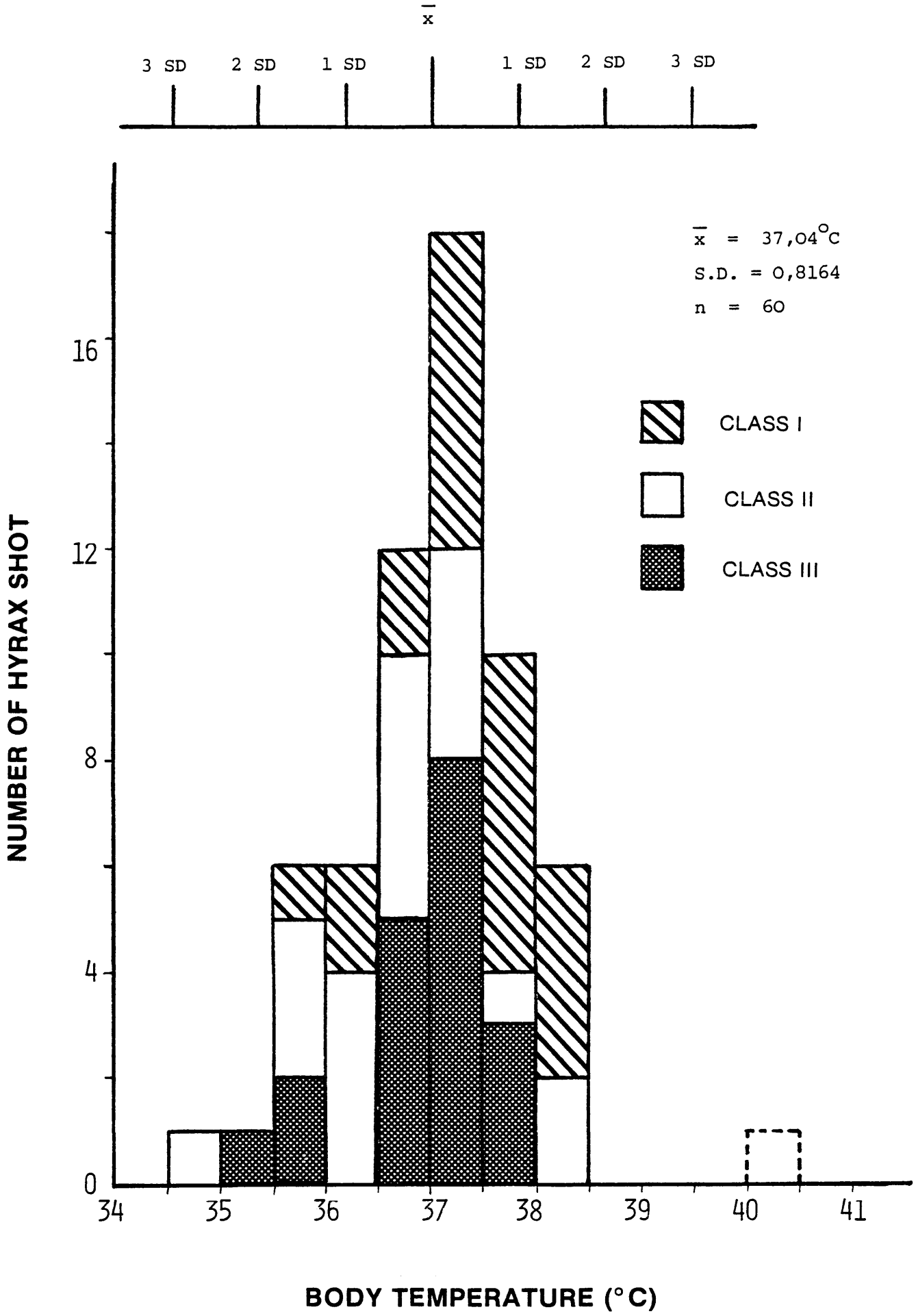

Figure 16: Relative occurrence of various Tb in the shot hyrax

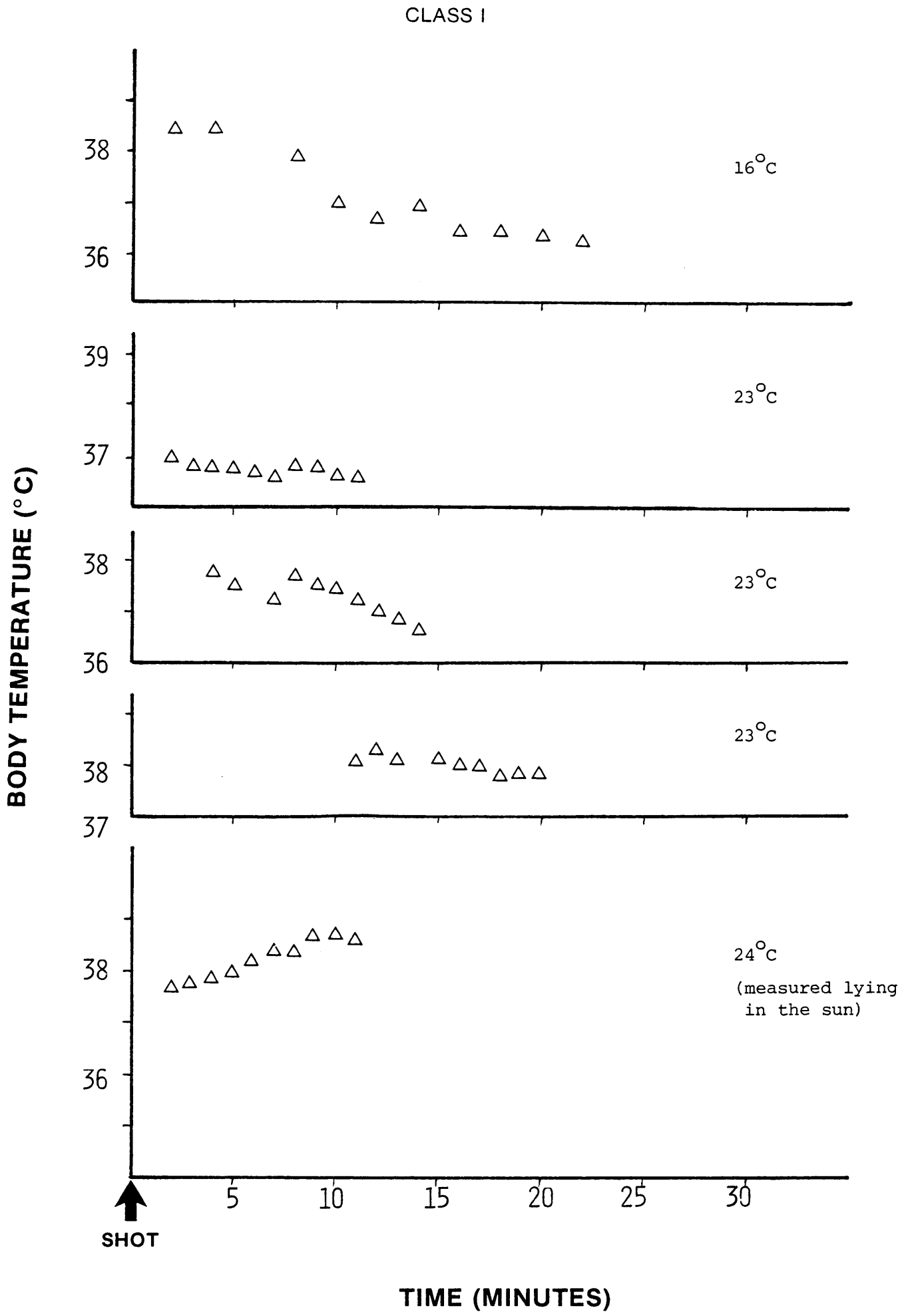

Figure 17: Tb profile post mortem - Class I

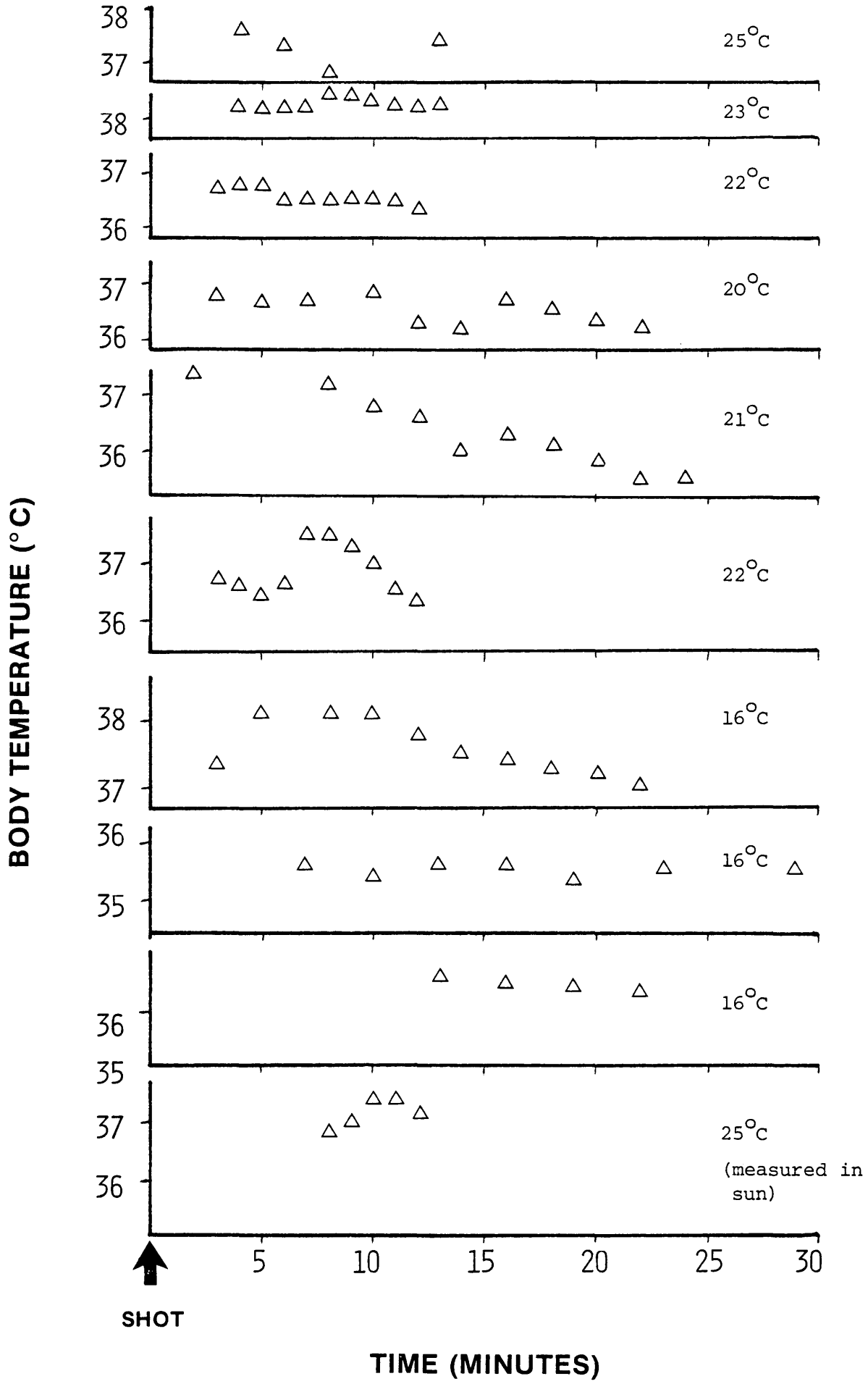

Figure 18: Tb profile post mortem - class II

CLASS III

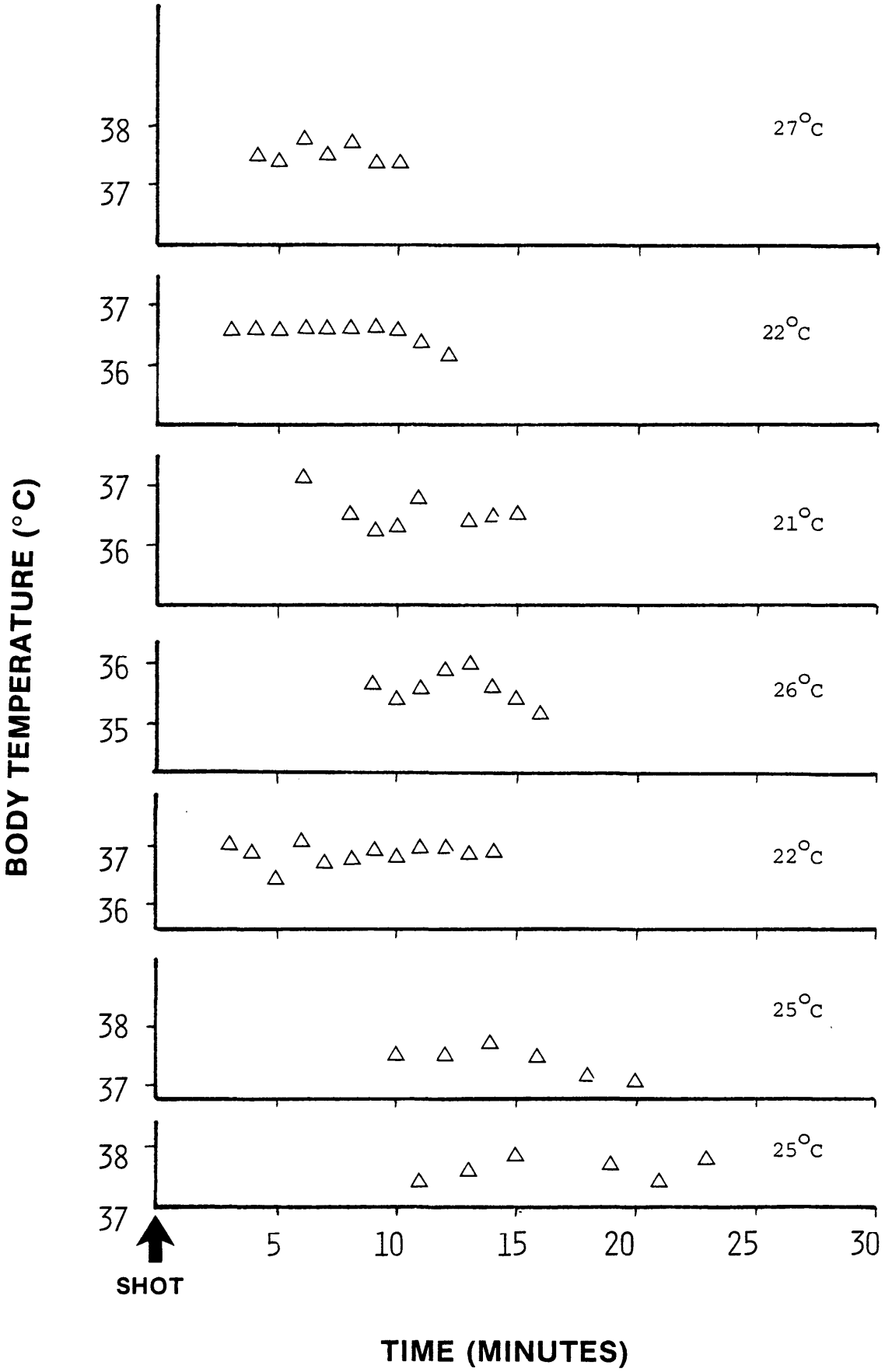

Figure 19: Tb profile post mortem - Class III

examined.

Figures 20, 21 and 22 show body temperature plotted against time of day for Classes I, II and III. No clear circadian pattern can be seen, but it should be borne in mind that the sample sizes for the individual groups are quite small, and thus conclusions at the best, might be hazardous.

It must be taken into account that the data were collected throughout the year and thus 08h00 in summer would expose the hyrax to totally different environmental temperatures to those pertaining at 08h00 in winter. Thus it is logical to examine body temperature as compared to environmental (ambient) temperature. Figures 23, 24 and 25 compare Class I, II and III hyrax body temperatures at different ambient temperatures.

Telemetrically monitored body temperatures taken during one hour exposures to varying ambient temperatures, are shown in Figure 26. These were measured concurrently with VO_2 measurements quoted earlier. The measurements were commenced at 30°C and terminated at 5°C, and are the means from five juveniles and five adults (means and S.D.'s are in the appendix). As can be seen, the body temperatures are at a maximum when measured at an ambient temperature of 30°C and then the body temperature falls until , in the case of the juveniles, it levels off below an ambient temperature of 20°C. The adult's body temperature, however, continues to fall and even at an ambient temperature of 5°C it has not levelled off, although it does seem to be flattening out slightly.

The body temperature of two adult hyrax as measured at a constant ambient temperature over a 24h period, are shown in Figure 27. The Tb data for 26° and 10°C are the means of two animals taken over three days. The data for 15°C are from one animal on one day only, and as such, should be viewed

