THE ECOPHYSIOLOGY OF THE AFRICAN GIANT RAT

CRICETOMYS GAMBIANUS (Waterhouse)

by

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ABSTRACT

Thermoregulation, digestion, gastrointestinal tract morphology, growth, movement patterns and burrow structure and contents were studied in the African giant rat, Cricetomys gambianus. Adult giant rats showed general inability to withstand high ambient temperatures (Ta). Resting metabolic rates (RMR) and conduc= tance (C) were both greater than predicted by body mass. Evapo= rative water loss (EWL) was found to be the most important mecha= nism regulating heat loss. Increase in juvenile mass, showed a decrease in RMR, C and EWL. Gross gut morphology showed adap= tations associated with omnivorous and herbivorous habits. The preferred food was found to be soft fleshy fruits. Growth and behavioural development in altricial young were found to be slow. Giant rat home ranges were smaller than predicted and more accurate estimates were determined with the linked cell method (LC) than with the minimum area method (MAM). Burrows were constructed in the cool shaded habitats.

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

Until recently <u>Cricetomys</u>, the African giant rat, was regarded
as a representative of the Murinae, however it has been re-
classified under the Cricetidae as the molars are biserial with
a variable number of supplementary and minor cusps (Rosevear
1969). Genest-Villard (1967) reduced the genus <u>Cricetomys</u>,
which is widely distributed over Africa (Fig. 1), to two defined
species, <u>gambianus</u> and <u>emini</u>. The two species have been sepa=
rated mainly on their different postures, fur texture, a few
skull dimensions, calls and habitat. <u>C. emini</u> is restricted
to the closed forest block from West Africa to Tanzania, while
<u>C.gambianus</u> has a much wider distribution, confined predominant=
ly to the moist savannah (Rosevear 1969) with an annual preci=
pitation of 800 - 1400 mm (Fig. 2). In southern Africa, Roberts
(1951) and Ellerman, Morrison-Scott & Haymann (1953) recognised
four subspecies of <u>C. gambianus</u>, with the material from the
Soutpansberg mountains, northern Transvaal, ascribing to the
form <u>C.g. haagneri</u>.. However, little is known on local and geo=
graphical variation of the species, and sub-species were not
recognised by Smithers (1983).

In the northern Transvaal, <u>C. gambianus</u> is recorded from the
woodland savannah only (Rautenbach 1978) and it appears they
prefer cool mesic habitats covered by reasonable amounts of
undergrowth (Ajayi, Tewe & Faturoti 1978; Smithers & Wilson 1979).
Giant rats also appear susceptible to high temperatures as Ajayi

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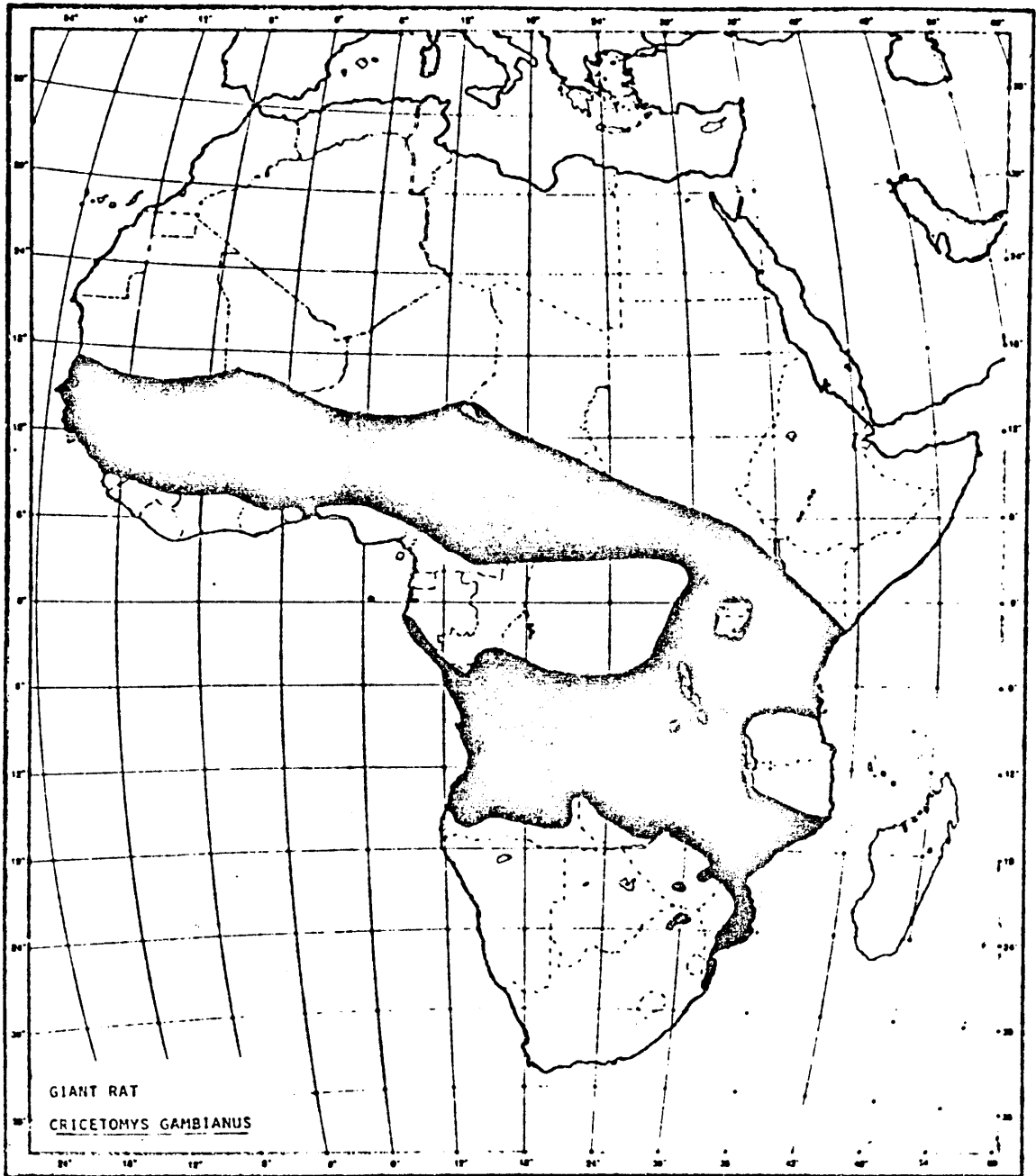
Fig. 1 : The distribution of the African giant rat (Smithers 1983).
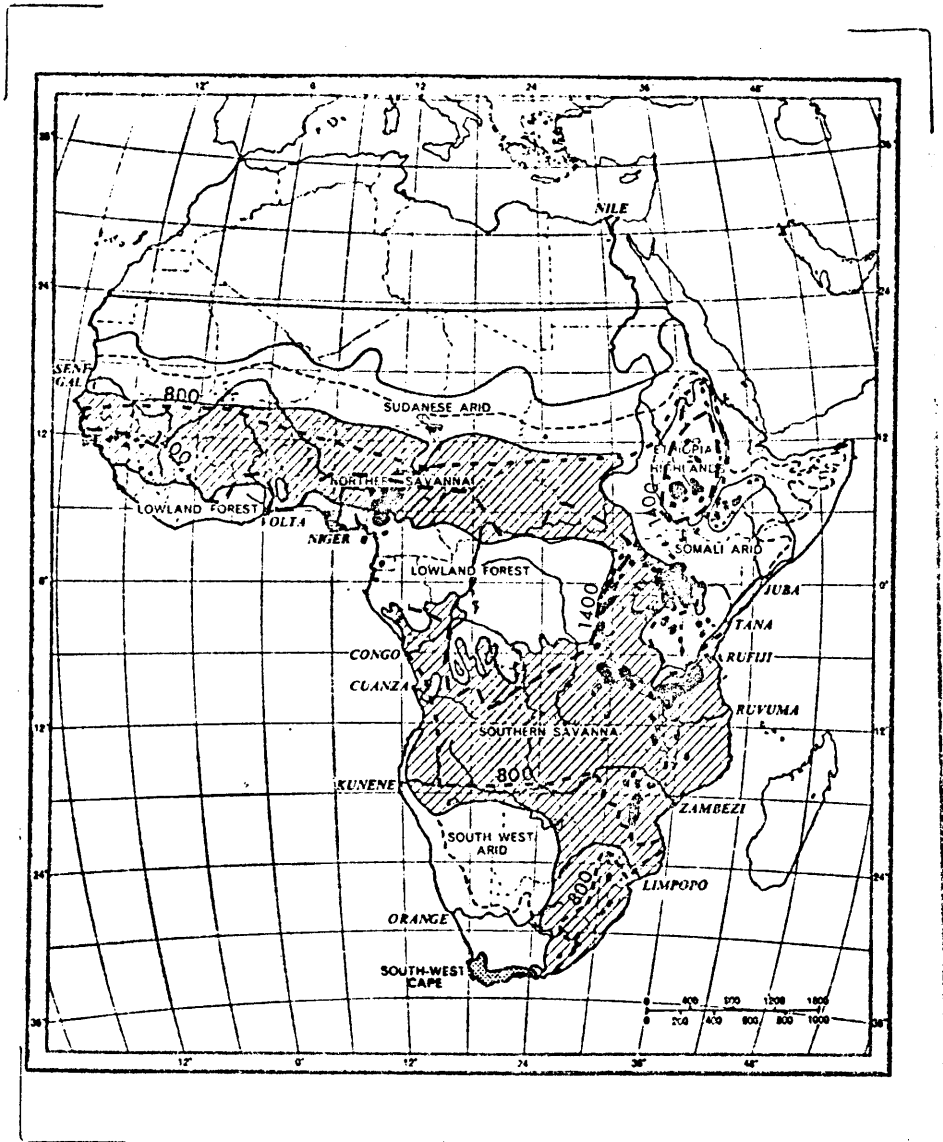
Fig. 2 : Biotic zones of Africa with 800 & 1400mm annual
rainfall average isohyetals (Adapted from Smithers
1983).

(1975 a) found that in hot dry seasons in Nigeria, 5o% of mor=
tality of caged animals was due to heat prostration at about
32°C.

Very little is known about the giant rat in the wild. Ewer (1967)
and Ajayi et al (1978) found from behavioural studies of captive
animals that they were docile, nocturnal and active burrowers
which become very tame after one generation. They are extensive
food hoarders, collecting food, and pieces of rubbish such as iron
(old pot parts) and storing these under their bedding within
their burrows. Giant rats are primarily terrestrial but have
been noticed to climb (Ewer 1967 ; Rosevear 1969). Burrows of
giant rats are predominantely located in cool, shaded environments
(Ajayi 1977) and are usually constructed at the base of large trees
or in termite mounds.

Giant rats have been reported to be gramnivorous (Roberts 1951),
herbivorous (Smithers 1966, 1975, 1979) and omnivorous (Morris,
1963; Ewer 1967; Ajayi 1974). The last classification is more
apt as they have been noted to eat termites and snails (Rosevear,
1969). Ajayi & Tewe (1978) found from food presented, that
maize was the preferred grain. Giant rats have also been found
to be inefficient digesters of food with more than 10% crude
fibre content (Faturoti, Tewe & Ajayi 1982). In the Soutpans=
berg giant rats are considered pests in commercial fruit orchards
taking avocado pears, macadamia nuts and pecan nuts.

In the wild they have been found to reproduce during the wet season (Morris 1963, Smithers 1966; Rosevear 1969; Ajayi 1975 b) however in captivity in Nigeria they reproduced throughout the year (Ajayi 1975 b).   The gestation period was found to vary from 27 to 36 days, with litter sizes ranging from one to four, the young being weaned after 30 days and reaching sexual matu= rity by five months of age (Ajayi 1974).

Since giant rats are an important source of protein in West Africa, Ajayi (1974) and Ajayi et al. (1978) have directed their studies at determining how well giant rats could be domesticated and bred for meat production.   They found that these animals were easily tamed, cheap to feed and reproduced well in captivity and if managed correctly could become a viable part of a farming enterprise.

Considering all the information on giant rats the present study was undertaken to determine the relationships of their distribu= tion, habits and habitat with their physiology and anatomy.
The following key questions were posed:

1. What are the giant rats' home ranges, activity periods and habitat use?
2. How is their growth and development adapted to their environ= ment?
3. What are the giant rats' energy requirements?
4. Are there any digestive adaptations associated with their feeding habits?
5. What are the thermoregulatory characteristics of giant rats?

CHAPTER 2

MATERIALS AND METHODS

STUDY AREA

The field work in the present study was undertaken on the farm
Studholme (22° 57' S, 30°01 ' E) 17 km north east of Louis
Trichardt, northern Transvaal, South Africa. The study area
was situated on the top of the Soutpansberg mountain range, 1472 m
above sea level. The sandstone mountains range in elevation
from 769,6 m to 1536 m above sea level.

Occasional trapping for laboratory animals was undertaken on the
farm Vreemdeling (22°59' S, 30°01' E), 12 km north east of Louis
Trichardt.

The vegetation of the study area is described as North-Eastern
Mountain Sourveld (Acocks 1975) and characterised by the follow=
ing plants:
Xymalos monospora, Clausena anisata, Rhamnus prinoides, Acacia
ataxacantha, Grewia occidentalis, Maytenus heterophylla, Peddia
africana, Cussonia spicata, Pellaea viridis, Ptenidium acquilium,
Behnia reticulata, Ziziphus mucronata, Eckebergia capensis,
Vepris undulata, Carissa bispinosa, Schefflera umbellifera,
Rhoicissus tridentata, Maesa lanceolata, Mundulea sericea,
  Caesalpinia decaptela, Endata spicata, Tricalysia capensis,
  Vangueria infausta, Syzygium gerrandii, Fauria saligna;
  Olea capensis; Bequertiodendron magalismontanum, Mimisops
  zeyeri, Senecia babertonicus, Oxycanthus sp., Solanum sp.,
  Cucumus sp., Lorathus sp., Brachylaena sp.

Louis Trichardt, which is the closest weather station to the study area receives 730 mm rain annually, with most precipi= tation from September to March (Fig 3) (Walter & Leith 1960). During the winter months misty days frequently occur. The mean annual temperature is 18,9°C.

THE BURROW

The burrows were located through searching and following par= tially anaethetised animals to their burrows. The burrows were excavated and mapped, noting the depths, size of tunnels and dimensions of chambers. The soil and nesting material in the sleeping chambers were removed and examined for presence of food and seed remains.

Burrow temperatures were determined with a copper- constan thermocouple pushed as far down an occupied burrow as possible. The temperature was read on a Kay May 2002 digital thermometer. A thermocouple was also suspended at 5 cm above the surface. Temperatures were recorded at sunrise and sunset during field trips. Maximum and minimum ambient temperatures were also recorded with a maximum and minimum thermometer suspended 5 cm above the ground in the forest.

RADIO TRACKING

The rats were captured with traps (wire, fall door cages; 80x30x30 cm) set within or adjacent to tracts of indigenous forest. The rats were restrained with a hand held crush in

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Louis Trichardt   (961 m)
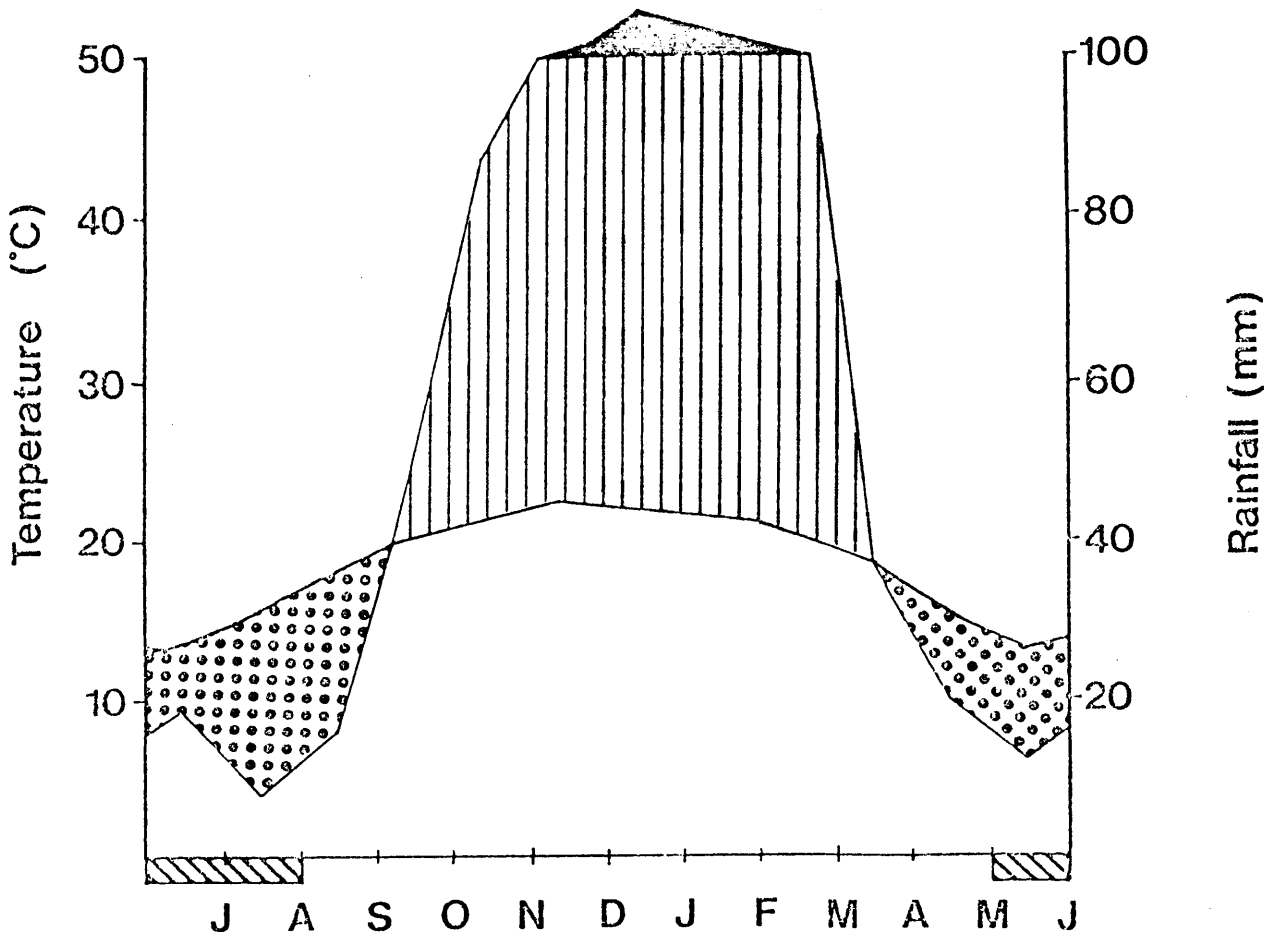
18·9 °C - Mean annual temperature

6·2 °C - Mean daily minimum temperature - coldest month

-1·7 °C - Absolute minimum temperature

730 mm - Mean annual sum - total of precipitation

▨ - Arid period

▥ - Humid period

▩ - Rainfall > 100 mm

▨ - Absolute minimum temperature below 0 °C

Fig. 3 :   Climatological   data of Louis Trichardt, northern

Transvaal (Walter & Leith 1960).

order to administer an anaesthetic. An injection into the thigh
muscle of 20 mg $.kg^{-1}$ of ketamine hydro-chloride (Ketalar; Parke-
Davis, Cape Town) was used to anaethetise the animals.

All radio-tracking equipment was designed and supplied by AVM
instrument Co., Dublin, California. Two types of pulse trans=
mitters were used. SMI transmitters, with BT collars, powered
by a 1,27 volt (v) Hg-601 battery. The expected battery life
was estimated at three years with a maximum range of reception
being 600 m. The total weight of the collar was 46,2 g, three
percent of the average body mass. SB2 transmitters with BT
collars were also used and were powered by
1,27 V lithium $^2/_3$ A battery. The expected life of this
battery was six months and the predicted range one km. The
average collar weight was 48,0 g. Each transmitter had
unique pulse rates lying between 150,7 to 151,1 MH_3.

Radio-tracking was conducted over two to three week periods every
two to three months from the 23 July 1981 to 12 April 1983.
During this period six rats were collared and radiotracked.
Two of the rats were radiotracked on three separate occasions
and the rest only once. During most study periods two rats
were followed simultaneously. The rats were located through
triangulation from fixed points using a hand held, four element
Yagi-antennae (Amlaner 1980) and a portable receiver (model LA
12-AVM). Pitch variation was used to identify activity of
transmitter bearing rats (Voigt & Tinline 1980). Successive

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fixes were taken every 10 to 20 min.   Observations were made·
during the nocturnal period   for six to seven h.   At   the
end of the radio-tracking period, the rats were recaptured,
weighed, the collars removed and the rats released.

Fixes were asigned to grid cells on a map of the study area,
with the sizes of the cells representing the triangulation
errors.   The data were analysed following the method of Voigt
& Tinline (1980).   A fix labelled 'active' was said to also
mark the eight cells surrounding the marked cell (influenced
cell procedure), while a fix labelled 'stationary' only regis=
tered in the marked cell and not in the surrounding cells.
To account for movement of the animal the linked cell (LC) method
 of Voigt & Tinline (1980) was also used.   Where succesive fixes
were closely related in time and far enough apart for the animal
to be travelling in a staight line, the cells along the path
were recorded as used.   At the end of such a path an active
status influenced the eight surrounding cells (Voigt & Tinline
1980).   Only travel rates greater than 0,1 km/h^{-1} qualified for
the linking.   The data were analysed on an IBM 4341 and printed
with an IBM 3203 printer and plotted on 3-D contour maps using
the SURFACE II package (Sampson 1975).

GROWTH AND DEVELOPMENT

One litter of two young was born in captivity and one litter
of four young were obtained in the field when they were about
five days old.   Their masses, measurements (head - body, tail,

hind-foot, pinnae, vibrissae, dorsal and ventral fur length)
were recorded every three to four days for the first two
months and every week for the next two months.
The young were also noted for the following morphological
developments; opening of the eyes, free pinnae, separate
digits, pattern of fur emergence, commencement of pigmentation,
eruption of teeth and presence of auditory meatus.

Behavioural development was studied using the following tests:
righting reflex, cliff dropping aversion, negative geotaxis,
grasp reflex, moving ability, rooting reflex, contact test,
isolation test, vibrissae reaction and nasal development
(Williams & Scott 1955, Baker & Meester 1977). The develop=
ment of locomotion, grooming, social behaviour and aggression
within the litter were noted.

The following body measurements, were recorded for all giant rats
trapped in the field: head body, tail, white tail tip, hind foot,
pinnae, neck, girdle, dorsal fur and ventral fur lengths. The
dorsal and ventral fur lengths were taken between the scapula's
and above the sternum respectively.

DIGESTION

DIGESTIBILITY TRIALS

Five rats were kept individually in metabolic cages (60x45x29 cm)
under a 12 L : 12 D light cycle and acclimated to ambient tem=
peratures (T_a) of 24°C and 10°C on different occasions. The rats

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were acclimated to the ambient temperatures for a minimum of two weeks prior to the commencement of the seven day long digestibi= lity trials. The rats were fed a low crude fibre (2,1%) and high crude protein (22,0%) diet for a week prior to collection. Water was provided ad libitum.

The rats were weighed at the beginning and end of the seven day trials. Each day the rats were given 100 g of the diet, mixed with 200 ml of water, and the faeces and urine of the previous day were collected. The remaining food and faeces were dried at 70°C and weighed once the constant dry weight was attained. The volumes of urine produced were recorded and samples frozen. Consumption equalled the difference between the dry weight of food presented and food remaining and apparent digestibility equalled 100 minus the percentage of consumed diet that was egested as faeces. Samples of the food and all the faeces were ground and combusted in a Gallenkamp adiabatic bomb calorimeter. Aliquots (4 ml) of urine were freeze-dried and a sample of known weight was combusted in the same apparatus used for the faeces. Metabolizable energy was calculated by subtracting urine energy from the digestible energy (Batzli & Cole 1979).

If the experimental rats gained or lost weight during the course of the digestibility trial the following corrections were made (Drodz 1975). For a gain in weight the costs of deposition were reduced by 37.68 $kJ.g^{-1}$ and for a loss in weight 29.31 $kJ.g^{-1}$ were added to the cost of maintenance.

RATE OF PASSAGE

The rate of passage was determined using plastic pieces (2x2 mm) and brilliant blue dye (Van Soest, Uden & Wrick 1983) on separate occasions.   The rats were acclimated to room temperature and a 12 L : 12 D light cycle.   Prior to the trial the rats were starved for 24 h, then presented with the marked food for only three h.   After a 12 h interval, the collection trays were in= spected every three h for 80 h then at six h intervals for the next 40 h followed by 12 h intervals until no more markers were found in the faeces.

DIGESTIVE SYSTEM AND MORPHOLOGY

Specimens were obtained by kill trapping in the field and labora= tory animals which died of natural causes.   Fresh specimens were either immediately processed or the digestive tract preserved in AFA and later studied.   Body mass and standard body measurements were always taken.   On dissection the number of liver lobes and presence or absence of a gall-bladder were noted.   The pH of the different gut regions was recorded with a portable Digital Data Systems 800 pH/Mv meter.   For the stomach the pH of the cardiac and pyloric regions were also noted by inserting the electrode of the meter through a small slit in each region.   The dimensions of the stomachs were noted, recording the lengths and widths of the corpus and antrum.   The approximate zonations of the squamous and cuboidal glandular epitheliums were mapped with the aid of a binocular dissection microscope.

The lengths and widths to the nearest millimetre were recorded
for the small and large intestines, intestinal loops and the
caecum.   The caecum was dried to shape by blowing dry atmos=
pheric air through it to reveal the external and internal micro=
scopic structures.   The different gut sections were filled with
water to determine their maximum volume.   For microscopic ob=
servations, sections were made from the different gut regions
and salivary glands and fixed in AFA and later mounted in wax.
Sections were cut to 7 µm and stained with Erhlich's hematoxylin
and counter stained with eosin and Masson's trichome (Humason
1962).   Light micrographs were taken through a Carl Zeiss
photomicroscope II.

THERMOREGULATION AND EVAPORATIVE WATER LOSS

ADULTS

Five giant rats (three females, two males), were caged separate=
ly and subjected to a 12 L : 12 D light cycle and acclimated on
different occasions to ambient temperatures (T_a) of 10°C and 24°C.
They were allowed to acclimate for a minimum of two weeks prior
to experimentation.

Experiments were conducted in the light phase of the daily photo-
period cycle.   Oxygen consumption was determined in an open-
circuit system (Depocas & Hart 1957).   A 2,8ℓ perspex metabolic
chamber was used.   Beneath the perforated platform, a layer of
paraffin oil was added to prevent evaporation of moisture from
urine and faeces voided while the rat was in the chamber.

Compressed air was dried through columns of silica gel and flowed at a rate of 1015 ml .min^{-1} through the chamber. Excurrent air was also passed through columns of silica gel before enter= ing a Beckman OM-14 polarigraphic oxygen analyser. Output from the oxygen analyser was recorded by a linear analog recorder.

Animals were individually tested at the following ambient tempera= tures: 5°C, 10°C, 15°C, 20°C, 25°C, 28°C, 30°C, 32°C and 33°C. Rats acclimated to 24°C were also measured at 34°C, 36°C and 37.5°C. The chamber was sub-merged in a regulated water bath. The chamber temperature was regulated to within 0,2°C of the desired temperature. The internal temperature of the chamber was determined with a copper-constantin thermocouple linked to a Kay-May 2013 digital thermometer. The animals body masses to the nearest 0,1 g were recorded prior to experimentation and the animals tested were not in a post absorptive state.

Each animal was allowed to acclimate to the ambient temperature for 1,5-2 h in the dark before oxygen consumption values were taken. When the oxygen consumption values became minimal and repeatable, (for about 15 min), evaporative water loss (from pulmocutaneous evaporation) was collected in a pre-weighed column of silica gel (Scheck 1982). The columns were re-weighed to the nearest 0,1 mg on a Mettler H 35 balance. If the animal became active during the collection period, the results were discarded. For the metabolic determinations, minimal oxygen consumption was recorded every three min. until five consecutive readings had similar values. All results were corrected to

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standard temperature and pressure (STP).

After oxygen measurements, the animal was removed from the cham=
ber and the body temperature (T_b) measured by inserting a copper-
constantin thermocouple (connected to a Kay-May digital thermo=
meter) 4 cm into the rectum.

JUVENILES

Young of ages one month (549,03 $\pm$ 82,50 g) to four months (1401,10
$\pm$ 32,50 g) were subjected individually to an ambient temperature of
of 25°C and their oxygen consumption was recorded with the same
apparatus used for the adults. The rats were together housed out=
side and the measurements were conducted from the 29 March 1983 to
15 June 1983.