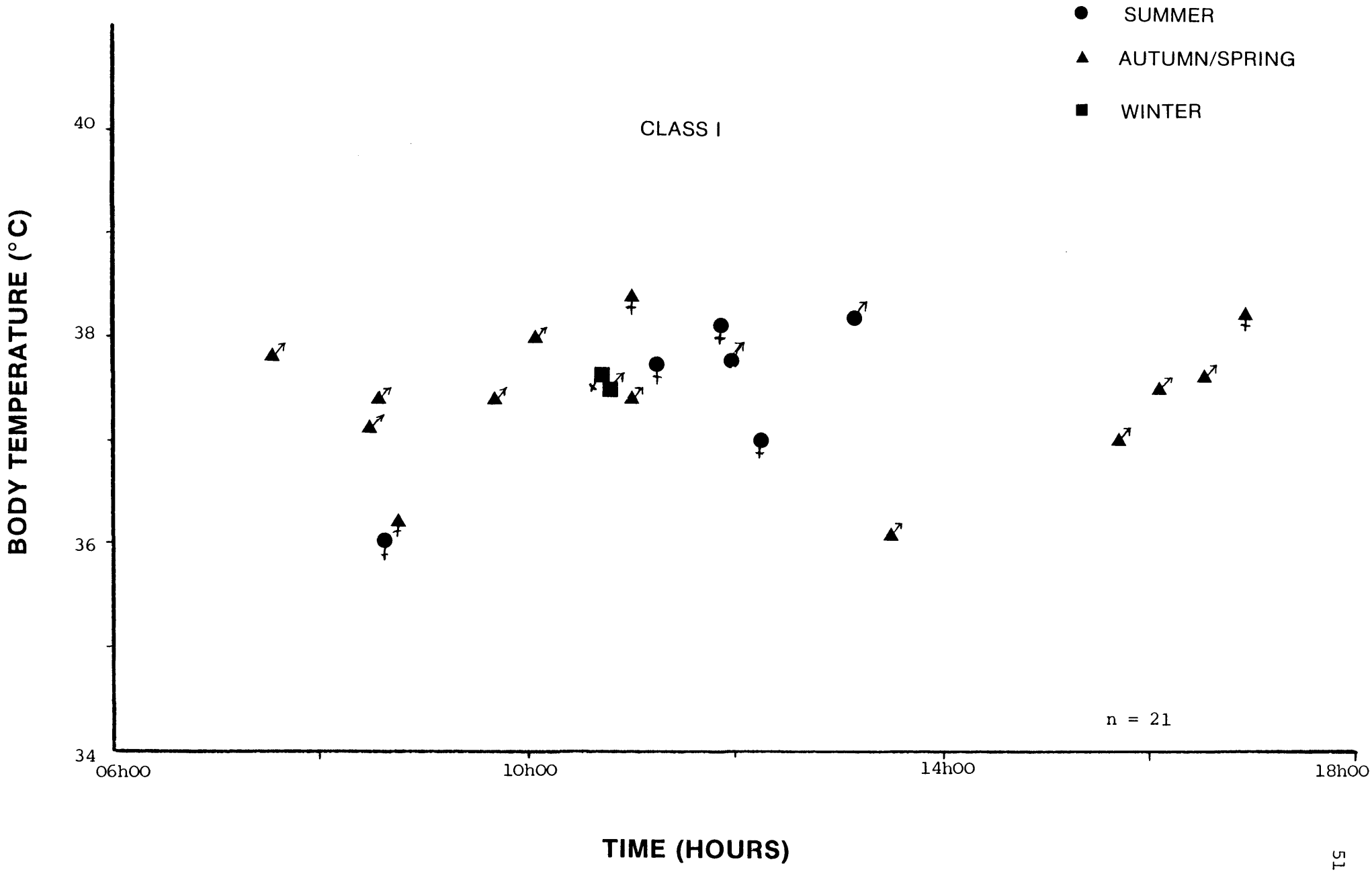

Figure 20: Tb at various times of day - Class I

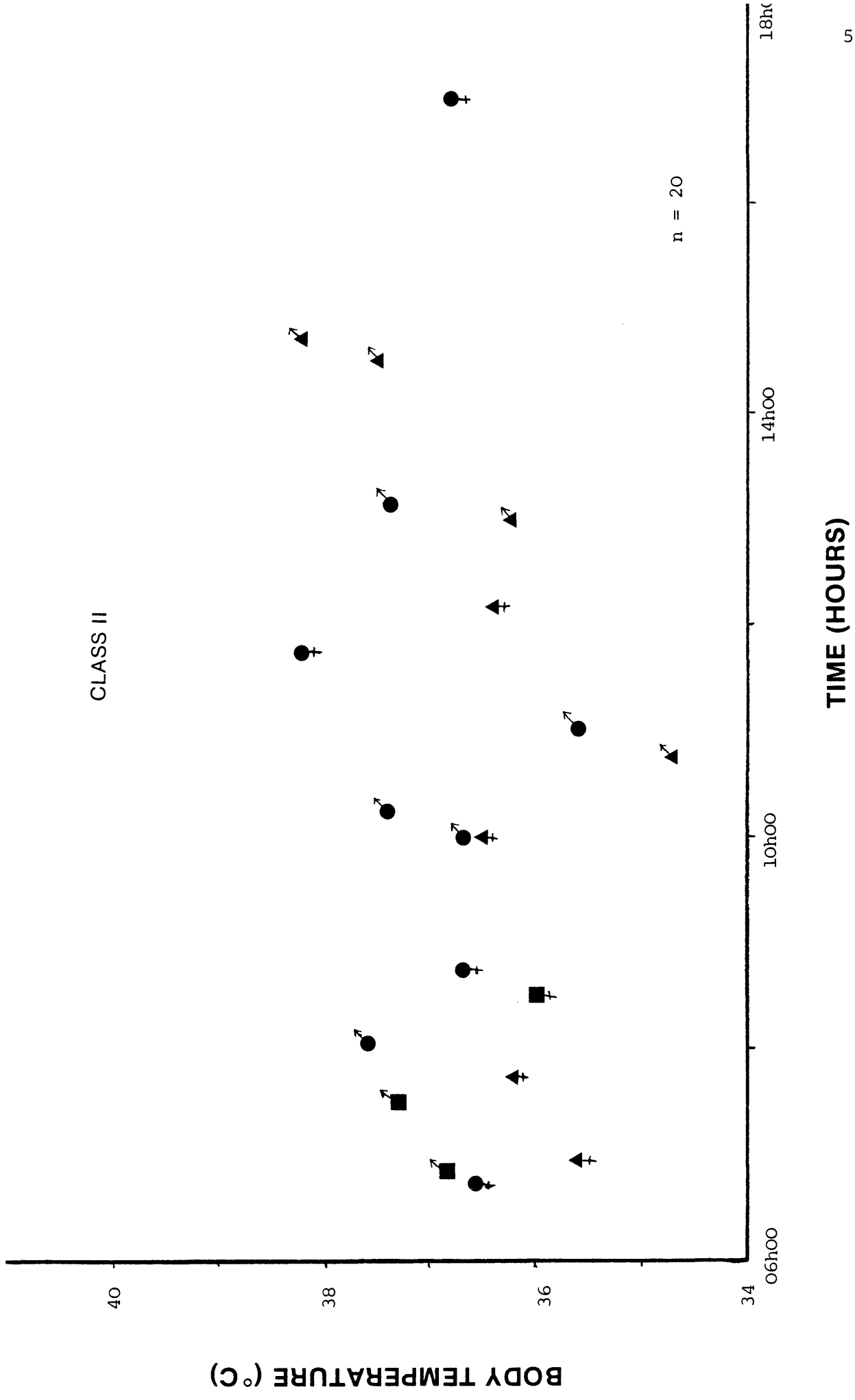

Figure 21: Tb at various times of day - Class II

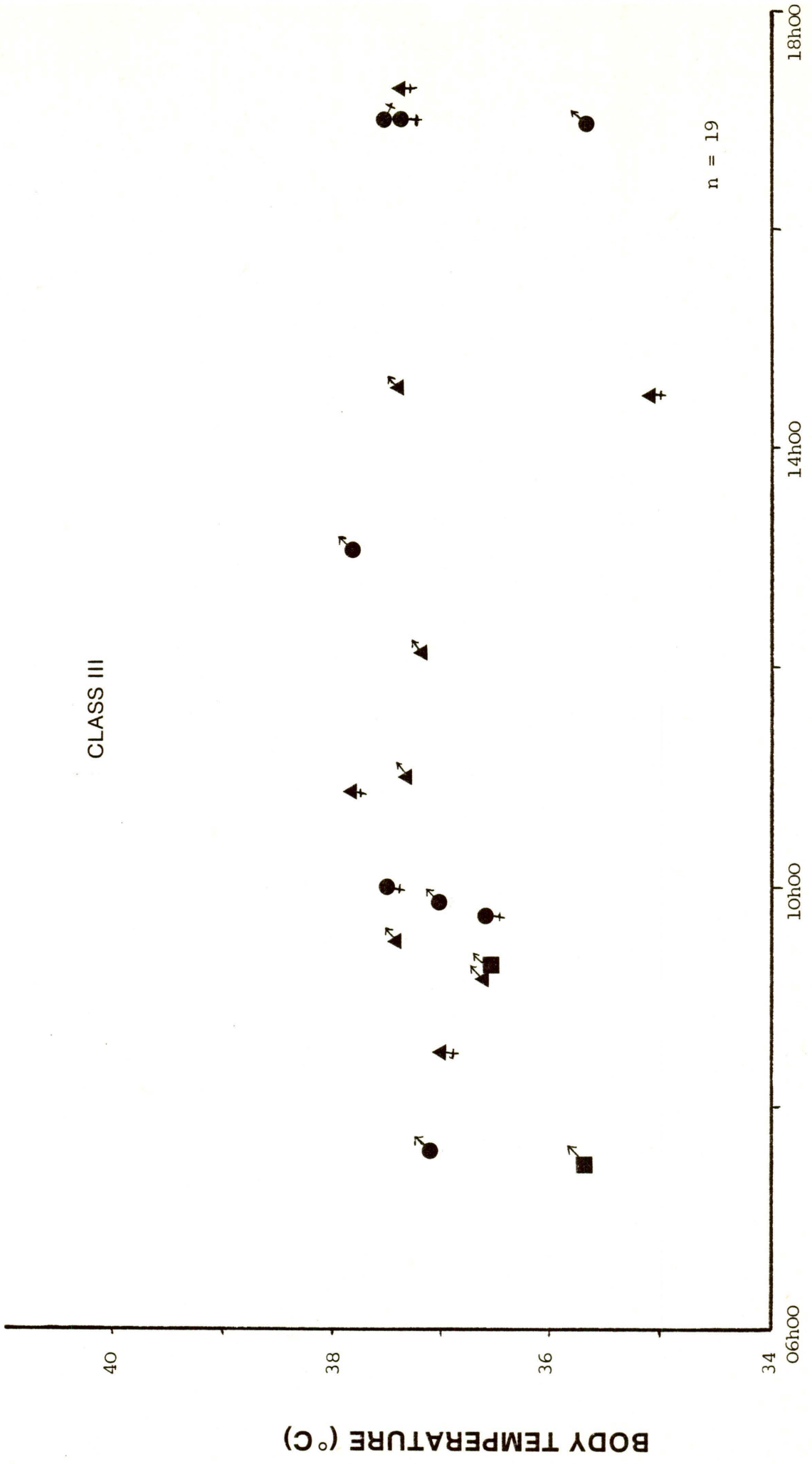

Figure 22: Tb at various times of day - Class III

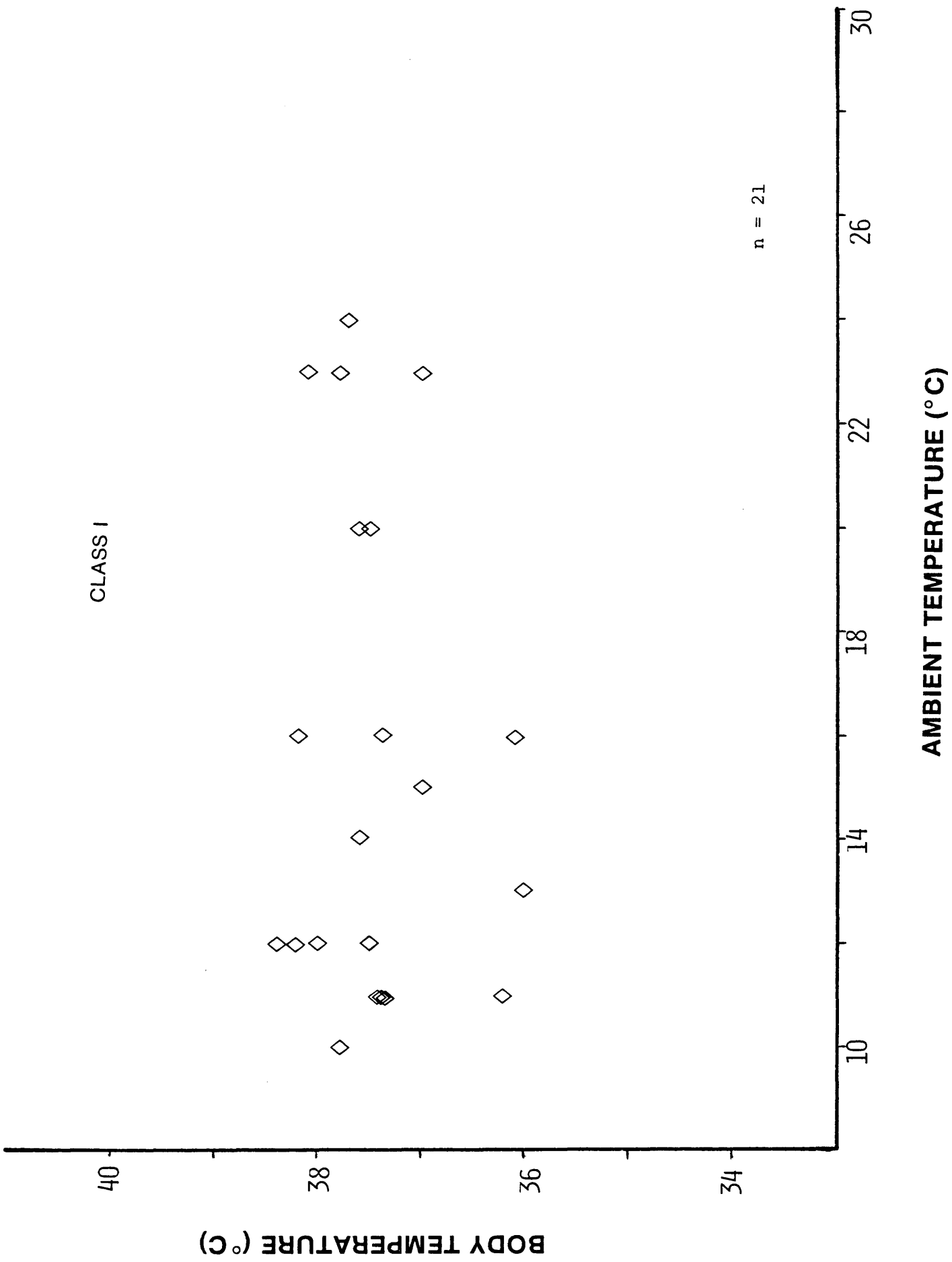

Figure 23: Tb at different ambient temperatures - Class I

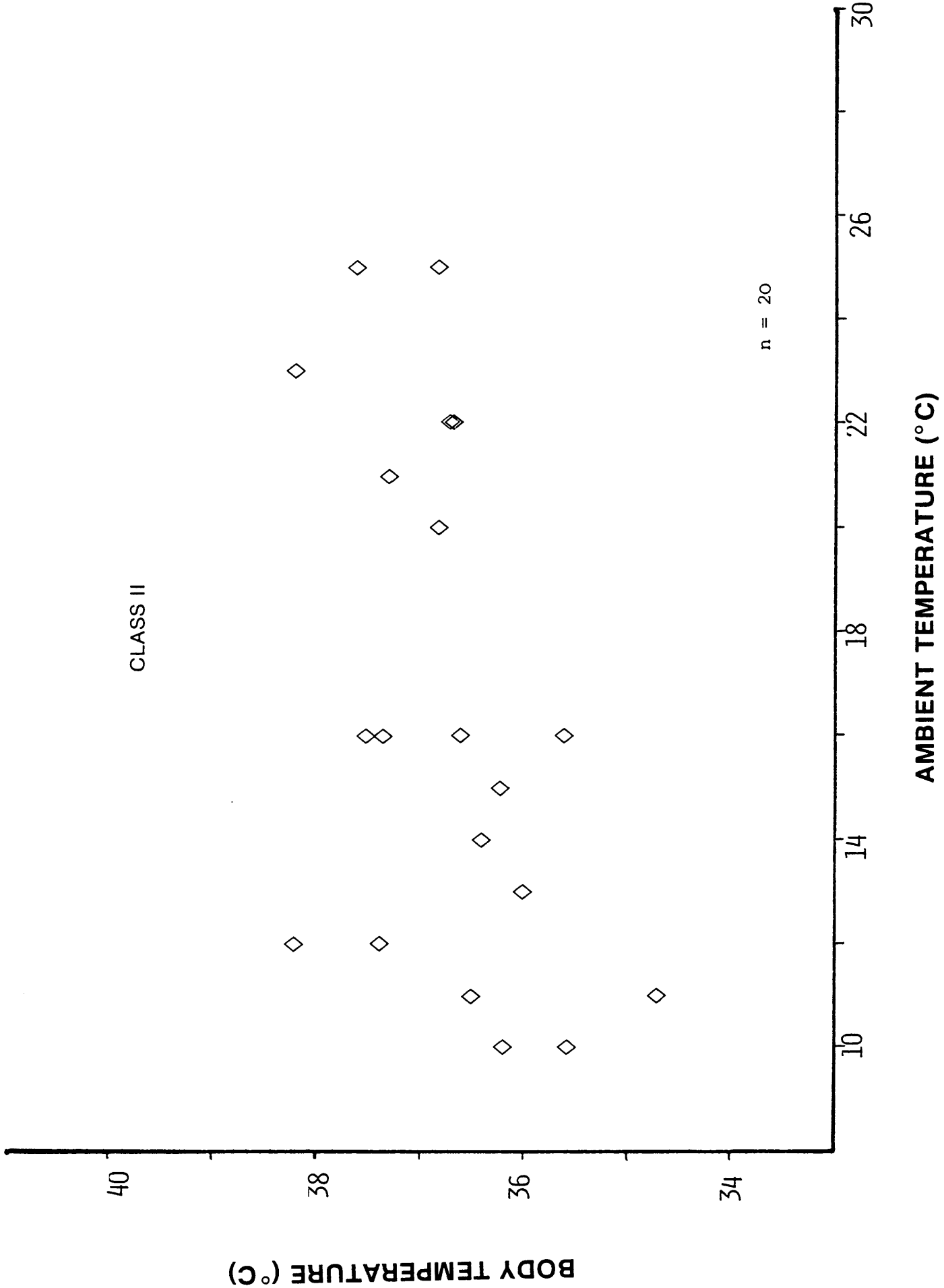

Figure 24: Tb at different ambient temperatures - Class II

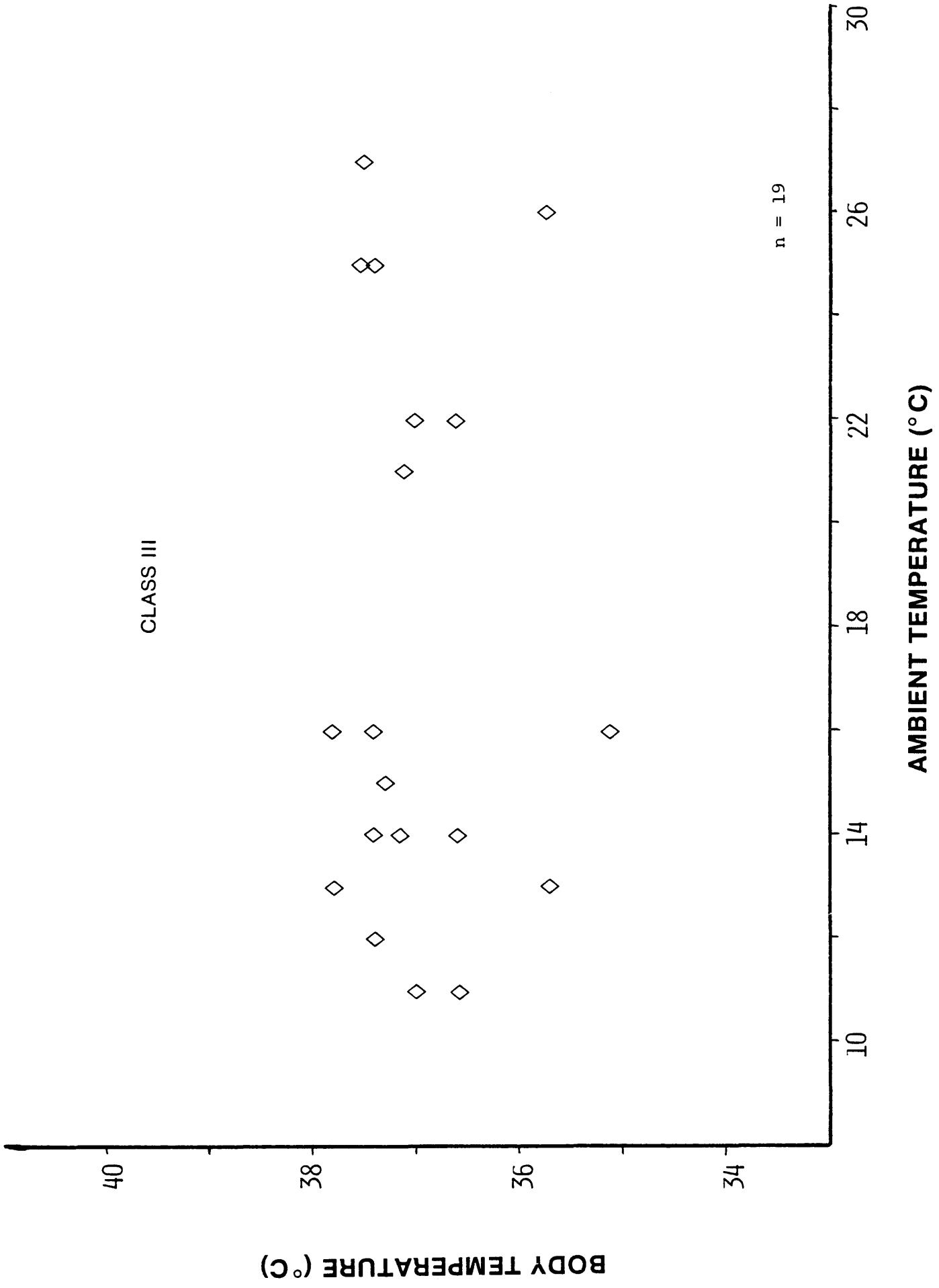

Figure 25: Tb at different ambient temperatures - Class III

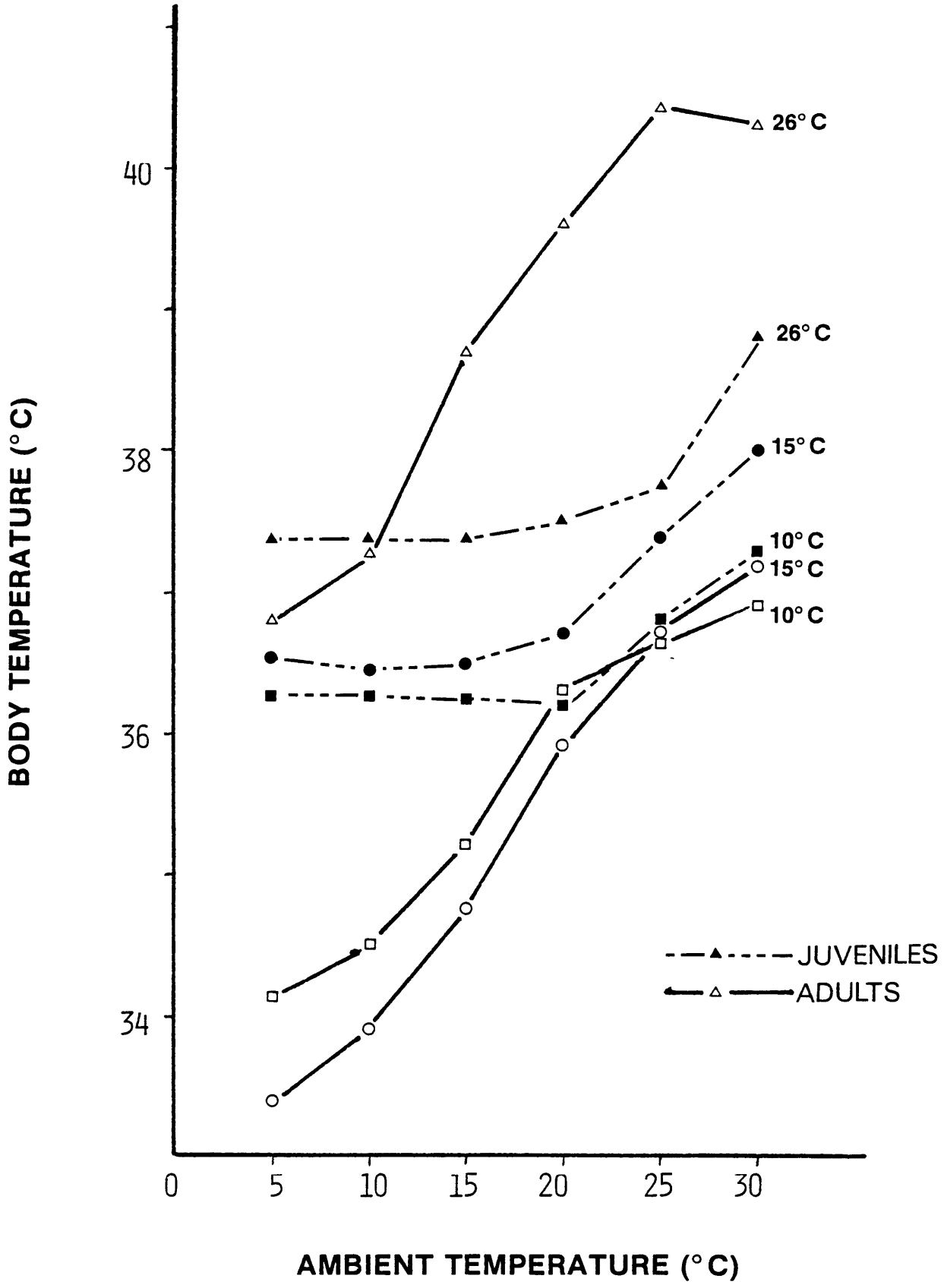

Figure 26: Tb of adult and juvenile hyrax at various ambient temperatures in the laboratory

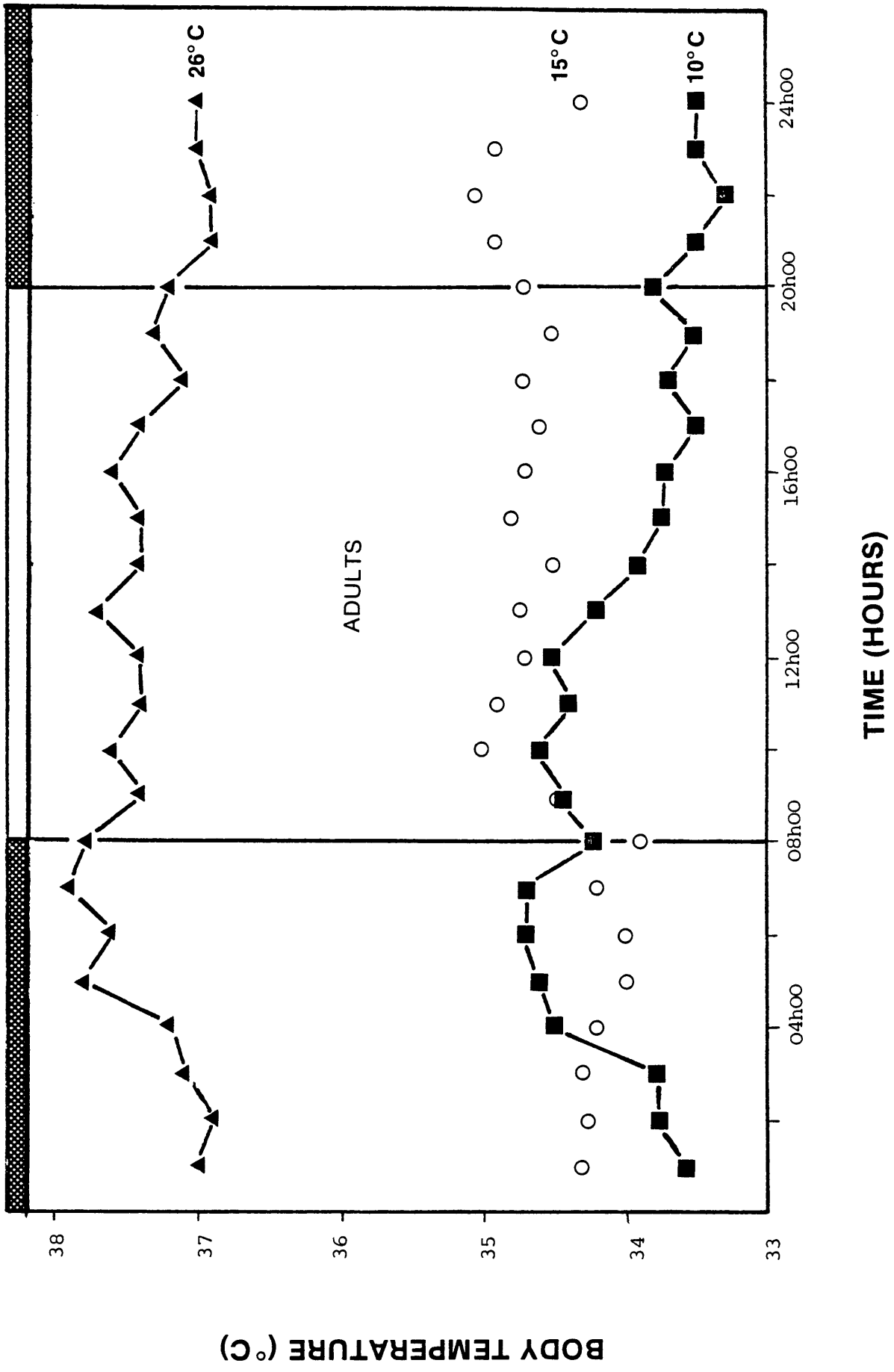

Figure 27: 24h Tb profiles of adult hyrax at constant acclimation temperatures

with due caution. The animals were habituated to the lights switching on at 08h00 and increases in body temperature at both 26° and 10°C acclimated animals were observed to have peaked one hour earlier. Thereafter, there was a gradual decline until a minimum was reached between 22h00 and 02h00. As can also be seen, there is a magnitude difference between the overall body temperature at 26°C and those at 10°C which suggests an overall lower body temperature at lower ambient temperatures.

METABOLIZABLE ENERGY (ME)

Figure 28 shows the metabolizable energy in $kJ(g.24h)^{-1}$ of adults (mean mass 3457g) as measured at various acclimation temperatures. The lower of the two juvenile metabolizable energy lines represents the actual values as measured at the acclimation temperatures. The upper line is the corrected data to counteract the effect of the increase of mass in the juveniles and represents a value as though the juveniles had maintained a constant mass during the study and had not grown. This would hopefully counteract the decreased metabolic rate caused by an increase in body mass and thus allow changes in metabolizable energy due to ambient temperature to be more visible. As is predicted by Poczopko (1979), metabolizable energy values for adult hyrax where urine and methane fractions have been included in the calculation (Eloff 1981), yielded lower results than those obtained in this study. Those data of Eloff (1981) are included in Figure 39.

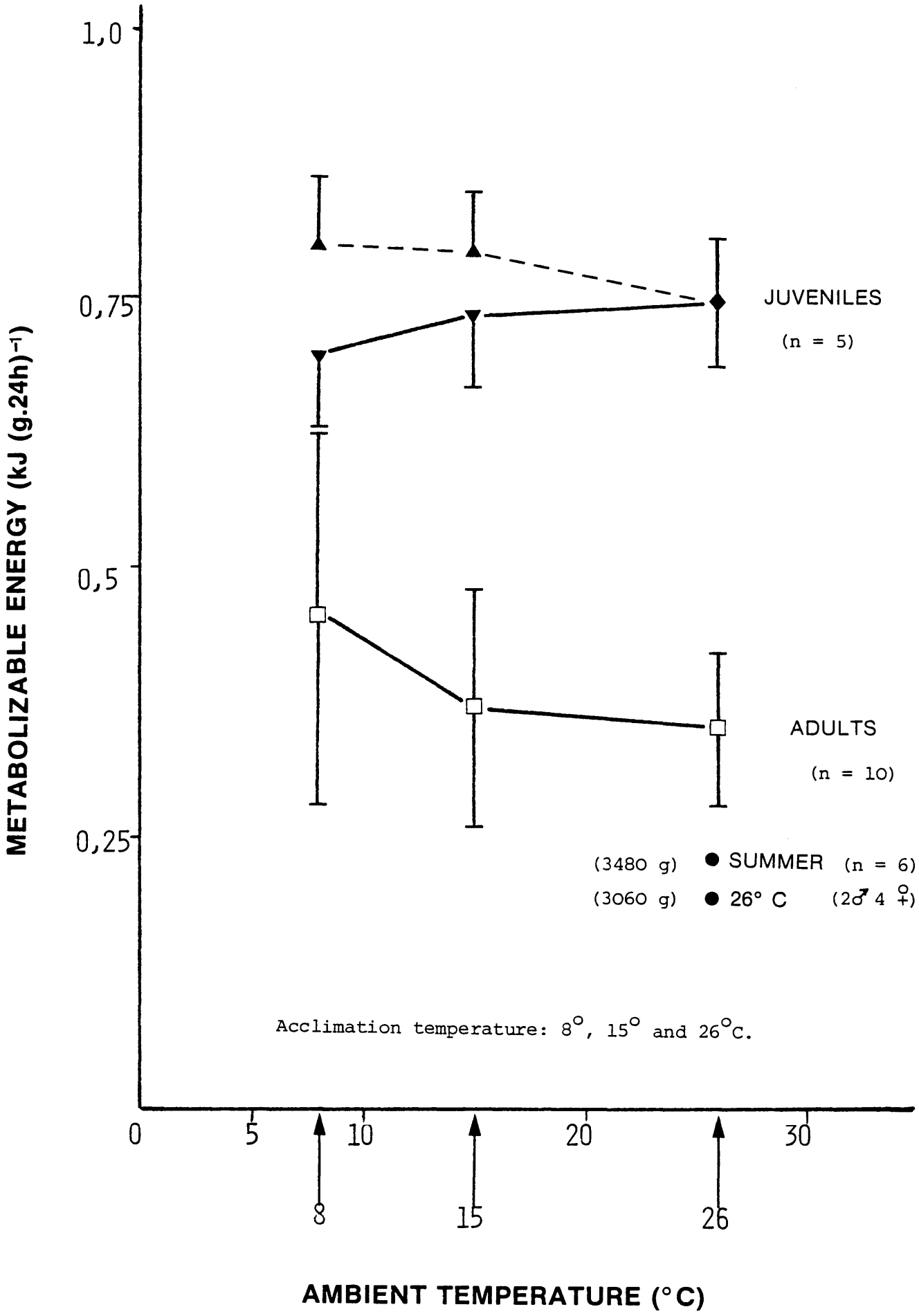

Figure 28: Metabolizable energy of adult and juvenile hyrax at acclimation temperatures (The two solid dots represent values for groups of

RADIATED HEAT (Tr)

The absorption of radiant heat at different acclimation temperatures is illustrated in Figure 29 by the increase in body temperature of the hyrax. However, leaving that for a while and looking at the radiant temperature of the pelage measured behind the shoulder, it can be seen that there is an increase in temperature (Tr) with exposure to Infra-red radiation. The increase in Tr is far greater in animals acclimated to a lower ambient temperature. At 26°C, however, the animals radiated at a temperature of 35°C which increased to 37°C after heating in front of the lamps. The hyrax heated from lower ambient temperatures radiated at 32° and 30°C.

NON-METABOLIC HEATING

In Figure 29 it can be seen that heating from a non-metabolic source (IR lamps) caused an increase in body temperature. Animals acclimated to 26°C increased their body temperature fractionally, while animals kept below thermoneutrality increased their body temperature from 36,95° to 39°C (those acclimated to 10°C) and from 37,2° to 38,1°C (those acclimated to 15°C).

ACTIVITY PATTERNS

The first indication of activity can be gained from the numbers of hyrax shot at different times of day as this may suggest at what times of day hyrax

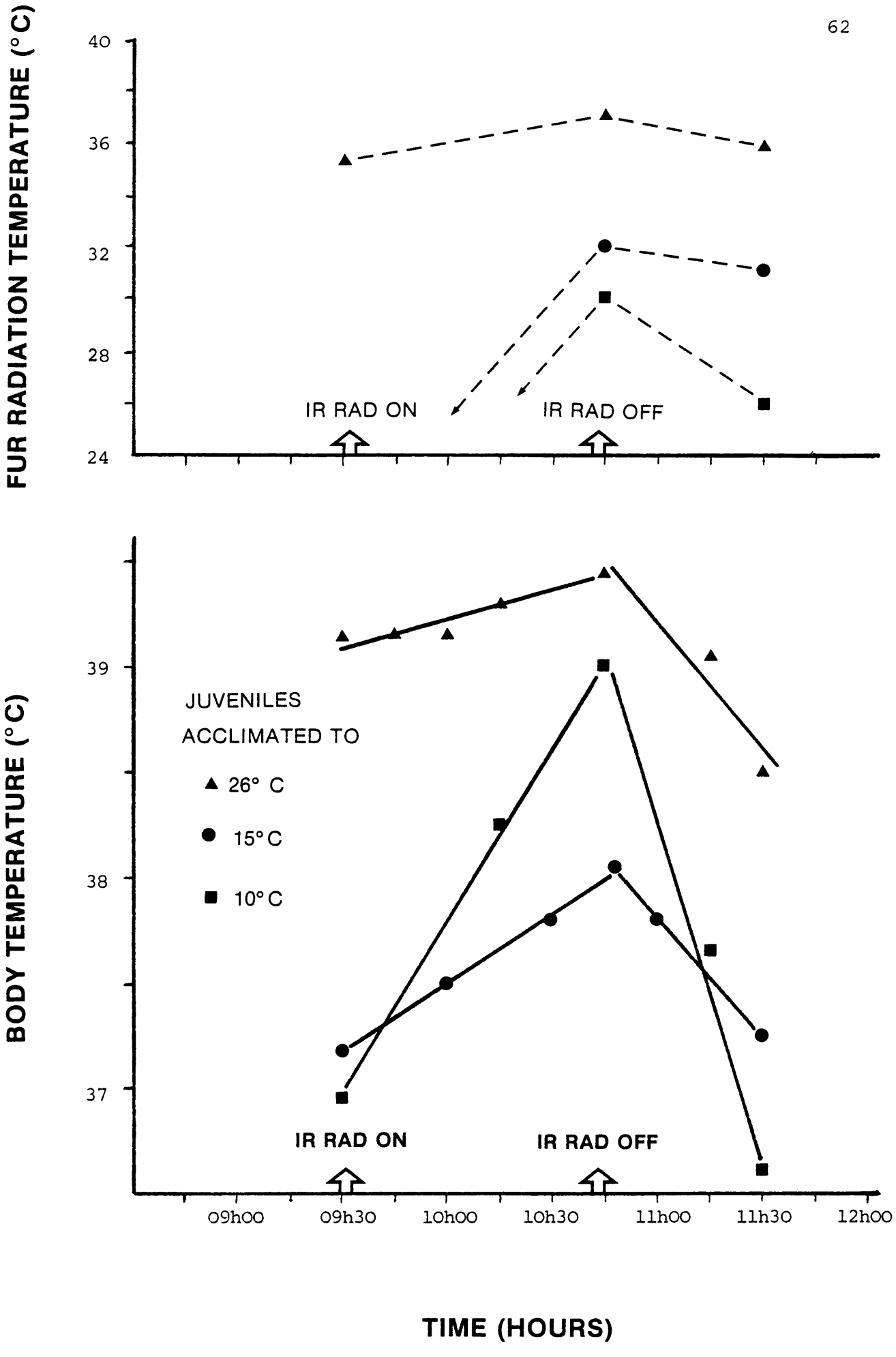

Figure 29: Fur radiation temperature and non-metabolic heating in hyrax at acclimation temperatures

are more active, providing that the researcher is consistently active throughout the day. Figure 30 shows the relative number of hyrax shot during Summer, Spring/Autumn and Winter at different times of day.

Another index of activity was the percentage of animals visible, at the Experimental Farm at any moment in time. Figures 31 and 32 show the pattern in Summer and Winter. As is expected, hyrax are far more active during the day (both Summer and Winter), as they are essentially diurnal animals. The big difference in activity between Summer and Winter is based on the fact that hyrax seem to become active later on a Winter's morning (than in Summer), and their activity tapers off far sooner in the early evening in Winter. During the night in Summer more hyrax are visible but these animals may be just as inactive as those within the sleeping boxes, and as a result, one cannot be categorical about this subjective analysis of activity.

Figure 33 shows the percentage of time spent by a focal animal on specific activities during the daylight hours. In summer it can be seen that the hyrax is "not visible" for 32% of the time, it is "lying, sitting or grooming" for 40% of the time and "moving" (walking or running), "feeding" and "fighting" for 28% of the time. In winter these figures change to "not visible" 12%, "lying", "sitting" etc. 52% and "feeding", "moving" etc. 36%. These relatively gross, arbitrary subdivisions are more neatly delineated in Figure 33.

The last aspect examined under activity was the relative heart rates of each of the activities designated above. These heart rates, in Figure 34, can be seen in the light of the percentage of time spent carrying out the activity, and from this an idea can be gained of the average heart rate during a total period, which can thus later be extrapolated to metabolic rate.

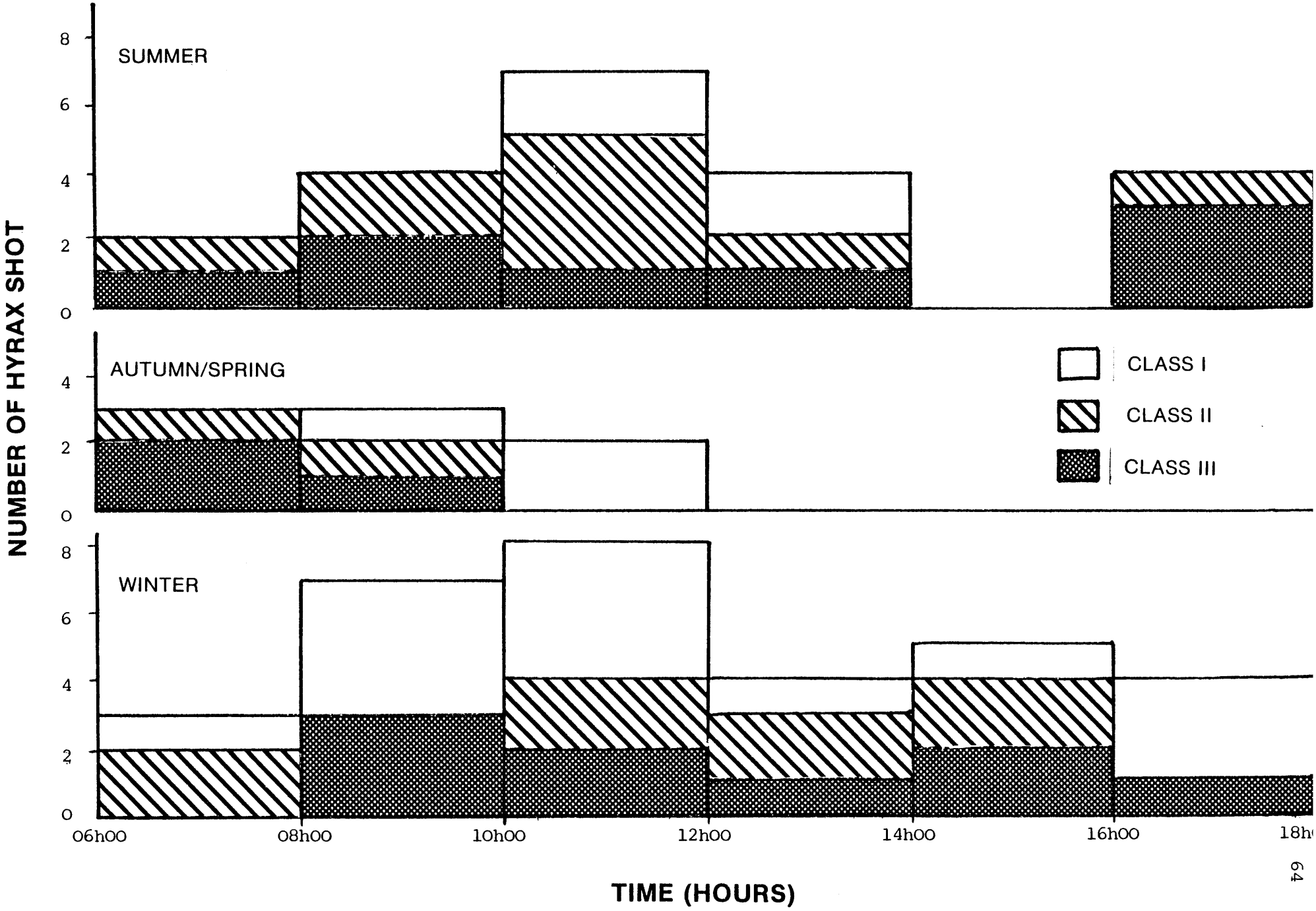

Figure 30: Times of day at which hyrax were shot

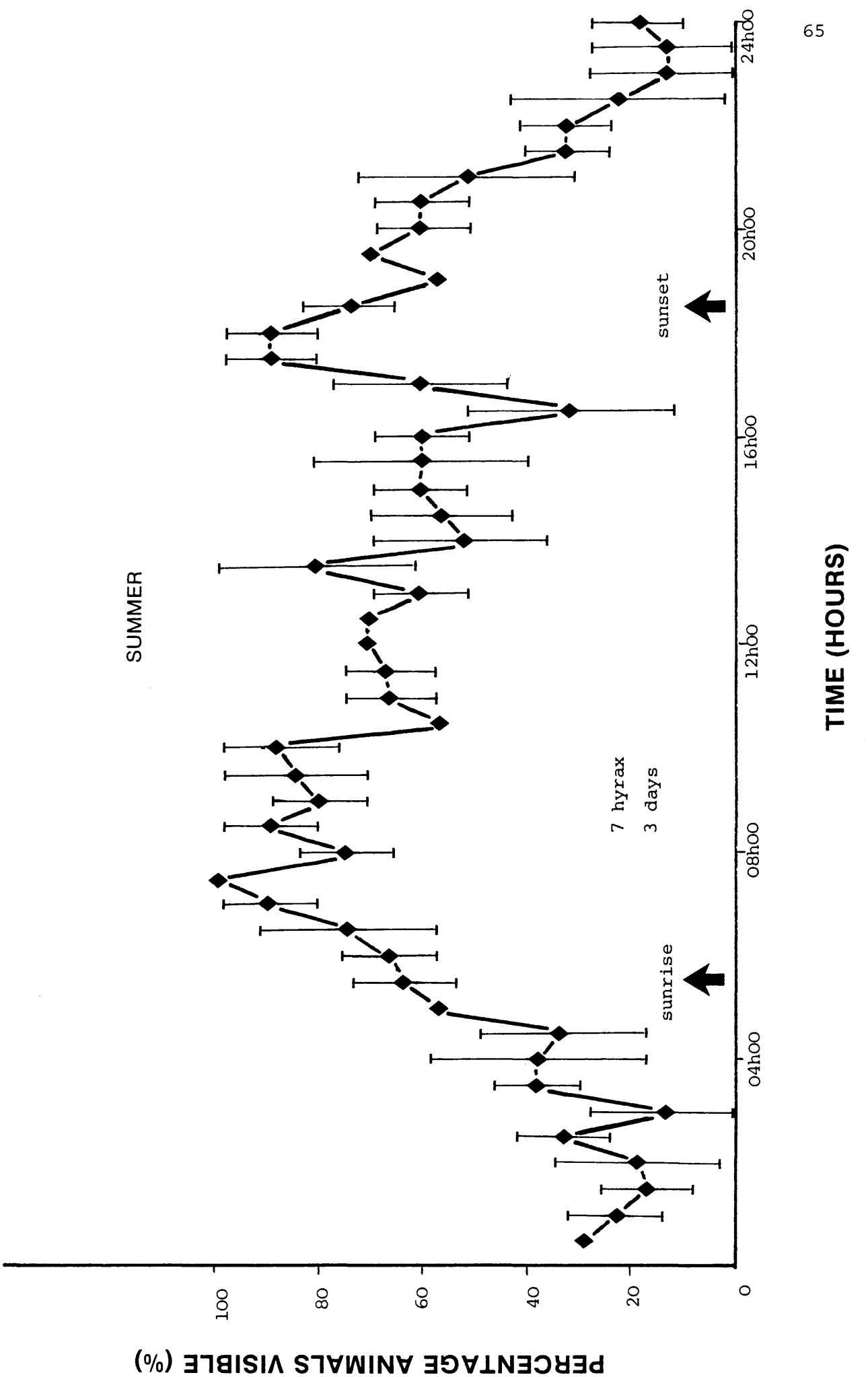

Figure 31: Percentage hyrax visible over a 24h period (Summer)