STATISTICAL ANALYSES

All data, where more than one sample was utilized are presented
as means ($\bar{x}$) with standard deviations (SD), unless otherwise
stated. Regression equations were calculated by the method of
least squares (Cass 1973). Significance of differences between
the means were first tested using analysis of variance (F test)
to determine if parametric or non-parametric statistical tests
could be used. For parametric data, the paired Student-t test
was used (Gass 1973) and for non-parametric data the Mann-
Whitney U and randomization tests (Siegel 1965) were used.
The chi squared distribution was used to analyse sets of frequen=
cies (Cass 1973). The minimum accepted level of significance
used in the present study was $P < 0,05$.

CHAPTER   3

THE   BURROW

RESULTS

BURROW STRUCTURE AND CONTENTS

The burrows of giant rats were usually constructed in old termite

mounds, under boulders or at the bases of large trees and were

always covered by vegetation.   Of the six burrows excavated

the number of entrances were found to vary from one to three

with a mean diameter of 19,60 $\pm$ 8,55 cm.   The main entrances

were never found sealed as reported by Morris (1963), but usually

a 'pop hole' (a tunnel extending to the surface, stopping a few

centimetres below the surface) was found in each burrow system

(Fig. 4).   One to four blind tunnels were also found in each

burrow and the burrow tunnels averaged 13,67 $\pm$ 3,83 cm in diameter.

The number of chambers varied from one to five but only one nes=

ting chamber was usually present in each burrow and could be

distinguished by the presence of stored food and nesting material.

The chambers had an average diameter and height of 45,46 $\pm$ 18,77

and 25,64 $\pm$ 9,82 cm respectively, and were 72,71 $\pm$ 9,01 cm below

the surface.   The entrances into the nesting chamber were often

found sealed with sand and rocks on excavation of burrows, giant

rats were noted to actively seal off their nesting chambers than

rather escape via one of the other burrow entrances or pop holes.

a.

Tree

Entrance

Pop-Hole

Nest

Blind Tunnel

b.

Tree

0   80 cm.
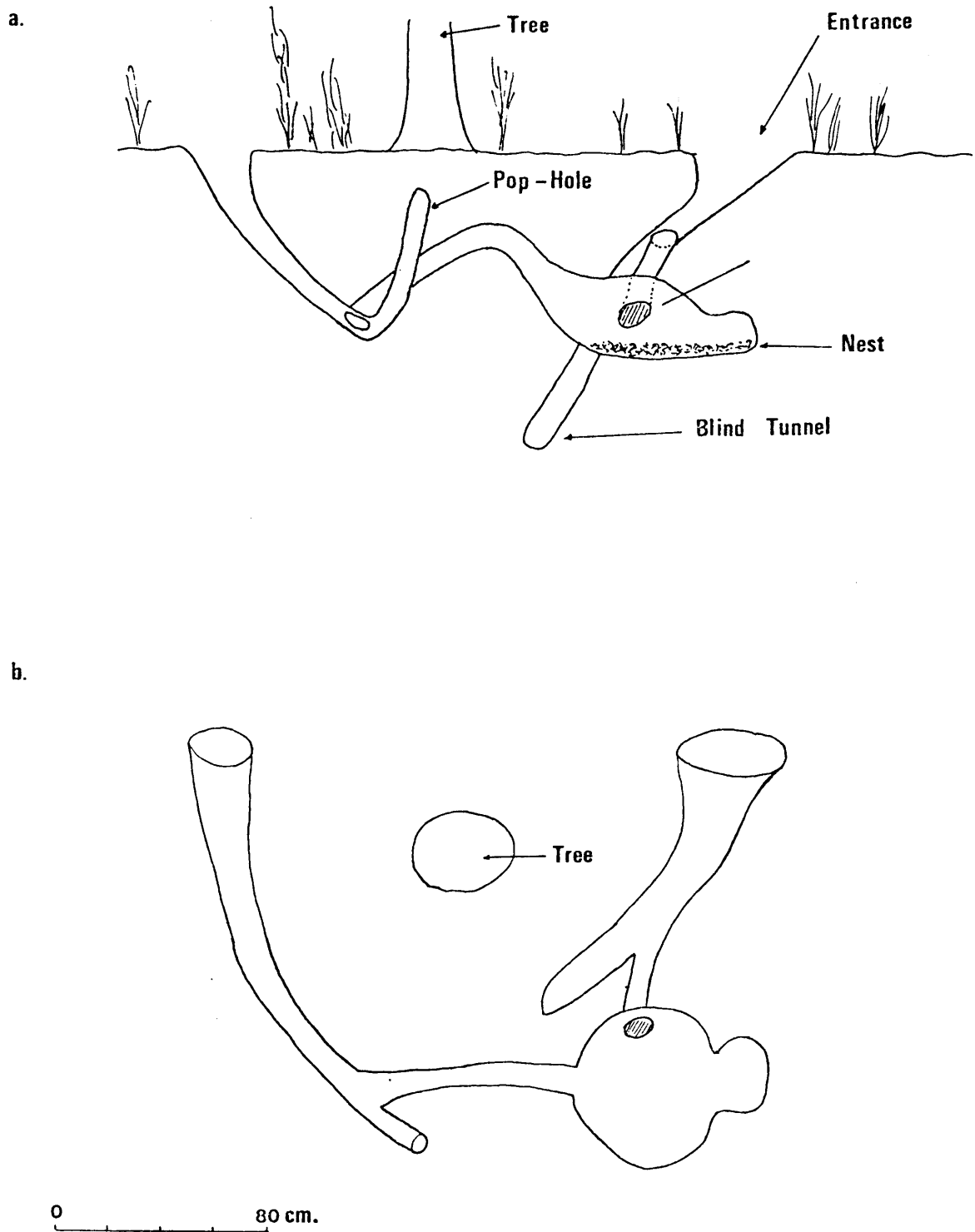
Fig. 4 :   a.   A burrow system of a giant rat in profile.

          b.   From above.

The nesting material consisted of leaves and sticks. The leaves being predominantly from trees in close proximity to the burrow, such as: macadamia (Macadamia integrifolia), avocado (Persea americana), Cape ash (Eckebergia capensis) and Cape chestnut (Calodendrum capensis). The nest of one burrow, containing a litter of four young, was made up entirely of pieces of burnt grass. Food stored within the nesting chamber was found scattered in the nesting material.

Burrows in the indigenous forest were found to contain fruit and seed remains of a large variety of plants (Table 1), but whether or not, they were used for food or just hoarded is not known. The majority of seeds collected were from fleshy fruits and many of the seeds were clearly husked as indicated in Table 1. From burrows adjacent to macadamia nut plantations large quantities of gnawed open macadamia nuts were found, and from one burrow 8,70 kg of opened nuts were removed. Animal remains, both in= sect and bones of mammals and birds were found with some of the bones showing signs of gnawing.

Separate shelters outside the burrows were used for defaecation and feeding. Both shelter types were characteristically pro= tected on three sides and from above. Feeding shelters were also found to contain seed and animal remains and all the seeds were from fleshy fruits (Table 2). Some of the seeds showed signs of being husked and particularly large quantities of shelled Ziziphus mucronata seeds were found in some shelters. From Tables 1 and 2, it is evident that fruit is available to giant rats throughout the year.

Table 1   Plant and animal remains found in six giant rat burrows.

PLANT AND ANIMAL REMAINS	FRUIT TYPE	TIME OF THE YEAR FRUITS DEVELOP
PLANTS		
Caesalpinia decapetala	* pod	
Calodendrum capense	* capsule	January - May
Cassia floribunda	pod	
Grewia occidentalis	* berry	January - May
Linociera foveolata	* fleshy	November - July
Mimusops zeheri	* fleshy	April - October
Vangueria infausta	* fleshy	January - April
Rhoicissus sp.	* fleshy	
Rhus sp.	fleshy	
Acacia karroo	pod	
Olea africana	fleshy	
Capparis sp.	* berry	
Persea americana	* fleshy	
Macadamia integrifolia	* nut	March - June
Acanthosicyos sp.	fleshy	
Datura ferox	capsule	July - September
Passiflora edulis	fleshy	November - January
Ricinus sp.	capsule	
Coffea	* fleshy	
ANIMAL		
Bones		
Insect		

* Seeds found husked.

Table 2   Plant and animal remains found in five giant rat

feeding shelters

PLANT AND ANIMAL REMAINS	FRUIT TYPE	TIME OF THE YEAR FRUITS DEVELOP
PLANT		
Mimusops zeyeri	* fleshy	April - October
Sclerocarya caffra	fleshy	April - June
Bequaertiodendron magalies-montanum	* fleshy	December - February
Zizphus mucronata	* fleshy	November - February
Vepris undulata	fleshy	May - July
Rhus sp	fleshy	
Asclepiadaceae		
ANIMAL		
Beetles		
Millipedes		
Snails		
Bird and mammal bones		

* Seeds found husked

FOREST AND BURROW AMBIENT TEMPERATURE

The mean forest temperature of 9,65 $\pm$ 2,07°C for June was signifi= cantly lower than that recorded for October (z = 3,24; P < 0,0007), January (t =68,85; P < 0,05) and April (t = 9,09; P < 0,05) (Table 3). The highest mean forest temperature of 20,50 $\pm$ 2,63 °C was recorded in January and was significantly different from April (u = 7,5: P < 0,05) but not from October (U = 14,5; P < 0,05).

The highest mean maximum forest temperature of 31,08 $\pm$ 3,94°C was recorded in April (t = 2,20; P < 0,05) but not October (t = 1,50; P < 0,05);(Table 3). The mean minimum temperatures showed no significant differences between the three sample periods.

The lowest mean maximum forest temperature of 12,67 $\pm$ 1,86°C was recorded in June and only differed significantly from those recorded in January (t = 17,73; P < 0,05) (which had the highest mean burrow temperatures of 18 ,63 $\pm$ 0,23°C) and April (u = 0,00; P < 0,05) (Table 3).

DISCUSSION

The dimensions and site of construction of giant rat burrows in the present study appeared to be similar to those found in Malawi (Morris 1963), West Africa (Rosevear 1969) and Nigeria (Ajayi 1977). The burrows were constructed in well shaded habitats under boulders, in termite mounds and at the base of large trees

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Table 3　Mean ambient temperatures (°C) recorded for the indigenous forest (at 5 cm above ground level) and mean burrow temperatures (approximately 70 cm deep).　Mean $\pm$ standard deviation and n = number of days.

SITE	JUNE '82 n = 7	OCTOBER '82 n = 6	JANUARY '83 n = 7	APRIL '83 n = 10
Forest temp. (°C)	MAX. *---	$^{ab}23,00 \pm 3,79$	$^{b}31,08 \pm 3,93$	$^{a}20,28 \pm 3,86$
Mean forest temp. (°C)	MIN. *---	$^{a}15,00 \pm 1,73$	$^{a}15,83 \pm 0,75$	$^{a}15,10 \pm 0,94$
	$^{a}9,65 \pm 2,07$	$^{bc}17,50 \pm 5,95$	$^{b}20,50 \pm 2,63$	$^{bc}17,14 \pm 1,21$
Mean burrow temp. (°C)	$^{a}12,67 \pm 1,86$	$^{ac}14,42 \pm 1,07$	$^{bc}18,63 \pm 0,23$	$^{bc}18,29 \pm 0,86$

* Maximum and minimum temperatures not recorded as thermometer was damaged.　Values without common superscript in rows are significantly different (P<0.05).

for what appears to be three reasons. First, the shaded envi=
ronments provided cool constant burrow temperatures which
are important for the survival of giant rats in the tropical
environments because it has been found (Chapter 7) that they
are not well adapted to withstand ambient temperatures greater
than about 30 - 34°C. Kenagy (1973) also found that the con=
struction of burrows under thick vegetation by Dipodomys microps
D. merriami and Perognathus longimembris was crucial in main=
taining cool burrow temperatures for the survival of these ro=
dents in arid environments. Second, the shaded habitat around
the burrows probably provides protection for the giant rats from
predation, as it has been found in the radio tracking study
(Chapter 4) that giant rats confined most of their activity to
habitats with plenty of cover. Until now only raptors have been
noted to take giant rats (Chapin 1932; Gargett 1977; Pitman &
Adamson 1978).

Third, construction of burrows under trees and boulders may be for
structural reasons, to prevent caving in, as the tunnels and
chambers are large in size.

In the Soutpansberg mountains the soil in the indigenous forests
(where most of the burrows were situated) was found to be of
a softer texture and moister, than that found in adjacent open
areas. Giant rats are known for their poor digging adaptations,
namely their small insignificant claws and fore paws (Rosevear
1967). But the soft forest soil facilitates digging.

The burrow contents analysed in the present study indicated that giant rats are omnivores, with a preference for fleshy fruits. Since these fleshy fruits are noted to ripen at different times of the year (Palgrave 1977) this source of food is available all year round.   In the thermoregulatory study(Chapter 7) it was found that giant rats are dependant upon water especially for regulating heat loss at high ambient temperatures and therefore these fruits are probably important in providing them with the necessary moisture.   Other studies on giant rats (Morris 1980; Rosevear 1969; Ajayi 1975 a, 1977; Iwala, Braide & Moduka 1980) have also reported on their omnivorous diet with a preference for fruits and tubers.   However, no tubers were found in the burrows during the present study, probably because no disting= uishable remains, such as husks or seeds were left.   Moreover giant rats are unable to digest fibrous food efficiently (Faturoti, Tewe & Ajayi 1982) which may account for their pre= ference for soft fruits.

In conclusion the distribution of giant rats appears to be deter= mined by their need for cool environments and moist, fibreless foods.

CHAPTER 4

RADIOTRACKING

RESULTS

ACTIVITY PERIODS

Giant rats displayed nocturnal behaviour patterns. Of the noc=
turnal period they spent an average of 67,07% (8,7 h) sedentary
in the burrow, 9,49% (1,2 h) active within the burrow and 23,44%
(3,1 h) active outside the burrow (Fig. 5). The overall activi=
ty appears to be bimodal, with the first and most active period
lasting from 19h00 to 22h00 and the second period from 01h00 to
05h00. The decreased activity in the 03h00 - 04h00 period did
not differ significantly (X = 0,72; df = 1; P>0,05) from that
recorded in the 02h00 - 03h00 period.

Giant rats were never active outside their burrows during the
diurnal period. Activity within the burrow appears to be
greatest at sunset and just before sunrise, with 18,60% and
17,10% of the burrow activity recorded between 18h00 to 20h00
and 04h00 to 08h00 respectively.

HOME RANGES, FORAGING DISTANCES AND RUNNING SPEEDS

The minimum area (MAM) (using convex polygons) estimate of home
ranges were in all cases significantly greater (randomization
test; P < 0,005) than the home range calculated by the linked
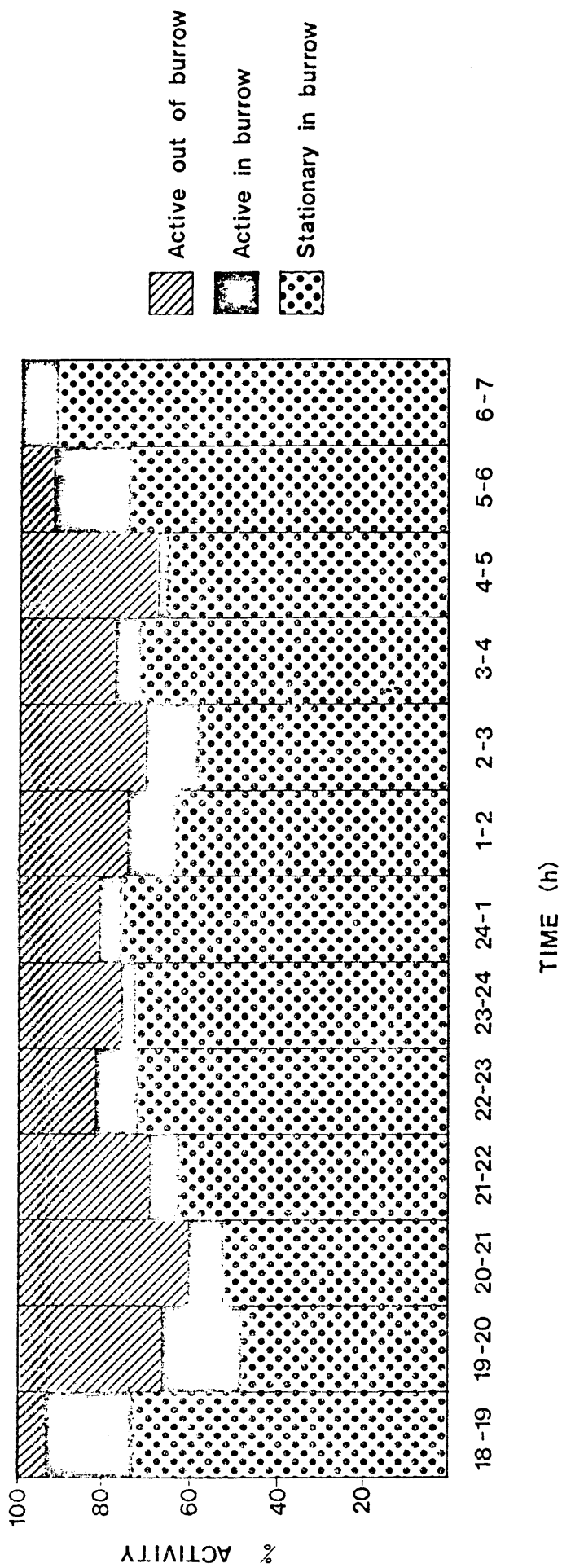
Fig. 5 : Activity periods of four radio-collared giant rats.

cell (LC) technique (Table 4). The mean LC estimate of home ranges was $4,95 \pm 4,18$ ha, with a range of 2,23 to 11,10 ha while the mean MAM estimate of home ranges was $27,12 \pm 33,28$ ha with a range of 8,90 to 77,01 ha. It appears that male giant rats have larger home ranges than females, but the small sample size prevents a definite answer. However the sexes differ in their use of the home ranges. Giant rats spend 95,43% of their outside activity within 200 m of their burrows, with the greatest percentage, 32,28% within 50 m of it (Table 5). Between 201 and 350 m from the burrow they spent only 4,43% of their outside activity. Figures 6, 7, 8 and 9 which illustrate the frequency of use of giant rats home ranges are each divided into two sec= tions. Section a illustrates the frequency of use of the home range using all the radiotracking data for each animal. Owing to the great amount of time spent within the burrows and the scaling down effect of the programme, the outer areas are overshadowed by the importance of the burrow. Therefore section b shows the same data excluding those recorded for the burrows to emphasise more clearly the frequency of use of the outer areas of the home range. In all cases the activity shows a concentration around the burrow, except for female 9 (Fig. 8) which had an extra area of use extending to the north of her burrow and the activity recorded between the two burrows for female 7 (Fig. 6) and male 8 (Fig. 7).

Females tend to concentrate their activity significantly closer $(X^2 = 27,58; \text{ df } = 1; \text{ P} > 0,01)$ to the burrow than males did. Of the radiotelemetric locations for females, 54,17% were within

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Table 4   The minimum area method (MAM) and linked cell (LC)
estimates of home ranges of four adult giant rats.

Animal no	MAM (ha)	LC (ha)
10♂	77,01	11,01
9♀	11,71	4,14
8♂	10,84	2,23
7♀	8,90	2,39
Mean	27,12 $\pm$ 33,28	4,95 $\pm$ 4,18

Table 5. The frequency (%) of radiotelemetry locations of active giant rats at different distances from their burrows

	Distance from burrows (m)						
	0 - 50	51 - 100	101 - 150	151 - 200	201 - 250	251 - 300	301 - 350
Combined ♂♂ and ♀♀	32,28	22,15	29,11	12,00	1,27	2,53	0,63
♂♂	15,12	22,09	38,37	16,28	2,83	4,65	1,12
♀♀	54,17	22,22	16,67	6,94	0,00	0,00	0,00
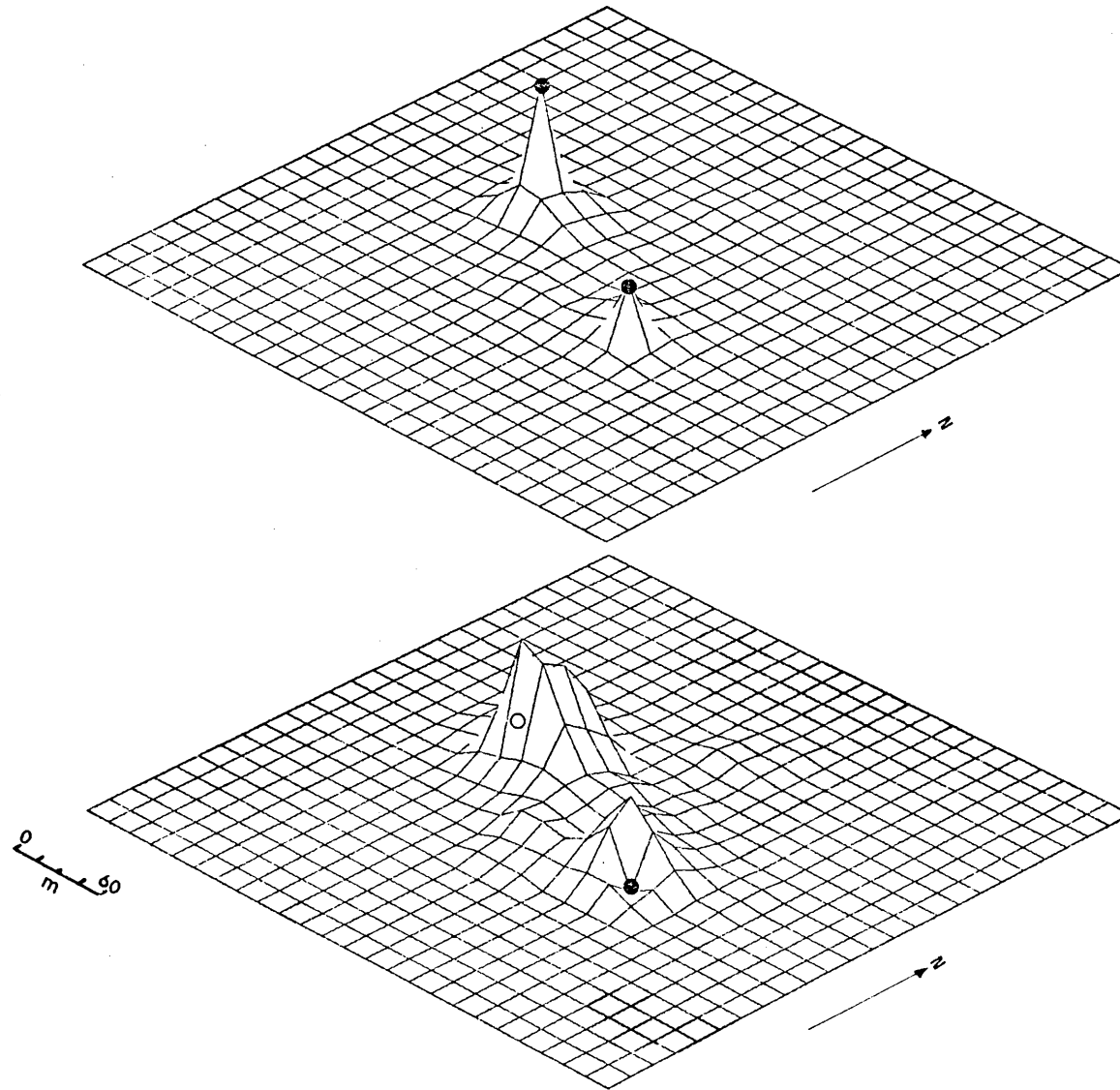
Fig. 6 :   a.   Frequency of use of the home range by a giant
              rat (No. 7♀), including burrow data.

          b.   Excluding burrow data.   ● = burrow.
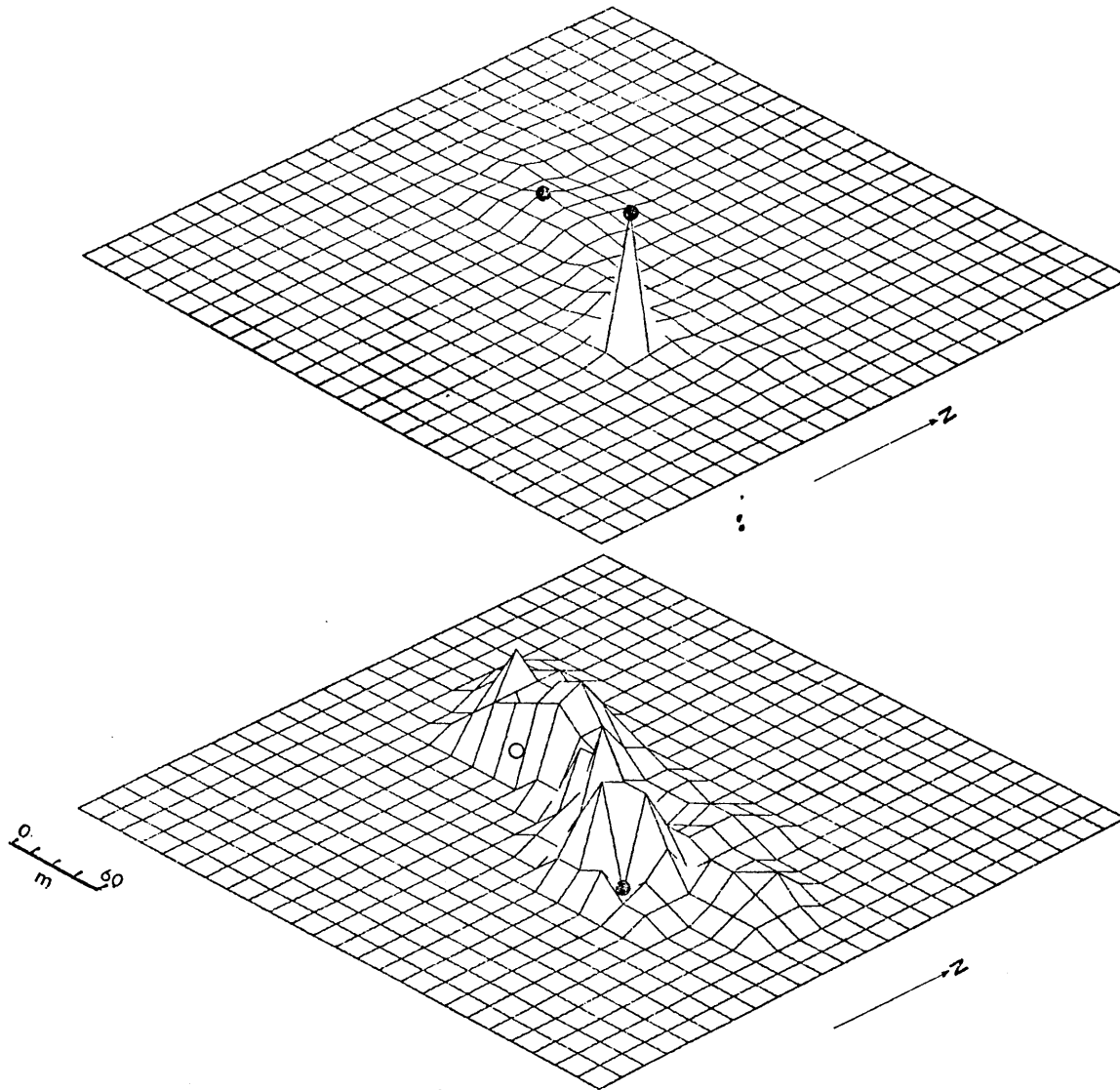
Fig. 7 : a. Frequency of use of the home range by a giant
rat (No. 8♂) including burrow data.