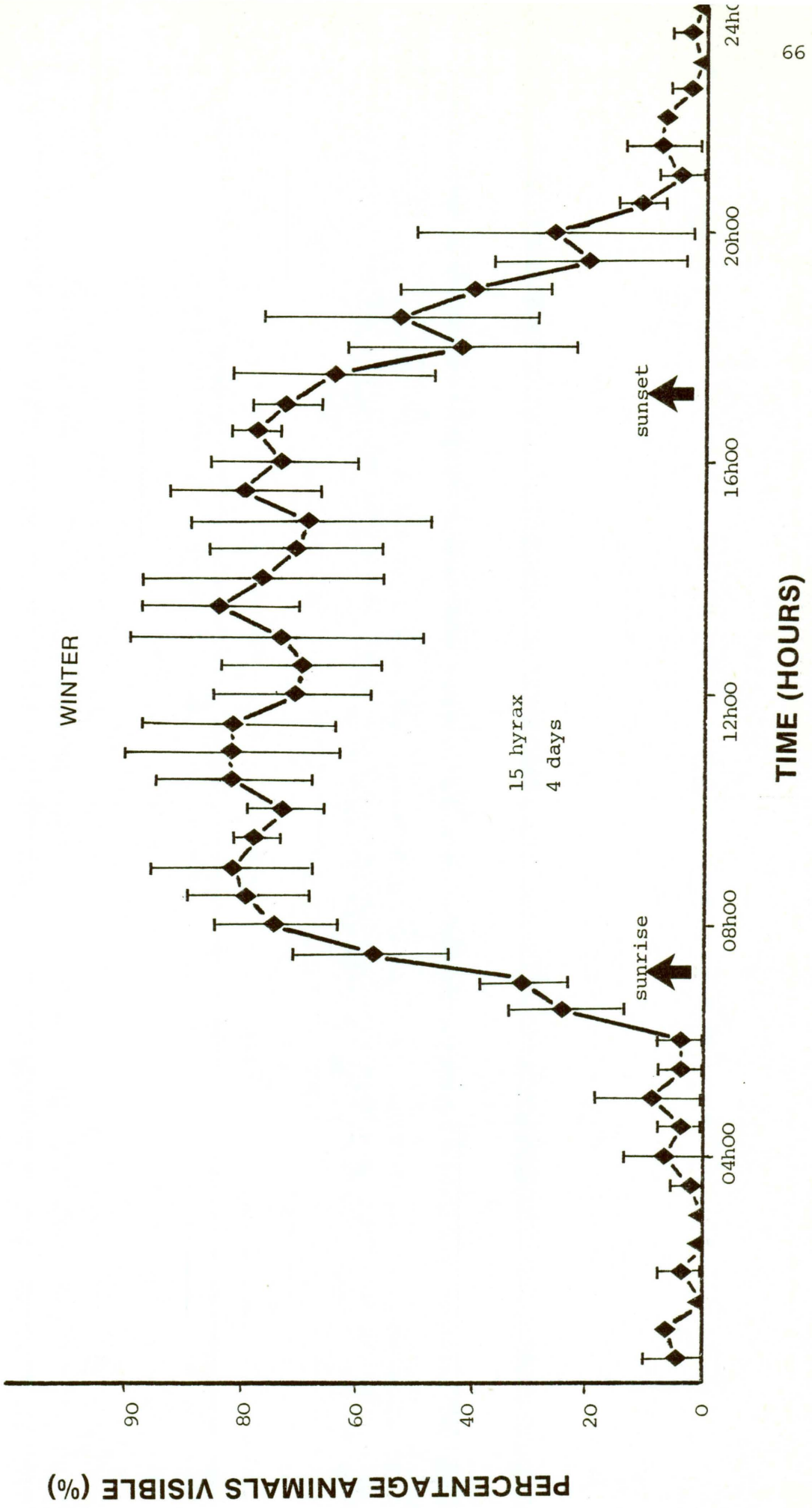

Figure 32: Percentage hyrax visible over a 24h period (Winter)

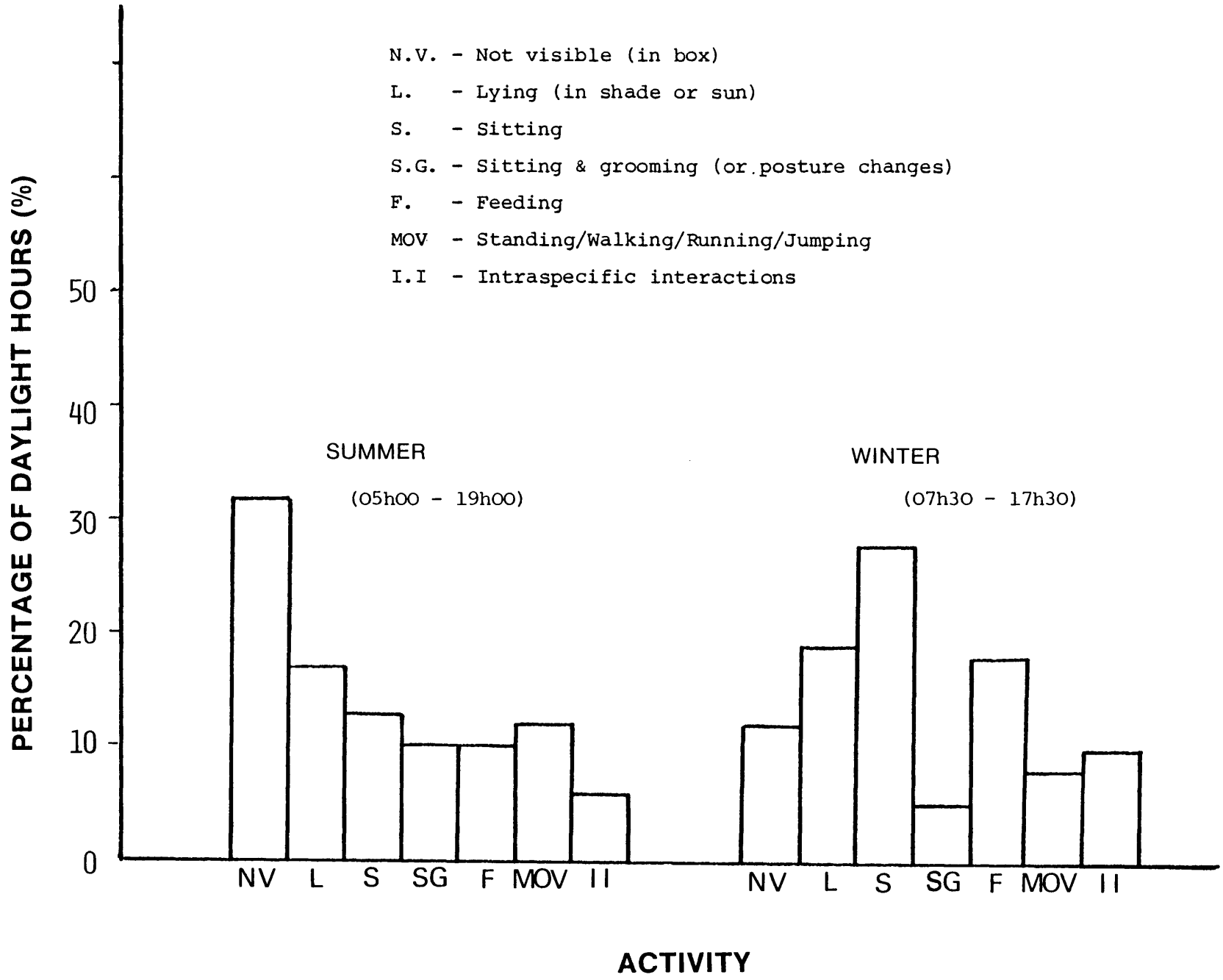

Figure 33: Percentage of daylight hours spent by a focal animal on specific activities (summer and winter)

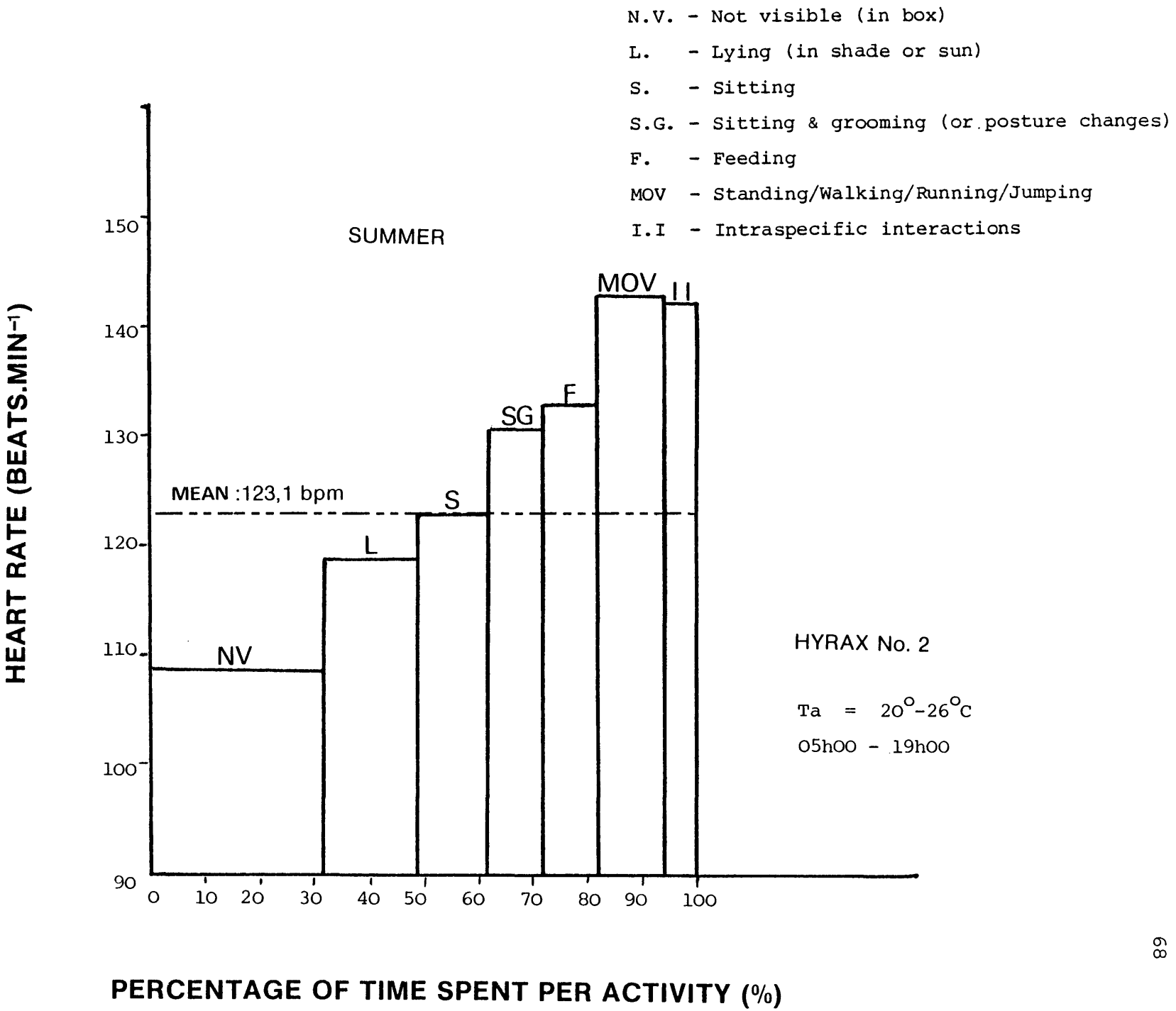

Figure 34: Heartrate and percentage time spent on each activity during daylight period (summer)

The relationship between VO_2 and HR is shown in figures 35 (adults) and 36 (juveniles). It can be seen that there is a linear relationship between these two parameters in both cases, however the difference between adults and juveniles is of importance at a later stage and should thus be borne in mind.

THYROID GLANDS AND HORMONES

Hormones

Data on serum T4 and T3 concentrations in adult hyrax, are shown in Table 1. Because of the small sample size, statistical analyses of the data should be interpreted with caution.

The TNZ is between 20° and 30°C, and thus the values for T4 and T3 at 26°C should be representative for the thermoneutral zone. No significant differences between different acclimation temperatures or between different seasons could be shown. It does seem however, that the T4 values for field hyrax were lower than those for captive hyrax, while the T3 values seem to suggest the opposite trend.

Free T4, comprising some 0,04% of total serum T4, is the major thyroid metabolic regulator (Beesson & McDermott 1975). The Free-T4 values for laboratory and field animals do not differ significantly ($P = 0,05$), while the Free-T4 in the laboratory at 8°C was significantly higher (one way ANOVA, $P < 0,05$) than the laboratory values at 15° and 26°C. The same was not found in the field data.

The Free Thyroxine Index ((T4 x T3-retension) x 10^{-2}) which is a widely

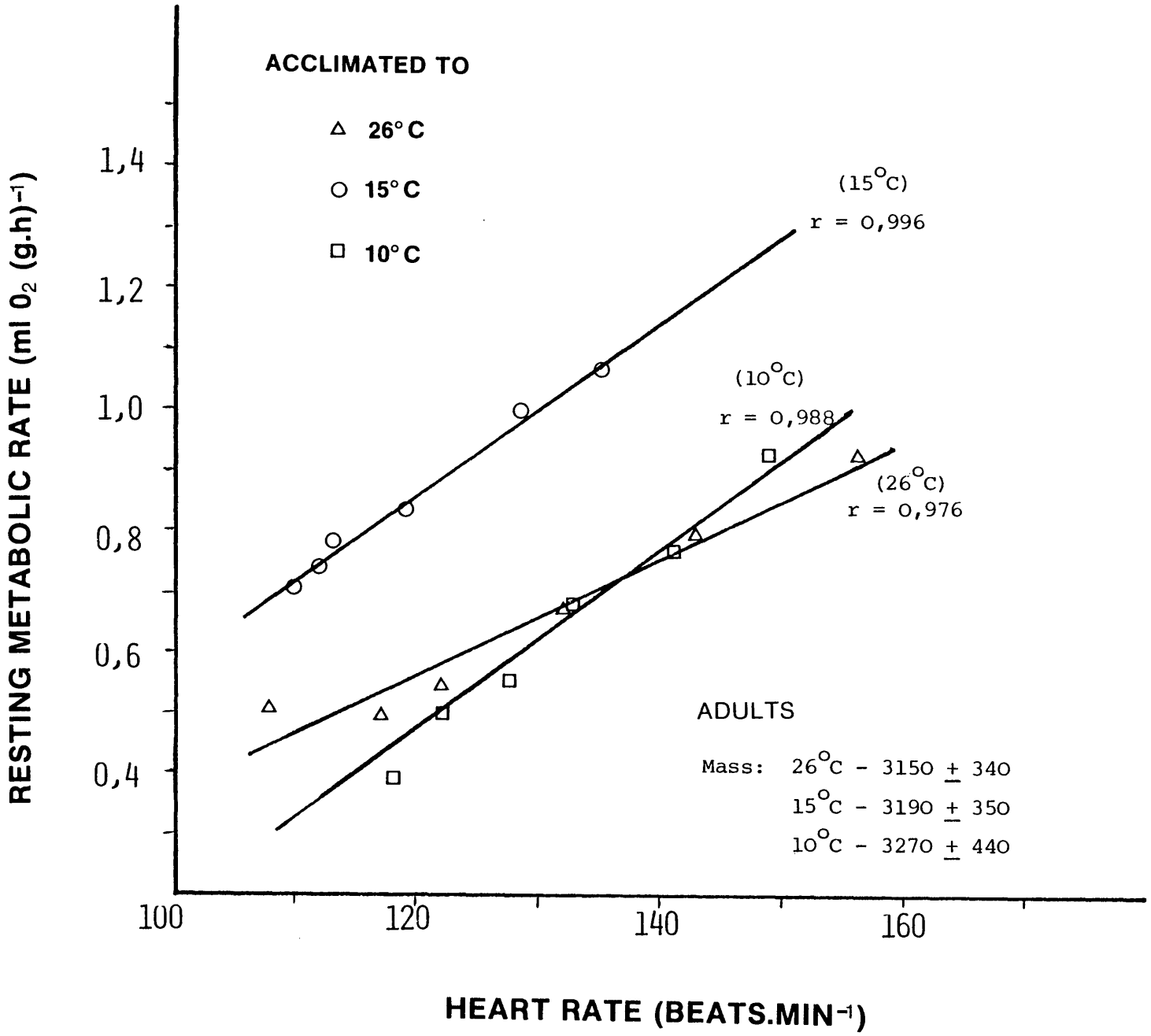

Figure 35: Correlation between VO_2 and HR in adult hyrax at three acclimation temperatures

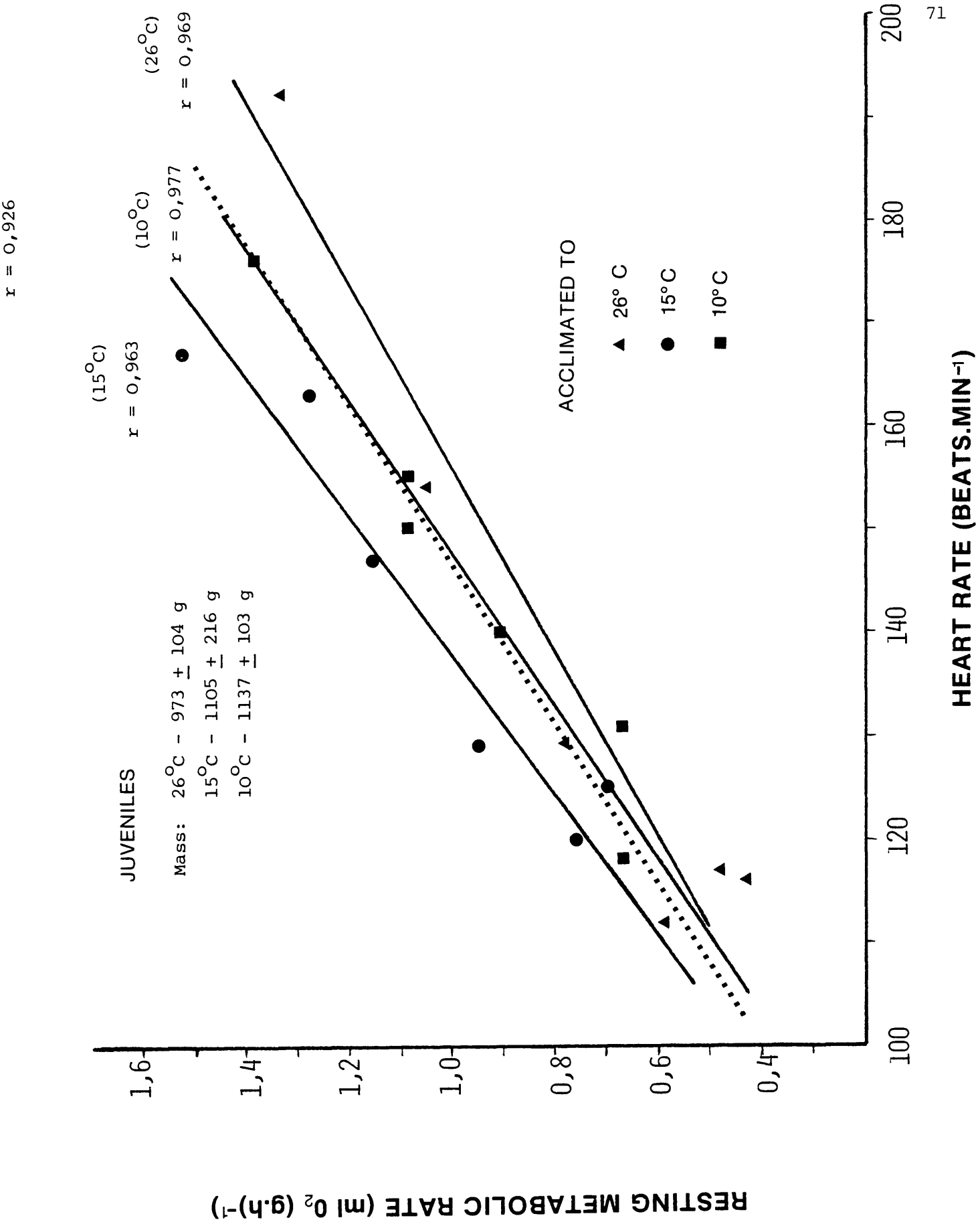

Figure 36: Correlation between VO_2 and HR in juvenile hyrax at three acclimation temperatures (The broken line represents the combined 10°, 15° and 26°C data).

TABLE 1. Serum L-thyroxine (T4) and triiodo-L-thryonine (T3) concentrations and indices in P. capensis.

	SERUM CONCENTRATION OF HORMONES (nmol/l) T4	T3	(ng/dl) Free-T4	FREE THYROXINE INDEX	T3:T4 ⊕ ratio x 10^2
LABORATORY					
26°C (3)	227 ±136	5,6 ±1,3	1,05 ±0,4	81 ±48	2,9 ±1,1
15°C (2)	153 ±35	5,7 ±0,2	1,09 ±0,35	61 ±7	3,8 ±0,9
8°C (3)	251 ±82	6,6 ±1,9	2,04 ±0,09*	78 ±1	2,7 ±0,2
FIELD					
Summer (3)	172 ±41	6,1 ±1,4	1,56 ±0,24	65 ±16	3,6 ±0,1++
Spring (3)	152 ±17	8,6 ±0,6	1,85 ±0,14	52 ±6	5,7 ±0,9
Winter (2)	140 ±47	6,7 ±2,1	1,32 ±0,62	45 ±20	4,8 ±0,1

All data are shown as mean ± S.D. (sample size in parentheses). Data of serum T4 and T3 were subjected to one way analysis of variance, but no significant differences could be shown.

* Free-T4 at 8°C was significantly higher ($P < 0,05$) than at 26° and 15°C (one way ANOVA).

⊕ T3 : T4 ratio was significantly higher (two sample t-test, $P < 0,01$) in wild hyrax than in captive hyrax.

++ T3 : T4 ratio in summer was significantly lower ($P < 0,05$) than in spring or winter (one way ANOVA).

used indicator of thyroid function in humans (Prof.P.Prinsloo, pers. comm.), does not show any significant differences between acclimation temperatures or seasons in the present study.

The ratio of T3:T4 has recently been used by Kamis (1980) and Leatherland & Ronald (1981) as an indication of thyroid activity. The overall T3:T4 ratios were found to be significantly higher (t-test, $P < 0,01$) in field hyrax than in captive hyrax.

At the same time, the field data for T3:T4 showed the Summer value to be significantly lower (one way ANOVA, $P < 0,05$) than Spring and Winter. The same could not be shown for the laboratory data and it should be borne in mind that the laboratory animals were exposed to a constant 12 h:12 h light : dark photoperiod.

Finally, thyroid-stimulating hormone (TSH) levels were determined for all the samples. The technique utilised to measure TSH is inherently inaccurate between 0-2 mE/l, while from 2mE/l up to 10 mE/l (or higher) it can be considered extremely accurate. With the exception of three values, all the hyrax TSH data fell between 0 and 2 mE/l and as a result could not be considered to be meaningful.

Thyroid histology.

The index of thyroid activity (d/n) values obtained for the 21 hyrax thyroids examined, resulted in a range from 2,31 to 5,01. These values are without meaningful units, as they are derived from d (inner diameter) in um and n (number of cells surrounding the follicle). Figure 37 illustrates the relationship between d/n index values and the seasonal acclimatisation or

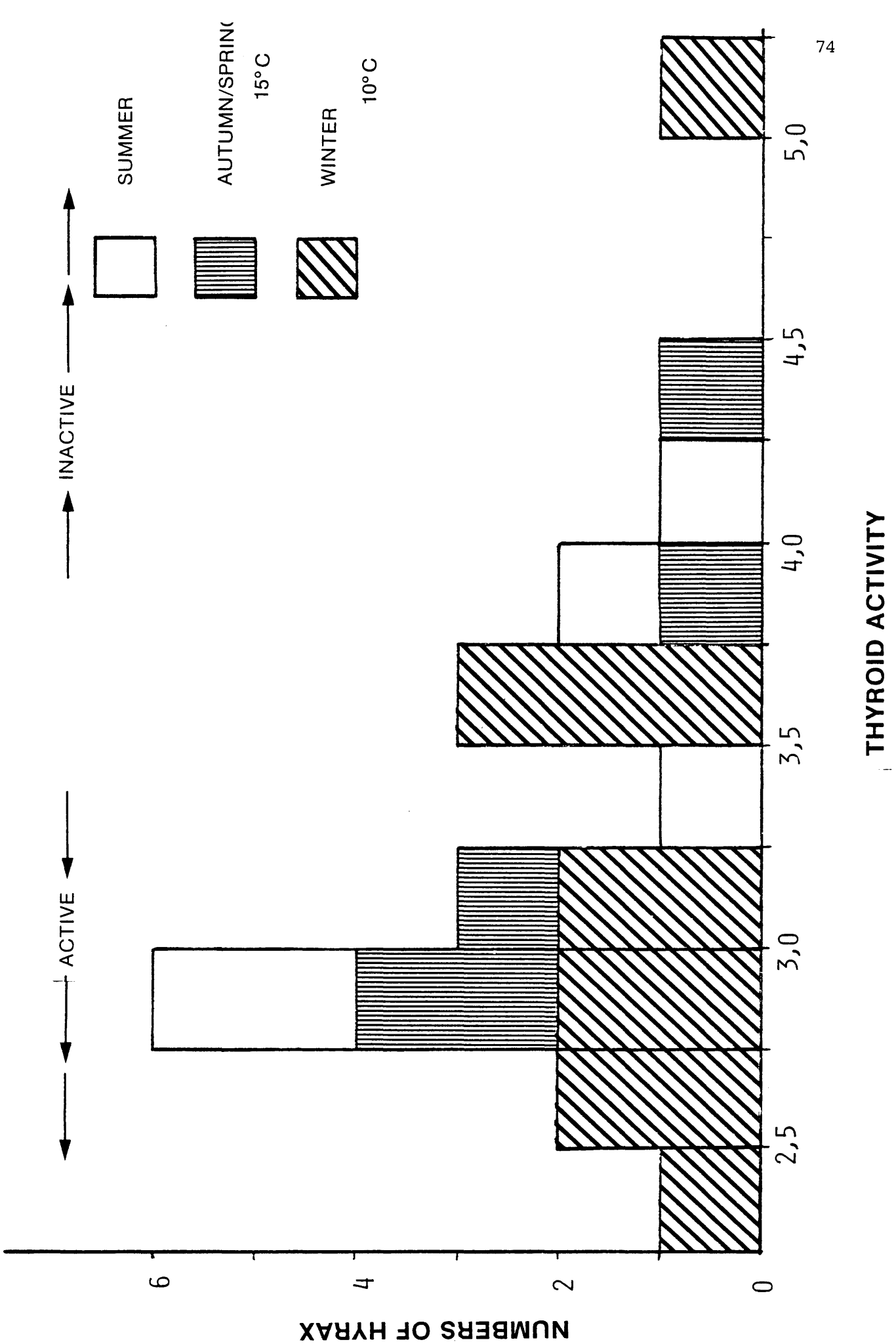

Figure 37: The numbers of hyrax expressed relative to thyroid activity.

laboratory acclimation in the 21 hyrax. As can be seen, there is no clear separation of "active" (low d/n index values) or "inactive" (high d/n index values) thyroids to any particular season.

CHAPTER FIVE : DISCUSSION

Initially the adult and juvenile hyrax will be discussed separately, where data for both groups are available. In the sections where no distinction is made between the age classes, attention shall be drawn to that fact.

ADULTS

VO_2 and Conductance

The thermoneutral zone (TNZ) in adult hyrax (mass 3150 g) acclimated to 26°, 15° and 10°C, can be seen in Figure 8 to range approximately from 20°C to 30°C. The lower critical temperature (Tlc) suggested here as being in the region of 20°C, concurs with the value given by Taylor & Sale (1969) of 20°C. Bartholomew & Rainy (1971), referring to Heterohyrax brucei quote a figure of 25°C, but this could be as a result of the size of their animals. The resting VO_2 observed within the TNZ was 0,499 $mlO_2(g.h)^{-1}$, which is only 1,6% lower than the theoretical basal value of VO_2 of 0,507 $mlO_2(g.h)^{-1}$, calculated by means of the equation based on metabolic mass;

$$VO_2\ (mlO_2(g.h)^{-1}) = 3,8W^{-0,25} \qquad (1)$$

where W is mass in grams (Kleiber 1961, Schmidt-Nielsen 1979). Considering the inherent inaccuracy of these metabolic rate measuring systems, this difference does not amount to anything. A basal VO_2 of 0,52 $mlO_2(g.h)^{-1}$

was reported for H. brucei (mean mass 1310 g) by Bartholomew & Rainy (1971), which is 17,6% lower than the predicted value. Taylor & Sale (1969), working with a very limited sample of two P. capensis (mean mass 2630 g), obtained a basal figure of 0,42 mlO_2 $(g.h)^{-1}$, which is 21,6% lower than equation 1 predicts. Leon (1981) working with P. capensis (mean mass of 2940 g), obtained a basal metabolic rate of 0,27 $mlO_2(g.h)^{-1}$, which was 41% lower than the predicted value.

It seems anomalous that results from the present study, should coincide so closely with the predicted values, while the literature consistently refers to hyrax as having a lower than predicted VO_2. The reason for this, seems simply to be that the VO_2 referred to in the literature is basal metabolic rate (BMR), while the present study centered upon resting metabolic rate (RMR). The reason for measuring RMR and not BMR in the present study, was based on the disadvantage of starving the hyrax for eight hours prior to commencing the experiment and then measuring for up to another eight hours, particularly if the animal was going to be used on several consecutive occasions. Another reason for choosing to measure RMR, was that it would be more valid to attempt to extrapolate RMR values (as coupled to HR values) to predict an average daily metabolic rate, than it would be to use BMR values which represents a condition in which the animal rarely finds itself in the wild.

Another very important consideration, suggested by Fairall (pers. comm.), was that it seemed possible that all the so-called BMR values in the literature obtained after eight hours starving, may actually not be basal values. Eloff's (1981) data on the rate of passage of digesta through the digestive tract, would tend to support this hypothesis. She found that the digesta first reached the caecum (where a large amount of volatile fatty acid production occurs) about 10 h after feeding. Food was still arriving at the

caecum up to 22 h after feeding. This would suggest that any metabolic readings taken before at least 22 h had elapsed after feeding, would not be representative of a post-absorbtive condition, which is one of the prerequisites for basal metabolic rate measurement. It is suggested that all the BMR values published to date are in actual fact neither basal values, nor are they resting values (RMR) but are the results obtained from partially starved animals. This makes these values hard to compare with the theoretical values, with each other, or with data from the present study. The theoretical (predicted) BMR is calculated by using the Brody-Kleiber formula (equation 1) and the fact that the data of Taylor & Sale (1969), Bartholomew & Rainy (1971) and Leon (1981) are far lower than the predicted value, does indicate that the actual BMR may be lower than the theoretical value. However, the great variability of results in their studies,(21%, 17,6% and 41% lower than predicted), would suggest that the animals were subject to varying degrees of digestive activity and were all less digestively active than the present study, though certainly not post-absorptive.

It has been suggested, that had VO_2 been measured in the present study in the same manner as other researchers had done, the values might have been lower, thus concurring more closely with the published data. There is, however, no evidence in the present study to support this suggestion. Another factor to consider, is the size of the animals. The hyrax in Bartholomew & Rainy's (1971) study had a mean mass of 1310 g. In this study, juveniles were classified as having a mass of up to 1500 g and as, will be shown later, these small hyrax thermoregulate differently from the larger adults.

As was stated earlier, a linear relationship between VO_2 and ambient temperature below thermoneutrality was observed (Figure 8). This response of a metabolic rate increase at lowered ambient temperatures, was moderated by a concomitant drop in body temperature (Tb), shown in Figure 26, and also found

by Bartholomew & Rainy (1971), Louw, et al. (1973) and McNairn & Fairall (1979). The slopes of the regression lines (Figure 8) reflect thermal conductance (C) according to Herreid & Kessel (1967), McNab (1970, 1980), Bradley & Deavers (1980) and Aschoff (1981). The measured conductance at 26°C was 0,0265 $ml O_2(g.h^oC)^{-1}$ (r=0,997); at 15°C was 0,0241 $ml O_2(g.h^o)^{-1}$ (r=0,983) and at 10°C was 0,0287 $ml O_2(g.h^oC)^{-1}$ (r=0,995). It can thus be seen, that there does not seem to be a large change in conductance with acclimation to lower temperatures in adult hyrax. It does appear however, that with a decrease in acclimation temperature from 26° to 15°C, there is a slight increase in RMR and a marked drop in overall Tb (Figures 26 and 27). From 15°C to 10°C there is no further great decrease in overall Tb and, in fact, no further increase in RMR. In actual fact, the RMR line seems to sink towards that of levels measured at the acclimation temperature of 26°C. This may mean that the metabolic response of adult hyrax is no greater when acclimated to 10°C, than when it is acclimated to 15°C. The other interpretation is that the three weeks at 15°C resulted in a "short term acclimation", while after five weeks at 15°C (3 weeks acclimation, 2 weeks experimenting) and three weeks at 10°C, a "long term acclimation" was the result, which was less energetically expensive than the short term acclimation at 15°C. A third interpretation could be that the hyrax are, in fact, not reacting to 15° and 10°C as different acclimation temperatures, but as a single "cold" acclimation and that the differences in results are purely artifacts. This is possible, as no significant difference could be shown between the values at 15° and 10°C. The juveniles seem to show the same trend, albeit non-significant.

Body temperature

Before considering the vagaries of body temperature in these hyrax, it is

important to clarify the choice of the site of temperature measurement. Rectal temperature (Trec) has long been used as the easiest and most practical method of monitoring body temperature in animals. One major problem however, is the question of how much Trec differs from core temperature. In man, for example, Trec can be up to 0,5°C warmer than the blood leaving the left side of the heart (Bligh 1973), while at other times, can be lower than core temperature. The major factor that causes Trec to be unsuitable for dynamic studies, is that there is a 5-10 min delay before a change in temperature at the heart is reflected at the rectum (Bligh 1973). Thus when Tb is changing rapidly, Trec is not a practical monitor of Tb. For this reason, the temperature sensitive transmitters were placed intraperitoneally, near to the diaphragm.

The significance of the highly labile Tb (Figure 26) as shown at 26°C (Tb varies by 3,5°C), 15°C (Tb varies by 3,8°C) and 10°C (Tb varies by 2,75°C), has already been mentioned in terms of moderating the increase in VO_2 at lower ambient temperatures (at each acclimated temperature). In other words, conductance (Figure 8) should be interpreted while considering the magnitude of drop in Tb at the same time (Figure 26). The metabolic response to falling ambient temperature would be more marked if the animal remained homeothermic at all times, thus the labile body temperature must be seen as an energy conserving mechanism. A similar situation is found in Abert's squirrels, Sciurus aberti (Golightly & Ohmart 1978), melanistic grey squirrels, Sciurus carolinensis (Innes & Lavigne 1979) and the red squirrel, Tamiasciurus hudsonicus (Pauls 1979). Therefore, the contribution of the decreased Tb is even greater, energetically, than the value calculated from the approximation of conductance derived from the slope of the regression of VO_2 on ambient temperature.

The decrease in Tb commenced with the first decrease in ambient

temperature (ie. from 30° to 25°C, within the TNZ), with the exception of adult hyrax acclimated to 26°C (Figure 26), where Tb only began to drop when the ambient temperature was below 25°C. The reason for this apparent resistance to cooling in the 26°C acclimated animals, remains a puzzle.

The Tb continued to fall over the rest of the range of ambient temperatures right down to 5°C. By the time an ambient temperature of 5°C had been reached, there was a trend towards levelling off which was not nearly as clearly seen as in the juveniles (Figure 26).

To obviate mortalities due to hyperthermia, all measurements were conducted $\leq$ 30°C, as the upper lethal temperature was previously found to be $\pm$ 35°C for juvenile hyrax, and was quoted to be between 34° and 40°C for adult hyrax by Louw, et al. (1973). It would seem therefore, that adult hyrax may be able to withstand a higher ambient temperature than juveniles. This would agree with the fact that adult hyrax, acclimated to 26°C and measured at 30°C, maintain a higher Tb than juveniles do under the same conditions (Figure 26).

At this point it might be prudent to review Taylor & Sale's (1969) postulation regarding a hypothetical nycthemeral fluctuation in Tb. They suggested that acclimation activates the energy conserving mechanisms rather than causing a drastic increase in BMR (or RMR). The idea was that a nocturnal hypothermia was coupled to a metabolic and solar rewarming in the morning. This idea is partially vindicated by the moderated metabolic response to cold, along with the continuous drop in Tb (Figures 8 and 26). It is further supported by the 24 h Tb profiles obtained at 26°, 15° and 10°C (Figure 27), where a nocturnal lowering of Tb is followed by an early morning metabolic rewarming. If the animals at 15° and 10°C had been exposed to solar radiation during the light period, the diurnal Tb

temperatures may have been far closer to the "normality" experienced at 26°C. This is supported by the Tb increases shown in Figure 32 when hyrax were exposed to infra-red radiation. Taylor & Sale (1969) also suggest that a hyrax would select its thermal environment so as to be able to avoid having to increase it's metabolism to generate heat or increase it's evaporation (presumably via respiration) to keep cool. This hypothesis is supported by personal observations in that, when the wind is blowing strongly enough to ruffle the pelage of hyrax, the hyrax retreat into the crevice entrances where they are still able to bask but are protected from the wind.

The difference in overall Tb in adults maintained at constant acclimation temperatures of 26°, 15° and 10°C, is apparent in Figure 27. Animals acclimated to 26°C and measured at a constant 26°C, maintained a higher overall Tb (including any fluctuations) than those animals at 15° or 10°C. This coincides with the Tb measured at various ambient temperatures. This is another aspect of the energy conserving mechanism, as an animal exposed to a constantly low environmental temperature will be able to maintain a constantly lower Tb which will require less energy than a strategy involving a great fluctuation in Tb with higher peaks and lower troughs.

Thermolability in the hyrax might not just be an energy conserving mechanism but may be a prerequisite of survival for these animals which are found in an environment where they could be exposed in winter to a low of -2°C (no wind- chill factor included) up to 25°C in the early afternoon, or in summer to a peak of close to 40°C dropping to 10°C later. In other words, they can be exposed to very great fluctuations in ambient temperature. This idea, that thermolability has survival potential, was put forward by Bruck & Wunnenberg (1967) after they found that guinea pigs "allowed" their core temperature to fall on cold acclimation. They then attempted to cold acclimate and heat acclimate guinea pigs at the same time, and found that

this resulted in a lowering of Tlc and a raising of Tuc, with a resultant widened TNZ (Bruck, Wunnenberg, Gallmeier & Ziehm 1970). This is very similar to what has been found in the present study of P. capensis. They went further, however, and stated that this change in the pattern of the central (autonomic) control of Tb, would allow the animals to withstand wider fluctuations in ambient temperature by allowing their Tb to fluctuate passively (become thermolabile), than could be endured if the animal strove to maintain thermostability. In this way, it is felt that thermolability in the hyrax has survival potential, and is of selective advantage to an animal that is exposed to immense environmental fluctuations.

JUVENILES

VO_2 and Conductance

The TNZ in juveniles seems to be from approximately 25° to 30°C (Figure 8) and the resting VO_2 observed here was 0,483 $mlO_2(g.h)^{-1}$ (mean mass 1016 g), which was 28,3% lower than the theoretical VO_2 of 0,673 $mlO_2(g.h)^{-1}$ calculated by means of the Brody-Kleiber formula. When this percentage difference is compared to that of Bartholomew & Rainy (1971) which was 17,6% lower than predicted for their animals (mean mass 1310 g), it could be suspected, that the far lower metabolic rates may be a juvenile characteristic that is not retained as strongly in the adult. Furthermore the Tlc in their study was 25°C, the same as for the juveniles in the present study. In addition, the decrease in VO_2 at 30°C found in juveniles in the present study may be ascribed to being within the thermoneutral zone or it may, when compared to the anomalous decline in VO_2 reported by Bartholomew & Rainy (1971) to occur at 35°, 40° and especially 42,5°C , be that juvenile hyrax are unable to thermoregulate properly from 30°C

upwards and that there is in fact, no clear upper critical point to the thermoneutral zone. This situation was not found to occur in adult hyrax.

The measured conductance at 26°C was 0,053 $ml O_2(g.h^oC)^{-1}$ (r=0,992) at 15°C was 0,037 $ml O_2(g.h^oC)^{-1}$ (r=0,991) while at 10°C was 0,029 $ml O_2(g.h^oC)^{-1}$ (r=0,932) (Figure 8). This, it can be seen, is totally different to the situation in adults. It is clear that the conductance decreased when the juveniles were acclimated to ambient temperatures below 26°C. This decrease of conductance should be borne in mind when the Tb in juveniles is discussed.

It is clear from Figure 26 that there is a decrease in overall Tb in juveniles when acclimated at 26°, 15° and 10°C. This is not as marked as in adults, but, it should be remembered, there is no change in conductance in adults. Therefore juveniles acclimated to 26°C and then to 15°C and finally 10°C , show an increase in $\dot{V}O_2$ (Figure 8), a decrease in conductance (Figure 8) and a moderate (relative to adults) decrease in Tb (Figure 26). Unlike adults there seems to be no major change between 15° and 10°C. This may be explained by the fact that the juveniles are more vulnerable to low environmental temperatures due to being smaller, thus having a larger relative surface area and concomitant greater danger of heat loss below thermoneutrality, and therefore 15° and 10°C are both hazardous and differ purely by degree.

The change in conductance shown in juveniles may be explained by examining the posture adopted by juveniles during the study. While acclimated to 26°C, no particularly unusual postures were noted. At 15° and 10°C however, the juveniles were seen to be standing in a hunched up position with the pelage ruffled and the head quite deeply retracted into the shoulders. The appendages were held very closely against the body. This

hunched up posture is simply an attempt by the hyrax to adopt as near a spherical shape as possible, which is of course energetically the best in low ambient temperatures. The ruffled, hunched up posture can be seen in very young hyrax up to a few weeks old, at almost any time of day or any environmental condition, except possibly the very hottest of days. Adults did not adopt this posture at any ambient temperature in the laboratory and the only animals seen to be in this posture at the colony was the occasional very old (+6 years) and infirm animal that was invariably found dead within a few days of being observed adopting this posture repeatedly.

As was stated earlier, there was no significant difference between adult VO_2 data at 26°, 15° and 10°C, while there was a significant difference between juvenile data at 26°, 15° and 10°C ($P < 0,05$). When the adult data were compared to juvenile data at 26°C there was no significant difference. This is to be expected as juveniles would not be expected to thermoregulate differently from adults when acclimated to a temperature within both groups' thermoneutral zones. However at 15° and 10°C there was a significant difference ($P < 0,05$) between adults and juveniles and this further emphasises the different approaches taken by adults and juveniles to thermoregulation.

The thermolability of the juveniles is another point where they differ slightly from adults (Figure 26). At 26°C the Tb varied by 1,4°C in juveniles (c.f. 3,5 °C in adults), at 15°C it was a 1,5°C variation (3,8°C in adults) and at 10°C it was only a 1°C variation (2,75°C in adults). The major difference here however, is that the juveniles Tb began to level off below 20°C ambient temperature, regardless of acclimation temperature, and thus the slightly lower Tb was maintained constantly down to an ambient temperature of 5°C. This is very important when seen in the light of decreased conductance shown at lower acclimation temperatures.

Conductance theory

Before proceeding it is necessary to finally clarify the situation regarding the validity of utilising conductance as a value to represent anything. This discussion applies to all age classes.

The concept of utilising the slope of the regression line of the metabolic response to lowered ambient temperature as an indication of thermal conductance, is discussed by Herreid & Kessel (1967) and McNab (1970). This so called conductance should be expressed in the same units as are used to denote measured metabolic rate. Herreid & Kessel (1967) suggested the use of

$$C = 1,023W^{-0,505} \quad (2)$$

where W is mass in grams, to calculate a theoretical conductance in $ml O_2 (g.h^{o}C)^{-1}$. However, Bradley & Deavers (1980), after examining the conductance values for 192 mammals, proposed a new formula:

$$C = 0,76W^{-0,426} \quad (3)$$

where W is again mass in grams.

McNab (1980) made the point that thermal conductance estimated from the slope of the linear regression of VO_2 values below thermoneutrality is only valid if the extrapolated value ($VO_2 = 0$) on the ambient temperature axis is the same as Tb. He states that otherwise the conductance value will be an underestimate due to the animal making use of both "physical" and "chemical" thermoregulation. He also feels, that unless the animal is STRICTLY

homeothermic below thermoneutrality, the conductance value will again be incorrect. As far as terminology is concerned, I prefer to classify McNab's "physical" thermoregulation, as behavioural thermoregulaltion. While his "chemical" thermoregulation could rather be called autonomic thermoregulation (Bligh 1973) as this is the control behind these processes. The reasoning behind the reclassification is that essentially both behavioural thermoregulation and autonomic thermoregulation are PHYSIOLOGICAL thermoregulation. The behavioural aspects of heaping, huddling, basking, avoidance of heat, avoidance of wind or posture changes, which are coordinated via the cerebral cortex, are the first processes to be activated by a change in the thermal environment, and these obviate or delay the onset of autonomic thermoregulation. Therefore behavioural thermoregulation is just a part of the greater whole, namely the thermoregulation of the animal. For this reason it is felt that it is not valid to reject conductance, calculated from the metabolic response, where the animal makes use of more than just autonomic (chemical) thermoregulation. In the same way, if the animal is not strictly homeothermic but is thermolabile (heterothermic), this is a strategem being utilised while thermoregulating, and conductance should be seen in the light of these strategems, not as an inflexible physical characteristic.