b. Excluding burrow data. ⊙ = burrow.
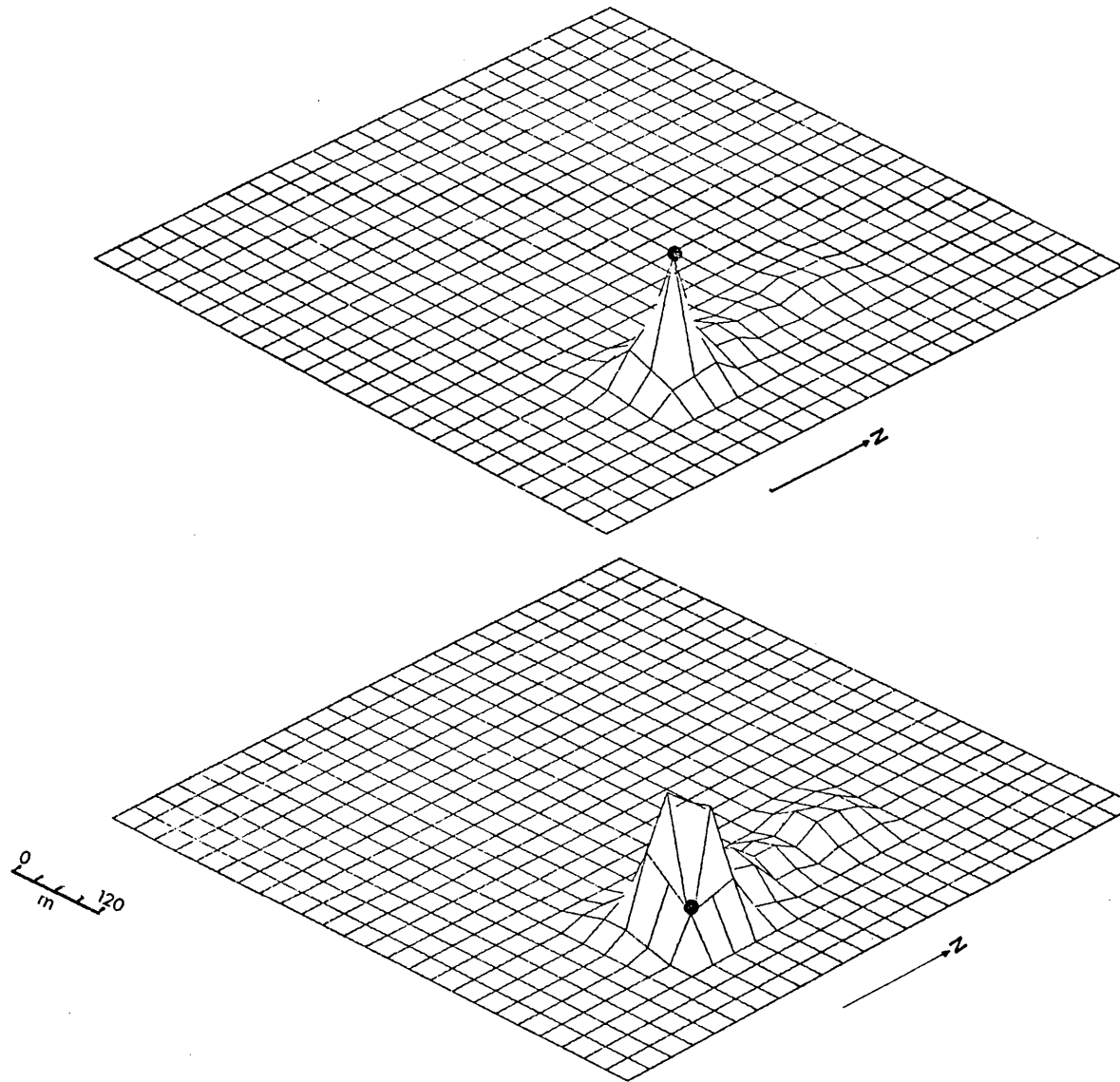
Fig. 8 : a. Frequency of use of the home range by

a giant rat (No. 9♀) including burrow

data.

b. Excluding burrow data.   ☻ = burrow.
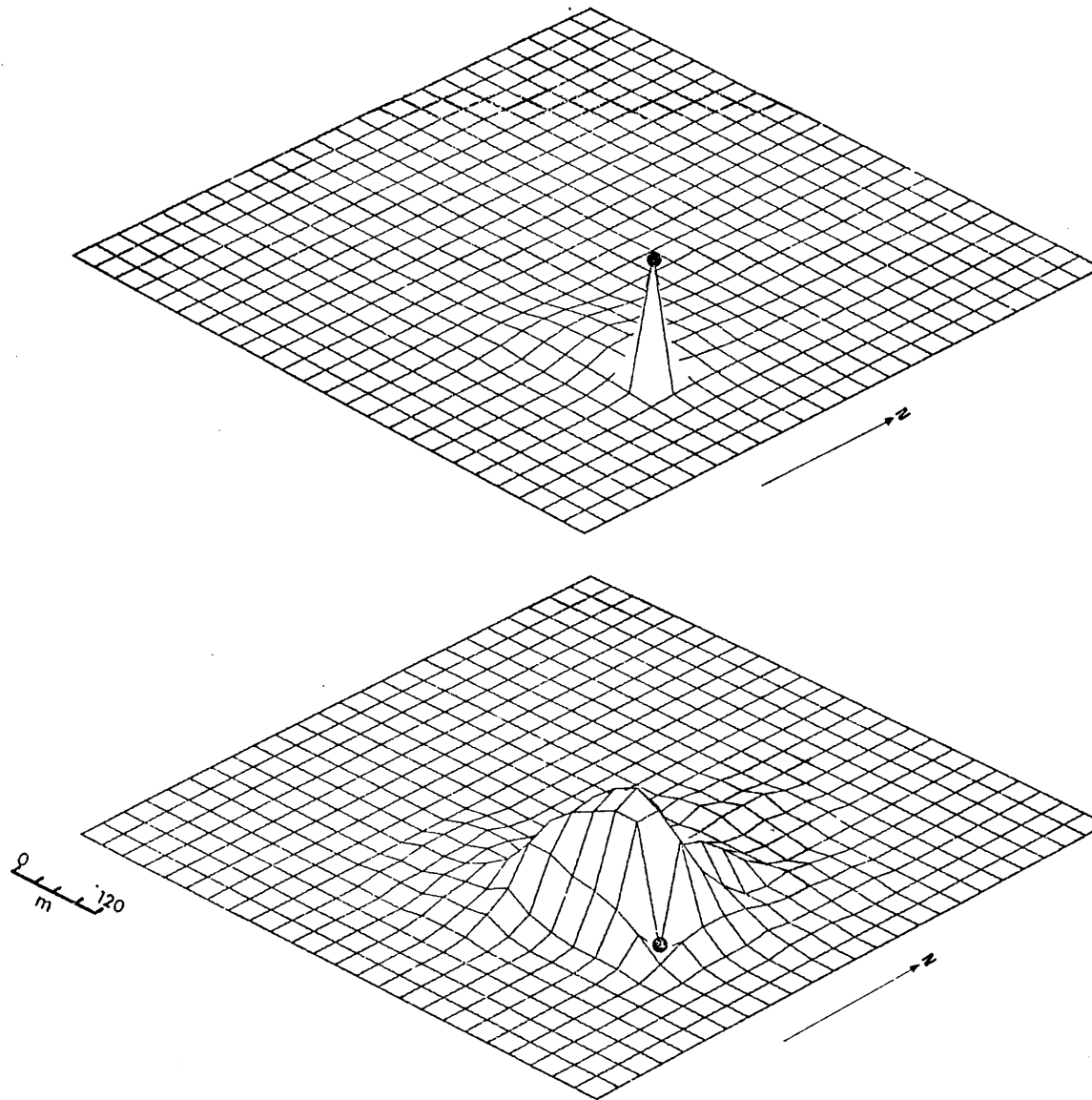
Fig. 9   a. Frequency of use of the home range by

a giant rat (No. 10σ) including

burrow data.

b. Excluding burrow data. $\odot$ = burrow.

50 m of the burrow (Table 5). Beyond this the number of loca=
tions decreased, with the maximum distance from the burrow being
196 m. This concentration of activity around the burrow is seen
as a high, steep sided hill in the three-dimensional (3D) re=
presentation of the home range of females 7 & 9 (Fig 6 b & 8 b).

The males on the other hand concentrated their activity further
from the burrow than the females (Fig. 7 b & 9 b). Within 50 m
of the burrow only 15,21% of the locations were recorded, while
the greatest percentage of 38,37% were recorded in the 101 to
150 m range (Table 5). Beyond this the percentage of locations
decreased, with the maximum distance recorded from the burrow
being 313 m.

Giant rats generally occupy one burrow except in the case of female
7 (Fig. 6) and male 8 (Fig. 7) which were found together frequently
in each others burrow in April 1982. However in June 1982,
male 8 disappeared and female 7 continued to use both burrows.
Male 10 and female 9 occupied the same burrow but on different
occasions and were found not to use any other during the study
periods.

The mean round trip distance (from burrow and back) for rats was
344,63 $\pm$ 232,17 m with a mean trip time of 94,52 $\pm$ 50,38 min.
From this a mean travelling speed of 0,23 $\pm$ 0,08 km.h^{-1} was found
(Table 6). The mean round trip distance (t = 1,98; P< 0,05)
and travelling speed (t = 1,86; P< 0,05) of males were signifi=

Table 6   The mean round trip distances, times, and travelling

speeds of active giant rats.   Mean $\pm$ standard

deviation and n = number of observations.

	Mean round trip distance (m)	n	Mean round trip time (min)	n	Travelling speed $(km \cdot h^{-1})$
Combined ♂♂ and ♀♀	344,63 $\pm$ 232,17	27	94,52 $\pm$ 50,38	26	0,23 $\pm$ 0,08
♂♂	*431,25 $\pm$ 245,26	16	99,94 $\pm$ 53,94	16	*0,26 $\pm$ 0,07
♀♀	*218,64 $\pm$ 143,03	11	86,64 $\pm$ 46,02	10	*0,18 $\pm$ 0,08

*   Means in columns bearing a superscript were significantly

different using t-test, P<0,05.

cantly greater than those found for the females but there was no
difference (t = 0,67; P>0,05) in the trip times between the sexes.
The fastest travelling speed recorded for a giant rat was 1,53
km.h^{-1}.

Giant rats tend to use paths near their burrows as was found in
the field from linking radiotelemetry locations in chronological
order.   The use of paths was evident around the burrow of male
10 (Fig. 10) and between the two burrows of male 8 (Fig. 11).
While foraging trips further afield illustrated the use of paths
less clearly except for the examples with dotted lines in Fig. 10.

HABITAT UTILIZATION

Giant rats were found to be active within the closed forest and
forest scrub, 56,20% and 36,50% (a total of 91,70%) of their time
which were greater than the meagre 1,46%, 2,92% and 2,92% found
for the open grass areas, Eucalyptus and avocado pear plantations
respectively (Table 7).

DISCUSSION

The radiotracking study confirms that giant rats are shy noctur=
nal rodents, active for short nocturnal periods in habitats pro=
viding ample cover.   As a result and because of the difficulty
in moving through the thick indigenous forest they inhabited,
allowed giant rat movement to be determined only through triangu=
lation.
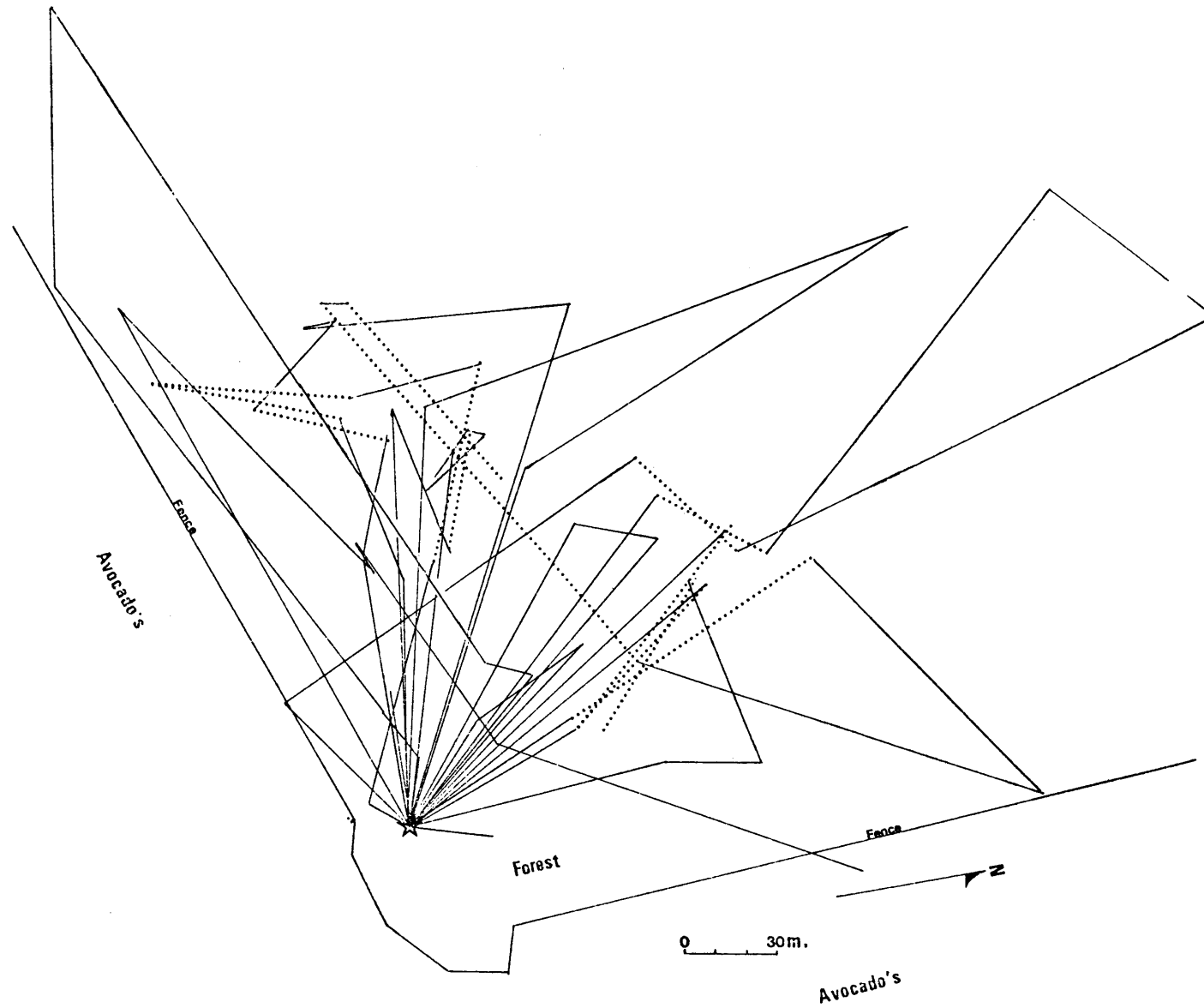
FIG. 10: Travel paths used by giant rat No. 10♂. Dotted lines indicate possible paths used further afield. ✿ = burrow.

N

Avucado

Forest

0 5 10 m.

Fence

Fence

Fence

Fence

Track
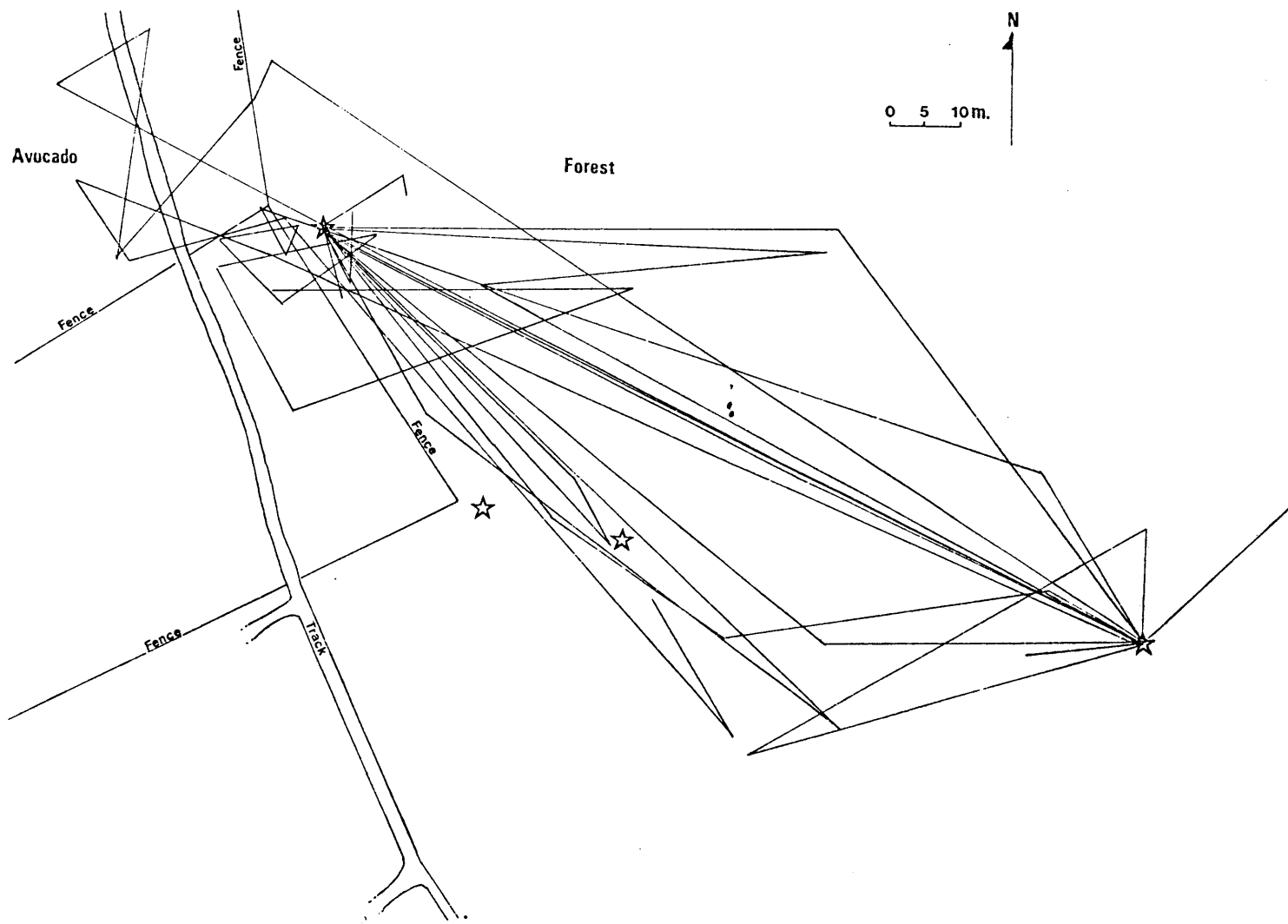
FIG. 11: Travel paths used by giant rat No. 8 . ✿ = burrow.

Table 7   Percentage habitat utilization of four radiocollared

adult giant rats.

Closed forest	Forest scrub	Open grass	Eucalyptus plantations	Avocado pear trees
56,20	36,50	1,46	2,92	2,92

Ewer (1967) found a bimodal activity pattern in giant rats kept in captivity, and Majer (1973) also recorded a similar pattern for C. emini while doing random night road cencuses in Ghana. This bimodal pattern is contrary to the trimodal activity patterns that Emmon (1981,1983) found in other forest dwelling, nocturnally active rodents, such as the bamboo rat, Dactylomys dactylinus, and the brush-tailed porcupine, Atherurus africanus. The bimodal activity pattern and the very short activity period outside the the nest (23,44% or 3,1 h of the night) were methods to reduce the time out of the burrow. Therefore giant rats could be classi= fied as 'time minimizers' (Schoener 1971), but it depends on the consideration of other factors such as nutritional requirements and predation (Pyke 1977). The reduction in time out of the nest could therefore be a result of; abundant and easily collec= ted food supply, efficient foraging behaviour, hoarding behaviour or a means to avoid predation. Measuring abundance and avail= ability of the food in the field would be no easy task. However the results in Tables 1 and 2 indicate that veld fruits were available to giant rats all year round. Foraging efficiency is enhanced by hoarding food because the animal can eat food in the safety of the burrow, thereby saving foraging energy and reducing exposure to predation.

Avoidance of predation appears to be very important to giant rats because first, a limited time is spent out of the burrow; second, (91,70%) outside activity occurred predominantly in the forest scrub which provided the most cover of all the habitats they fre= quented; third the use of feeding and defaecation shelters that

offered shelter from three sides and above; and finally the habit of sealing off the burrow once inside. Reports of predation on giant rats are rare but a few records have been made of predation by raptors (Chapin 1932; Gargett 1977; Pitman & Adamson 1978) and snakes (Ajayi 1975). Avoidance of predation by confining activity to areas of cover have also been reported for Neotoma lepida lepida (Thompson 1982), N. fuscipes (Cranford 1977) and Rattus norvegicus (Taylor & Quy 1978). Predator avoidance is very important because if taken by a predator it is the ultimate loss of fitness.

Only recently has attention been focussed on the risk of predation and how it affects foraging behaviour (Pyke 1977; Krebs 1980). But not until it can be properly quantified can predation risk really be used in optimal foraging theories. Therefore, the cost-benefit hypothesis by Schoener (1971) is too simple in describing foraging behaviour.

Little information is available on speed of movement of rodents in the field. Taylor & Quy (1978) found that R. norvegicus moved at an average speed of 0,90 km. h^{-1} with a maximum of 1,47 km. h^{-1} and Emmons (1983) found A. africanus moved at 1,50 km.h^{-1}. These rodents were travelling between burrow and feeding patches. Giant rats were found to move at slower speeds, averaging 0,23 $\pm$ 0,08 km. h^{-1}, with a maximum of 1,53 km. h^{-1} and this may result from giant rats actively searching for food while moving rather than just travelling between two points as found for R.norvegicus.

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Male giant rats travelled further on foraging trips and con= centrated their activity further from the burrow than did the females and it could be a function of their larger body size and energy demands or territorial patrolling. Triangulation unfortunately only provides information on movement and not on actual behaviour while travelling and only through detailed be= haviour studies can the foraging behaviour be determined. No direct evidence of territoriality was obtained, except that, foreign males were only ever trapped outside the burrows of females and never outside those of the resident males, which may indicate aggression between males needed for teritorial defence. Defaecation was restricted to latrines within the burrow and also shelters in the home range. Urine dribbling was noticed in both sexes in captivity and probably has a dual function of marking their paths while foraging and also their home ranges. The females have a large clitoris, very similar in size to the retracted penis of the males, which probably facilitates urine dribbling. This large clitoris often caused difficulty in sexing young unperforated female giant rats.

Home range is a concept employed to indicate the area used by an animal during its routine activities (Calhoun & Casby 1958) and it can be calculated in a variety of ways as reviewed and assessed by Mac Donald, Ball & Hough (1980) and Voigt & Tinline (1980). Home ranges of giant rats calculated by the minimum area method (MAM) (using convex polygons) over-estimated by an average of 24,23% those calculated by the linked cell method (LC) (Table 4). The latter method defines more closely the actual area used by

giant rats to satisfy their energy requirements while the MAM
encompasses large unused areas in the home ranges.

A close relationship between home ranges and body mass (McNab
1963) and home range and trophic status (Harestad & Bunnell 1979,
Gittleman & Harvey 1982, Mace & Harvey 1983) exists in mammals
and birds. The MAM estimate of home range for giant rats (used
for comparative purposes as MAM is used widely in the literature)
was found to be 43,56% less than the home range predicted for
omnivores (Harestad & Bunnell 1979) using:

$$\text{home range (ha)} = 0,059 \ W^{0,92}$$

where W = adult body mass (g)

The LC estimate of home range was found to be 89,70% less than
that predicted. The small home range size of giant rats could
be a result of a number of factors. First, the predicted home
range could be over estimated because of small sample sizes and
the use of MAM. Second, the giant rat habitat could be very
productive producing suitable foods in large quantities on which
giant rats feed, and third, the giant rats may be very efficient
foragers.

Very little information exists for rodents of similar size to
giant rats. However, the brush - tailed porcupine, A. africanus
(Emmons 1983), which are forest dwelling omnivores feeding pre=
dominantely off fallen fruit and weighing about 3,0 kg have home
ranges averaging 13,31 ha which is 85,82% less than that predicted
by body mass. Similarly, Emmons (1975 cited in Emmons 1983)
found that the forest squirrel, Epixerus ebii, which also are

omnivores, feeding predominantly on fruit, had home ranges 33,50% less than those predicted by body mass. This implies that either animals living predominantely off fruit have characteristically small home ranges or that the home ranges are rather the result of the productive habitats which produce food all year round. The latter is probably the more correct assumption. Therefore, habitat types should be considered when describing relationships between body mass and trophic status with home ranges.

Giant rats show the classical habitat use found in central place foragers where the home ranges are clearly organised around an intensively used, frequently visited area (Kramer & Nowell 1980, Getty 1981) and in the case of giant rats it is the burrow (Fig. 6 - 9).

Males tend to concentrate their activity further from the burrow than females, and as mentioned earlier, this may result from their greater energy demands or territoriality.

In conclusion giant rats appear to restrict their activity to small home ranges with sufficient cover, for short periods of the night to avoid predation. The small home ranges are probably a result of foraging efficiently and the productive habitat providing cover and fruit all year round.

CHAPTER 5

GROWTH AND DEVELOPMENT

RESULTS

GROWTH

The mean birth mass was not determined, however at two days of age body mass of two pups averaged 27,43 g (1,86% of adult mass) and increased rapidly to 461,70 $\pm$ 34,79 g by day 52 (Fig 12). Over this period the percentage increment was 6,70% but between days 52 and 94 the percentage increment dropped to 3,57%, where a mean mass of 963,40 $\pm$ 101,84 g was found (Fig. 13). Between day 94 and day 129 the body mass further increased to 1331,27 $\pm$ 106,57 g (90.26 % of adult mass) with the increment of 13,10%, after which it decreased. The rats attained adult mass (male data Table 8) after about 134 days after which it rose to a high 1632.23 $\pm$ 144,89 g after 227 days.

The head body length at two days was 8,6 cm (22,50% of adult) and increased rapidly to 20,45 $\pm$ 0,82 cm after 28 days, with a percentage increment of 8,00% (Fig. 12 & 13). There was a slight decrease in growth rate between 20 and 23 days. After 43 days the percentage increment dropped to a low 3,48 % after which it rose again to a peak of 10,90 % at 72 days where a mean length of 28,00 $\pm$ 0,41 cm (73,24% of adult) was recorded.
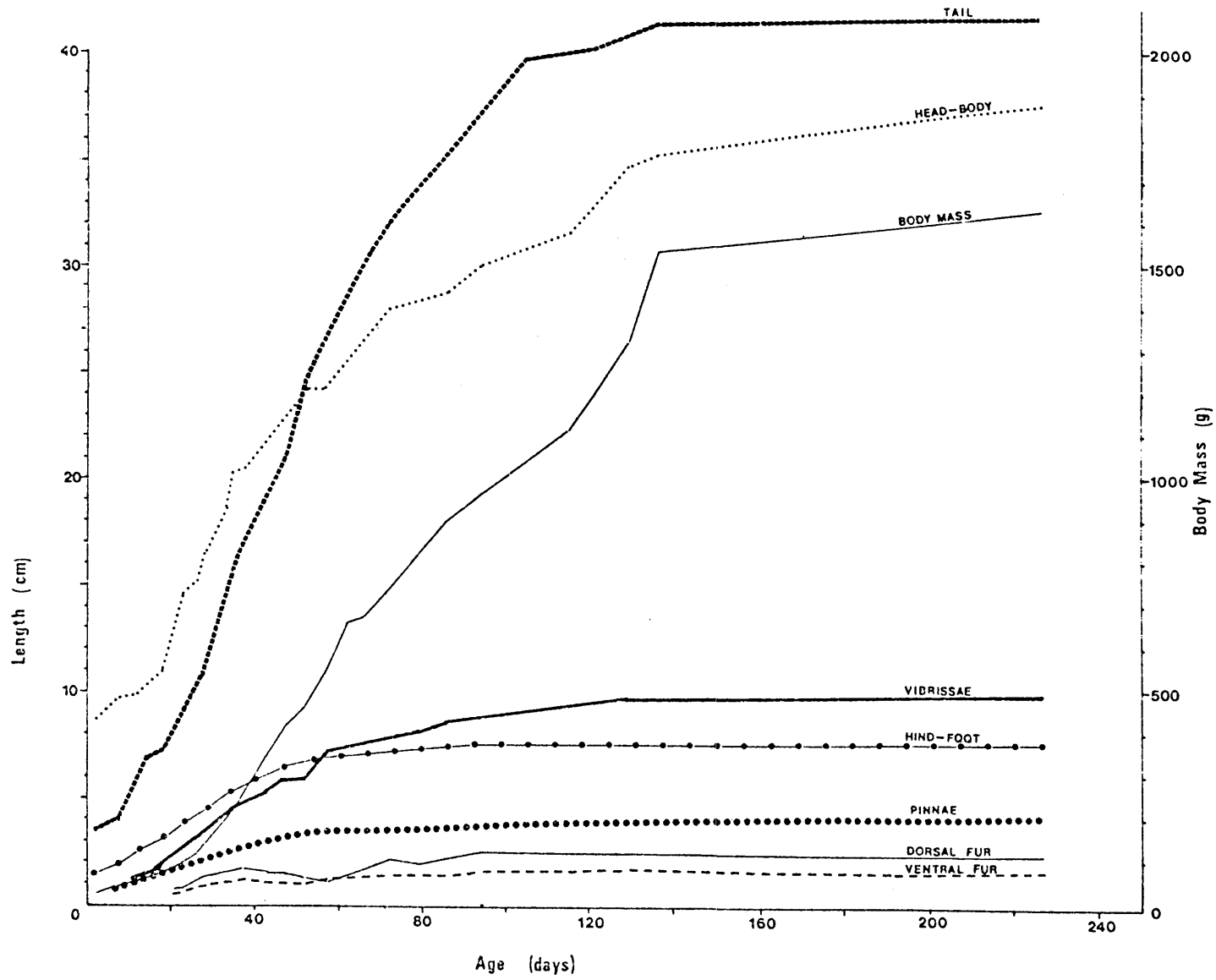
FIG. 12: Growth curves of giant rats. N = 6.
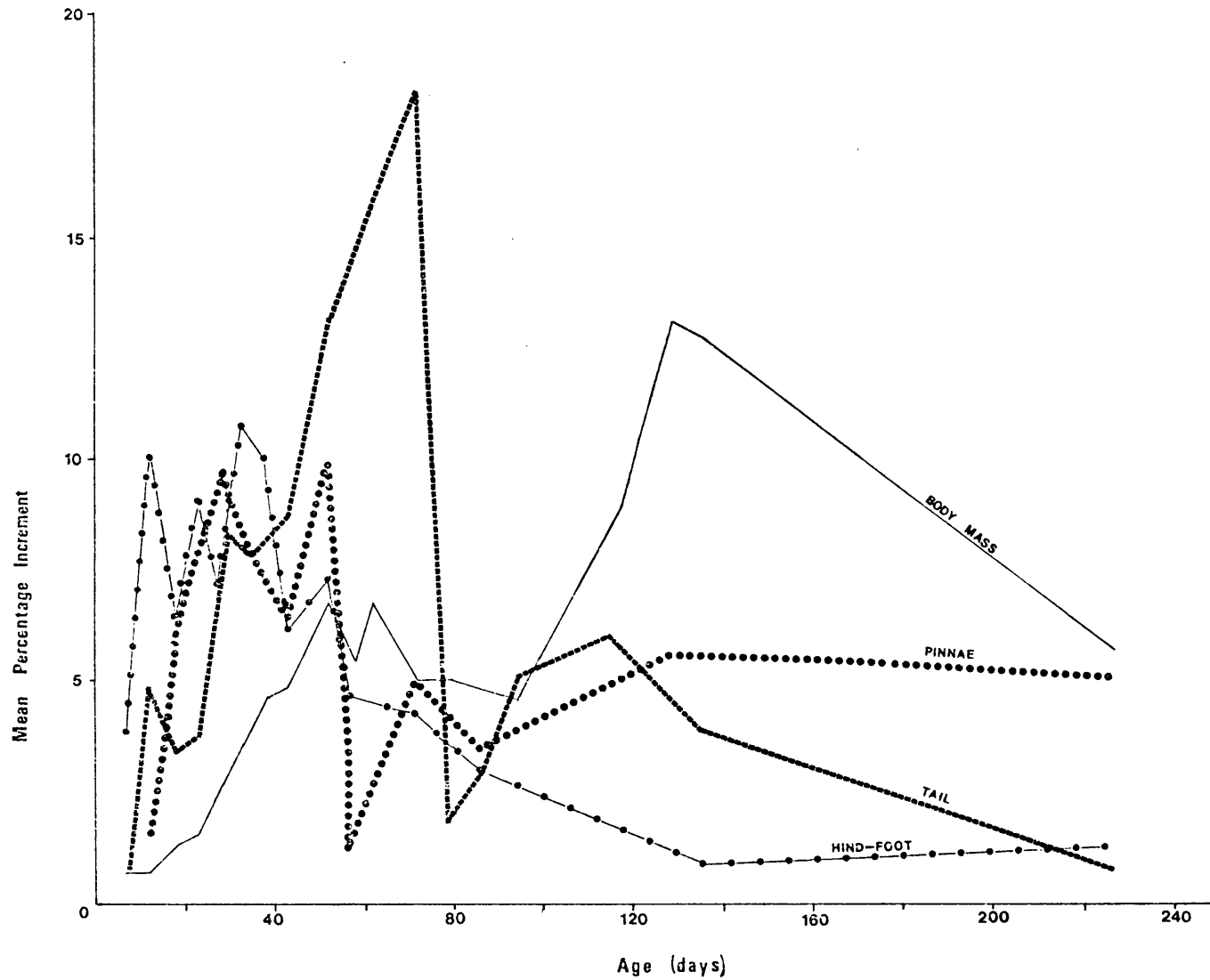
FIG. 13: Mean percentage growth increments of body mass, tail, hind foot and pinnae. N = 6.

After 86 days the increment dropped to the lowest of 0,80%, with it rising again to 7,50% after 129 days. They attained 92,47% of adult head body length after 136 days.

The tail at two days was 3,55 cm long, 8,39 % of adult length. It showed the greatest growth of all the linear measurements, having the highest percentage increment of 18,18% after 72 days at which stage it reached 32,18 cm, 72,09% of adult length (Fig. 12 & 13). However, during this rapid increase there were two declines in the growth rate, the first after 18 days and the second after 35 days. By 79 days the growth rate dropped to the lowest value of 1,82%, and again increased to an increment of 6,00% after 115 days, when the tail reached 93,83% of adult length.

At two days the hind foot was 1,50 cm long, 20,19% of adult length, and grew rapidly to reach adult length after 86 days (Fig. 12 & 13). The greatest percentage increment of 10,75% was found after 35 days, after which it declined reaching a low 0,90% after 136 days. The rate of growth prior to 33 days was characterized by two declines, one at 18 days and the other at 28 days of age.

Free pinnae were not present at birth, only becoming free after seven days and measuring 1,20 cm, 29,63% of adult length (Fig. 12).

The growth of the pinnae was also characterised by a rapid but fluctuating growth to reach $3,67 \pm 0,12$ cm (90.62% of adult length) after 86 days (Fig. 13). The highest percentage incre= ment of 9,83% was found at both 28 and 52 days. Declines in the growth rate were found after 43,57 and 86 days with low in= crements of 6,44%, 1,23% and 3,44% respectively (Fig. 12).

Giant rats are born with vibrissae and by 12 days reached a mean length of 1,2 cm. The vibrissae, reach 9,0 cm in length (91,09% of adult length) after 72 days (Fig. 12). At 38 and 79 days of age declines in growth rate were found with the increment dropping to 4,56% and 9,63% respectively (Fig. 14). Beyond 129 days the growth rate was found to decrease to a low 2,29% at 227 days.

The fur emerged 9 days after birth and at 23 days the ventral and dorsal fur were found to be $0,53 \pm 0,05$ and $0,73 \pm 0,12$ cm long respectively (Fig. 12). They both grew rapidly with the ventral and dorsal fur reaching $0,88 \pm 0,05$ cm (69,80% of adult length) and $1,18 \pm 0,96$ cm (69,01% of adult length), each with a growth rate of 12,12% and 17,71% respectively after 28 days (Fig. 14). At 38 days the ventral and dorsal fur were $1,25 \pm 0,06$ and $1,58 \pm 0,05$ cm long, but by 52 days they had both decreased in length to $1,03 \pm 0,15$ and 1,28 + 0,15 cm, showing negative growth rates of -16,67% and -8,42% respectively. Between 52 and 72 days they increased to $1,50 \pm 0,10$ (84,50% of adult length) and $2,20 \pm 0,16$ cm (85,70% of adult length) for the ventral and dorsal fur respectively. At 72 days the growth rates were found to be 8,24% for the ventral fur and 45,83% for the dorsal fur. The dorsal

52/.....
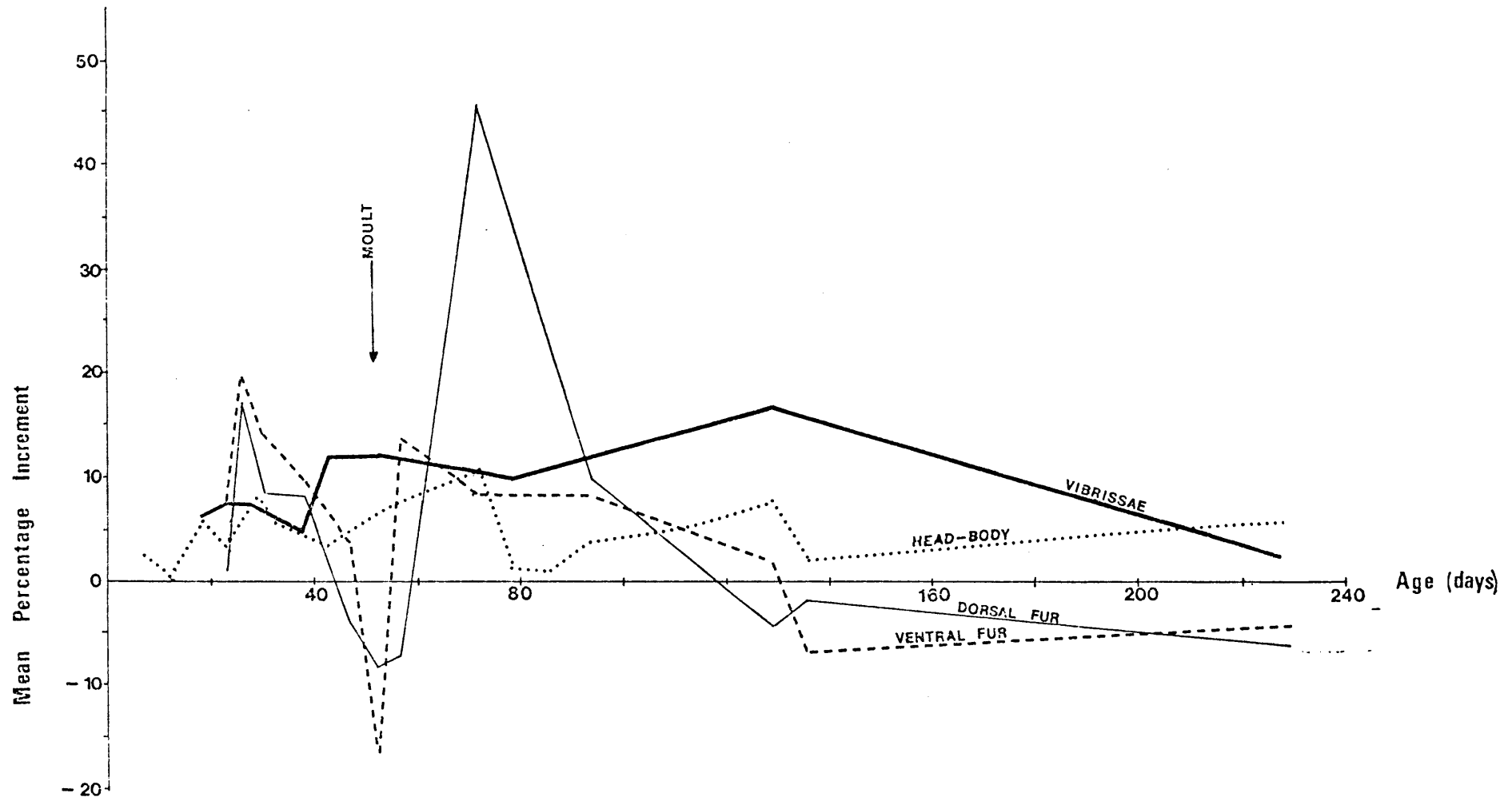
FIG. 14: Mean percentage growth increments of head-body, vibrissae and dorsal and ventral fur of giant rats. N = 6.

fur was at its longest, 2,57 $\pm$ 0,46 cm at 94 days, and decreased to 2,2 cm after 227 days, while the ventral fur reached its longest, 1,78 $\pm$ 0,26 cm after 129 days and also decreased to 1,53 $\pm$ 0,15 cm after 227 days. The decrease in the fur length would probably further continue to that found in adults, where the dorsal and ventral fur averaged 1,71 $\pm$ 0,16 (n = 15) and 1,26 $\pm$ 1,45 (n = 15) cm respectively.

DEVELOPMENT

The four major development periods in the giant rat are based on the Williams & Scott (1953) division of behaviour of neonatal mice, and are summarised in Figure 15.

Period 1 Neonatal: Birth To Nine Days

This period could be identified as one in which there was mainly physical development, with few behavioural patterns developing.

Physical Development

The newborn pups were atricial at birth, being dark pink dorsally and lighter ventrally and hairless except for small vibrissae. By day seven they became a darker pink, the digits separated and the pinnae became free, but remained relatively flat against the head. The tail of the pups was uniformly pink, with the tip being slightly darker in colour which later developed into the charac= teristic white tip (Plate 1). They did not react to sound during

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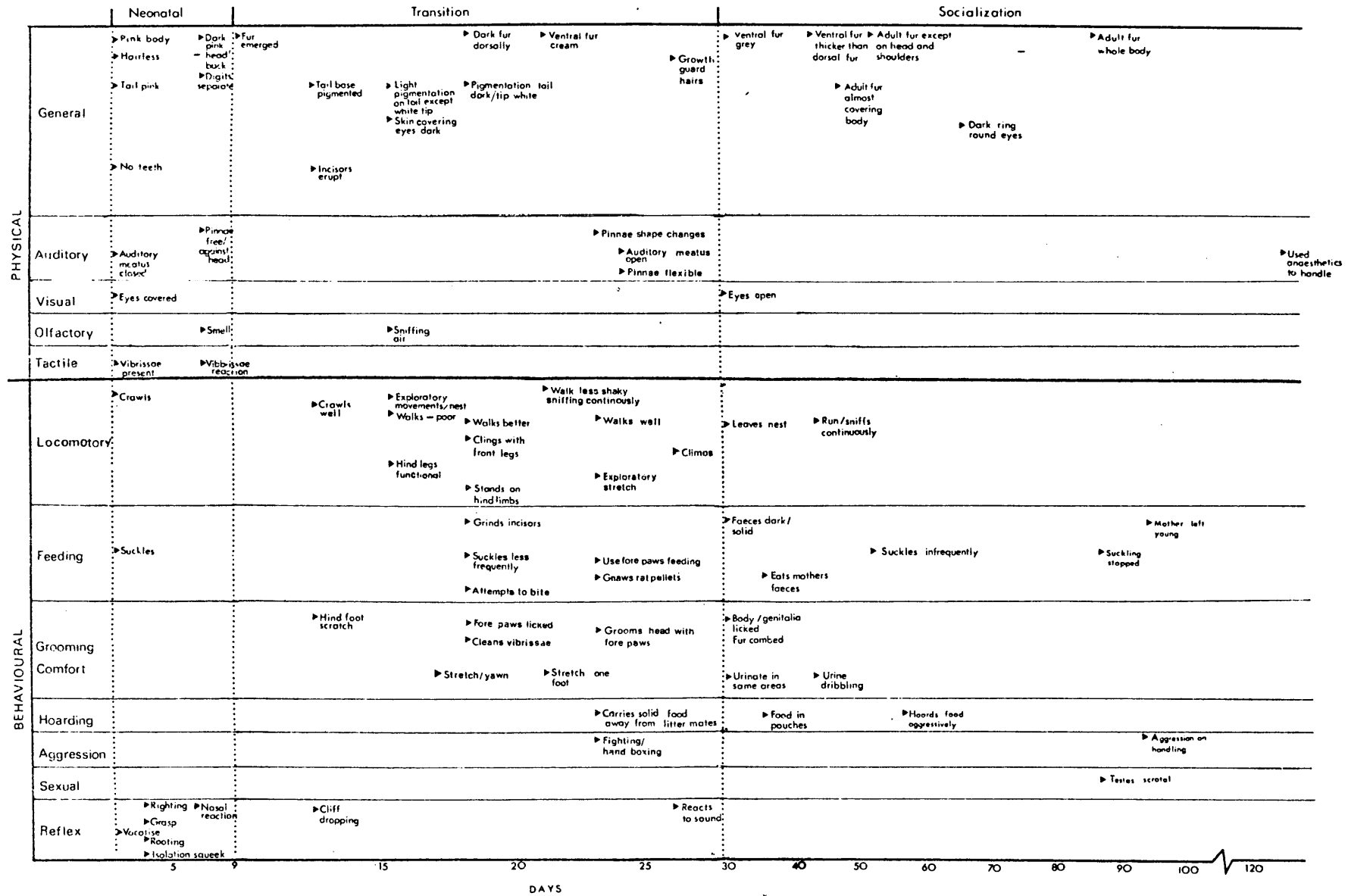
FIG. 15: The general development and development of reflex responses and behaviour patterns in young giant rats. N = 6.
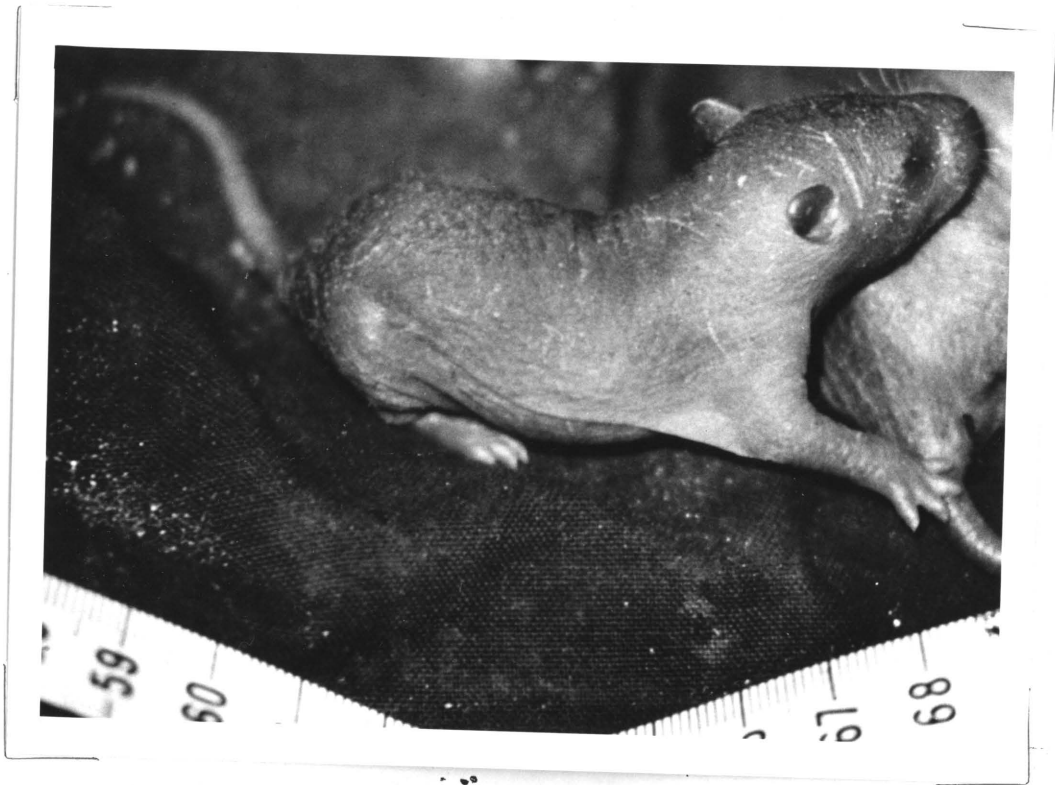
Plate 1 : Five day old giant rats.

Plate 2 : Twelve day old giant rat. Note
development of the fur and darkening
at the proximal end of the tail.

this first period, but by day seven reacted to smoke being blown in their faces.   By day nine the fur emerged.

Behavioural Development

From birth the pups could crawl, pulling themselves with their forelimbs.   Suckling began immediately after birth, using all pairs of nipples on different occasions.   By day two the righting, rooting and grasp flexures were evident, and by day seven the negative geotropic reflex and vibrissae reaction were also developed.   When the pups sniffed the vibrissae were always erected forward.   From birth they sometimes made high pitched squeeks when handled or left alone.

Period II.   Transition: From Six to   28 days.

This period was marked by changes in sensory and motor capacities resulting in the development of adult behaviour patterns.

Physical Development

The fur first appeared on day nine, being dark dorsally and cream coloured ventrally.   The skin covering the eyes became darker by day 15 and so did the tip of the pinnae.   On day 12 the base of the hairless tail became pigmented (Plate 2) and by day 15 the pigmentation had become slightly darker and spread to 2,2 cm from the tip, which still retained its pink colour (Plate 3).   By day 18 the pigmented part of the tail was darker

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Plate 3 : Fifteen day old giant rats. Note the
white tail tip and darkening and
the thickening of the fur.

Plate 4 : Eighteen day old giant rat. Beginning
to bite.

still making the non-pigmented tip more prominent (Plate 4). The incisors erupted on day 12.

Guard hairs appeared in the fur by day 26, but the fur still re= mained soft and fluffy. On day 23 the pinnae became more flexi= ble and began to take more of an adult shape but once the audi= tory meatus opened on day 24, the pinnae became very flexible, twitching in response to sound. The eyes opened on day 28.

Behavioural development

By 12 days crawling was good but still shaky. The hind legs became functional and a shaky walk was first observed on day 15. They were noted at the same time to move around more, stopping to sniff the air and when exploring a new area they stretched out, sniffing continuously, placing most of the body weight on the hind feet to enable them to react quickly. During this ex= ploring stretch their skin was noted to twitch more than usual.

Hind foot scratching was noted on day 12. The development of four-paws, licking, vibrissae cleaning, stretching and yawning and standing on their hind feet using their tails for support were all noticed to coincide with more coordinated walking on day 18. The stretching was performed while lying on their sides, hunching their backs and stretching out their legs and toes and yawning simultaneously. By day 22 the characteristic adult stretch was observed when they stood up, outstretched one front leg, arched their backs and yawned. About this period the incisor grinding

behaviour was noted and the pups attempted to bite littermates
and other articles (Plate 4). On day 23 they were seen gnawing
rat pellets but were still seen suckling frequently. This in=
creased incidence of biting and taking solid food also coincided
with fighting, hand boxing and the start of hoarding behaviour
on day 23. The hoarding behaviour consisted of the pups taking
solid food, and carrying it between their incisors away from
the other littermates. The first sign that they were eating
solid food was on day 28 when their faeces were black, instead
of light brown colour.

The cliff dropping reflex developed later than the other reflexes
being noticed on day 12. Reaction to sound was observed once
the auditory meatus had ruptured.

Period III. Socialization: From 28 to 86 Days.

The most marked change occurring during this period was the opening
of the eyes at the beginning and weaning at the end.

Physical Development

The eyes opened on day 28 (Plate 5). The ventral fur turned
grey on day 30 and the development of adult fur began on the
ventral surface on day 43. At that stage it was thicker than
the fluffy dorsal fur and moved round to cover the dorsum
apart from the head and shoulders by day 52. This patch of
juvenile fur decreased in size to a small patch between the

60/.....

Plate 5 : Twenty eight day old giant rat. Note the opened eyes and thin dorsal fur, and large, flexible pinnae.

pinnae by day 72 and finally disappeared after day 86. The characteristic dark rings around the eyes of giant rats, de= veloped in the pups by day 66.

Behavioural Development

Once the eyes opened the pups began to leave the nest (Plate 5) and were seen to run by day 43. Suckling decreased throughout this period finally ending on day 86, with only the inguinal nipples latterly being suckled. Urine dripping was observed on day 43. With eating more solid food, hoarding was noted more frequently with the pups stuffing their cheek pouches on day 35, and on day 55 aggression was noted with hoarding where one littermate tried to steal food from another.

Period IV   Juvenile: From 86 to 129 Days

This period covers the time from weaning to sexual maturity and the attainment of adult size.

Physical and Behavioural Development

The pups reached adult size in 129 days. Sexual maturity was not determined. On day 94, after suckling had ceased the mother left the pups. During this period the pups became more aggres= sive to handling and aneaesthetics were used in order to record their body measurements.

ADULT BODY MEASUREMENTS

The tail, white tail tip, hind foot, neck and girdle lengths of adult male giant rats were significantly greater than those of adult females (Table 8). While the head body, pinnae and body masses did not differ between the sexes.

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Table 8   Body measurements of adult male and female giant rats.

Parameter	MALES (cm ± SD)	n	FEMALES (cm ± SD)	n	Test	P
HB	38,23 ± 5,18	12	36,33 ± 3,95	7	t = 0,84	>0,05
T	42,29 ± 1,91	12	40,28 ± 2,43	7	t = 2,01	<0,05
Wh	18,06 ± 1,52	12	16,13 ± 1,50	7	t = 2,68	<0,01
HF	7,43 ± 0,34	12	7,14 ± 0,27	7	t = 1,92	<0,05
P	4,05 ± 0,12	12	4,03 ± 0,16	7	t = 0,31	>0,05
Ne	15,89 ± 1,33	12	14,29 ± 1,07	7	t = 2,70	<0,01
G	23,86 ± 1,73	12	21,30 ± 1,51	7	t = 3,25	<0,01
DF	1,69 ± 0,17	4	1,80	1		
VF	1,23 ± 0,11	4	1,40	1		
V	9,95 ± 1,25	4	9,53	1		
Mass (g)	1475,00 ± 174,80	12	1324,36 ± 245,49	7	t = 1,56	> 0,05

HB = head body; T = tail; Wh = white tail tip; HF = hind foot; P = pinnae; Ne = neck; G = girdle; DF = dorsal fur; VF = ventral fur; V = Vibrissae.

DISCUSSION

Growth and development recorded in the present study were similar to those reported by Ewer (1967) and Ajayi (1975), except for the fact the Ewer (1967) noted an earlier weaning age of 18 days (Table 9).

Comparing the birth and weaning weights and growth rates of giant rats with that predicted by the formulae developed by Millar (1977), giant rats showed in all cases values less than those predicted (Table 9). The birth and weaning weights and growth rates of the lumped data from the three giant rat studies were 30,50%, 38,61% and 29,86% respectively less than those predicted from body weight and well outside the 95% confidence limits of the curves. These low values could be a result of many inter= related factors such as burrowing habits, genetic influences, diet, predation, litter sizes and foraging 'strategies', as Case (1978) and Millar (1977) suggested.

Since giant rats live within burrows that provide protection and a stable insular environment, it is to be expected that they would have altricial young because long pregnancies resulting in heavier precocial neonates would handicap the mother and could influence her ability to escape and chances of being preyed upon. Increased growth rates should also be expected as has been found in other altricial young rodents, as McClure & Randolph (1980) found in Neotoma. They suggested that during the early growth stages when the young lacked insulation and were virtually eco= thermic, energy was directed into growth and not wasted in thermo=

Table 9   Growth data of giant rats according to Ewer (1967), Ajayi (1975 a)

and present study.

	Present study	Ajayi	Ewer	Predicted values
Number of litters	2	17	9	
Adult mass (g)	1324,38 $\pm$ 245,5	1000,0		
Birth mass (g)		22,38	33,40	[a]32,94
Weaning mass (g)	140,40 $\pm$ 7,0	120,91 $\pm$ 34,0	99,40 $\pm$ 7,8	[b]195,84
Age to weaning (days)	28	26	18	
Litter size	3	3,06 $\pm$ 1,2	2,56 $\pm$ 1,0	
Birth mass/ Adult mass		0,02	0,02	
Weaning mass/ Adult mass	0,10	0,10	0,07	
*Growth rate (9/day)		3,79	4,22	[c]5,71

* Growth rate = (Weaning mass - birth mass)/days to weaning.

a = Birth mass (g) = 0,20 $M^{0,71}$ (Millar 1977)

b = Weaning mass (g) = 1,03 $M^{0,73}$ (Millar 1977)

c = Growth rate (g/day) = 0,04 $M^{0,69}$ (Millar 1977)

M = adult mass

regulation. Why therefore do giant rats have low growth rates?
It could be the result of first, some energetic trade-off between
the mother and young (i.e. decreased demands by the young means less
foraging by the mother, so reducing her chances of predation and
increasing the chances of survival of the young). Second a poor
conversion of assimilated energy into production in the young as
Randolph, Randolph, Mattingly & Foster (1977) found in the voles,
Microtus arvalis and Clethrionomys glareolus or third, a result
of a lower than predicted birth weight as suggested by Case (1978).
Giving birth to smaller young is associated with larger litters
(Case 1978).

The smaller weaning weights than predicted and similar weaning
age to that found in other cricetid rodents (Meester & Hallet 1970;
Millar 1977; Scott 1979) means less energy spent in lactation by
the mother. But mothers probably compensate for this low wean=
ing mass by giving extended maternal care after weaning, because
it was noted by Ewer (1967) and in the present study, that the
young remained with the mother until about 95 days of age. In
the field young giant rats were infrequently captured, with the
smallest ones weighing 670 and 990 g, approximately 60 and 98 days
old respectively. Possibly the need to feed young solid foods
for extended periods after weaning was one of the selective fac=
tors in the development of hoarding behaviour in the giant rat.

Therefore the low birth weights, growth rate and weaning weights
appear to be a mechanism to reduce the energetic cost of raising

the young prior to weaning but the mother has to compensate with the burden of post weaning maternal care. Difficulty arises in defining when weaning takes place because it is more of a gradual process rather than a specific day and was based on the taking of solid food and appearance of solid food traces in the faeces (Layne 1968). Giant rat pups were observed to handle solid food at 23 days but remains were only detected in the faeces at 28 days. Suckling was noted to cease after 86 days, thus indi= cating that weaning in giant rats appears to be a long process. However, day 28 has been used as the weaning date for compara= tive purposes, and if it was longer, the growth rate would be even that much smaller.

The pinnae, tail, hindfoot and vibrissae all grew rapidly reaching greater than 90% of adult lengths by about 86 days. The pre= sence of vibrissae at birth and quick attainment of adult length indicates their importance to giant rats in sensing their environ= ment. Even adult giant rats seem to make more use of their olfaction, hearing and vibrissae rather than eyesight in sensing their environment. The early development of the hindfoot and tail are indicative of their importance in locomotion and balan= ce for climbing (Ewer 1967). Since the smallest giant rats caught in the field were between 64 and 99 days old, as mentioned previously, young giant rats leaving the burrow will probably have hind foot, pinnae, tail and vibrissae all approximating adult lengths to enhance their chances of survival.