McNab (1980) did propose the following formula to predict conductance in thermolabile animals:

$$C = VO_2 \, (Tb - Ta)^{-1} \qquad (4)$$

Recently Aschoff (1981) examined the results of Bradley & Deavers (1980), and came to the conclusion that a small further refinement should be made.

Animals measured during their active period (during the day if diurnal, or at night if nocturnal) should be treated as one group, while those examined during their passive (resting) period should be treated as another. He developed the following formula for predicting conductance in animals measured during the active period:

$$C = 1{,}539\ W^{-0{,}517} \qquad (5)$$

where W = mass in grams.

Comparing the previous four methods of predicting conductance against the results obtained in this study, the following was found (Table 2).

- Bradley & Deaver's (1980) method resulted in conductance values (for adults) between 86 and 102% of the measured values. While, for juveniles, it was between 75% and 157%.

- Aschoff's (1981) system gave results as good, adults 84-99% and juveniles 81-148%.

- The established method of Herreid & Kessel (1969) resulted in values between 61 and 72% of the adult readings and 58 to 107% of juvenile results.

- McNab's (1980) suggestion of utilising both VO_2 and Tb at each ambient temperature resulted in a conductance value for each experimental point. The percentage accuracy to obtained values, was at lowest 104% (adults) and 64% (juveniles), while the highest was 185% (adults) and 195% (juveniles).

TABLE 2. Thermal conductance of adult and juvenile hyrax and values based on various authors predictions.

Acclimation temperature	26°C		15°C		10°C	
	C	%	C	%	C	%
Adult conductance (3150 g)	0,0265		0,0241		0,0286	
Predicted a	0,0246	93	0,0246	102	0,0246	86
Predicted b	0,0239	90	0,0239	99	0,0239	84
Predicted c	0,0175	66	0,0175	72	0,0175	61
Predicted d(20°)	0,0276	104	0,0447	185	0,0304	106
Predicted d(15°)	0,0284	107	0,0425	176	0,0333	116
Predicted d(10°)	0,0292	110	0,0419	174	0,0316	111
Predicted d(5°)	0,0293	111	0,0378	157	0,0318	111
Juvenile conductance (1016 g)	0,0529		0,0371		0,0285	
Predicted a	0,0398	75	0,0398	107	0,0398	137
Predicted b	0,0429	81	0,0429	116	0,0429	148
Predicted c	0,031	58	0,031	83	0,031	107
Predicted d(20°)	0,0341	64	0,0574	155	0,0564	195
Predicted d(15°)	0,0349	65	0,0541	146	0,0509	176
Predicted d(10°)	0,0385	72	0,0485	131	0,0413	142
Predicted d(5°)	0,0429	81	0,0488	132	0,0444	153

C = Conductance (ml $O_2(g.h^oC)^{-1}$)

% = Percentage of measured value

a. $C = 0,76W^{-0,426}$ Bradley & Deavers 1980.

b. $C = 1,539W^{-0,517}$ Aschoff 1981.

c. $C = 1,023W^{-0,505}$ Herreid & Kessel 1967.

d. $C = VO_2(Tb - Ta)^{-1}$ McNab 1980.

These comparisons were only an academic exercise however, as in themselves they are hypothetical. To be able to compare conductance in other, totally different, species, it is necessary to find a method that is universally acceptable. What is of importance here is to be able to see whether the SAME animals changed their conductance during the course of the study. For this purpose the relative values are of importance and not the actual figures. If a system to predict P. capensis conductance were required, I would suggest the use of Bradley & Deaver's (1980) formula, as it comes closest to the actual figures obtained in this study.

Within the Hyracoidea a quick comparison of thermal conductance in a few species is interesting (Table 3). The mean mass of each group follows the specie's name, thereafter the first conductance figure is the one actually measured, followed by the predicted value based on Bradley and Deaver's (1980) formula.

It can be seen that in general the predicted values are not far from the actual values measured, with three exceptions, P. capensis juveniles in the present study, P. johnstoni adults from Taylor & Sale's (1969) study and P. capensis adults in Leon's (1981) study. The great variability of the juvenile conductance should suffice to explain this apparent anomaly as far as juvenile P. capensis is concerned. No explanation can be given for the P. johnstoni value of Taylor & Sale (1969) or those of Leon (1981).

TABLE 3. Thermal conductance in four species of the hyracoidea.

Species	Mass(g)	Measured	Predicted*	Units	Author
Procavia capensis	1016	0,0529	0,0398	$ml O_2 (g.h^oC)^{-1}$	(d)
Heterohyrax brucei	1310	0,039	0,0357	$ml O_2 (g.h^oC)^{-1}$	(a)
Heterohyrax brucei	2000	0,031	0,0298	$ml O_2 (g.h^oC)^{-1}$	(b)
Procavia habessinica	2250	0,031	0,0284	$ml O_2 (g.h^oC)^{-1}$	(b)
Procavia capensis	2630	0,020	0,0265	$ml O_2 (g.h^oC)^{-1}$	(b)
Procavia johnstoni	2750	0,016	0,0260	$ml O_2 (g.h^oC)^{-1}$	(b)
Procavia capensis	2940	0,0137	0,0253	$ml O_2 (g.h^oC)^{-1}$	(c)
Procavia capensis	3150	0,0265	0,0246	$ml O_2 (g.h^oC)^{-1}$	(d)

* - predicted value $C = 0,760W^{-0,426}$ Bradley & Deavers (1980)

a - Bartholomew & Rainy (1971)

b - Taylor & Sale (1969)

c - Leon (1981)

d - Present study (animals acclimated to 26°C).

Postural thermoregulation

The behavioural thermoregulation of hyrax exposed to low ambient temperature has already been discussed and mention has been made of basking as a thermoregulatory strategem. The means of testing whether or not basking actually does offer the hyrax the opportunity to raise its body temperature passively (therefore without metabolic cost) was simply by exposing the animals to infra-red (IR) lamps and observing changes in body temperature and surface temperature (or radiant temperature, Tr). Figure 29 shows the body temperatures of juvenile hyrax acclimated to 10°, 15° and 26°C prior to exposure to IR radiation. After a little more than one hour of "sunning" all three groups' Tb's had risen. The 26°C group had increased by ± 0,4°C, the 15°C group's had increased by 0,9°C while the 10°C group's Tb had risen by 2,0°C. On cessation of IR heating, the temperatures all fell precipitously, suggesting a return to the Tb levels prior to heating. During this whole process the radiant temperatures (Tr) of the four hyrax were monitored. Again in all three instances the Tr increased suggesting a conductance increase. To state that this conductance increase was only postural would be circumstantial and would be ignoring the obvious effect of pelage change, but it is of interest to examine the posture changes in a hyrax in the field (ambient temperature 12°C, no wind from 09h40 to 10h35) in Figure 38.

Figure 38a shows the animal soon after emerging from a crevice. Its legs are folded underneath its body and the body is orientated at right angles to the sun's rays. Figure 38b shows the hyrax beginning to stretch out. In Figure 38c the hyrax is presenting a larger lateral surface to the sun and is beginning to adopt a "rock hugging" posture as it presumably gets warmer. Figure 38d shows the same animal just after moving to a new position (0,5 meters from the previous position) where the hyrax is beginning to make

Ta = 12°C No wind

a

09h40

b

09h56

c

10h08

Figure 38 : Posture changes in a basking adult hyrax in the field

d
10h21

e
10h35

Figure 38: (Continued)

itself comfortable. In Figure 38e the hyrax can be seen in a typical "warm" stretched out basking position. This type of posture will be maintained for hours if the weather is mild, or will be alternated with disappearance into the cool crevices on a hot day.

The increased radiant temperature of the fur, along with the passive increase in Tb at constant ambient temperature while exposed to a radiant heat source, support the hypothesis that these animals make use of solar radiation as a supplementary non-metabolic energy source to assist in rewarming after a nocturnal hypothermia (or any other hypothermia).

Visual examination of the pelage shows a thick (±0,5 cm) dark brown to light brown layer of coarse hair covering the dorsum and flanks. The belly hair is lighter in colour, close to the colour of the sub-terminal bands of the dorsal hair. Bothma (1966) stated that the colour variation within 93 P. capensis examined, varied from quite pale to very dark, and this variation he described as a clinal one and did not involve taxonomic differences. The animal is further covered by a sprinkling of tactile guard hairs, or vibrissae, which are longer than the rest of the fur and are supposed to have a sensory function (Sale 1970b).

There is no evidence of P. capensis from a warm climate being meaningfully different in colour to those from cooler areas. What has been noted however, is that with a change in posture there is often a change in the appearance of the pelage. There is clear pilo-erection in juveniles (in the laboratory) when acclimated and exposed to cold (Ta < 15°C).

When there is no pilo-erection, the pelage presents a very shiny and quite reflective appearance, which would help obviate too much heat uptake

from the environment. As the temperature falls and pilo-erection occurs, the fur becomes dull and matt looking, probably facilitating heat uptake. Not only was this most apparent in juveniles in the laboratory but some adults in the field seemed to exhibit pilo-erection in the early morning on cool days. A personal observation of hyrax in the field was that, when it was warm, hyrax could be spotted far more easily on the rocks by virtue of their lighter, shining fur. On cold mornings however, it required far more careful scrutiny through binoculars to spot the basking animals.

Pelage quality does seem to change with the seasons and the best covered animals were collected in July - October; however the laboratory animals' pelage did not visibly improve or deteriorate with acclimation to different temperatures. This is not contradictive as, although it seems safe to correlate ambient temperature with pelage quality, it is not necessarily the only environmental factor influencing the pelage. Yeates (1955) showed that in cattle the density and depth of the pelage seemed to be related to day length and light intensity through gonadotrophic activity of the anterior pituitary and not to concommitant changes in ambient temperature *per se*.

Sweating

While considering the pelage and heat absorption, it is logical to examine heat loss in relation to sweating. Bartholomew & Rainy (1971) stated that 21,5% of evaporative water loss, when H. brucei were exposed to heat stress, originated as sweat on the soles of the feet, the rest being contributed by respiratory water loss. Taylor & Sale (1969) also pointed out the absence of sweat glands on the body of the animal. This seems to suggest that the hyrax are not adapted to cope with high ambient temperatures by sweating but rather by avoidance of high temperature conditions. This would concur with the fact that hyrax do not often drink free water and in fact strive toward water conservation (Leon 1981). Another interpretation of the sweating on the foot pads of hyrax was suggested by Adelman & Taylor (1974) and Adelman, Taylor & Heglund (1975) when they showed that the friction coefficient, and resultant steepness of slope that hyrax could traverse, increased with increased sweating on the foot pads. Secondly they showed that the sweat rate from the foot pads more than doubled as the hyrax ran at 1 km/h at 20°C. This is substantiated by the reasons behind the action of the adrenergic "fight or flight" reaction.

Field temperature data

After having examined body temperature in the laboratory and possible relationships to posture changes, it is of interest to see how the field data relate to this laboratory information.

Figure 16 shows the relative occurrence of different body temperatures found in hyrax collected at various times of day and season. The mean Tb was 37,04°C (±0,81) for the 60 animals with the range being from 34,7° to

38,4°C. These are animals that are able to make use of both behavioural and autonomic thermoregulation (as they were wild hyrax) but still they show a large degree of thermolability. These results differ markedly from those of Leon (1981) who commented on a singular lack of thermolability in her "field" hyrax.

When examining Tb as related to time of day, within each age class, the fact that the hyrax were collected in Summer, Winter and Spring/Autumn, tends to confound the situation. Thus the conditions at 08h00, for example, would be totally different, environmentally speaking, at different times of the year. The sample sizes for each season were too small to examine time of day Tb data for each season. The only other environmental approach to use was to couple Tb and ambient temperature, and the result can be seen in Figures 23, 24 and 25. The three size classes were examined separately and the mean Tb for class I was 37,43°C (±0,68), for class II was 36,72°C (±0,88) and for class III was 36,95°C (±0,53). There was no significant difference between these three groups.

Essentially there was no real difference between the age classes and this was not quite as expected from the laboratory study. The laboratory juveniles (comparable to class I) were less thermolabile than the adults (equivalent to class II and III). The field data showed a range of 2,5°C in class I but only a difference of 3,5°C and 3°C in classes II and III respectively (the sample sizes for each of the classes was 20 and 19).

The major reason for not being able to correlate body temperature with ambient temperature in the field, is that there were other variables (wind, cloud cover, humidity, overnight temperature, previous rainfall and intraspecific interactions) which could not be delineated or excluded. The field data do not disagree with the laboratory data, they are just too

limited to draw any conclusions.

Control of thermoregulation

Earlier there was an attempt to explain some aspects of thermoregulation in terms of autonomic and behavioural control. It will now be attempted to describe it in greater detail.

Bligh (1966) postulated his so called "Two-tier theory of thermoregulation", where there was a narrow band of fine control and a wide band of coarse control of body temperature. The coarse control, he suggested, only became operative when a critical high (>40,7^{o}C) or low (<36^{o}C) body temperature was reached, otherwise this coarse control was normally inoperative. Schmidt-Nielsen, Schmidt-Nielsen, Jarnum & Haupt (1957) showed that the camel did not sweat until a body temperature of between 40,5^{o} - 41^{o}C had been reached. At the lower end, Bligh (1966) stated that the camel did not begin shivering until the body temperature had dropped to about 35^{o}C. This coarse control of the "wide band" would seem to be autonomic, with sweating and panting at the high end and shivering at the lower end.

The advantage of "wide band" control is that it prevents "run-away" effects of changes in body temperature outside the "narrow band" due to the Arrhenius effect (ie. body temperature drop causes a metabolic rate slowing, causing a body temperature drop, and so on in a vicious cycle), it therefore has survival value. The wide band control does allow for necessary changes in body temperature which occur outside the narrow band, namely fever, exercise and functional hypothermia, without the danger of the body temperature going below 36^{o}C or above 41^{o}C. It therefore prevents the occurrence of lethal hypothermia or hyperthermia.

The logical question is, what is the point in having a narrow band of fine control within this wide band? It would seem that this is eminently practical as it allows the animal to maintain a body temperature close to optimum by means that are energetically cheap, namely behavioural thermoregulation.

By stating that narrow band thermoregulation is fine controlled by behavioural means, while wide band thermoregulation is controlled by autonomic means, we seemingly create a paradox. This requires that the sensor of body temperature, the hypothalamus, has either two sets of set points - which is not logical, or that at times, the hypothalamus is sensitive to narrow band control while at other times is sensitive to wide band control, which is equally doubtful. There is another approach which requires the existence of extrahypothalamic temperature control. There is evidence that ablation of the anterior hypothalamic tissue inactivates the fine control of body temperature and that a second line of defence against over-heating (or fatal cooling) is located further back in the brain (Keller & McClaskey 1964, Andersson, Gale, Hökfelt & Larsson 1965, Bligh 1966). Thus it is suggested, that narrow band thermoregulation is fine controlled by the hypothalamus and therefore, this behavioural thermoregulation is governed by the temperature of the blood flowing through the hypothalamus. Wide band thermoregulation (or coarse control) is arbitrated by extrahypothalamic sensors and these are only brought into play when the blood bathing those areas reaches temperatures outside of the high and low set points.

To summarise, whilst the body temperature (and blood flowing to the hypothalamus and extrahypothalamic sensors) is close to "normal" (within the narrow band), neither processes of thermoregulation are brought into play. As soon as the body temperature deviates away from the set point of "normal"

body temperature, the hypothalamus registers this and behavioural thermoregulation is begun (the extra hypothalamic sensors are still not activated). Should this be insufficient to maintain body temperature within the narrow zone, the temperature is allowed to rise or fall (within the confines of the wide band) without autonomic (extrahypothalamically triggered) thermoregulation being used. Only when body temperature exceeds the upper or lower set points of the wide band does the extrahypothalamic tissue begin to activate autonomic thermoregulation, and sweating and panting or shivering begins (hypothalamically controlled behavioural thermoregulation has been continuing all the time).

Heart rate

The concept of measuring heart rate in the present study is based on the requirement for an indirect index of energy expenditure in free-ranging animals. According to Johnson & Gessamen (1973) and the inferred relationship of energy metabolism = f(HR), it should be feasible to predict metabolic rate from heart rate. This is substantiated by the literature, where it has been found true for decreases in ambient temperature below thermoneutrality in a number of mammals and birds; the pigmy possum (Bartholomew & Hudson 1962); Australian flying foxes (Bartholomew, Leitner & Nelson 1964); pigmy mouse (Hudson 1965); California mastiff bat (Leitner 1966); blue winged teal (Owen 1969); 4 species of ground squirrel (Morhardt & Morhardt 1971); bush hyrax (Bartholomew & Rainy 1971); black duck (Wooley & Owen 1977) and rock hyrax (McNairn & Fairall 1979) to name but a few examples.

Lund (1979) agrees with the basic premise provided that certain limitations are accepted.

The inference that

$$\text{Energy metabolism} = f \times \text{heart rate} \quad (7)$$

is based on the physiological relationship of

$$\text{Energy metabolism} = f \times \text{ambient temperature} \quad (8)$$

as could be seen in Figure 8, and

$$\text{Heart rate} = f \times \text{ambient temperature} \quad (9)$$

which is shown in Figure 9.

On examination, Figure 9 shows that the relationship of heart rate to ambient temperature below thermoneutrality is linear, with correlation coefficients of -0,842 for adults and -0,896 for juveniles (if the three acclimation temperature groups are grouped together). When these groups are kept separate the correlation improves considerably.

The heart rates within thermoneutrality are expected to be minimal and this is indeed the case with a mean of 115,8 $\pm$ 6,6 beats per minute being found in adults, while in juveniles it was found to be 123,0 $\pm$ 5,1 beats per minute. These values are far lower than the 180 beats per minute (3150 g) and 237 beats per minute (1016 g) predicted from the equation:

$$HR = 241W^{-0,25} \quad (10)$$

that has been suggested by Stahl (1967). These lower values coincide with the overall trend towards energy conservation, particularly in view of the

fact that

$$VO_2 \text{ (energy metabolism)} = f \times HR \qquad (7)$$

Before examining the VO_2 : HR relationship, it is necessary to consider another approach to determining a formula, $VO_2 = f \times HR$.

Morhardt & Morhardt (1971), Johnson & Gessaman (1973), Bartholomew (1977) and Pauls (1980) all make use of the formula :

$$VO_2 = HR \times SV \times A\text{-}V\ O_2 \text{ diff.} \qquad (11)$$

in the derivation and justification of stating that :

$$VO_2 = f \times HR \qquad (7)$$

$$\text{where } f = SV \times A\text{-}V\ O_2 \text{ diff.} \qquad (12)$$

The individual parameters of the original formula are examined in Table 4.

When the animals are exposed to ambient temperatures lower than thermoneutrality, there is an increase in VO_2 which can be seen in the second column. This extra oxygen has to be transported from the lungs to the tissues, where there is an increased O_2 demand. This increased transport can be accomplished by :

1) increased heart rate,
2) increased O_2 carrying capacity of arterial blood,
3) decreased PO_2 in venous blood, ie increased A-V O_2 difference or

TABLE 4. Oxygen pulse and the concept "VO_2 = HR x SV x A-V O_2 diff"

	Cardiovascular parameters			.	% increase above last temperature		
	VO_2	HR	O_2 pulse	.	VO_2%	HR%	O_2 pulse%
ADULTS (3150 g)							
TNZ	0,595	116,8	267,4	.	-	-	-
20°C	-	-	-	.	-	-	-
15°C	0,729	127,9	299,2	.	22	9,5	12
10°C	0,858	137,6	327,4	.	17,5	7,5	9
5°C	0,978	146,8	349,8	.	14	7,0	7
JUVENILES (1016 g)							
TNZ	0,617	121,4	98,3	.	-	-	-
20°C	0,823	127,3	124,9	.	33	5	27
15°C	1,009	143,0	136,4	.	22,5	12	9
10°C	1,139	157,8	139,5	.	13	10	2
5°C	1,437	178,8	155,4	.	26	13	11

4) by increasing the volume of blood pumped in each beat ie stroke volume increase.

It can be seen that there is an increase in heart rate over the whole range of temperatures and this increase, on a percentage basis, is reasonably regular. It is simple to test whether the heart rate increase was sufficient to carry the extra oxygen utilised at each temperature, by examining the volume of oxygen in each beat, the so called O_2 pulse (Müller & Jaksche 1980). If the heart rate increase was sufficient, the O_2 pulse would remain constant. It can clearly be seen from Table 4, column 4, that this is not the case and that the percentge increase varies from 2% to 27%.

Thus there remain two unmonitored variables in formula 11, SV and A-V O_2 diff, and according to Johnson & Gessaman (1973) both of these increase with increasing VO_2.

Morhardt & Morhardt (1971) equated O_2 pulse with $VO_2 \times HR^{-1}$ which is what it actually is, thus if

$$VO_2 = HR \times SV \times A\text{-}V\ O_2\ diff \qquad (11)$$

$$\text{then } VO_2 \times HR^{-1} = SV \times A\text{-}V\ O_2\ diff \qquad (13)$$

$$\text{thus } O_2\ pulse = SV \times A\text{-}V\ O_2\ diff \qquad (14)$$

Therefore the O_2 pulse increase can be seen as representing the combined increased stroke volume and increased Arterial-Venous O_2 difference. According to Rushmer (1965) the increase in A-V O_2 difference is relatively constant over the whole range of VO_2 changes, where the SV

increase tends to flatten off toward the higher VO_2 levels. The two seen in conjunction, however, seem to be more constant and if they are expressed as;

$$SV \times A\text{-}V\ O_2\ diff = k \qquad (15)$$

where k is a constant, then the equation

$$VO_2 = f \times HR \qquad (7)$$

becomes valid.

For the sake of this study the SV x A-V O_2 diff. will be treated as equal to a constant and then through examining the VO_2 : HR relationship it will be possible to see if there was any validity in that supposition.

It is interesting to compare the measured O_2 pulse values obtained in this study with the predicted values calculated by using:

$$O_2\ pulse = 0{,}061W^{0{,}99} \qquad (16)$$

quoted by Åstrand & Rodahl (1977). The prerequisite is; animals at rest within the thermoneutral zone. Adults (3150 g) measured 267,4 $\mu l.beat^{-1}$ which was 50,8% higher than the predicted value of 177,3 $\mu l.beat^{-1}$. Juveniles (1016 g) were 98,3 $\mu l.beat^{-1}$ which was 70,1% higher than predicted (57,8 $\mu l.beat^{-1}$). These values suggest a greater than normal stroke volume, or possibly a greater A-V O_2 difference, but at rest that seems more unlikely than an increased stroke volume.

Now it is possible to examine the VO_2 : HR relationship. Figures 35 (adults) and 36 (juveniles) showed the extremely good correlations obtained

when plotting metabolic rate against heart rate. The adults VO_2:HR relationship seems to vary according to acclimation temperature while the juvenile relationship does not. This agrees with the postulated difference in thermoregulation between adults and juveniles as discussed earlier.

The importance of this VO_2 : HR correlation will be shown when the activity budgets of these animals are examined along with the concomitant activity related heart rates.

Figure 11 shows the heart rate fluctuations over a 24 h period of an adult hyrax exposed and acclimated to 25°C. The same situation is shown in Figure 12 except that the hyrax is exposed and acclimated to 15°C. The great variability of the data collected over a three day period, results in it being impractical to attempt to directly interpret these data. The similarity of these patterns to those of the summer and winter activity patterns (figures 31 & 32) should not be overlooked, however.

Heart rate for the specific activities was measured and Figure 10 shows the mean heart rates for each activity. It can clearly be seen that there is an increase in heart rate as the degree of effort involved in each activity increases. Thus the lowest heart rates (107 beats.min^{-1}) were obtained when the hyrax were not visible which meant that they were inside the sleeping box probably lying or huddling. Animals lying in the sun or shade but visible to the researcher had a mean heart rate of 119 beats.min^{-1}. While those adopting a posture where the legs were beneath the animal and thus were able to groom or move without much effort, were judged to be sitting and these showed a mean heart rate of 123 beats.min^{-1}. Animals actively involved in grooming, posture changes or just generally restless, were in the next group, which had a mean heart rate of 130 beats.min^{-1}. This was not very different from the 133 beats.min^{-1} of the animals busy feeding, which is not

surprising, as the feeding hyrax (in the colony) were not involved in a very strenuous activity. The animals busy moving from one area to another, by walking, running or jumping, and the animals involved in direct agonistic interactions showed a mean heart rate of 143 beats.min^{-1}.

It is now possible to assign an approximate energetic cost to these activities and to see, when considering the percentage of time spent carrying them out per day, what the total daily "cost" is for an animal moving and interacting freely with other hyrax. These values may be derived from heart rates that show a degree of fluctuation, but it is proposed that they do give an idea of the energetic cost involved, and as, such are valid as an approximation. The metabolic rate values are derived from the VO_2 : HR correlation for adults at 26°C in figure 37 and are as follows:

Not visible	- 0,44 ml	O_2 $(g.h)^{-1}$
Lying	- 0,55 ml	O_2 $(g.h)^{-1}$
Sitting	- 0,59 ml	O_2 $(g.h)^{-1}$
Sitting grooming	- 0,65 ml	O_2 $(g.h)^{-1}$
Feeding	- 0,69 ml	O_2 $(g.h)^{-1}$
Moving	- 0,81 ml	O_2 $(g.h)^{-1}$
Intraspecific interactions	- 0,80 ml	O_2 $(g.h)^{-1}$

This suggests that there is only approximately an 80% increase in metabolic rate as a result of normal non-stressful activity in adult hyrax. This compares favourably with the 85% increase in VO_2 in 26°C acclimated adult hyrax when exposed to ambient temperatures from thermoneutrality to 5°C.

It seems therefore that hyrax do not involve themselves in activities

that are energetically very expensive. This concurs with what Lieb & Marcum (1979) found in elk (Cervus canadensis nelsoni) and Mautz & Fair (1980) found in white-tailed deer (Odocoileus virginianus) using the same method as utilised in this study. Interestingly enough, Holter, Urban, Hayes, Silver & Skutt (1975) found that white-tailed deer make use of body posture extensively to maintain energetic equilibrium, just as P. capensis seems to do.

The good correlation between heart rate, metabolic rate and activity under both resting and active conditions is perhaps quite surprising as Best, Ronald & Øritsland (1981) found it impossible to accurately define different levels of activity in polar bears and also discovered that cardiac rates of resting animals were not accurate enough to be used as indices. They did however, get accurate results in active or walking animals.

Thus, approximate metabolic rates for various arbitrary activities have been measured and will be extrapolated further to see whether or not they might give a reasonably accurate indication of average daily metabolic rate.

While busy with these heart rate investigations, it was felt that it would be of interest to see whether the hyrax,an animal that hides from predators and doesn't attempt to outrun them, would show tachycardia or bradycardia when exposed to an external "fright" stimulus. Swamp rabbits, Sylvilagus aquaticus (Smith, Sims & Vich 1981); eastern chipmunks, Tamias striatus (Smith, Johnson & Martin 1981) and the woodchuck, Marmota monax (Smith & Woodruff 1980) all show fear bradycardia.

The hypothesis is that animals that "freeze" when frightened, or that dive into a convenient shelter, are likely to show bradycardia, and not tachycardia, when frightened.

Figure 13 shows that when a hyrax was exposed to the very close proximity of the researcher (50 cm apart), the heart rate increased and this tachycardia resulted in a mean increase in heart rate of 35 beats.min^{-1}.

The resultant recovery profile was very similar to that of bighorn sheep (Ovis canadensis canadensis) heart rate response to harassment (MacArthur, Johnston & Geist 1979) except that complete recovery of heart rate took up to 9 to 12 min in hyrax and only 3 min in sheep under some circumstances (in others it took up to a few hours). The possibility then suggested itself that this tachycardia was not as much fear related as being due to aggresion on the part of the hyrax. Its aggresion being directed toward the close proximity of the researcher.

The hyrax were then exposed to an unexpected loud noise (no persons being visible to the animals). Bradycardia then became apparent. Figure 14 shows that the change in heart rate, delta HR, varied from a decrease of 14 bpm to a decrease of 34 bpm. The big difference here however, is the time scale involved, as the recovery took a mean of 7,25 seconds ($\pm$2,2 n=4) to occur.

These two seemingly opposed reactions of tachycardia (concurring with the adrenergic "fight or flight" reactions), and bradycardia (found in many animals that crouch and hide), are not contradictory as they are a result of two totally different stimuli.

Smith, Sims & Vich (1981) question the validity of using heart rate as an accurate indicator of oxygen consumption because fear can cause a variety of unrelated changes in HR and VO_2.

Their doubts however, are ungrounded in the present study as care was taken to place the hyrax in an environment where they would not be under stress or fear while the HR : VO_2 relationship was being investigated. The hyrax was confined in a small, dark metabolic chamber, very similar to the conditions found in hyrax holes and shelters in the wild, and under observation showed no visible tension or discomfort.

An attempt to evaluate the effect of exercise on heart rate failed due to the treadmill being too large for the hyrax, and secondly, because it was not realised that it would be necessary to take the time initially to teach the hyrax to run on the treadmill. What was demonstrated here however, was the effect of exaggerated stress (combined with limited exercise) on heart rate. In Figure 15 it can be seen that three repeated attempts resulted in delta HR of 56 bpm, 60 bpm and 72 bpm; greater tachycardia than obtained through aggression and displacement activities alone. The recovery time was again in the region of 9 min, the same as in milder tachycardia.

According to Baudinette (1978) the maximum steady state heart rate (max. HR) that can be maintained by an animal can be expressed by the formula :

$$\text{Max. HR} = 375\ W^{-0,19} \qquad (17)$$

where W = mass in kg. This would suggest that the maximum heart rate of almost 220 bpm in this study is nowhere near the maximum rate possible, as the predicted value for a 3,15 kg hyrax is 301 bpm.

The relationship between heart rate and certain activities is shown in Figure 10. Activity can now be examined from a number of view points.

Activity

An initial idea of when hyrax are active, can be gained from examining at what time of day they were shot during the field portion of the study. There are obviously a number of unrelated external factors that will effect this, but it still relies on one simple fact, the hyrax have to be visible to be shot. Figure 30, representing a sample size of 60, indicates the time of day when the hyrax were shot, comparing Summer, Spring/Autumn and Winter. Taking the extreme vagueness of this method into account, it is apparent that the results don't disagree with the double peak in activity that both Sale (1965) and Hoeck (1975) reported. Going one step further, the times of these two peaks in Sale's (1965) study were 09h00 to 12h00 and from 17h00 to 19h00 which are not very different from what was found.

The greatest limitation of the previous method is that it ignores the dark hours when it was not possible to see the hyrax. Sale (1965) states that Procavia habessinica are not active at night but Fox (1933), Coe (1962) and Fourie (1974) all state that hyrax are active at night (as well as during the day) or state that they are more easily caught in traps on moonlight than dark nights, which infers that they must be active and moving around at night. It must also be remembered that predators may have an effect on hyrax activity. As far as aerial predators (black eagle, Aquila verreauxi and martial eagle, Polemaëtus bellicosus) are concerned, it would be practical for hyrax to extend their activity period into the dark hours when the raptors are grounded. However, in areas where leopard (Panthera pardus) or caracal (Felis caracal) are very active, the hyrax are far safer inside their shelters at night.

The number of hyrax visible at any moment in time expressed as a

percentage of the total number of hyrax known to be in the colony, is what is shown in Figures 31 and 32. As can be seen in the Summer situation (Figure 31), the number of individuals visible are at their highest during the daylight hours, albeit not as active. There seems to be a peak of activity in the earlier morning and late afternoon, with a gradual decline at night. In Winter (Figure 32), however, there seems to be no pre-dawn activity and the daytime activity seems constant. The nocturnal activity in Winter is curtailed to a great extent. This method of estimating activity does have its pitfalls, in that the observer does not know whether a spot he considers to be in the open (i.e. a visible hyrax) is actually still under cover (and thus not visible) in the eyes of the hyrax. Despite the inherent weaknesses, the system still gives an indication of hyrax activity. Personal observations on hyrax in the wild record the finding of hyrax already out feeding (in areas up to 800m away from shelter) at dawn, which would suggest that they were already active and feeding a good while before dawn. There were also observations of hyrax actively feeding late at night (between 22h00 and 24h00). All these observations were made in Summer. Hyrax were never obviously active at night in Winter on the occasions when I would have been aware of it.

A possible reason for the difference in the Summer and Winter activity patterns is thermoregulatory, as the terrestrial and aerial predator situation in the study area (Brits) did not seem to vary during the year. Secondly the colony at the experimental farm was not exposed to normal predation pressure but still exhibited a similar pattern to the field hyrax. For these reasons it is felt that the contribution due to predators can be excluded.

A possible reason for inactivity in nocturnal Winter hyrax, relative to the Summer conditions, is that the animals would be exposed to low

environmental temperatures which would not be energetically economic. In Summer the animals active at night would not be exposed to stressful temperatures and thus activity and feeding at night would be profitable. In Winter the morning activity seems to begin very suddenly which would suggest that the hyrax are waiting for the optimum conditions, in terms of the warming sun, before they cease heaping and huddling in their shelters, and emerge to face a new day. In Summer the decline in activity that seems to occur between 11h00 and 17h00 may be as a result of the heat, as this coincides with the period of maximum temperature during the day. The researcher has observed hyrax basking throughout the day in Winter, but in Summer their basking seems to be limited to the late afternoon in particular. Possibly in both Summer and Winter they utilise the increase in body temperature just before nightfall, as a heat-sink against the cool to cold night, much like the eland (Taurotragus oryx) and oryx (Oryx gazella) do (Taylor 1969).

Another method of estimating activity is to observe a focal animal exclusively and to express the different activity patterns observed, relative to the total number of hours that the animal was observed. Figure 33 shows the percentage of daylight hours spent by a single hyrax on the different activities discussed earlier. The problem with this method is that it is exceedingly difficult to observe an animal at night well enough to identify just what it is doing and as a result these data are limited to the daylight hours. It is apparent that there is an anomaly in that during the day the hyrax in Winter seem to spend less time inside the shelter ("not visible") than in Summer, but according to Figures 31 and 32 almost no animals were visible outside the shelter in Winter at night. The reason for this difference can be seen in Figure 33, as it is the daylight hour activity that can be seen and not a 24 h period. This then agrees with the previous Figures as it appears that the hyrax in Summer did spend a lot of time avoiding the

high ambient temperatures experienced outside the shelters during the day. Another difference between Summer and Winter is that hyrax seem to spend far more time "lying" or "sitting" in Winter. This is logical as basking would be included under "sitting" or "lying" and according to the argument developed all through this thesis, hyrax use basking as a supplementary non- metabolic energy source, which is particularly necessary in Winter. Finally in Winter, hyrax seem to spend more time feeding during the day than in Summer. This can partly be explained by an increased energetic requirement in Winter, though it is equally probable that the difference is due in Summer to hyrax feeding at night as well as during the day.

Examining the Summer activity pattern in more detail, with regard to the respective heart rates for each activity (Figure 34), a mean daily heart rate, taking the percentage of time dedicated to each activity can be worked out. This can be done by multiplying the heart rate for that activity by the time dedicated to it. All these values are then added together and divided by 100 to obtain a percentage. This it can be seen, results in a mean Summer daily heart rate of 123,1 beats.min^{-1}. Before any further conclusions are drawn here, it is necessary to examine metabolic rate as expressed by metabolised energy (ME) (Figure 28). The reason for measuring ME was that it was a non-invasive technique that could be carried out on a captive animal without having to confine it to a metabolic chamber. Ultimately the ME results could be compared with VO_2 data to gain an indication of the accuracy of these two systems when used on hyrax.

Gessamen (1973) evaluated A = I = E (where A = assimilation energy, I = ingested energy and E = egested energy) as an indicator of metabolised energy and found it to be effective within certain limitations.

As can be seen, the juvenile ME is far higher than the adult value, as

should be expected. The difference caused by acclimation to lower ambient temperatures was non-significant and would tend to support the idea that the thermoregulation of these animals, inside the wide band control by behavioural means and by thermolability, is so successful that the animals energetic requirements do not increase dramatically when exposed to low environmental temperatures.

The two points below the adult value at 26°C, represent two groups of hyrax, one in the climatic room and one in a cage exposed to the elements during Summer. These animals were allowed to freely interact (as a small family group) and their total food intake was combined, as was their faeces production.These were treated as single values. These were then divided by the total mass of the group to get a ME value in $kJ(g.24h)^{-1}$. As can be seen, these results are slightly lower than the isolated adult value at 26°C, which may be explained by the fact that through heaping and huddling, they would be able to conserve energy, and as a result, lower the ME values obtained. Another contributary factor may be that they are under less stress in a group than they are when kept individually in cages.

Returning to Figure 34, an attempt can be made to extrapolate the data available to see if the average daily metabolic rate (ADMR) can be predicted from the parameters that have been isolated. First a relationship between VO_2 and HR is needed which is supplied in Figures 37 and 38. It is found in adults that:

$$VO_2 = 0,0097\ HR - 0,599 \qquad (18)$$

acclimation temperature 26°C (r = 0,976),

$$VO_2 = 0,0144\ HR - 0,859 \qquad (19)$$

acclimation temperature 15°C (r = 0,996),

and $$VO_2 = 0,0145\ HR - 1,26 \quad (20)$$

acclimation temperature 10°C (r = 0,988).

In juveniles the values of the three acclimation temperatures were sufficiently similar to be treated as one group, which resulted in:

$$VO_2 = 0,013\ HR - 0,899 \quad (21)$$

where r = 0,926.

The heart rate values in Figure 34, which are associated with the various activity patterns, will be the values used to calculate ADMR. A mean DAILY heart rate of 123,1 bpm has already been calculated. This was measured in an adult in Summer, so the VO_2 : HR relationship to use would be the adult value measured at 26°C, namely:

$$VO_2 = 0,0097\ HR - 0,599 \quad (18)$$

Therefore with a mean daily heart rate of 123,1 bpm an oxygen consumption of:

$$0,595\ ml O_2\ (g.h)^{-1}$$

is calculated. However it must be remembered that the mean heart rate was based on activity monitored from 05h00 to 19h00; that is for 14 h during daylight only. Knowing that 1 litre O_2 = 20,08 kJ (Schmidt-Nielsen 1979) it

is found that the

$$VO_2 \text{ for } 14 \text{ h} = 8{,}33 \text{ ml}O_2.g^{-1}$$

and thus there is a total metabolic requirement (TMR) of:

$$TMR_{14} = 0{,}167 \text{ kJ(g.14 h)}^{-1}.$$

This is only for 14 h, however. If the remaining 10 h of darkness are treated as though the animal had the same metabolic requirement as during the daylight hours (however unlikely), the following is found :

$VO_2 = 0{,}595 \text{ ml}O_2\text{(g.h)}^{-1}$ during the 10 h darkness

VO_2 for 10 h $= 5{,}95 \text{ ml}O_2.g^{-1}$

$TMR_{10} = 0{,}119 \text{ kJ(g.10 h)}^{-1}$

and thus the ADMR = $TMR_{14} + TMR_{10}$, which results in an ADMR value of

$$0{,}287 \text{ kJ(g.24 h)}^{-1} \qquad \text{ADMR (B)}$$

If the remaining 10 h (darkness) were not treated in the above manner however, but rather as though they were the same as the metabolic requirement during the "not visible" (N.V.) activity period, and thus having a heart rate of 108,7 bpm (therefore a $VO_2 = 0{,}455 \text{ ml}O_2\text{(g.h)}^{-1}$, the following TMR_{10} would be found:

$VO_2 = 0{,}455 \text{ ml}O_2\text{(g.h)}^{-1}$ (10 h darkness)

VO_2 for 10 h = 4,55 $ml O_2 . g^{-1}$

TMR_{10} = 0,0914 $kJ(g.10\ h)^{-1}$

and therefore an ADMR = TMR_{14} + TMR_{10} = 0,258 $kJ(g.24\ h)^{-1}$ which becomes ADMR (A).

Thirdly, using the data shown in Figure 11,(24 h profile for heart rate at 26°C in the laboratory) a mean heart rate over 24 h of 135,7 bpm was calculated. This heart rate, when inserted into:

$$VO_2 = 0,0097\ HR - 0,599 \qquad (18)$$

gave a VO_2 value of:

$$0,717\ ml O_2 . g^{-1}$$

which for a 24 h period resulted in:

$$VO_2 = 17,207\ ml O_2 . g^{-1}$$

$$TMR_{24} = 0,346\ kJ(g.24\ h)^{-1}$$

but ADMR = TMR_{24} therefore:

$$ADMR\ (C) = 0,346\ kJ(g.24\ h)^{-1}.$$

Therefore, to summarise these three methods of calculating ADMR, the following was found :

1. ADMR (A)

was based on HR and activity patterns for the 14 h of daylight and the calculation of the 10 h darkness on the basis of being the same as the "not visible" activity group. The ADMR for this treatment should give an underestimate and is therefore seen as the lower estimation.

$$\text{ADMR (A)} = 0{,}258 \text{ kJ(g.24 h)}^{-1}.$$

2. ADMR (B)

was based on treating the 14 h daylight period as in the previous group, but the 10 h darkness period was treated in the same manner as the daylight period. This ADMR should therefore be an overestimate and can be considered the upper estimate

$$\text{ADMR (B)} = 0{,}287 \text{ kJ(g.24 h)}^{-1}.$$

3. ADMR (C)

is an estimate where the animal is in a cage in the climatic room (unlike A and B which are of animals under semi-natural conditions at the colony. ADMR (C) is calculated from the mean HR calculated from a 24 h HR profile.

$$\text{ADMR (C)} = 0{,}346 \text{ kJ(g.24 h)}^{-1}.$$

Finally, as far as extrapolations are concerned, it was of interest to see whether or not it was possible to predict ADMR from RMR. This is purely an academic exercise as RMR does not include activity or the metabolic requirements for thermoregulation. The result, as can be seen in Figure 39, is a value very similar to the ME value of Eloff (1981), and also to the ADMR

values just calculated.

Figure 39 contains, from the left hand side :

1. ME values for adults and juveniles as measured in the present study.These are the highest values and are for individually caged hyrax in the climatic room.

2. ME value from Eloff's (1981) study where the hyrax were treated in the same manner as in the present study, except that the urine and methane fractions were taken into account in the calculation.

3. ME data for the two groups of hyrax (6 per group) that were not confined in cages but were allowed to interact with one another.

4. RMR values transformed into $kJ(g.24\ h)^{-1}$. No activity taken into account.

5. ADMR (A) as calculated from "HR - activity" and "VO_2 - HR" relationships (minimal values) for a free-living colony.

6. ADMR (B) as in the previous case but using maximal values.

7. ADMR (C) for a caged hyrax on its own in the climatic room.

Thyroid activity

As can be seen in Table 5, the T4 values in the literature varied from as low as 13 to 120 ng/ml, while T3 data fluctuated from 0,6 to 25,6 ng/ml.