The behavioural development of giant rats was relatively slow,

comparable to that found in other altricial young such as <u>Mys=</u>
<u>tromys albicaudatus</u>, <u>Tatera</u> <u>brantsi</u> (Meester & Mallett 1970),
<u>T. leucogaster</u> (Scott 1979) and <u>Malacothrix typica</u> (Knight &
Skinner 1980). Altricial species have no hair, closed pinnae,
sealed auditory meatus, fused toes and no incisors at birth
(Scott 1979). Characteristically, all the above species have
burrowing habits, while <u>Otomys irroratus</u> (Scott 1979) and
<u>Thamnomys dolichurus</u> (Panagis & Nel 1981) both live above ground
level, the former being entirely terrestrial and the latter
arboreal and they both have precocial young. Therefore, the
late development of physical phenomena such as opening of eyes
and auditory meatus and behavioural characteristics such as
walking, grooming and some of the reflexes are probably due to
the influence of the protected burrow environment.

The development of fur in young rodents is usually associated
with the onset of thermoregulation (McManus 1979; Maxwell & Morton
1975). The fur of giant rats appears after 9 days and only
develops adult characteristics of rough, bristly fur by day 86.
The moult of the pups fluffy fur takes place after 50 days (Fig.
20), beginning on the ventral surface, moving round to the dor=
sum. Delayed development of thermoregulation of the young
would be energetically important for the mother because once
thermoregulation commences, energy demands of the young increase.
Therefore, by delaying the development of thermoregulation, the
young can direct more energy into growth and less into thermo=
regulation. However, lactation is energetically more demanding
than pregnancy (Randolph <u>et al</u> 1979) therefore introducing young
giant rats to solid food at low weaning masses would decrease

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the demand posed by lactation and the energy burden on the mother.

The large decline in the percentage growth increments of hind= foot, vibrissae and ventral and dorsal fur around days 20 and 43 were probably associated with the introduction to solid food and reduction in lactation respectively. While the sharp incremental declines witnessed in the growth of the tail, head and body, pinnae and dorsal fur from day 72 to 86 were probably caused by the termination of suckling. These sharp declines in the growth increments may also be a result of the small sample size.

In conclusion further study in the development of thermoregu= lation in the young of giant rats and the cost of reproduction should be undertaken in order to determine the type of develop= mental 'strategy' employed by giant rats.

Concerning the physical stature of adult giant rats, there appears to be no variation throughout their distributional range as the standard body measurement of giant rats collected in the Soutpans= berg mountains were similar to those recorded for animals trapped in West Africa (Ewer 1967, Ajayi 1975 a).

CHAPTER 6

DIGESTION

RESULTS

DIGESTIBILITY TRIALS

No significant differenceswere found for the digestible energy and metabolizable energy of giant rats acclimated to 10°C and 24°C (Table 10). The $0,68 \pm 0,03$ kJ $(g.h)^{-1}$ intake of giant rats acclimated to 10°C was significantly greater that the $0,44 \pm 0,02$ kJ $(g.h.)^{-1}$ intake of those acclimated to 24°C. Even though the body masses were not significantly different the mean metabolizable energy for giant rats acclimated to 24°C was corrected for a change in body mass to $0,47$ kJ $(g.24\ h)^{-1}$, 17,5% below the $0,57$ kJ $(g.24h.)^{-1}$ found for those animals acclimated to 10°C.

The apparent digestibilities for the 10 and 24°C acclimated giant rats were similar, being 89,3% and 89,5% respectively (Table 10). The urine production for the two groups were not significantly different, being 5,3% and 4,3% of the metabolizable energy for the giant rats acclimated to 10°C and 24°C respectively.

The faeces of 10°C acclimated giant rats contained 52,23% moisture (an average of $6,03 \pm 1,84$ g (n = 34) of water in an average

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Table 10   Intake, digestible energy (DE) and metabolizable energy (ME) of five giant rats accli= mated to 10°C and 24°C.   Mean $\pm$ standard deviation; NS: not significant; *: signifi= cantly different at P<0,05.

	Acclimated to 10°C	Acclimated to 24°C	Signifi= cance	Test	P
Mean body mass (W_b) (g)	1694,00 $\pm$ 201,57	1911,00 $\pm$ 206,71	NS	t = 0,31	>0,05
Intake g(24h)$^{-1}$	51,42 $\pm$ 6,76	37,26 $\pm$ 4,37	NS	t = 1,59	>0,05
kJ(24h)$^{-1}$	1150,34 $\pm$ 150,62	830,57 $\pm$ 97,50	NS	t = 1,57	>0,05
kJ(g.24h)$^{-1}$	0,68 $\pm$ 0,03	0,44 $\pm$ 0,03	*	t = 2,38	<0,05
Faeces g(24h)$^{-1}$	5,60 $\pm$ 0,77	3,81 $\pm$ 0,59	NS	t = 1,65	>0,05
kJ(24h)$^{-1}$	114,08 $\pm$ 14,60	87,35 $\pm$ 12,99	NS	t = 1,22	>0,05
kJ(g.24h)$^{-1}$	0,06 $\pm$ 0,00	0,05 $\pm$ 0,00	*	t = 3,27	<0,01
Apparent digestibility (%)	89,32	89,52			
Digestible energy (DE) kJ(24h)$^{-1}$	1118,11 $\pm$ 445,68	857,20 $\pm$ 184,65	NS	t = 0,24	>0,05
kJ(g.24h)$^{-1}$	0,65 $\pm$ 0,24	0,45 $\pm$ 0,09	NS	t = 0,73	>0,05
Urine ml(24h)$^{-1}$	74,09 $\pm$ 18,05	45,54 $\pm$ 18,93	NS	t = 1,17	>0,05
kJ(24h)$^{-1}$	73,29 $\pm$ 43,23	32,01 $\pm$ 9,31	NS	t = 0,75	>0,05
kJ(g.24h)$^{-1}$	0,03 $\pm$ 0,01	0,02 $\pm$ 0,00	NS	t = 0,35	>0,05
Metabolizable energy (ME) kJ(24h)$^{-1}$	961,16 $\pm$ 227,82	824,85 $\pm$ 177,85	NS	t = 0,12	>0,05
kJ(g.24h)$^{-1}$	0,57 $\pm$ 0,11	0,43 $\pm$ 0,09	NS	t = 0,29	>0,05
Corrected ME kJ(g.24h)$^{-1}$		0,47			
kJ(g.24h)$^{-1}$	0,02 $\pm$ 0,01	0,02 $\pm$ 0,00	NS	t = 0,20	>0,05
≠Predicted ADMR kJ(g.24h)$^{-1}$	0,23	0,22			
% Difference to ME	247,83	213,64			

≠ ADMR   kJ(g.24h)$^{-1}$ = 9,617 $W^{-0,5}$ (Grodzinski 1975)

faecal wet mass of 11,55 $\pm$ 2,87 g (n = 34)) being significantly

greater than the 25,95% moisture (an average of 1,24 $\pm$ 0,77 g

(n = 30) of water in an average faecal wet mass of 4,78 $\pm$ 1,55 g

(n = 30)) content of those acclimated to 24°C.

RATE OF PASSAGE

The mean 5%, 80% and 95% occurrence of plastic particles was found

to be 30, 141 and 205 h respectively after feeding (Fig 16).

The first (transit time) and last appearance of plastic pieces

were 27,8 $\pm$ 9,70 h and 217,50 $\pm$ 41,57 h respectively.   The peak

time (maximal faecal marker concentration) was found to be 57,5

h after feeding (Fig. 17), with the 80 - 5 h retention time

being 111 h (difference in time between 5 - 80% of marker (Balch

& Campling 1965)).   Two smaller peaks also occurred after 157,50

and 205,50 h.

With brilliant blue dye used as a marker, the mean first appearance

was recorded after 38,2 $\pm$ 11,2 h and was not significantly

different (U = 4,50; P>0,05) to that found with plastic pieces,

while the mean last appearance of 78,8 $\pm$ 5,77 h was significant=

ly (U = 0,08; P<0,05) shorter than that with the plastic pieces.

DIGESTIVE SYSTEM AND MORPHOLOGY

Macroscopic Morphology

The oesophagus enters the stomach in the non-glandular corpus

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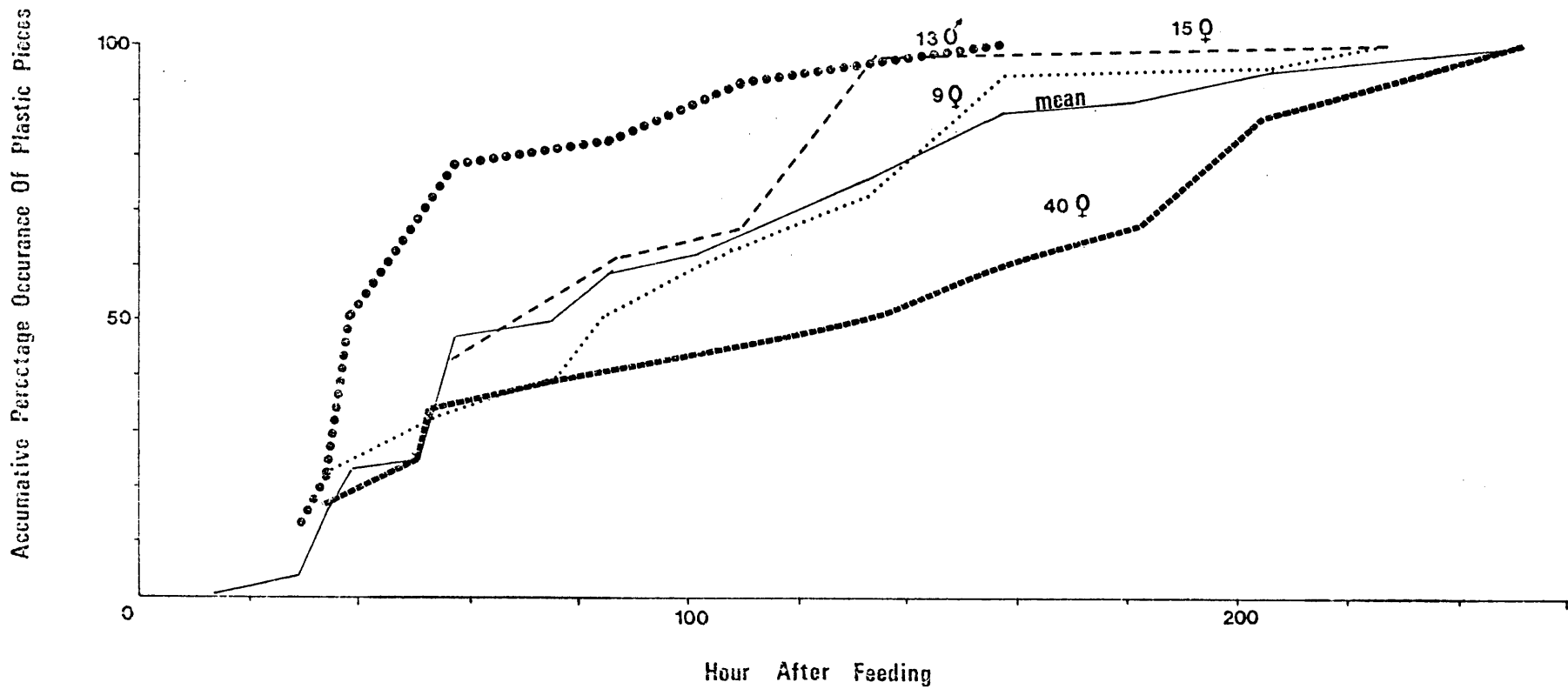
FIG. 16: Mean and individual passage times (h) of digesta marked with plastic pieces.
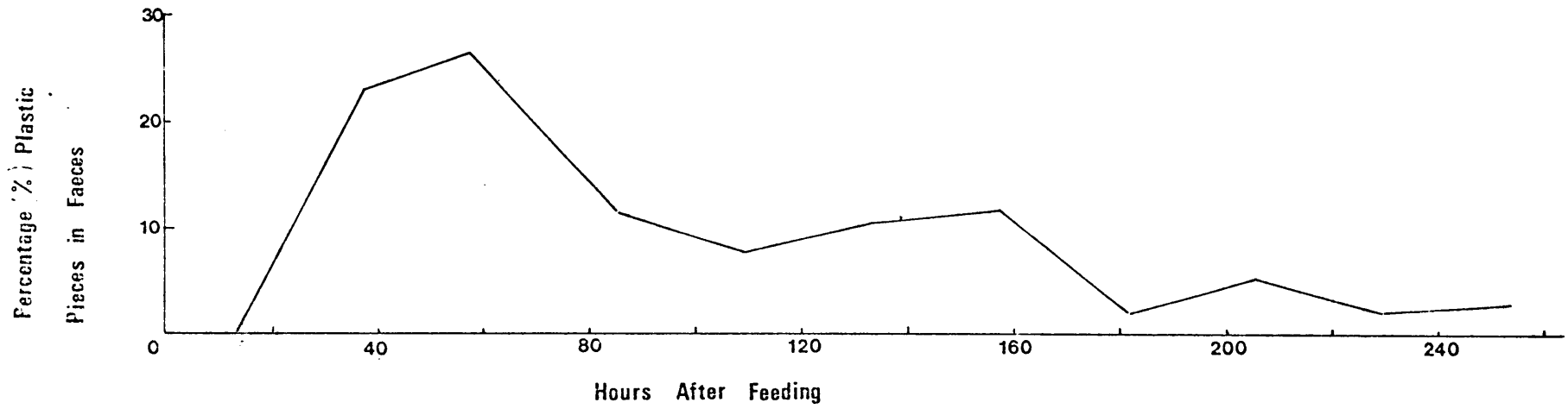
FIG. 17: Percentage occurrence of plastic pieces after feeding.

region (Fig. 18 and 19). The papillae covered corpus and fornix ventricularis was $7,80 \pm 0,12$ cm long and $3,95 \pm 0,98$ cm wide (n = 12) while the glandular antrum was smaller, being $4,70 \pm 0,15$ cm long and $3,94 \pm 0,54$ cm wide (n = 12). The stomach can be described as a unilocular hemiglandular stomach as it has a shallow angularis and wide channel $(1,67 \pm 0,75$ cm; (n = 12)). linking the non glandular and glandular regions (Fig. 19). The corpus, fornix ventricularis and oesophageal groove were found covered in stratified epithelium while the antrum was covered in glandular epithelium. The surface area of the corpus and fornix ventricularis $((62,50 \pm 7,40$ mm^2 (n = 12)) was significant= ly greater (t = 8,19; P<0,01) than that found for the antrum $((37,50 \pm 7,49$ mm^2); n = 12)) and the mean ratio between the two being $1,76 \pm 0,55$.

The small intestine was $101,09 \pm 49,00$ cm long and $0,87 \pm 0,45$ cm wide and led into a caecum $18,12 \pm 4,95$ cm long and $3,14 \pm 2,49$ cm wide (Table 11). The caecum had a varying number of sacculations $(16,8 \pm 11,2)$. The overall length of the colon was $63,24 \pm 5,60$ cm and it was 0,8 cm wide. Two colonic loops were noted, one immediately after leaving the caecum and the other halfway along the colon (Fig 18) and measured $11,60 \pm 3,01$ (n = 9) and $19,88 \pm 4,98$ cm (n = 12) long respectively. The mean lengths of the gut sections all differed significantly (t - test, P<0,01), with the small intestine, colon, colonic spirals and caecum com= prising 51,34%, 21,61%, 11,35% and 9,82% respectively of the total gut length (excluding stomach) (Table 11). Giant rats were also found to have an average of $6,33 \pm 1,11$ liver lobes and gall

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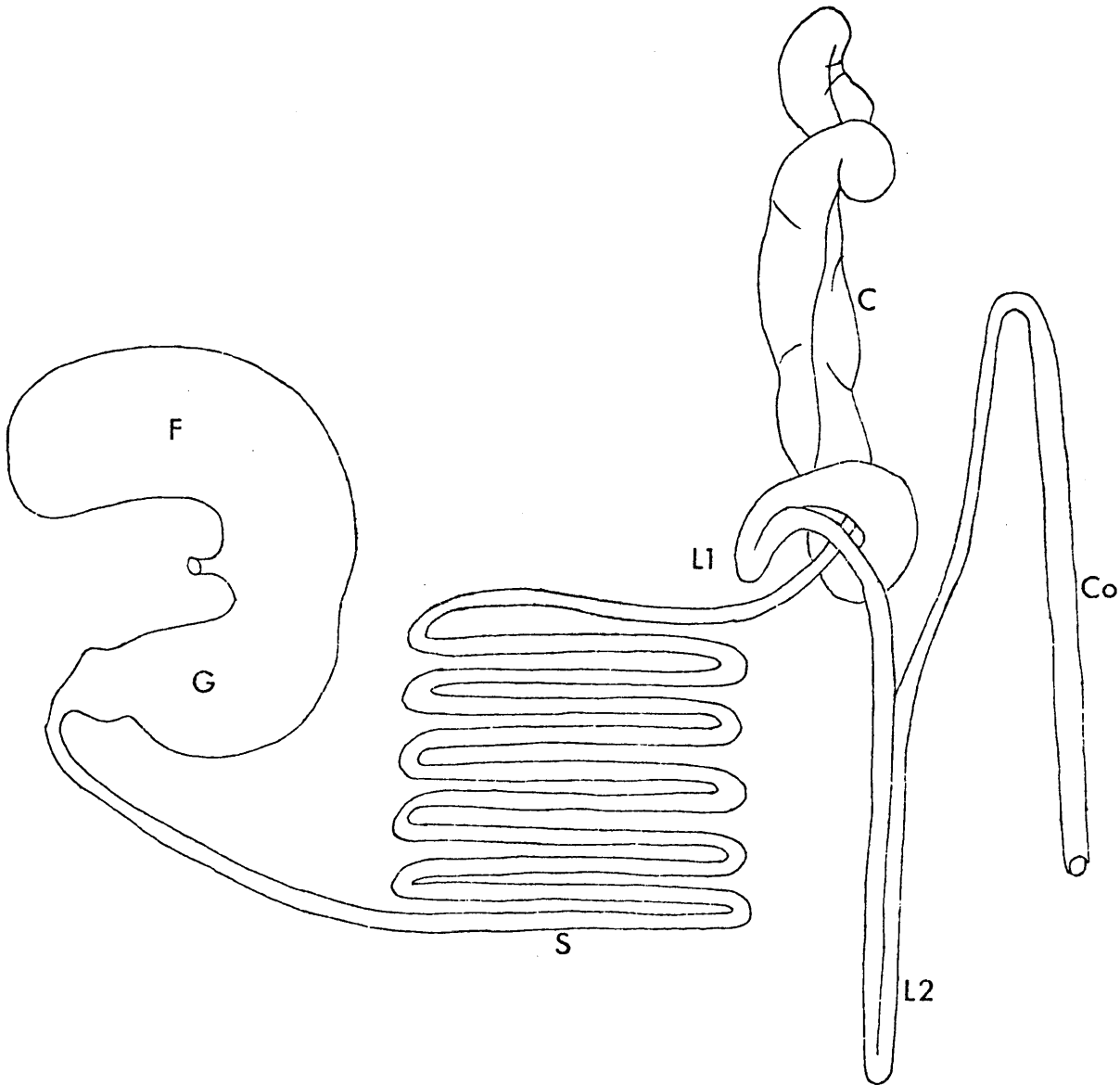
Fig. 18:   Schematic drawing of the gastrointestinal
           tract of the giant rat, extended to show
           continuity.   G = glandular stomach;
           F = forestomach;   S = small intestine;
           C = caecum;   L1 = 1st colonic loop; L2 =
           2nd colonic loop; Co = colon.
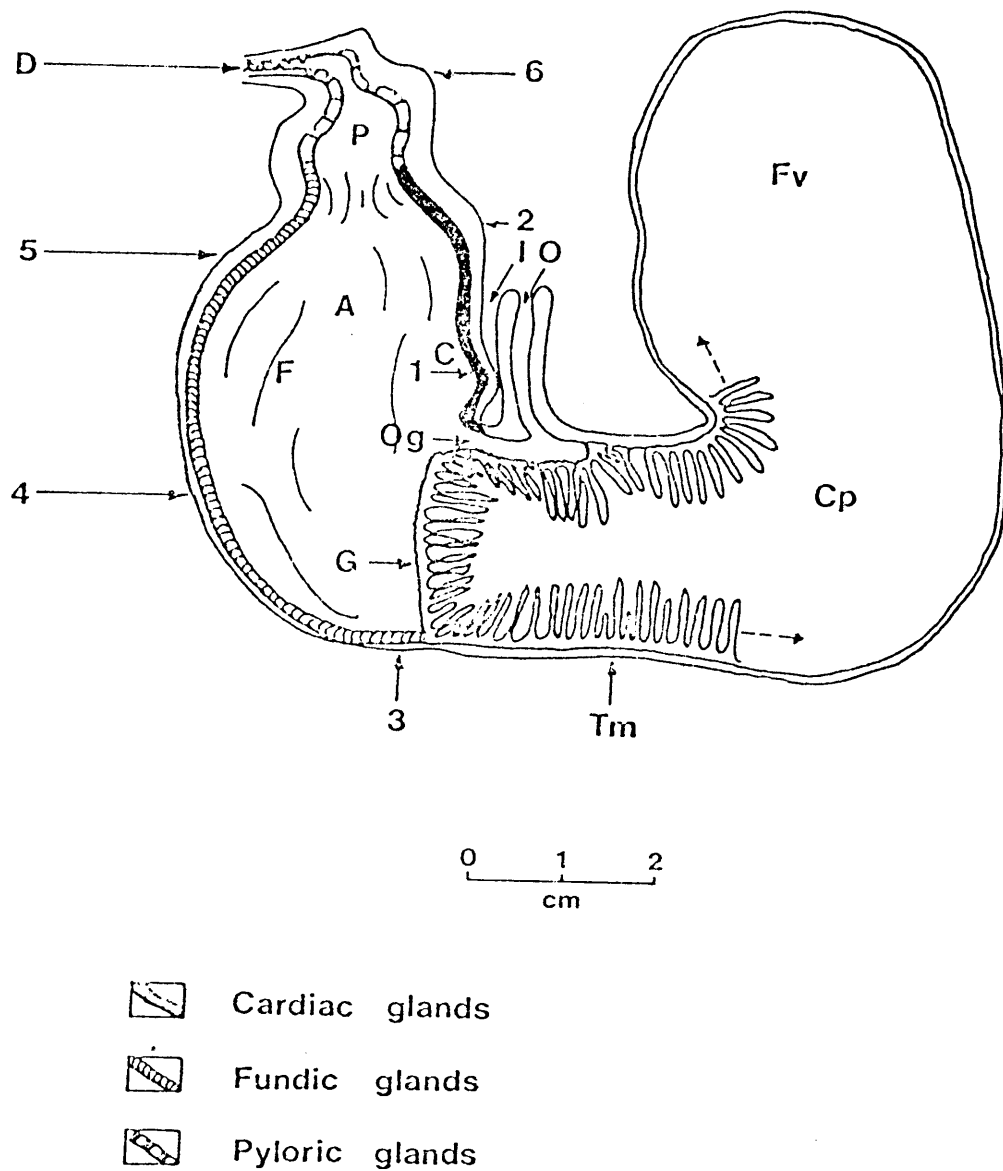
Fig. 19: Schematic drawing of the bisected stomach
          of the giant rat.   A = antrum; C = cardiac
          region; Cp = corpus; D = duodenum; F =
          fundic region; Fv = fornix ventricularis;
          G = grenzfalte;   I = incisaura angularis;
          O = oesophagus; Og = oesophageal grove;
          P = pylorus;   Tm = Tunica muscularis.
          Numbers correspond to those in Table 13.
          (Adapted from Kokkin 1981).

Table 11.   Mean gut lengths in giant rats. N = 15. Mean $\pm$ standard deviation .   Mean body
            mass = 1534,56 $\pm$ 357,49 g.

	Hindgut section lengths (cm)	Relative length of gut sections as % of total hind gut length	Head-body (cm)	Ratio of hind= gut to head- body length	Ratio of small intestine to large intestine length
			38,51 $\pm$ 3,81	1,30	1, 21
Small intestine	101,09 $\pm$ 49,79[a]	51,34			
Caecum	18,12 $\pm$ 4,95[a]	9,82			
Spirals	23,20 $\pm$ 3,31[a]	11,35			
Colon	39,84 $\pm$ 7,89[a]	21,61			

Values with like superfixes in columns differ significantly using Student-t test, P<0,01

bladders were present.

The caecum was divided into two sections, first the ampulla ceci into which the ileum entered and from which the proximal colon emerged and second, the larger corpus ceci which terminates in the blind sac, the apex ceci (Fig. 20). A narrow extension of the mesentery to the jejenoileum and colon runs along the corpus ceci forming two clockwise flexures in the corpus ceci.

The internal structure of the caecum revealed that the ileum enters the ampulla in the centre of the first flexure of the corpus (Fig. 21). The ileo-caecal orifice is much smaller in comparison to the diameter of the ileum. A fold extends from the top of the ileo-caecal orifice in a slightly spiral course for about two-thirds of the circumference of the ampulla. The ampulla is only separated from the corpus ceci by a very low fold extending through half of the circumference of the ampulla. In the proximal colon obliquely running folds (plicae oblique) were found.

The maximum volumes of the stomach, small intestine and large intestine did not differ significantly (t - test; $P < 0,05$). How= ever, the large intestine had the largest maximum volume being 47,08% (80,05 ml) of the total volume, followed by the stomach 30,50% (68,00 ml) and the small intestine with 30,28% (56,50 ml) (Table 12). Of the individual gut sections the small intestine had the largest maximum volumes but only differed significantly
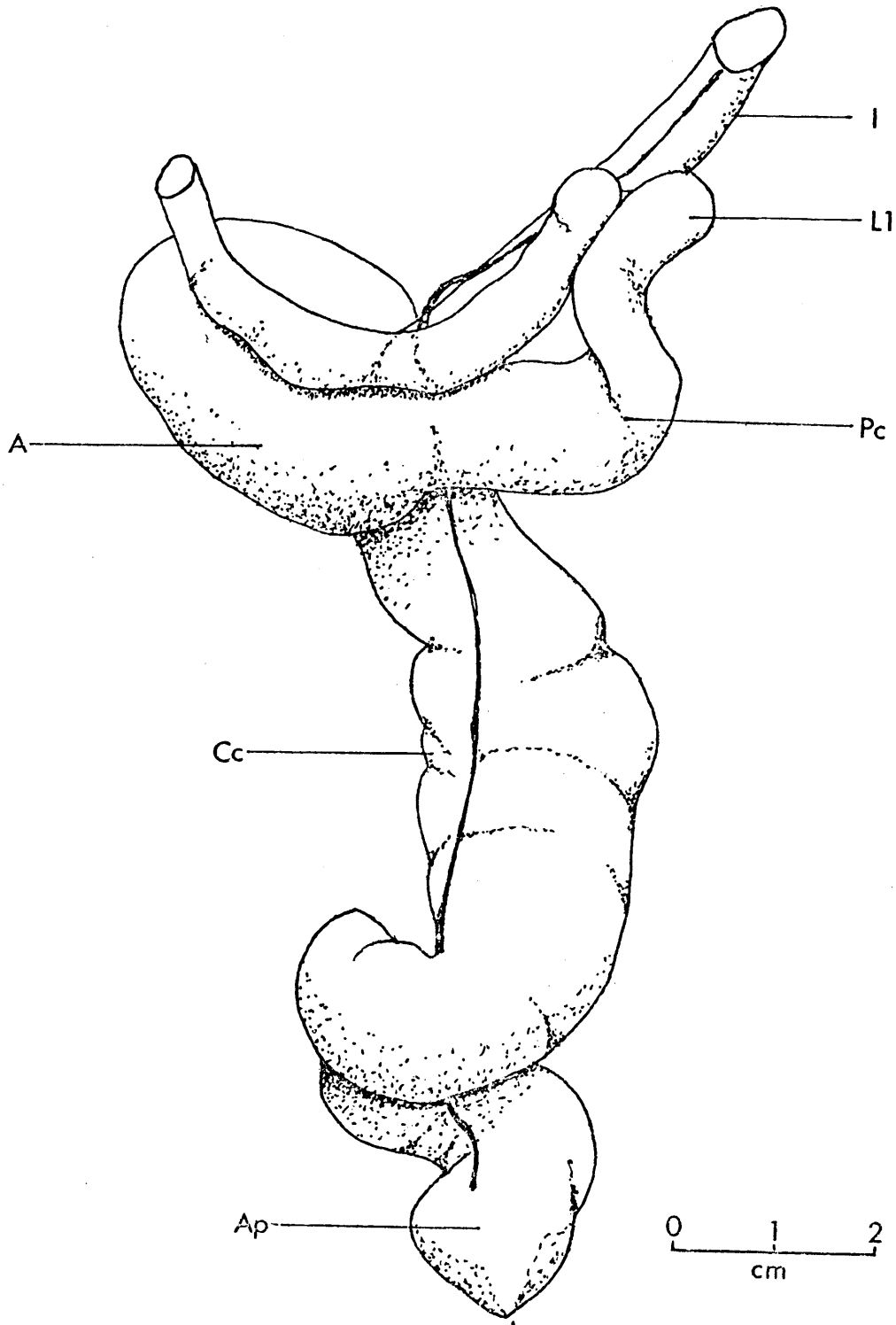
Fig. 20: Caecum of giant rats. A = ampulla ceci;
Ap = apex ceci; Cc = corpus ceci; I =
ileum; Ll = 1st colonic loop; Pc =
proximal colon.
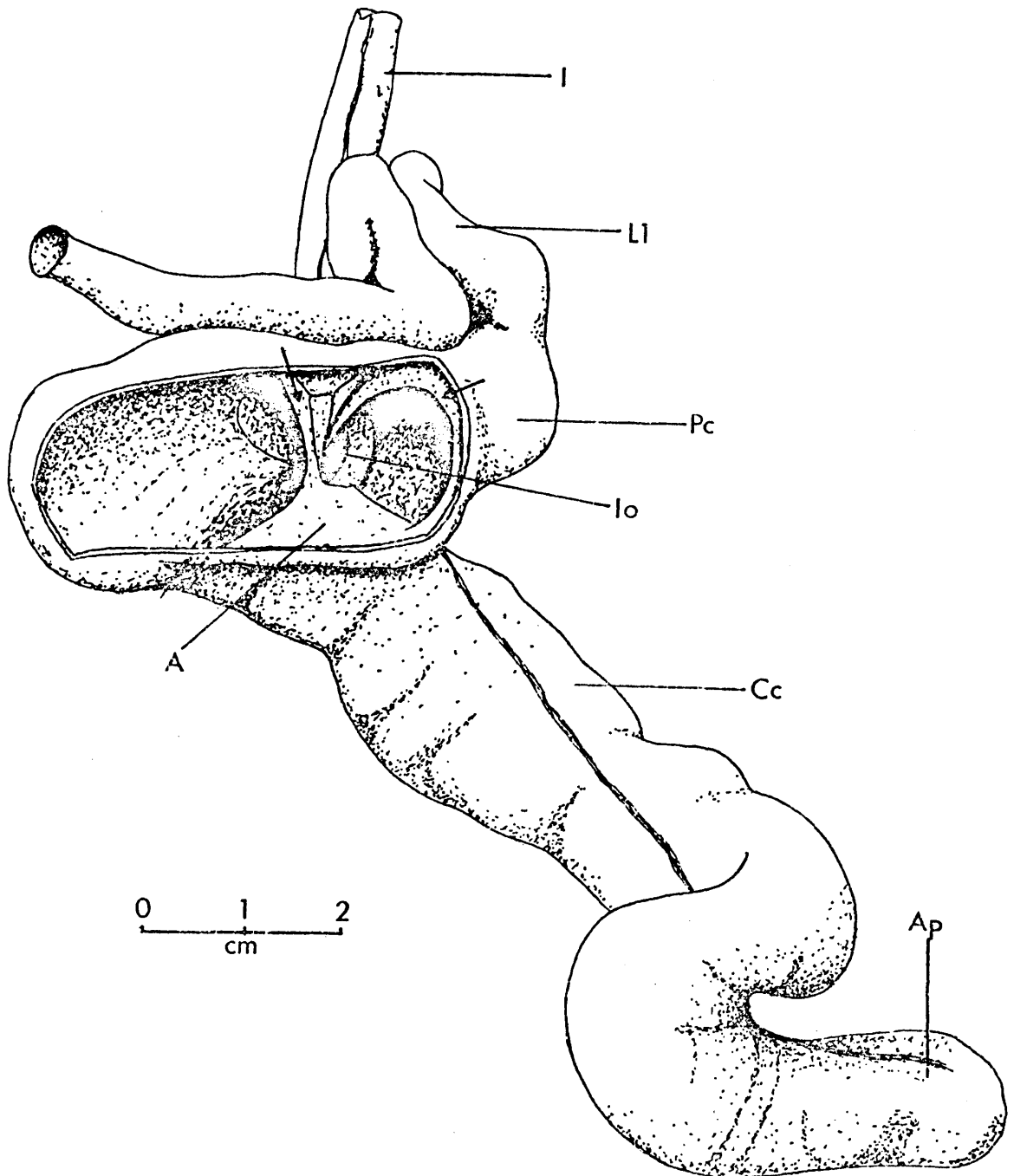
FIG. 21: Internal macroscopic structure of the caecum of giant
rats. A = ampulla ceci; Ap = apex ceci; Cc =
corpus ceci; I = ileum; Io = ileocaecal orifice;
Ll = 1st colonic loop; Pc = proximal colon; arrow =
folds.

Table 12   Maximum gut section volumes ($\pm$ standard deviations) and ratio of stratified to squamous glandular tissue of giant rats . N = 5

	Maximum volumes of stomach and hind gut sections (ml)	Relative maximum volumes as % of total gut volume	Ratio of stratified squamous to glandular tissue in stomach
Corpus and Fornix ventriculus	46,00 $\pm$ 17,70	21,50	1,76
Antrum	22,00 $\pm$. 2,35	9,00	
Small intestine	56,50 $\pm$ 24,45	30,28	
Caecum	49,80 $\pm$ 16,98	29,13	
Colon and spirals	31,25 $\pm$ 2,75	17,95	

from the colon (t = 2,05: P<0,05) and antrum (t = 3,19; P<0,05)

sections.   The corpus and fornix ventricularis had a signifi=

cantly (t = 3,00; P<0,01) larger maximum volume than the antrum

area of the stomach.   For the large intestine, the caecum had

a larger (t = 2,13; P<0,01) maximum volume than the colon and

spirals together.

Digestive Tract pH Values

The pH of 4,80 $\pm$ 1,20 of the corpus was significantly higher

(t = 2,83; P<0,01) than the 3,44 $\pm$ 0,64 of the antrum (Fig. 22).

The small intestine pH of 6,80 $\pm$ 0,34 was also significantly

greater than that of the corpus (U = 5,00; P<0,01) and antrum

(U = 12; P<0,05) but did not differ from the caecum (t = 0,63;

P<0,01) and long intestine.

Microscopic Anatomy

Corpus and Fornix Ventricularis of the Stomach

These sections were uniformly covered by papillae (Fig. 19) and

were lined with stratified squamous keratinised epithelium on

the lumen side and displayed the characteristic strata germina=

tivum granulosum, lucidum and corneum (Plate 6), similar to that

found in the oesophagus of giant rats.   The stratum germina=

tivum extended into the base of the papillae with a correspon=

ding larger stratum spinosum than is found in non papillated

epithelial sections (Plate 6).   The rest of the papillae con=

sisted entirely of stratum corneum.   The papillae were covered

by a dense brown mat probably being bacteria (Bacillus) which

Camain, Quenum, Kerrest & Goueffons (1960) have already reported.

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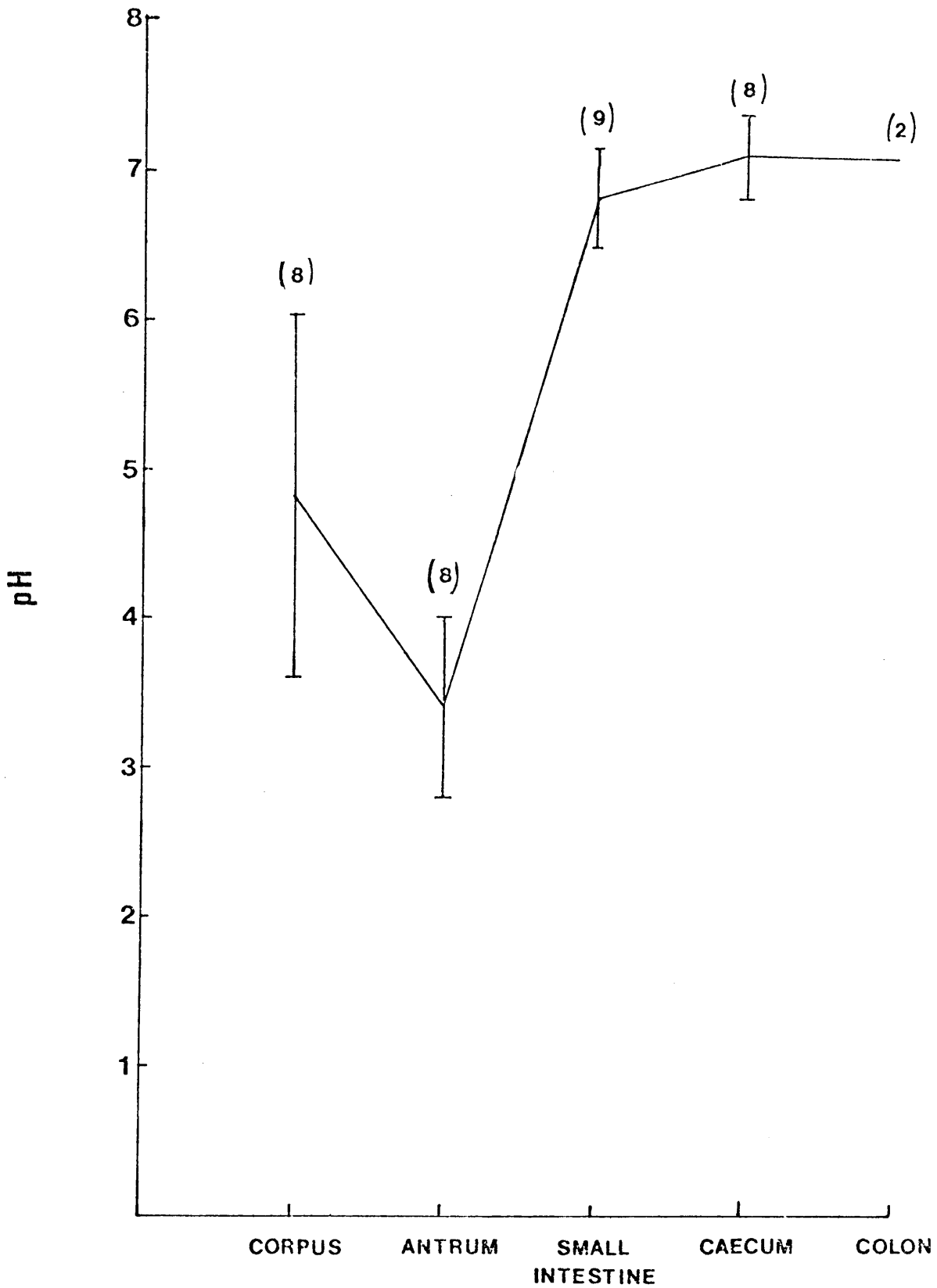
Fig. 22: Mean (± standard deviations) pH values of the different gastrointestinal tract parts. Sample sizes is parentheses.
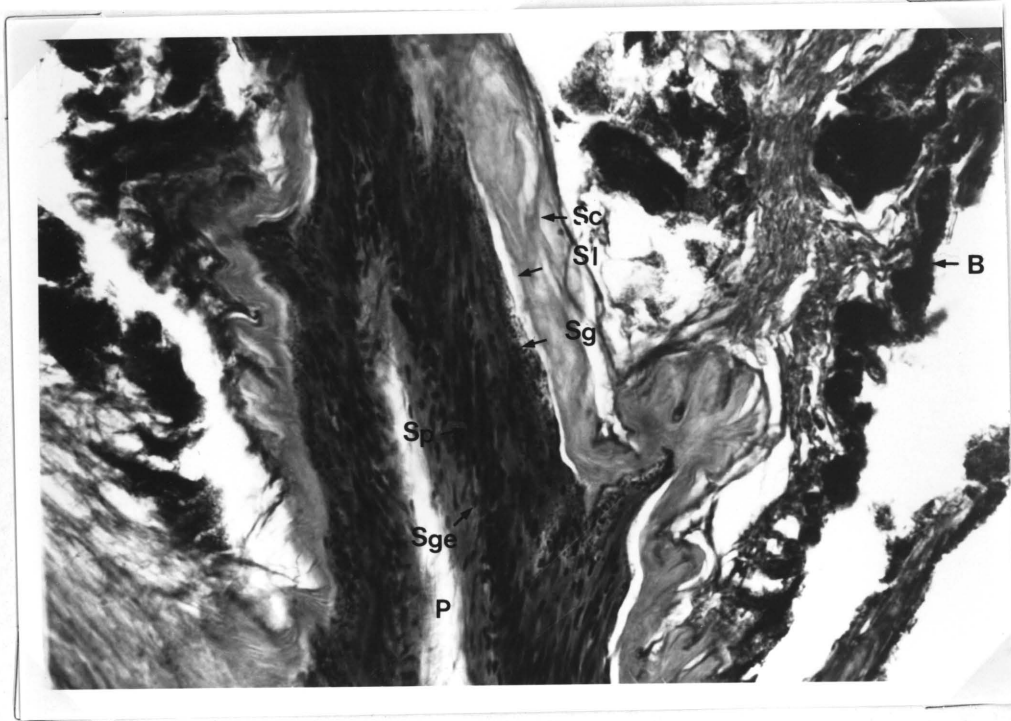
Plate 6 : Section of a papillae from the fornix
ventricularis, showing the stratified
squamous keratinised epithelium and
bacteria. B = bacteria; Sc = stratum
corneum, Sg = stratum granulosum,
Sge = stratum germinativum, Sl = stra=
tum lucidum, Ss = stratum spinosum,
P = papillae. X 32

The Tunica muscularis consisted of the typical mammalian pattern of inner circular and outer longitudinal muscle layers. It was found to be 0,47 $\pm$ 0,02 mm thick, significantly thicker than the Tunica muscularis of the cardiac region (t = 10,24: $P<0,002$) and two fundic regions on the greater curvature of the antrum (no 3 (U = 2; $P<0,002$) and no. 4 (t = 14,71; $P<0,01$) Table 13) but significantly smaller than that found in the fundic region near the pylorus (U = 0,00; $P<0,001$) and pyloric region (t = 12,74; $P<0,01$).

Cardiac Glands

The cardiac glands in the lamina propia were restricted to a small region of the antrum at the junction between the lesser curvature of the antrum and the corpus (Fig. 19). The glands consisted almost entirely of mucous secreting glands with a few scattered parietal cells (Plate 7). The Tunica muscosa of the cardiac region was the smallest (0,28 $\pm$ 0,03 mm) in the whole antrum but was only significantly smaller (t = 2,65; $P<0,05$) than that of the pyloric region (Table 13).

The Tunica muscularis showed a gradual increase in thickness from the 0,19 $\pm$ 0,01 mm adjacent to the oesophageal groove to 0,51 $\pm$ 0,05 mm next to that of the pyloric region. The muscular layers of both these regions were significantly thicker than those of the two corresponding fundic regions (no. 3 (t = 7,73; $P<0,01$) and no. 4 (t = 6,94; $P<0,01$)) on the greater curvature (Table 13 and Fig. 19).

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Table 13   : Thickness (mm) of the Tunica mucosa (oblique

lines) and the Tunica muscularis (dots) of

the glandular antrum and non glandular

corpus of the stomach of giant rats.

(Numbers correspond to those in Fig. 19).

Mean $\pm$ standard deviation.
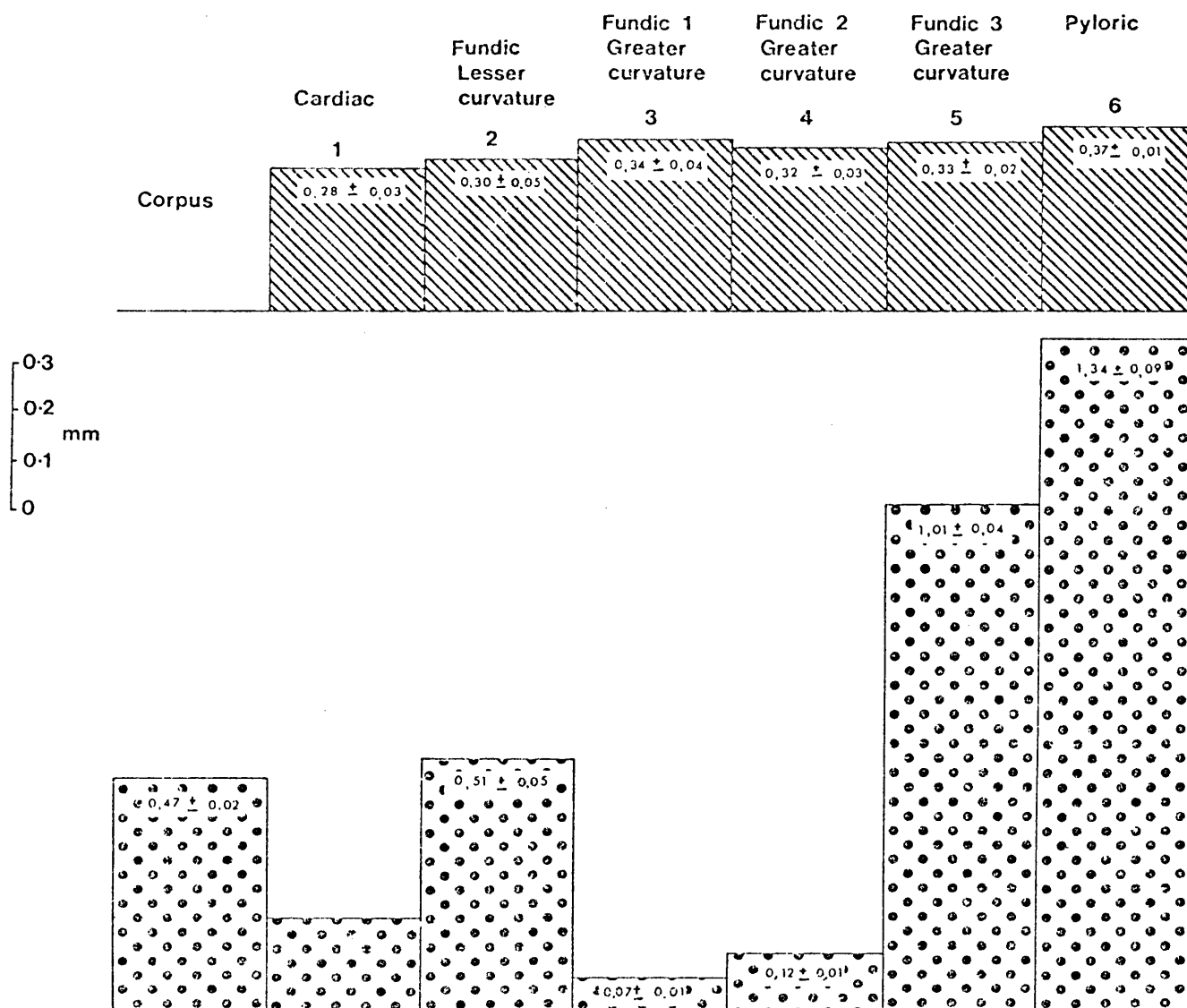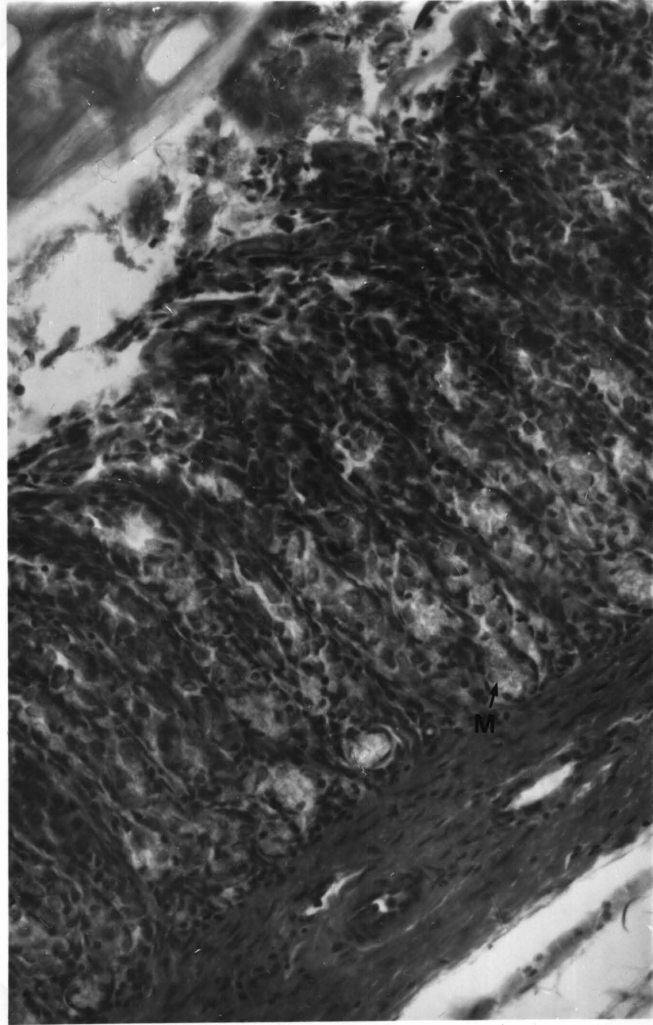
Plate 7 : Cardiac glands. M = mucous cells. X 32

Fundic Glands

Tubular fundic glands with shallow foveola were found from the
grenzfalte to the pyloris on the greater curvature (Fig. 19).
They consisted typically of mucous epithelium, zymogenic and
pariental cells (Plate 8).

The Tunica muscularis of the fundic region on the greater curva=
ture also showed an increase in thickness (but very much more
gradual than the corresponding thickening in the cardiac region)
from the grenzfalte to the pylorus. The fundic regions (No's
3 and 4, Table 13 and Fig. 19) were found to have the significant=
ly thinnest (t - test; P>0,01) Tunica muscularis of the whole
stomach, but rapidly increased in thickness near the pyloric
region.

Pyloric Glands

The pyloric glands were restricted to a small region adjacent to
the pyloric duodenal junction. They consisted entirely of the
columnar epithelium mucous cells with flattened nuclei (Plate 9).
The thickness of the tunica mucosa (0,37 $\pm$ 0,01 mm) was similar
to the other glandular epithelia, but the Tunica muscularis (1,01
$\pm$ 0,04 mm) was significantly (t-test; P>0,01) thicker than the
other muscle layers of the stomach (Table 13).

Ileum

The ileum had long villi extending into the lumen with their
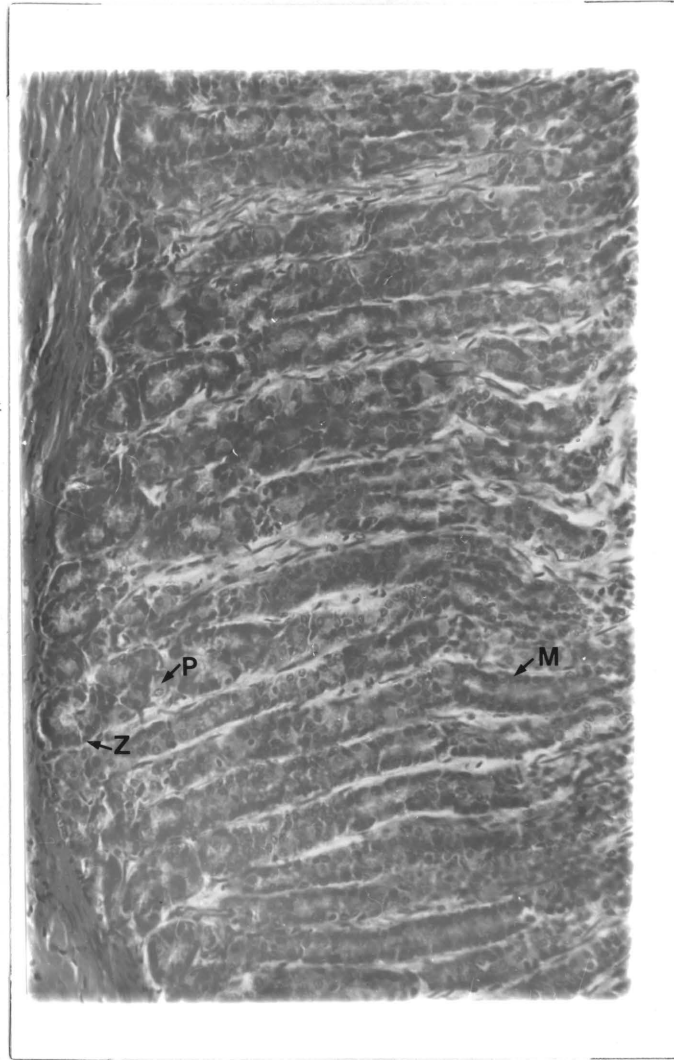
Plate 8 : Fundic glands. M = mucous cells, P = parietal cells. Z = zymogenic cells. X 32.

Plate 9 : Pyloric glands. M = mucous cells.X 32.

epithelium consisting of goblet and epithelial cells (Plate 10).
The Tunica mucosa of the ileum (0,81 $\pm$ 0,05 mm) was signifi=
cantly (t = test; P<0,01) thicker than that found in the caecum
and colon (Table 14).   The Tunica muscularis of the ileum (0,15
$\pm$ 0,16 mm) was significantly thicker than that found in the cor=
pus ceci (t = 2,31: P<0,05) and colon (U = 7; P<0,02) but was
thinner than that of the ampulla and colon loop.

Ampulla Ceci, Corpus, Proximal Colon, Colonic Loop and Colon

The epithelium of the caecum and remainder of the long intestine
consisted of columnar epithelial cells and varying numbers of
goblet cells.   The corpus and ampulla ceci and colon had few
goblet cells which were confined entirely to the depth of the
crypts while the proximal colon had more goblet cells also con=
fined to the crypts.   The first colonic loop had the largest
number of goblet cells in the large intestine predominantely in
the large crypts but also a few scattered on the exposed epithe=
lium.

Differences in the Tunica mucosa and muscularis and the degree
of folding of the lamina propia in the caecum and long intestine
were noted.

In the Tunica muscularis the inner circular and outer longitudinal
muscles were easily distinguishable.   In all cases the circular
muscle was significantly thicker (t-test; P<0,01) than the longi=

TABLE 14: Thickness (mm) of the Tunica mucosa (oblique lines) and Tunica muscularis (circular muscle = large dots and longitudinal muscle = small dots) in the ileum, ampulla çeci, corpus ceci, proximal colon, first colonic loop, and colon of giant rats. Mean $\pm$ standard deviation.