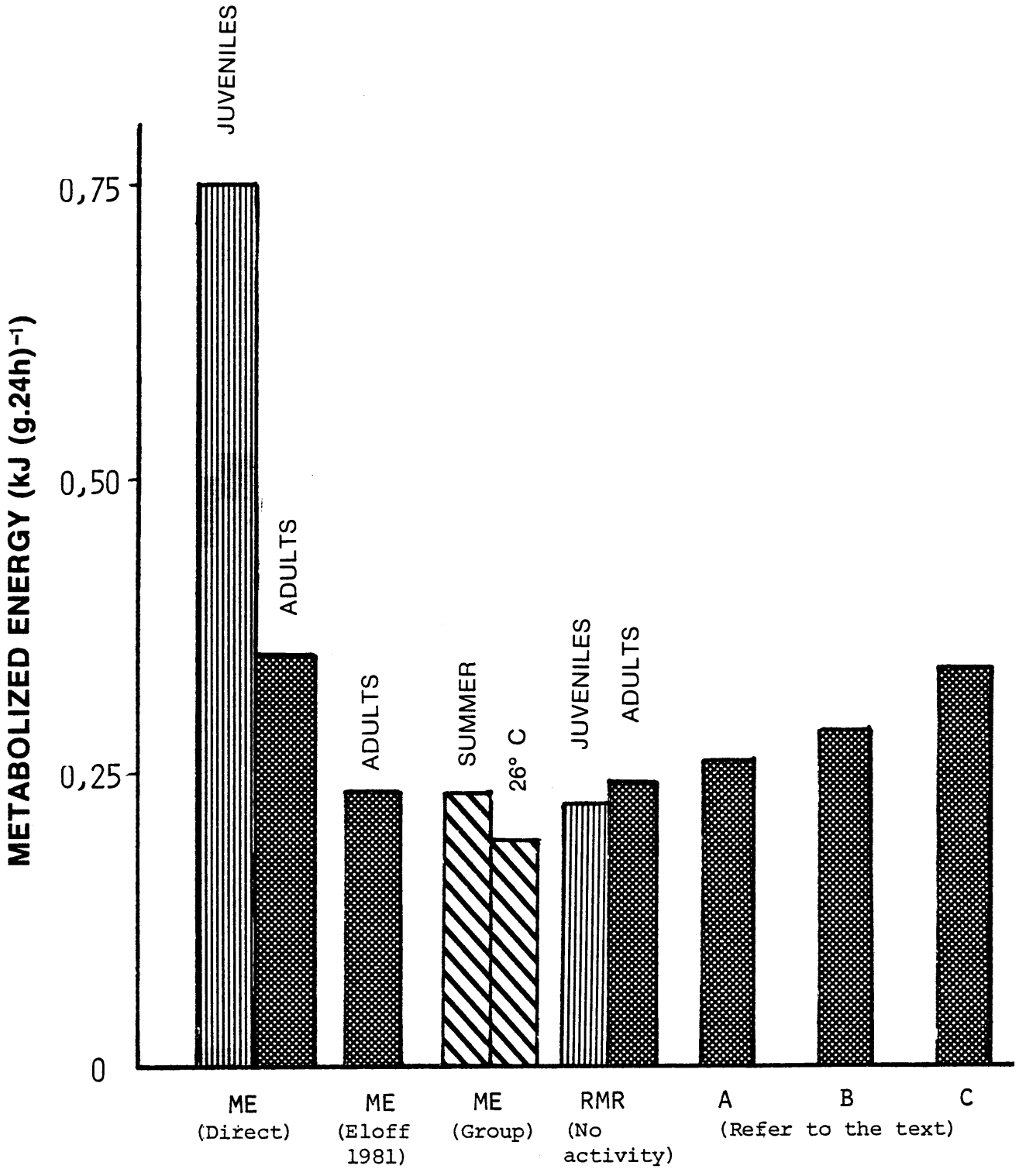

Figure 39: ADMR, ME and RMR extrapolated values for hyrax

TABLE 5: Comparison of T3 and T4 values in various species.

	T4 (ng/ml)	T3 (ng/ml)	T3/T4 x 10^2	Author
P. capensis (lab)	169 ± 74	4,6 ± 1,0	2,7	
P. capensis (field)	121 ± 25	5,6 ± 1,3	4,6	
Mouse deer	47 ± 3	0,6 ± 0,08	1,3 *	b
Human	120 ± 21	1,8 ± 0,2	1,5 *	d
Baboon	95 ± 27	2,1 ± 0,6	2,2 *	d
Dog	19 ± 5	1,2 ± 0,3	6,3 *	d
Cat	26 ± 8	0,8 ± 0,3	3,1 *	d
Horse	21 ± 6	0,9 ± 0,6	4,3 *	d
Cow	80 ± 26	1,2 ± 0,8	1,5 *	d
Goat	45 ± 6	1,9 ± 0,4	4,2 *	d
Pig	42 ± 10	1,1 ± 0,5	2,6 *	d
Sheep	57 ± 15	1,3 ± 0,4	2,3 *	d
Rabbit	80 ± 23	25,6 ± 16,9	32,0 *	d
Ground squirrel (hiben)	58 - 97	6,4 - 7,7	9,2 *	a ^
Ground squirrel (non-h)	13 - 39	1,3 - 2,6	7,3 *	a ^
Polar bear (feral)	31 - 52	0,68 - 1,5	2,3 - 3,1	c ^
Polar bear (captive)	35 - 49	0,46 - 1,1	1,1 - 2,6	c ^

All T3 & T4 data are shown as means ± S.D. except where indicated

* : Calculated from T3 & T4 values by researcher

^ : These T3 & T4 values are given as ranges

a : Demeneix & Henderson 1978

b : Kamis 1980

c : Leatherland & Ronald 1981

d : Reap, Cass & Hightower 1978

Thus the T4 results obtained for P. capensis were the highest values measured. The T3 data on the other hand was comfortably within the upper end of the majority of results. Leatherland & Ronald (1981) proposed that direct comparison of the T4 and T3 data was fallacious and that it would be safer to compare the data in the form of an index, T3/T4 x 10^2. With the exception of the rabbit, with its extrodinarily high T3 value, the T3/T4 ratios in juveniles varied from 1,1 tp 9,2, with P. capensis laboratory animals at 2,7 and field hyrax at 4,6. Interestingly enough, feral polar bears had a higher T3/T4 ratio than did captive animals, the same trend as shown in hyrax. It is suggested that the actual T3/T4 ratio is not significant when compared between species, however it may be of value for intraspecific comparison. The limited data offered here for P. capensis was sufficient to demonstrate a significant difference between laboratory and field hyrax ($p < 0,01$, Table 1) and in field hyrax, the T3/T4 ratio in Summer was significantly lower than for the other seasons ($p < 0,05$, Table 1).

The thyroid histology, on the other hand, did not show any clear pattern (Figure 35). Whether laboratory and field collected thyroid glands were treated as one sample or as two discrete samples, no distinct separation into Summer, Spring/Autumn or Winter groups, or 26°, 15° or 10°C acclimated groups, could be shown. The d/n index varied from just below 2,5 to just above 5,0. As a result no relationship with T3 and T4 values could be shown. Not even a relationship between T3/T4 ratio and thyroid activity based on histological criteria could be discerned.

In conclusion, with respect to the thyroid gland, it is suggested that radioimmuno assays for thyroid hormone titres can possibly be used to good purpose in the hyrax, but histologically based criteria do not seem to be of any practical use.

The Hypothetical Evolution of Thermoregulation in Procavia

The presence of unusual physiological strategems in P. capensis, namely a low metabolic rate and functional hypothermia coupled to thermolability, raises the question as to how these strategems evolved. Before postulating along this line, it is worth examining some definitions. Bligh (1973) defined non-temperature regulating (temperature conforming) animals as possessing a bradymetabolism, while temperature regulating animals were called tachymetabolic. What is of importance here, is the requirements for a tachymetabolic animal. These are first, a high rate of metabolism, and secondly, a regulating system of sensors, central control and thermoregulatory effectors. The question here, is whether or not these two factors evolved, or even needed to evolve, concurrently. Besides these physiological strategems, behavioural thermoregulation is an integral part of the tachymetabolic animal. It has been documented that the heliothermic reptiles carry out behavioural thermoregulation with consummate ease (Bligh 1973). It can be suggested therefore, that the Saurian ancestors to mammals may already have been in possesion of this very useful trait.

For further functional thermoregulation to occur, a variable blood flow to the skin is essential. This may possibly have originated in amphibia to control the exchange of respiratory gases through a moist skin, and therefore have become modified in dry skinned reptiles, to facilitate heat uptake and heat transfer to deep body tissues (Cowles 1958). It is suggested that the basic building blocks for thermoregulation could have been present early in the evolution of tetrapods, possibly as far back as in the Devonian (300 million years ago).

The capability for thermoregulation only becomes worth considering when the control mechanism is present. Bligh (1973) states that for behavioural control of body temperature to occur, a sensitive thermostat, which has been shown to be situated in the pre-optic area in ectothermic reptiles, is essential. This does suggest the presence of an ancestral region where later evolved the structure housing the hypothalamic thermostat.

This superficial hypothesising has led back to the question behind all this, that of thermolability. To state dogmatically that thermolability is primitive, risks being anthropocentric by suggesting that homeothermy (thermostability) is an ideal biological state towards which there must be a steady evolution. If it is presumed that homeothermy is the ideal state to strive for, it must be understood that for any extant mammalian species to exhibit thermolability, it must be assumed that strict homeothermy offers no advantage, or represents a distinct disadvantage, for the survival of that species. It would be reasonable to assume that fine control of body temperature (homeothermy) is advantageous in many mammalian species as it manifests itself regularly, though what the advantage is, is unclear. It should seem to be equally valid, on the other hand, to state that the reversion to, or retention of, a labile body temperature in other mammals holds advantages, especially under adverse environmental conditions.

For an animal to remain strictly homeothermic, it requires insulation and a continuous availability of food under cold conditions, or the presence of a variable insulator and sufficient water for evaporative cooling at high ambient temperatures. Therefore under conditions where one or more of the above are in short supply, and the animals are still exposed to extreme environmental conditions, it might be safe to suggest that heterothermia may be advantageous. This is, of course, what has been suggested in the case of P. capensis, based on the present, and previous, studies.

In considering the argument of "primitive" heterothermia versus "modern" homeothermia, it is valuable to examine the review of thermostability in monotremes, marsupials and some mammals, in Bligh (1973). There seems to be no evidence of a trend from a labile body temperature in monotremes to a stable body temperature in placental mammals, with marsupials occupying an intermediate position. Within all three subclasses there are species which demonstrate considerable thermolability. The remarkable morphological similarities between marsupial and placental mammals, which occupy comparable ecological niches, are accepted as being independant convergent adaptations to similar environments. In the same manner, the similar cases of thermostability on the one hand, and thermolability on the other, indicate that these variations in thermoregulation may also be independant convergent adaptations to similar environmental stresses, AND therefore of little value as indices of evolutionary history. It is suggested therefore, that the thermolability found in P. capensis, and probably in all hyracoidea, is not as a result of its phylogenetic history, but rather as a direct result of the adaptation of these remarkable animals to their semi- arid, harsh environment.

CONCLUSION

The hyrax, it seems, is an energy conserver which makes use of a reduced metabolic rate, a labile body temperature, behavioural avoidance of environmental extremes, postural orientation combined with basking to supplement rewarming following hypothermia and a mainly diurnal activity period flanked by crepuscular feeding periods. A degree of nocturnal activity seems to be governed by ambient temperature and season.

The low metabolic rate exhibited by the hyrax may well be a function of their environment, in that the limited food resources, especially in winter, prevent them from maintaining the highest metabolic rate possible, a trait towards which McNab (1980b) suggests all endotherms should strive.

Adults and juveniles show slightly differing approaches to environmental vagaries. Juveniles exhibit an increased metabolic rate (though less than predicted), and a reduction of conductance, possibly achieved by postural changes, when acclimated to low ambient temperatures. At the same time the thermolability that is exhibited is tempered by a tapering off of the lowered Tb to a constant value below the TNZ. The adults on the other hand, exhibit an increased metabolic rate, and a considerable reduction of Tb when acclimated to low ambient temperatures. There is no tapering off of the Tb below the TNZ. The adult conductance however, does not seem to change with acclimation. The TNZ in adult hyrax seems to be wider than in juveniles. In both instances, the Tuc is in the region of $30^{o}C$, while the adult Tlc is approximately $20^{o}C$ and the juvenile Tlc is approximately $25^{o}C$.

In both adults and juveniles the depressed Tb at low ambient temperatures would be of considerable importance to energy saving, as the hyrax would not be required to increase its metabolic rate to such a considerable extent, to maintain heat production, as would have been required, had these animals been strictly thermostable.

Besides considering the depressed Tb at low ambient temperatures to be of importance in the conservation of energy, it can also be suggested to be an inability (in the absence of solar radiation) to maintain a constant Tb. This suggestion however, should be seen in the light of Bligh's (1973) two-tier thermoregulation theory, where the wide band thermoregulation is autonomically controlled, while the narrow band is behaviourally regulated. This would therefore mean that it is not a question as to whether it is an inability to thermoregulate properly, but rather a non-requirement to make use of energetically expensive autonomic thermoregulatory processes, when "cheap" behavioural processes suffice. This then leads back to the hypothesis that thermolability is an energy saving strategem.

The suggestion that animals in possesion of a smaller body size were less thermolabile, and could not withstand as low a functional hypothermia as larger animals could, seems to be valid in the case of P. capensis. This conforms with what would be predicted when considering Newton's Thermodynamic Laws.

Metabolizable energy was found to be in the same region as metabolic rate measured by means of oxygen consumption.

Heart rate, in both adults and juveniles, showed a positive correlation with ambient temperature and, more importantly, with metabolic rate. The

equation VO_2 = f.HR for P. capensis could be substantiated by the data collected in the present study. When HR, in conjunction with activity, was extrapolated to give average daily metabolic rate, the resultant figures were favourably comparable to ADMR values measured more directly. One of the aims of the present study was to test whether or not it would be feasible to predict metabolic rate from HR, and thus, by measuring HR, gain an idea of the total energetic cost incurred by a hyrax under various conditions in the wild over a 24 h period. It required that activity also be taken into account. This use of heart rate, activity and metabolic rate to predict ADMR has been shown not only to be feasible, but also practical, providing that the telemetry equipment that can transmit the data over sufficiently long distances, and clearly through obstacles, while remaining small enough to be carried by a hyrax, is available.

Future research that can now be profitably conducted on P. capensis, could involve the accurate delineation of activity budgets for animals in the wild, combined with the monitoring of heart rate, and thus by extrapolation, metabolic rates. This would enable the delineation of total metabolic costs for animals in the wild. In conjunction with demographical data, this would facilitate the prediction of the impact of a population of hyrax on their environment. This is a question of continual interest to agriculturalists.

Another avenue open to more extensive study is the measurement of Tb in animals in the wild on a continuous basis, to examine how the indivdual, living within a population, copes with environmental fluctuations on a thermoregulatory level.

SUMMARY

The hyracoidea, and more specifically Procavia capensis, are small, gregarious members of the Paenungulata that mainly inhabit rocky, semi-arid habitats. Considering their extensive distribution, the question arose as to how the hyrax copes with low ambient temperatures associated with a relatively limited food supply.

In answer to that question, resting metabolic rate (RMR), conductance (C), and thermoneutral zone (TNZ) determinations were carried out on adult and juvenile hyrax (P. capensis) in the laboratory.

Body temperature (Tb) fluctuations under various conditions in both the laboratory and the field were investigated.

Heart rate (HR), as related to RMR and activity was studied in the laboratory and then measured in unrestrained hyrax in an exposed out-door holding facility.

Metabolizable energy in laboratory hyrax was measured and the data compared with RMR results.

Tb increases caused by infra-red radiation were utilised to examine non-metabolic heating.

Thyroid gland histology and thyroid hormone levels in serum were studied with a view to clarifying their role in the control of metabolism in the hyrax.

Hyrax were found to have a lower than predicted resting metabolic rate (RMR) and conductance (C). The thermoneutral zone was found to be from 20° to 30°C in adults, and from 25° to 30°C in juveniles. The body temperature (Tb) was highly labile in adults, ΔTb = 4,0°C, but less so in juveniles, ΔTb = 1,5°C. Acclimation to lower ambient temperatures caused an overall lower Tb to be maintained.

There was a positive linear relationship between heart rate (HR) and RMR, supporting the hypothesis $VO_2 = f.HR$. There was also a positive relationship between HR and the degree of activity.

Average daily metabolic rate calculated from HR, RMR and activity at the outdoor holding facility, was similar to values based on direct calorimetry.

Infra-red radiation (and by association, solar radiation) was indicated to be directly linked to the increase of Tb shown in basking hyrax otherwise exposed to constant ambient temperatures.

No clear relationship between the thyroid data and environmental conditions could be discerned.

The difference between adult and juvenile thermoregulation seems to be that adults show no change in conductance but exhibit considerable thermolability when exposed to low ambient temperatures, juveniles limit their degree of thermolability and exhibit a decrease in conductance when acclimated to low (10°C) ambient temperatures. It is suggested that the considerable thermolability shown by adults is of decided value in energy conservation, in that it allows the adults to limit the metabolic rate increase to a greater extent, than would otherwise have occured when exposed to low ambient temperatures with the concommitant limited food supplies

OPSOMMING

Die Hyracoidea, en meer spesifiek Procavia capensis, is klein, sosiale lede van die Paenungulata. Hulle word hoofsaaklik in rotsagtige, semi- dorre habitatte aangetref. As hulle wye verspreiding in ag geneem word, ontstaan die vraag; hoe die dassie dit reg kry om lae temperature geassosieer met moontlik relatief beperkte voedsel bronne te weerstaan?

In antwoord hierop is rustende metaboliese tempo (RMR), geleiding (C), en die omvang van die termoneutrale gebied (TNZ) bepaal op volwasse en onvolwasse dassies (Procavia capensis) in die laboratorium. Liggaamstemperatuur (Tb) wisselinge is ook, onder verskillende toestande in die laboratorium, en veld, ondersoek.

Harttempo (HR) se verwantskap aan RMR en aktiwiteit, is in die laboratorium bestudeer. Hierna is dit gebruik op 'n vrybeweegende dassie in 'n hok blootgestel aan die omgewing om 'n skatting van metabolisme in die vrylewende dier te kry. Metaboliseerbare energie is ook in die laboratorium gemeet en die data is met RMR resultate vergelyk.

Die Tb verhooging veroorsaak deur infra-rooi bestraaling is gebruik om nie-metaboliese verhitting te bestudeer.

Histologie van die tiroïed klier en die gepaardgaande serum hormoonvlakke is ondersoek om die rol van die tiroïed in die beheer van metabolisme in die dassie te probeer verklaar.

Dassies se metaboliese tempo en geleidings vermoë is laer as die waardes voorspel vir soogdiere in die algemeen, en die TNZ lê, by volwassenes, tussen 20° en 30°C, terwyl dit by onvolwassenes, tussen 25° en 30°C voorkom.

Liggaamstemperatuur is by volwassediere uiters labiel, $\Delta Tb = 4,0^{\circ}C$, maar by onvolwassenes minder so, $\Delta Tb = 1,5^{\circ}C$. Aklimeering by laer omgewings temperature veroorsaak dat 'n algehele laer liggaamstemperatuur gehandhaaf word. Daar was 'n positiewe liniêre verwantskap tussen harttempo en rustende metaboliese tempo wat die hipotese, $VO_2 = f.HR$ by P. capensis, ondersteun. Daar was ook in positiewe verhouding tussen harttempo en die graad van aktiwiteit.

Gemiddelde daaglikse metaboliese tempo (ADMR) is vanaf harttempo, rustende metaboliese tempo en aktiwiteit, voorspel vir 'n vrylewende dassie in die buitelug aanhoudingshok. Die waardes is vergelykbaar met resultate verkry d.m.v. direkte kalorimetrie.

Infra-rooi bestraaling (en dus by assosiasie, son straaling) het geblyk om die oorsaak te wees van die toename in liggaamstemperatuur wat dassies blootgestel aan die bestraaling getoon het.

Geen duidelike verband tussen die tiroïedklier parameters wat ondersoek is en omgewings toestande kon bewys word nie.

Die verskil in liggaamstemperatuur beheer van volwasse en onvolwasse dassies is oenskynlik dat by blootstelling aan lae omgewings temperature, volwassenes geen verandering in geleiding toon nie, maar wel noemenswaardige thermolabiliteit. Onvolwassenes aan die anderkant beperk hulle graad van thermolabiliteit en toon in verlaagde

geleiding as hulle geaklimeer is aan 'n lae ($10^{o}C$) omgewings temperatuur. Dit word voorgestel dat die aansienlike thermolabiliteit wat deur volwassenes getoon word, van belang is by energie bespaaring in die sin dat dit die volwassene in staat stel om sy metaboliese toename tot 'n grooter mate te beperk as wat die geval sou wees by blootstelling aan lae omgewings temperature en gepaardgaande beperkte voedselbronne wat in die winter ondervind word.

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PERSONAL COMMUNICATION

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APPENDIX 1: VO_2, HR, Tb of Juvenile Hyrax.

Exp. Ta (°C) \ Accl. Ta (°C)		Acclimated at 26°C $\bar{x}$ Tb : 38,6 ± 1,6 °C $\bar{x}$ mass : 973,3 ± 104g N=3 (3♀)	Acclimated at 15°C $\bar{x}$ Tb : 37,2 ± 0,85°C $\bar{x}$ mass : 1105 ± 216g N=5 (2♂ 3♀)	Acclimated at 10°C Tb $\bar{x}$: 36,6 ± 0,14°C $\bar{x}$ mass : 1137,5 ± 103g N=5 (2♂ 3♀)	
30°C	VO_2	0,428 ± 0,021	0,704 ± 0,094	0,665 ± 0,099	ml O_2 $(g.h)^{-1}$
	HR	116,3 ± 6,35	125,4 ± 8,14	131,1 ± 9,61	bpm
	Tb	38,65 ± 1,6	38,02 ± 0,14	37,2 ± 0,0	°C
25°C	VO_2	0,483 ± 0,04	0,766 ± 0,106	0,654 ± 0,077	ml O_2 $(g.h)^{-1}$
	HR	117,2 ± 14,1	120,5 ± 14,97	117,9 ± 6,93	bpm
	Tb	37,75 ± 0,71	37,38 ± 0,35	36,75 ± 0,07	°C
20°C	VO_2	0,596 ± 0,103	0,959 ± 0,144	0,913 ± 0,066	ml O_2 $(g.h)^{-1}$
	HR	112,5 ± 18,3	129,4 ± 4,94	140,1 ± 7,65	bpm
	Tb	37,5 ± 1,06	36,7 ± 0,42	36,2 ± 0,0	°C
15°C	VO_2	0,782 ± 0,015	1,162 ± 0,353	1,082 ± 0,124	ml O_2 $(g.h)^{-1}$
	HR	128,6 ± 14,2	146,98 ± 19,21	150,5 ± 8,34	bpm
	Tb	37,38 ± 1,24	36,48 ± 0,34	36,25 ± 0,35	°C
10°C	VO_2	1,053 ± 0,017	1,282 ± 0,283	1,084 ± 0,129	ml O_2 $(g.h)^{-1}$
	HR	154,8 ± 10,2	163,4 ± 33,4	155,5 ± 8,2	bpm
	Tb	37,38 ± 1,24	36,44 ± 0,46	36,25 ± 0,35	°C
5°C	VO_2	1,388 ± 0,106	1,537 ± 0,115	1,387 ± 0,166	ml O_2 $(g.h)^{-1}$
	HR	192,6 ± 23,5	167,64± 17,52	176,1 ± 16,97	bpm
	Tb	37,38 ± 1,24	36,52 ± 0,48	36,25 ± 0,35	°C