Ileum

0·81 ± 0·05

Ampulla

0·28 ± 0·03

Proximal colon

0·26 ± 0·07

Corpus

0·13 ± 0·09

1st Colonic loop

0·14 ± 0·02

Colon

0·20 ± 0·04

0·3

0·2

mm

0·1

0

0·32 ± 0·07

0·33 ± 0·08

0·11 ± 0·01

0·12 ± 0·04

0·09 ± 0·01

0·09 ± 0·00

0·05 ± 0·01   0·05 ± 0·02   0·03 ± 0·00   0·11 ± 0·02   0·05 ± 0·01   0·02 ± 0·00
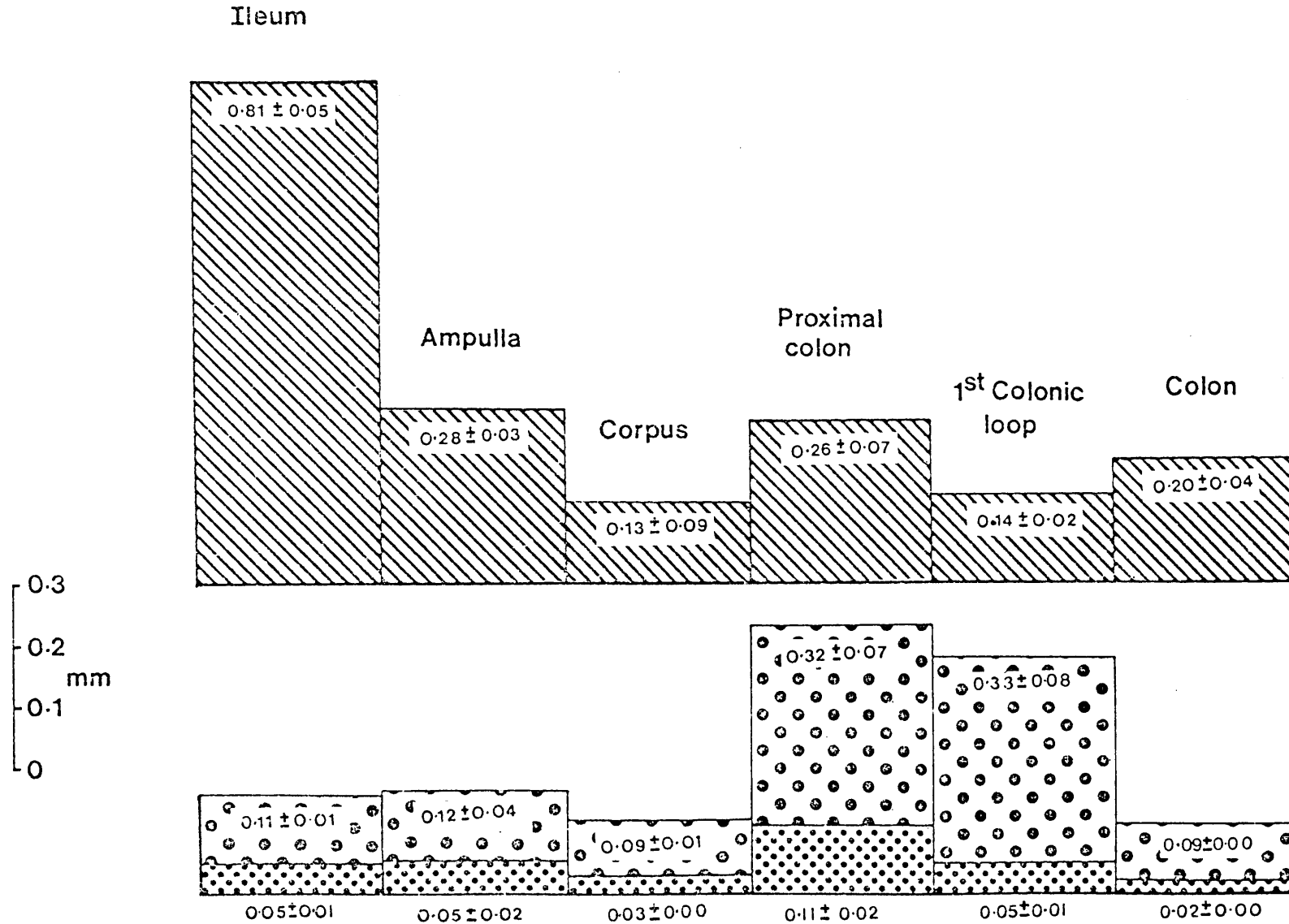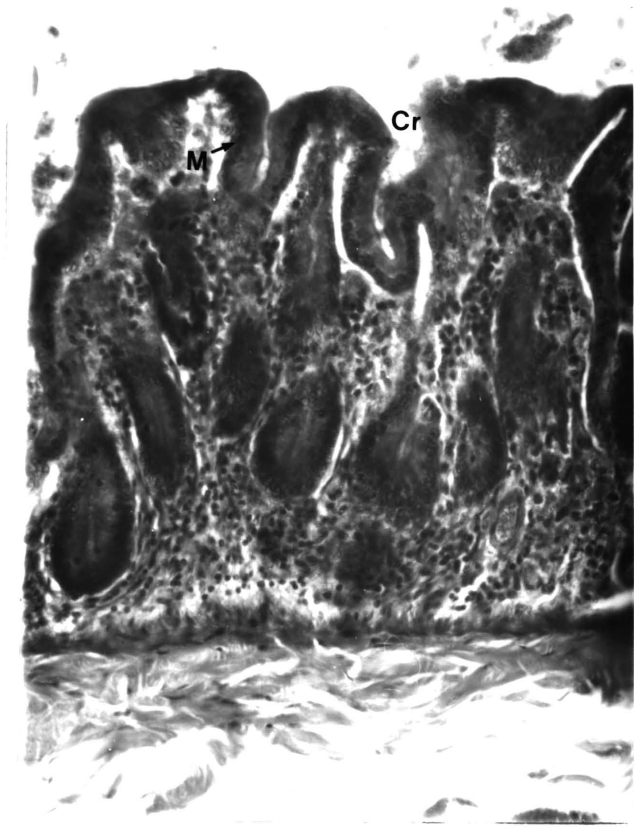
Plate 10 :   Ileum. Cr = Crypts of Lieł kühn,
              G = goblet cells. X 12,6.

tudinal muscle (Table 14). The uniform distribution of the longitudinal muscle in the caecum accounted for the fact that no taenia coli and haustra were noted. The Tunica mucosa of the ampulla was flat with no large folds (Plate 11). The mucosa was $0,28 \pm 0,03$ mm thick, similar to that found in the proximal colon but significantly thicker than the mucosa of the corpus ($t = 4,42$; $P<0,01$) and the large intestine (first colonic loop ($t = 4,04$; $P<0,01$) and colon ($t = 1,93$; $P<0,05$) (Table 14). On the other hand the Tunica muscularis was similar thickness to that found in the corpus and colon but significantly thinner than the muscle layers found in the proximal colon ($t = 2,64$; $P<0,01$) and colonic loop ($t = 2,35$; $P<0,05$) (Table 14).

The corpus ceci was the thinnest region in the caecum and large intestine with both the Tunica mucosa and muscularis diminished in thickness (Table 14).

The crypts of Lieberkühn were wider open than that found else where in the caecum and large intestine (Plate 12).

The proximal colon had obliquely running folds (plicae oblique) evident in Plate 13. The Tunica mucosa was of equal thickness on both sides of the plicae. Both the Tunica mucosa and mus= cularis were thick, being $0,26 \pm 0,07$ and $0,43 \pm 0,07$ mm respec= tively, making it the thickest region of the caecum and large intestine (Table 14).

The first colonic loop had very large plicae extending almost to

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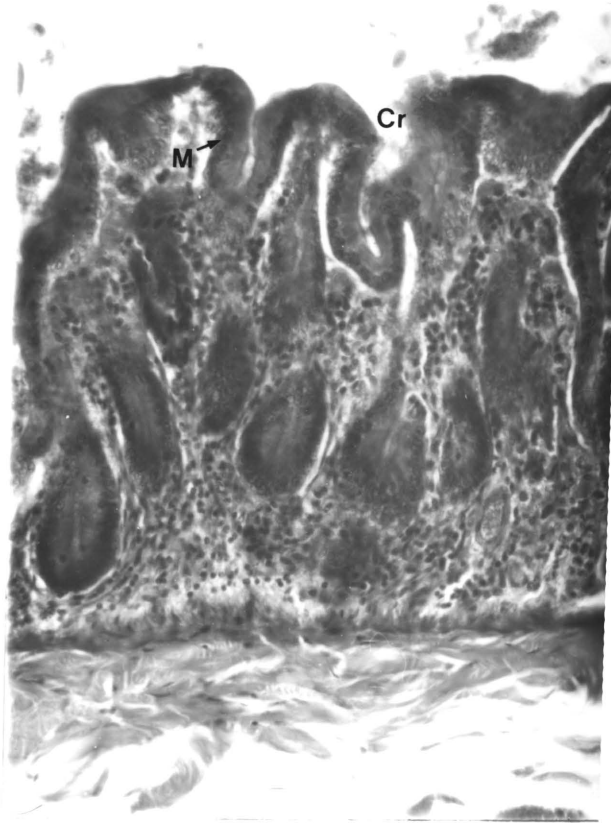
Plate 11 :   Tunica mucosa of the ampulla ceci.
Cr = crypts of Lieberkühn. M =
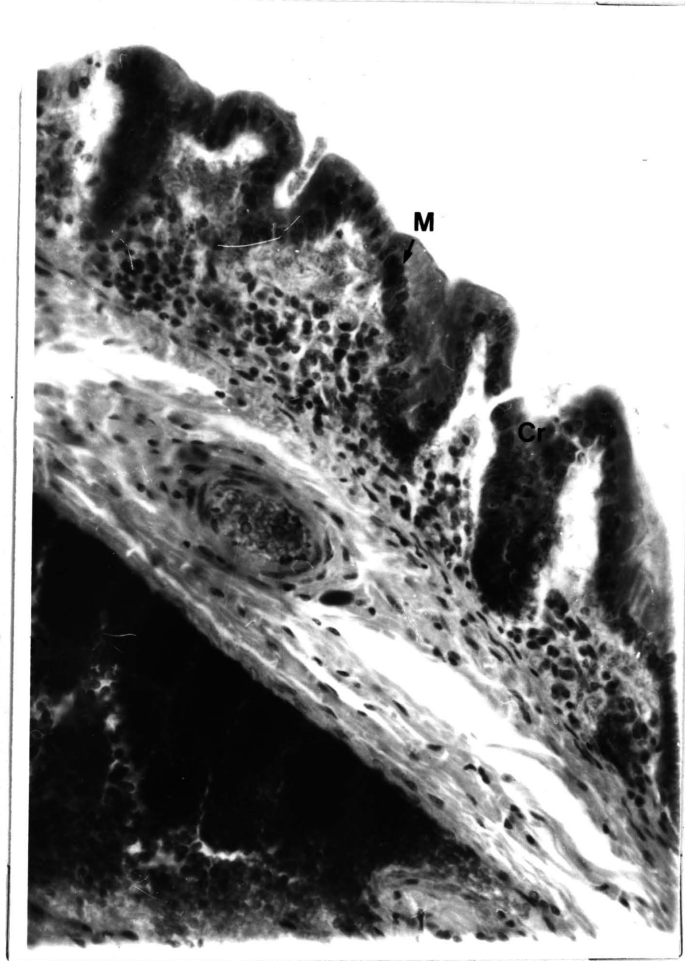
mucous cells. X 20

Plate 12 : Tunica mucosa of the corpus ceci.

Note the wide open crypts. Cr =

crypts of Lieberkühn, M = mucous cells.

X 20.
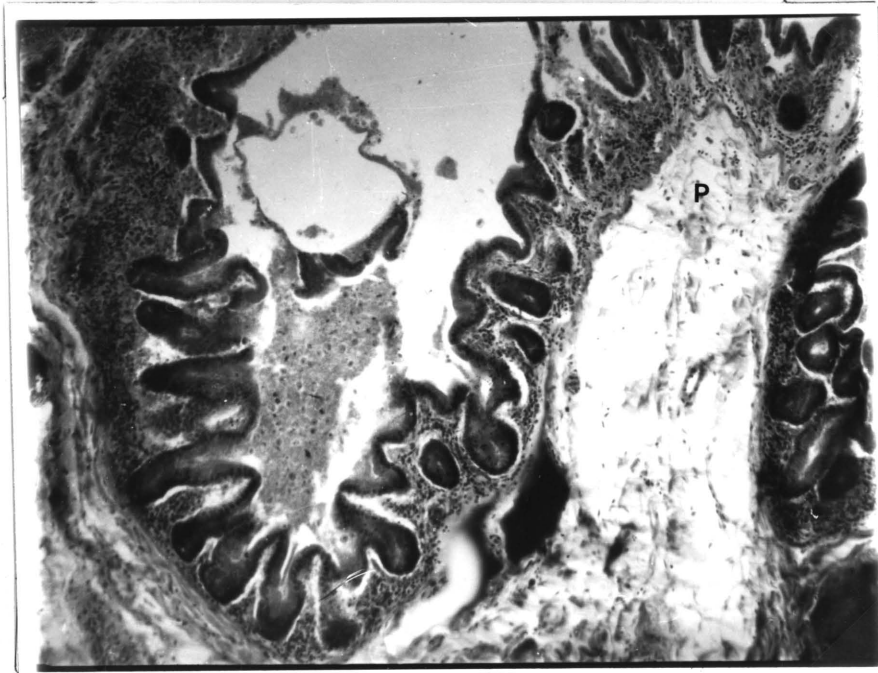
Plate 13:   Folded Tunica mucosa of proximal colon.

p = plique. X 20.

the centre of the lumen (Plate 14). The Tunica mucosa was not thick but similar to that of t⁴ⁿ corpus and colon but signifi= cantly thinner than the mucosa of the ampulla (t = 3,73; P<0,01) and proximal colon (t = 1,96; P<0,05) (Table 14). The Tunica mucosa was also of equal thickness on both sides of the plicae. The colonic loop had the second thickest Tunica muscularis, not significantly different (t = 0,39; P>0,05) to the proximal colon. The Tunica mucosa of the colon was intermediate in thickness between the colonic spiral and proximal colon, but the Tunica muscularis was significantly thinner than the muscles of the colonic spiral (U = 0,0; P<0,001) and proximal colon (U = 0,001; P<0,001) (Table 14). The Tunica mucosa had shallow crypts of Lieberkühn (Plate 15).

Salivary Glands

The submandibular and parotid salivary glands were only examined. Two-thirds of the submandibular salivary gland consisted entire= ly of , serous secreting salivary units while the remaining one-third was made up of mucous secreting units, with very few serous demilunes in their secretary units (Plate 16). The parotid was found to consist entirely of serous secreting units.

DISCUSSION

DIGESTIBILITY TRIALS

The change in ambient temperature appeared to have had a small

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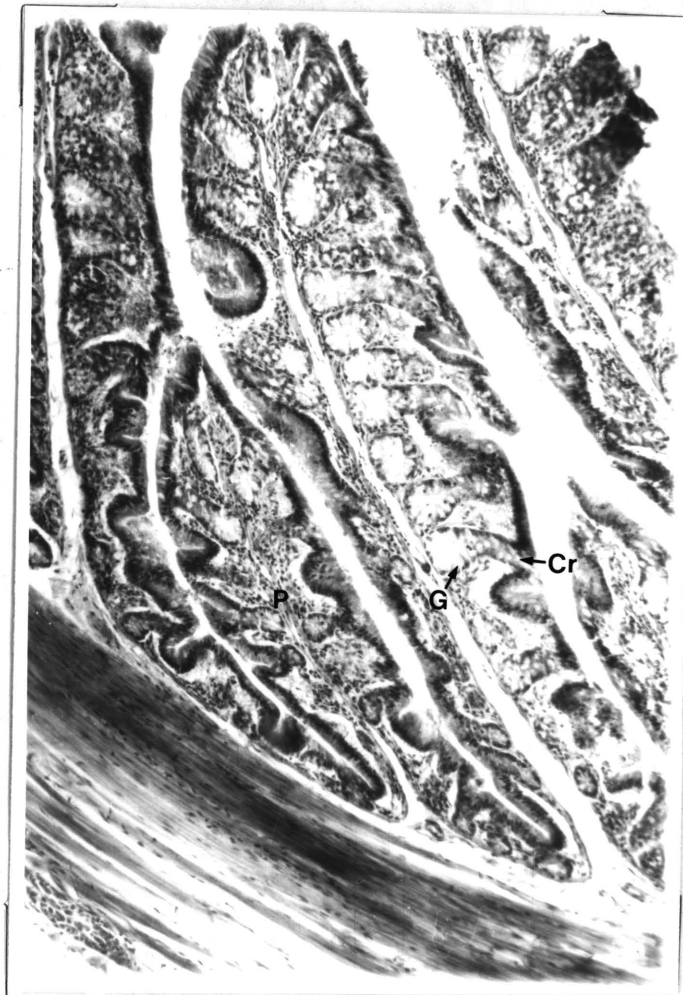
Plate 14 :   Large plique of the first colonic loop .

Cr= crypts of Lieberkühn, G = goblet cells

P = plique. X 10.
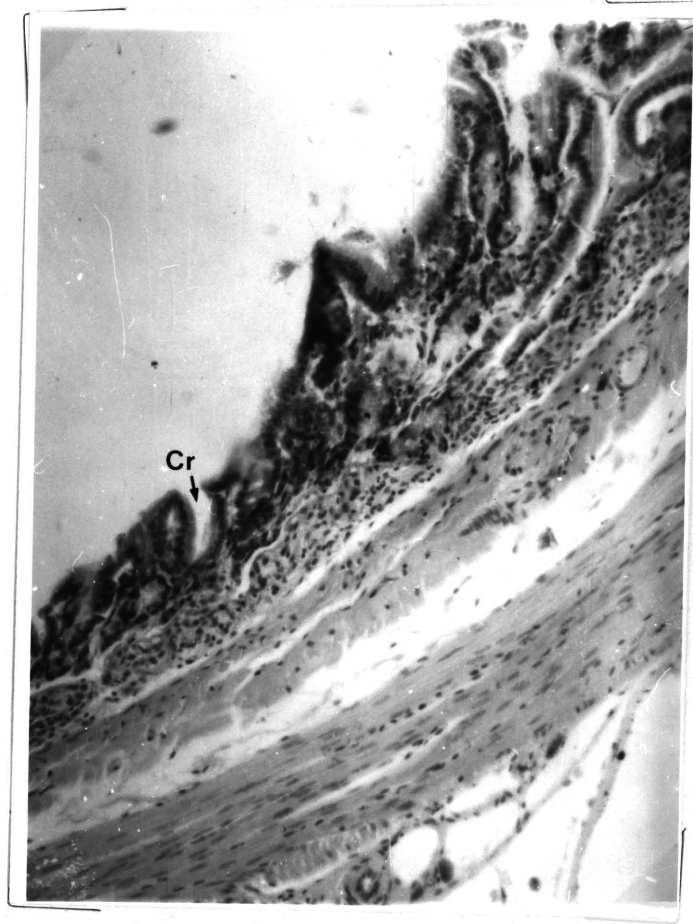
PLATE 15: Tunica mucosa of the colon. Note the shallow crypts
of Lieberkühn. Cr = crypts of Lieberkühn. X 126.
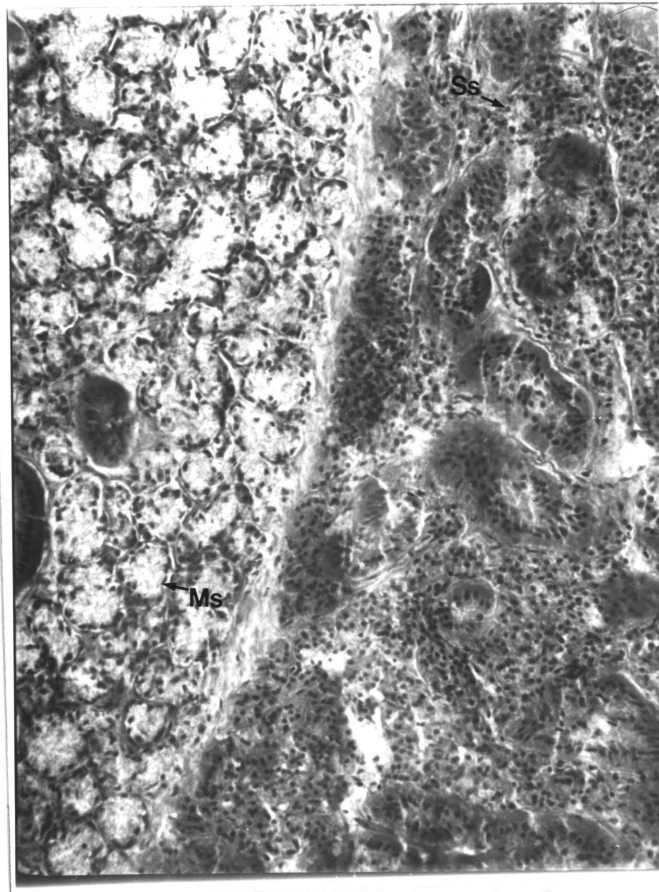
Plate 16 : Submandibular salivary gland. Ss = serous secretory unit; Ms = mucous secretory unit. x20.

but limited effect on the metabolism of giant rats acclimated to 10 and 24°C, even though their metabolizable energy values did not differ significantly (Table 10). The fact that the body masses of the two groups were not exactly the same, even though not significantly different, confounded the issue some= what. Assuming that the change in acclimation temperature had no effect on the metabolism of giant rats the difference in metabolism between the two acclimation groups in Table 10 should be due to the change in body masses alone, therefore the per= centage change between the two groups should be the same as the difference between that predicted by body mass. The metabolizable energy declined 17,54% from 0,57 $\pm$ 0,11 kJ (g.24 h)$^{-1}$ to 0,47 kJ (g.24 h)$^{-1}$ in the 10 and 24°C acclimated giant rats respectively, while the average daily metabolic rate (ADMR) predicted from body mass (Grodzinsky 1975) showed a decline of only 4,35% with the increase in body mass. Therefore the differences between the differentials cannot be accounted for by the change in body mass alone but by a change in metabolism in the two groups. Since the metabolizable energy of giant rats acclimated to 10°C was 247,83% greater than that predicted from body mass, as opposed to the 213,64% found for the 24°C acclimated rats, this indicated that the colder acclimated giant rats had a higher metabolic demand than the warmer acclimated group. This is to be expected because giant rats whether acclimated to 10 or 24°C showed an increase in oxygen consumption at T_a= 10°C (Fig. 24 and 25). Batzli & Cole (1979) found a similar response in metabolism in brown lemmings, Lemmus sibercus, to a change in ambient temperature.

The increase in metabolism on acclimation to 10°C was also indi=

cated by the increased food intake and faecal production over
that of the 24°C acclimated group.   The increased urine pro=
duction and faecal water loss would also have resulted from
increased metabolism and decreased evaporative water loss,
placing the rats in a positive water balance.

But why should the actual metabolizable energy values be so much
greater than predicted from body mass ?   The formula used
for ADMR calculations (Grodzinsky 1975):

$$\text{ADMR kJ (g.24h)}^{-1} = 9,617 \text{ W}^{-0,50}$$

was based on data from 36 rodent species ranging from 7 to 350 g
in mass and since giant rats are much larger, the formula
probably under estimates metabolism at higher masses.   How can
this information be applied to giant rats living in the field?
Since burrow temperatures were found to average 16,00 $\pm$ 2,93°C
throughout the year (Table 3) and assuming that the nest tem=
perature would be warmer, the data obtained from the giant rats
acclimated to 24°C probably are a closer estimate to the daily
energy demands of giant rats living within their burrows.   The
calculated metabolizable energy value of 824,85 $\pm$ 177,85 kJ
$(24h)^{-1}$ which according to Batzli & Cole (1979) is equivalent ;
to the ADMR when the animals are not growing, would account for
giant rats basal metabolism, cost of thermoregulation, specific
dynamic action (SDA) and activity metabolism such as those
associated with feeding and comfort movements (Gesseman 1973).
Taking into account the amount of time spent active out of the

burrows and the speed at which they travel, estimates of the cost of free existence (EM) can be made. Giant rats have been found to be active out of their burrows for 3,1 h (Fig. 5) a night and travel at an average speed of $0,23 \pm 0,08$ km. h^{-1} (Table 6). Therefore EM can be estimated by:

$$EM = ADMR + M_A$$

where ADMR is that determined for giant rats acclimated to 24°C but only over 20,9 h. The M_A is metabolism of activity (ml $O_2(g.h)^{-1}$) and has the form adapted from Wunder (1975) where:

$$M_A = 1,7 \ RMR \pm (8,46 \ W^{-0,40}) \ V$$

and RMR is resting metabolic rats (ml $O_2 \ (g.h)^{-1}$) of giant rats acclimated to 24⁶C (Fig. 24) exposed to an ambient temperature of 16,19°C (equivalent to the mean forest temperature (Table 3)). The coefficient with the value of 1,7 in the above formula is the cost of posture associated with activity and is found to be 1,7 times the basal metabolic rate (Taylor, Schmidt-Nielsen & Raab 1970). V is velocity in km.h^{-1}.

Therefore, using the combined average body mass of field caught male and female giant rats ($1414,75 \pm 213,60$ g)(n = 19), their EM is estimated at about 703,10 kJ. day $^{-1}$. To satisfy this a giant rat feeding entirely on avocado pears (calorific value of 912,77 kJ. 100 g.$^{-1}$ (Popenoe 1920)) or macadamia nuts (cal= orific value of 3288,99 kJ. 100 g.$^{-1}$ (Rodale 1961)) would only need 77g or 21 g of each fruit respectively. If the giant rats became conditioned to collect and eat these fruits they could become an economic pest. However since they only frequent avocado plantations 2,92% (Table 7) of their activity time, I

consider their impact to be minimal on the fruits. The rela=
tive proportions of different foods consumed in the wild, their
calorific values and their seasonal availability should be
determined to find out how the giant rat partitions its diet.

PASSAGE RATES

It appears that there is selective retention of fibre in the gut
of giant rats owing to the longer passage rates of small plastic
pieces in comparison to that found for the brilliant blue dye.
The times for 5% and 80% appearance of the plastic pieces are
longer than those reported in other hind gut fermenters such as
the capybara, rabbit (Parra 1978), guinea pig, rat (Clemens &
Stevens 1980) and brushtail possum (Wellard & Hume 1981) and
even some foregut fermenters such as cattle and sheep (Parra 1978).
The long 85% appearance time could have been due to the charac=
teristics of the plastic pieces (Clemens & Stevens 1980), stomach
and caecal anatomy and coprophagy. But the fact that first and
last appearances of the food marked with brilliant blue dye were
also long in comparison to those reported by Parra (1978) and
Clemens & Stevens (1980) indicated that giant rats tend to have
slow movement of digesta through the digestive tract. The pre=
sence of too smaller peaks after 157,5h and 205,5 h following
feeding emphasises either or both the influence of caecal reten=
tion and pulsative emptying or that of coprophagy in the diges=
tion process of giant rats.

A slow passage rate is generally associated with animals with low metabolic rates such as sloths (Montgomery & Sunquist 1978) and also in larger animals feeding on high fibre diets where slow passage rates enhance digestion. Because larger animals have a relatively lower mass specific metabolism, the demand for energy is not as great, therefore time can be spent digesting fibre to its fullest. But why then should the giant rat have a slow passage rate when it has a higher than predicted meta= bolic rate and feeds predominently on fruits containing a large proportion of soluble sugars? The answer may lie in the fact that giant rats can not ably conserve water owing to their high evaporative water losses. (Fig. 26) and their large urine volumes. A slow passage rate would enhance reabsorption of water, elec= trolytes and metabolites (Hume & Warner 1980) and this probably accounts for the drier faeces found in giant rats acclimated to 24°C than those acclimated to 10°C. A study of the effect of ambient temperature on passage rate should be undertaken to clarify this matter. Kostelecka - Myrcha & Myrcha (1964) suggested that the longer passage rates would also increase the digestion of starch, as they found the granivorous Clethriono= mys glareolus to have longer passage rates than the herbivorous Microtus arvalis.

Since giant rats predominantely feed on fruit (Chapter 3) this does not necessarily mean they cannot digest fibre, as Faturoti et al (1980) and Tewe & Ajayi (1982) found they could efficiently digest foods containing 10% fibre, for which a slow passage rate would be an advantage. Thus giant rats probably retain

the ability to digest fibre but that fibre intake is probably
dependant on the food containing a lot of water. This depen=
dance on moist food is supported by the presence of entire
lobes of mucous secretory units in the submandibular salivary
gland of giant rats, as rodents living on dry diets, such as
seeds, have a more watery saliva owing to increased serous
secretions (Suida & Szymanska 1961). Hume and Warner (1980)
also noted that most herbivores have a watery saliva to aid
mastication and swallowing of their dry food.

Therefore giant rats appear to have the ability to digest
limited amounts of fibre but prefer fleshy foods probably be=
cause of their need of water.

DIGESTIVE MORPHOLOGY

In comparison with the digestive system morphology of 19. species
of southern African myomorph rodents (Perrin & Curtis 1980),
the giant rat can be classified as a species with an intermediate
standing along the scale from omnivory to herbivory, with some
of the adaptations being typically herbivorous and other typi=
cally omnivorous.

With the postulated shift from foods high in protein and lipids
to ones high in cellulose in rodents, Vorontsov (1962, 1967)
predicted changes within the gastro-intestinal tract. He sugges=
ted that the tuberculous molars became more flattened, hypso=

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dontic and laminate to facilitate grinding of fibre, and that there was a reduction of the gastric glandular zone, with a subsequent compartmentalization of the stomach from its simple unilocular condition. With compartmentalization, stratified squamous epithelium increased to foster the existence of cellu= lolytic gastric symbionts. The relative length and volume of the small intestine would decrease and the caecum and colon increase to facilitate microbial existence within the gut. With the decreased proteinaceous diet the number of liver lobes would decrease and gall bladder disappear and with the increase in a herbivorous foods the serous secreting units of the salivary gland would become more proliferic.

As previously stated giant rats are omnivorous but they prefer soft fleshy fruits (present study (chapter 3); Tewe & Ajayi 1979). It is not surprising then that their molars are not particularly flat, nor laminated and have several associated cusps (De Graaf 1981). (Fig. 23).

The stomach of giant rats shows a degree of compartmentalization with a large papillated corpus and smaller glandular antrum. The large maximum volume (Table 12) and surface area of the corpus are indicative of its importance in the digestive process of the giant rats.

The papillae of the corpus and fornix ventricularis were covered in keratinized stratified epithelium, which in turn were covered
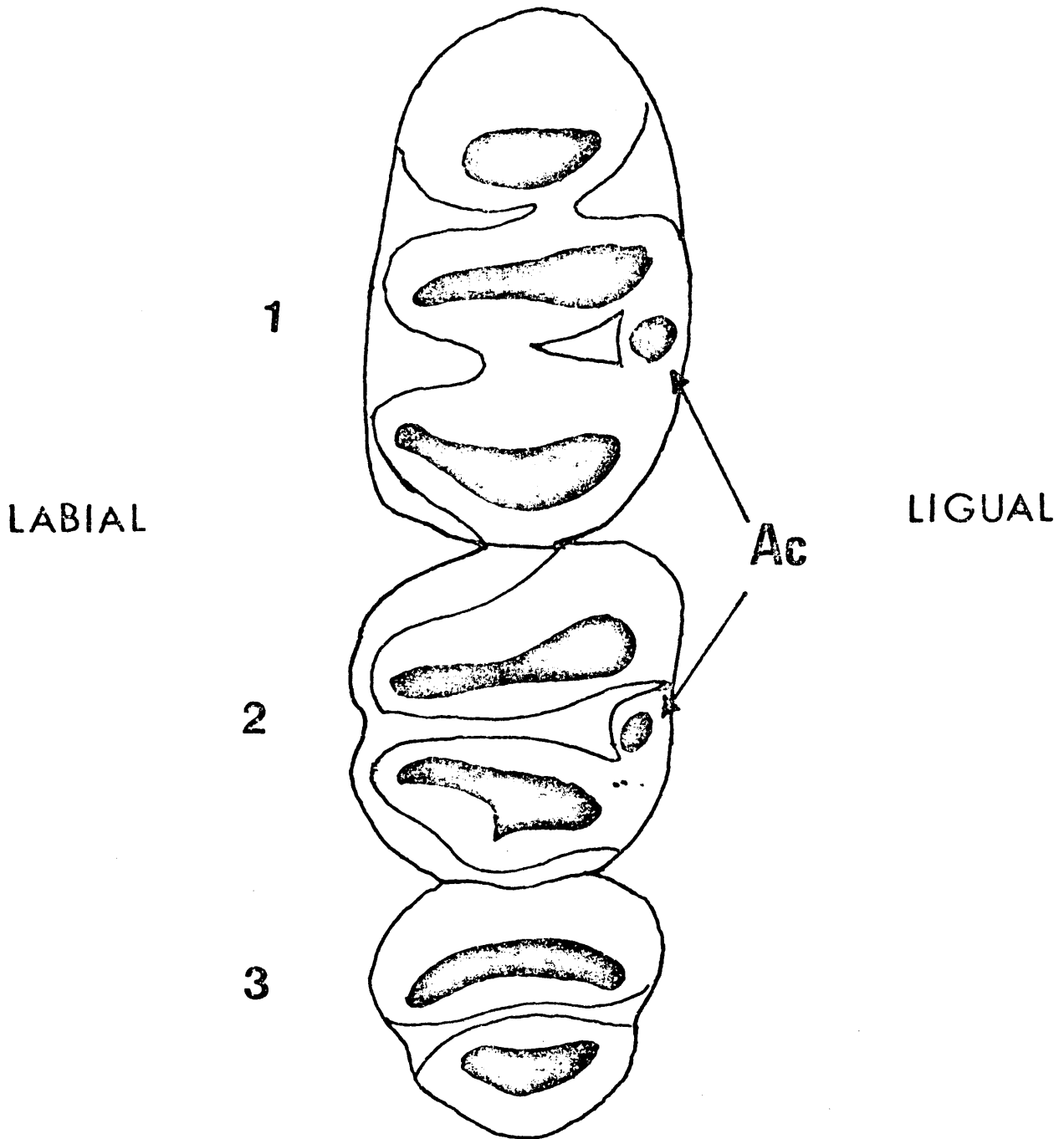
Fig. 23:   Occlusal surface of the molar teeth of
            the lower left jaw of the giant rat. Ac =
            accessory cusps.

by a mat of bacteria (Plate 6) which Camain et al (1960) and Kokkin (1981) identified as Bacillus.   Bacillus is associated with fermentation of glucose, production of acetyl methyl carbinol, hydrolysis of starch and the proteins casein and gelatin and nitrate reduction, but not the fermentation of cellu= lose (Camain et al 1960).   Therefore, the arguements of Vorontsov (1962) concerning pregastric fermentation do not apply to the giant rat but rather the large papillated corpus and fornix ventricularis probably provides a means to sustain sali= vary amylase digestion (as Carleton suggested (1973, 1981) for New World Cricetids and Microtine rodents) and the action of Bacillus.   The higher pH of the corpus, than that of the antrum (Fig. 22), would sustain the action of salivary amylase and the digestion of starch, as Perrin & Maddock (1983) found in the white tailed rat, Mystromys albicaudatus.   But how can the two compartments maintain their separate pH levels with a shallow incisaura angularis and wide channel (1,67 $\pm$ 0,75 cm) linking them?   The small fibria on the bordering fold (or grenzfalte) were noted to stand erect and not lie prostrate on the glandu= lar mucosa probably help maintain the separation.

The thick Tunica muscularis of the corpus and fornix ventricularis (Table 13) suggests that mixing is important which probably aids the digestion of starch and shifting the large bolus into the antrum.   The corpus was found not to be an area of absorption owing to the presence of few blood vessels close to the keratin= ised squamous epithelium.

The corpus of other omnivorous rodents such as M. albicaudatus (Maddock 1981) and the golden hamster, Mesocricetus auratus (Ehle & Warner 1978) were also found not to be pregastric fer= mentation vats and even in surgically removed forestomachs, the hamsters showed equally efficient digestion as compared to control animals.

Therefore the corpus and fornix ventricularis of giant rats appears to be a temporary storage chamber to prolong amylase activity, with the papillae increasing the surface area to accommodate a larger bacterial population to facilitate starch digestion.

The presence of cardiac, fundic and pyloric glands in the antrum indicate the importance of protein digestion which is to be expected considering their omnivorous diet. The pyloric pouch with its thick muscular walls are related to a milking action in the pylorus (Dearden 1969) probably to regulate that only small quantities of digesta enter the duodenum to facilitate efficient digestion and absorption.

The relatively long (Table 11) and voluminous (Table 12) small intestine can be equated to its importance in digestion and ab= sorption of proteinaceous foods. The differences in relative percentage lengths and volumes of the small intestine and other gut regions are a result of the two different methods. Since the capacity of the gut is probably more important to the animal than gut length, as it determines the actual amount of

food that can be held, the volumes are considered more important
in the present study.

The large plique and deep crypts of Lieberkühn in the small
intestine all enhance the absorptive and digestive capabilities.
The large number of goblet cells scattered on the epithelium
and within the crypts probably aid the movement of digesta through
the small intestine.

Since the caecum of giant rats is relatively short and voluminous
(29,13% of the total gut volume (Table 11)) it must play an im=
portant role in the digestion process.

The caecum is very similar to that found in the dwarf hamster,
Phodopus sungorus (Snipes 1979 a) and since both species are
myomorph rodents of the family Cricetidae, the similar caecal
structure could be a result of phylogeny, rather than similar
feeding habits. The giant rats' caecum is without taenia and
haustra but the corpus and ampulla were not as clearly disting=
uisable as those seen in the dwarf hamster. The two folds
separating the ampulla ceci (into which the ileum enters) from
the muscular proximal colon at one end and the corpus ceci at
the other end probably influences the flow of caecal contents,
restraining fibre for digestion within the corpus ceci. This
separation may have accounted for the long passage rates of
plastic pieces, but needs to be tested with radioactive isotopes,
such as ^{14}C-labelled polyethylene (PEG) which Björnhay (1972)
used successfully on rabbits.

The Tunica mucosa of the caecum of the giant rat was found to differ from that of the rest of the intestine, by having wide open crypts as opposed to the closed ones characteristic of the large and small intestines. This finding is in accordٍ with that found in other rodents such as the dwarf hamster (Snipes 1979 a), vole (Snipes 1979 b) and laboratory rat and mouse (Snipes 1981) and supports the hypothesis that the mucosal form of the caecum is probably a different tissue type to that found in the rest of the intestine. Snipes (1981) suggests that the wide open crypts probably increase the absorptive area of the caecum.

The presence of a flat ileocaecal orifice in the giant rat was very similar to that reported for the dwarf hamster (Snipes 1979 a), again indicating the close relationship between the Cricetids. The thicker Tunica muscularis of the ampulla in comparison to that of the corpus ceci is probably an adaptation to direct flow of digesta leaving the ileum into either the colon or corpus ceci. This sorting could also occur in the proximal colon owing to the presence of an even thicker muscle layer and plicae oblique which have been interpreted as permanent structures in= strumental in guiding digesta from the proximal colon back into the caecum (Behmann 1973). Björnhag (1972) found this pheno= menon to occur in the rabbit and it may also occur in many rodents, as Snipes (1979 a, 1979 b) reported thicker muscle layers in the proximal colon of the dwarf hamster and vole. This sorting mechanism probably accounts for the longer passage rates of plastic pieces and may be more common in those species

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practising coprophagy or caecotrophy.

The caeca of giant rats showed a reduction in the number of goblet cells compared to the large and small intestines.   This has been suggested (Snipes 1979 b) to be a possible advantage in absorp= tion because of the decrease in mucous secretion.   However, it is more likely a result of less direct flow of digesta through the caecum in comparison to the rest of the intestine, as goblet cells were more common in the proximal colon and even more so in the first colonic loop because of the increased resistance offered by the plique.   This does not negate the fact that the caecum is an important area for absorption (Rérat 1978).

The colonic spirals constituted 11,35% (Table 12) of the intes= tines length and are probably important in absorption and parti= cularly the first colonic spiral owing to the presence of large plique and accumulation of fat deposits around the loop.   The first loop may be responsible for absorption from the digesta leaving the caecum.   The second loop was of similar structure to that of the colon but had no fat accumulation.   It may be responsible for absorption of electrolytes and water.

The colon comprised 21,61% (Table 11) of the total hindgut length yet its maximum (including the spirals) volume was the smallest in the hindgut (Table 12).   The Tunica mucosa of the colon was very similar to that of the corpus ceci from the point of view of lacking plique and folds and also a reduced number of goblet

cells (but not to the same extent as in the corpus). The fewer goblet cells could be a result of less resistance offered to the flow of digesta or an adaptation to facilitate absorption. However, the lack of secondary structures in the colon may faci= litate the fermantative process of bacteria, as McBee (1977) found the colon of rats to be an important region of cellulose fermentation. Therefore, the colon and two colonic loops may have areas of differential absorption as Snipes,Clauss, Weber & Hörnicke (1982) found in the colon of rabbits.

The presence of $6,3 \pm 1,1$ liver lobes, and a gall bladder (which is associated with..lipid digestion) is indicative of a predominance of protein in the diet as opposed to cellulose.

In conclusion it appears from gut morphology that giant rats should have equal capacities to survive on a mixed protein, carbohydrate and cellulose diet, with the compartmentalized stomach digesting the starch and protein and the caecum diges= ting fibre. However, the feeding habits of giant rats show a preference for soft fruits (Chapter 3) and an inefficiency to digest fibrous foods (Faturoti et al 1980; Tewe & Ajayi 1982) does not support the deductions made from its gut morphology. This suggests that not all organs of the digestive tract are totally aligned to the animals feeding habits, perhaps providing flexibility should the diet change. Phylogeny may also play a significant rôle in determining the gut morphology as was indicated by the similarities between the giant rat and dwarf hamster.

Therefore, detailed digestion experiments and electromicroscopic work needs to be undertaken to determine the sites and extent of fermentation and absorption to clarify the functions of the forestomach and hindgut of the giant rat. The present study emphasises that the simple gross morphological analysis of rodent digestive systems are not adequate enough to fully describe the feeding habits of rodents.

CHAPTER 7

THERMOREGULATION

RESULTS

ADULTS

Giant rats acclimated to 24°C had a minimal oxygen consumption of 0,61 $\overset{+}{-}$ 0,05 ml O_2 (g.h)$^{-1}$ with the thermoneutral zone (TNZ) ranging from 23,5 to 34°C (Fig. 24). Below thermoneutrality a conductance (calculated by the relation $C = Vo_2/(T_b-T_a)$ where; C = conductance (mlO_2 (g.h.°C)$^{-1}$), T_b = body temperature (°C) and T_a = ambient temperature(°C)) of 0,04 ± 0,00 mlO_2 (g.h.°C)$^{-1}$ was found (Fig. 24). Giant rats acclimated to 10°C had a slight= ly lower minimal oxygen consumption of 0,55 $\overset{+}{-}$ 0,03 mlO_2 (g.h.)$^{-1}$ which did not differ significantly (t = 1,57; P>0,01) from those acclimated to 24°C (Fig. 25). The TNZ ranged from 18 to 30°C above which the oxygen consumption rose. The thermal conductance of 0,04 $\overset{+}{-}$ 0,01 ml O_2 (g.h.°C) did not differ significantly (u = 26; P>0,01) from that found for those acclimated to 24°C.

The body temperature of animals acclimated to 24°C was low, being 35,65 $\overset{+}{-}$ 0,45°C, when exposed to ambient temperatures from 10 to 30°C. However at higher ambient temperatures, the body tempera= ture increased to a maximum of 41,0°C when exposed to a maximum of 37,5°C (Fig. 24).

For those acclimated to 10°C difficulty was experienced in ob= taining body temperatures. However a significantly lower (Z = 1,98; P<0,02) body temperature of 33,5 $\overset{+}{-}$ 0,18°C was found

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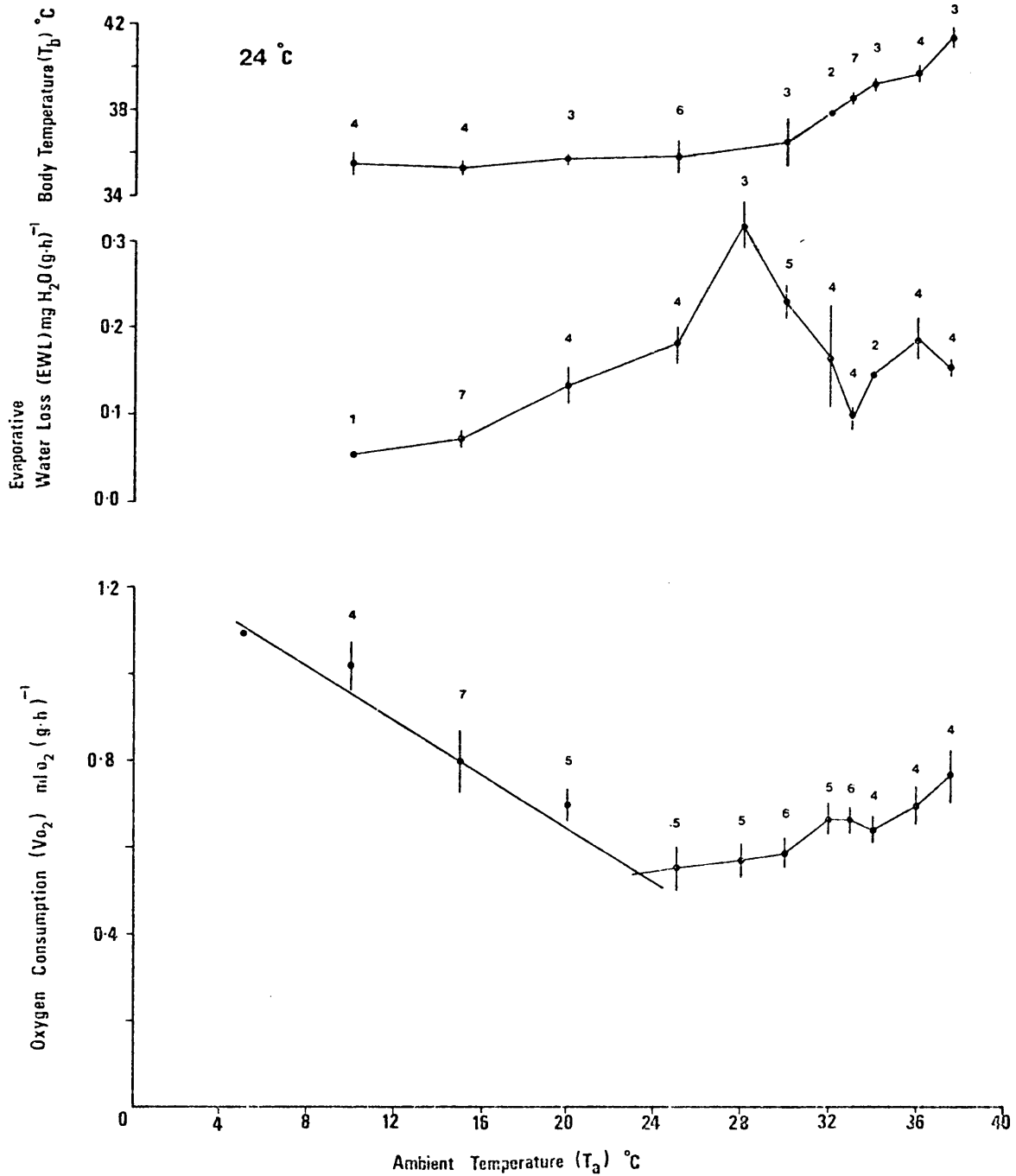
Fig. 24: Minimum oxygen consumption, evaporative
water loss (EWL) and body temperature
(T_b) of five adult giant rats acclimated
to 24°C.   Mean $\pm$ standard error.   Num=
bers above lines equate to sample size.
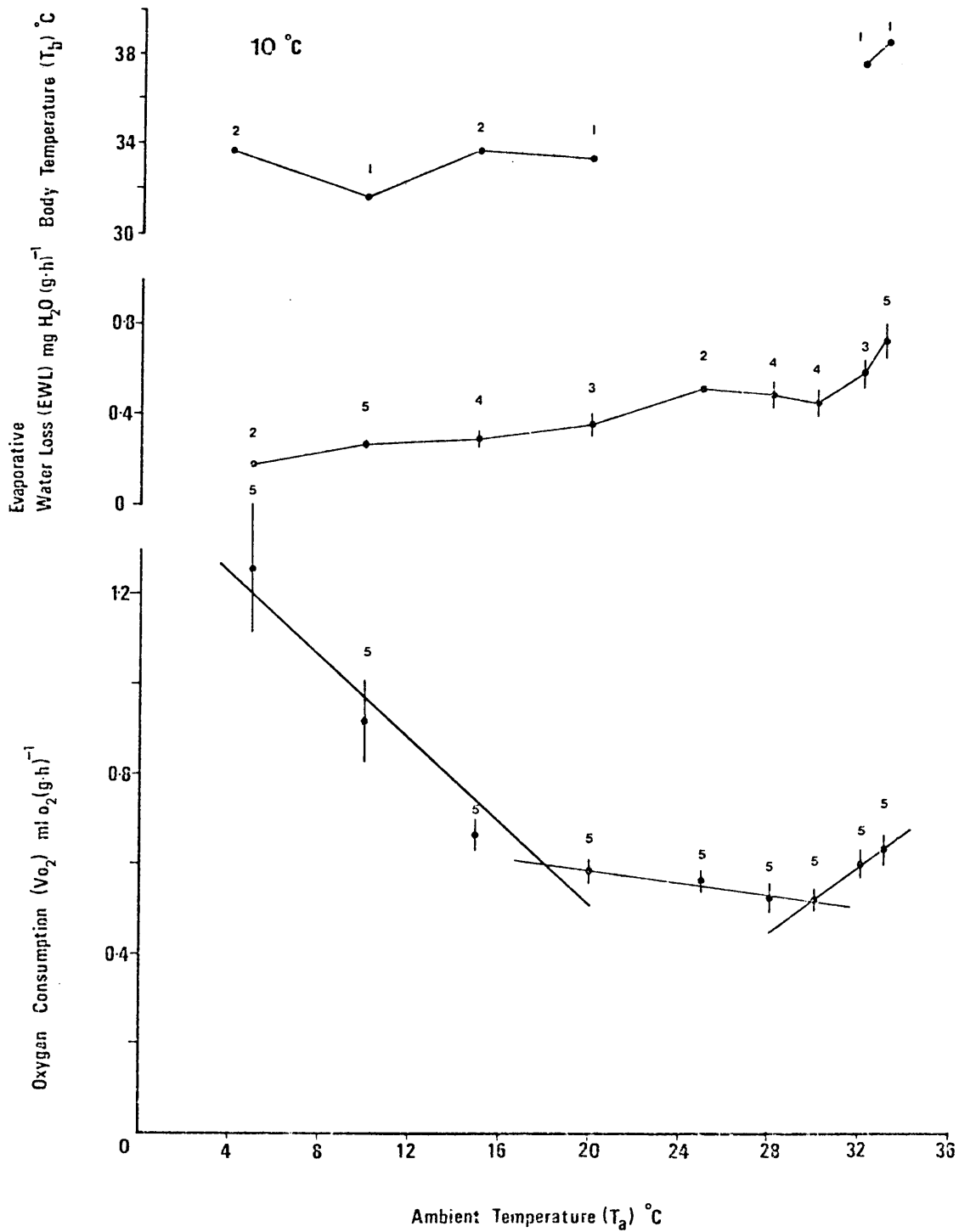
Fig. 25: Minimum oxygen consumption evaporative
water loss (EWL) and body temperature (T_b)
of five adult giant rats acclimated to 10°C.
Mean $\pm$ standard error. Numbers above
lines equate to sample size.

for giant rats exposed to ambient temperatures from 5 to 20°C (Fig. 25). At ambient temperatures of 32 and 33°C the body temperatures were found to be higher, 37,5 and 38,4°C respective= ly and were similar to those found for giant rats acclimated to 24°C at the same ambient temperatures.

The evaporative water loss (EWL) of giant rats acclimated to 10°C was significantly greater (U = Test; $P < 0,01$) than that found for those acclimated to 24°C at all temperatures (Fig 24 and 25). The EWL for those acclimated to 10°C showed a steady increase from 0,18 mg H_2O $(g.h.)^{-1}$ at Ta = 5°C to 0.73 $\pm$ 0,16 mg H_2O $(g.h.)^{-1}$ at Ta = 33 °C and the rate of increase was 0,02 mg H_2O $(g.h.°C)^{-1}$ ($r = 0,93$). However, for giant rats acclimated to 24°C, the EWL at a Ta = 10°C was 0,06 mg H_2O $(g.h.)^{-1}$ (only one reading) and increased at a rate of 0,05 mg H_2O $(g.h.°C)^{-1}$ ($r = 0,92$) to 0,31 $\pm$ 0,05 mg H_2O $(g.h.)^{-1}$ at Ta = 28°C (Fig. 24). Beyond Ta = 28°C, the EWL dropped to a low 0,09 $\pm$ 0,03 mg H_2O $(g.h.)^{-1}$ at 33°C, and again increased to 1,83 $\pm$ 0,05 mg H_2O $(g.h.)^{-1}$ at Ta = 36°C. The rate of increase of EWL at Ta's from 0 - 28°C for both groups of acclimated giant rats were not significantly diffe= rent (t=0,07; P>0,01).Assuming the combustion of 1 ml of oxygen requires 20,10 J (Gordon, Bartholomew, Grinell, Jorgensen & White 1977) and that evaporation of 1mg H_2O dissipates 2,4 J, the portion of total conductance due to evaporative cooling could be determined (Hudson, Deavers & Bradley 1972). It was found

that the evaporative energy loss of giant rats acclimated to
10°C is significantly greater than those acclimated to 24°C,
(Table 15).

The percentage of metabolic heat loss by evaporation (MHE) is
about three-fold greater, at all ambient temperatures, for giant
rats acclimated to 10°C than those acclimated to 24°C (Fig. 26).
For giant rats acclimated to 10°C, evaporative heat loss accoun=
ted for 45,8% of the total heat loss at Ta = 5°C and to 95,5%
at Ta = 20°C.   However, at Ta's of 32 and 33°C the evaporative
heat loss declined to 62,7%and 74,2% respectively (intermediate
results are lacking owing to lack of body temperature results).
For giant rats acclimated to 24°C, the evaporative loss accounted
for 16,3% of the total heat loss at Ta = 10°C and rose to 73,2%
at Ta = 25°C, there after declined to a 8,3% at Ta = 37,5°C.

JUVENILES

With an increase in body mass in growing giant rats there was a
subsequent decline in mass specific oxygen consumption tested at
Ta = 25°C (Fig. 27).   Giant rats, 55 days old weighing 548,00
$\pm$ 60,86 g had an average minimal oxygen consumption rate of 1,24
$\pm$ 0,16 ml O_2 (g.h.)$^{-1}$ and decreased to 0,71 $\pm$ 0,11 ml O_2 (g.h.)$^{-1}$
in 132 day old rats with average body mass of 1401,08 $\pm$ 82,50 g.

The Tb's did not increase significantly (t = 0,61, P>0,01) with
increase in body mass over the range tested (Fig. 27).   The Tb

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Table 15   Energy loss of evaporation at different ambient temperatures (T_a) in giant rats acclimated to 10°C and 24°C.

| T_a (°C) | ENERGY LOSS AND EVAPORATION $(J \ (g.h)^{-1} \pm SD)$ | | | | | |
	10°C acclimation	n	24°C acclimation	n	Test	P
5	0,42	2				
10	0,64 ± 0,01	5	0,13	1		
15	0,69 ± 0,16	3	0,16 ± 0,05	7	U = 0,00	0,008
20	0,85 ± 0,21	3	0,31 ± 0,08	4	U = 0,00	0,028
25	1,24	2	0,43 + 0,09	4		
28	1,16 ± 0,31	4	0,75 ± 0,12	3	t = 2,14	0,05
30	1,10 ± 0,30	4	0,54 ± 0,12	5	t = 3,89	0,01
32	1,38 ± 0,25	3	0,39 ± 0,28	4	t = 5,72	0,01
33	1,74 ± 1,76	5	0,22 ± 0,06	4	U = 0,00	0,008
34			0,35	2		
36			0,44 ± 0,12	4		
37,5			0,36 ± 0,05	4		
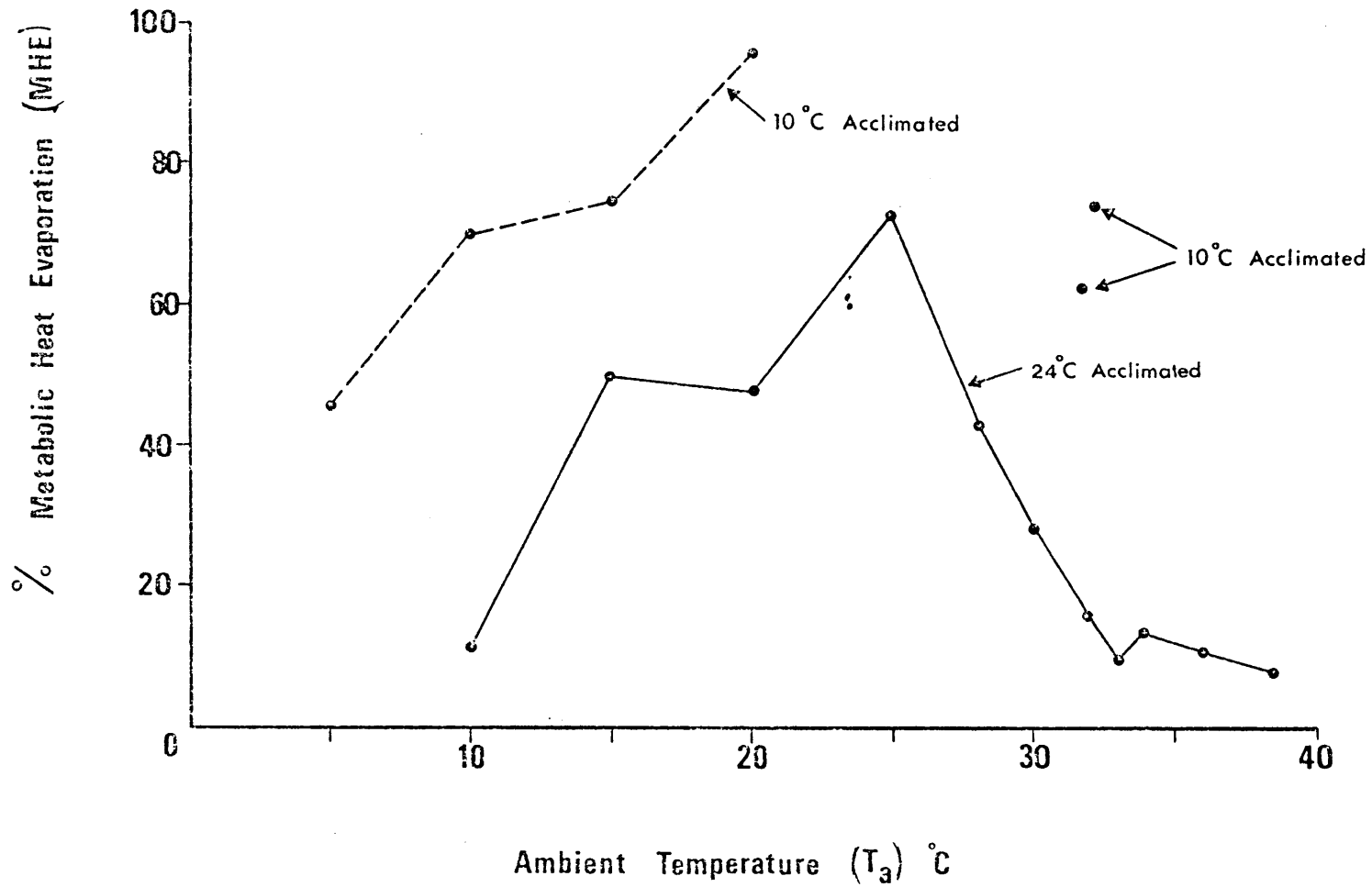
Fig. 26: Percent of metabolic heat loss dissipated by evaporation by five adult giant rats accli= mated to 24°C (solid line) and 10°C (dashed line). N = 10
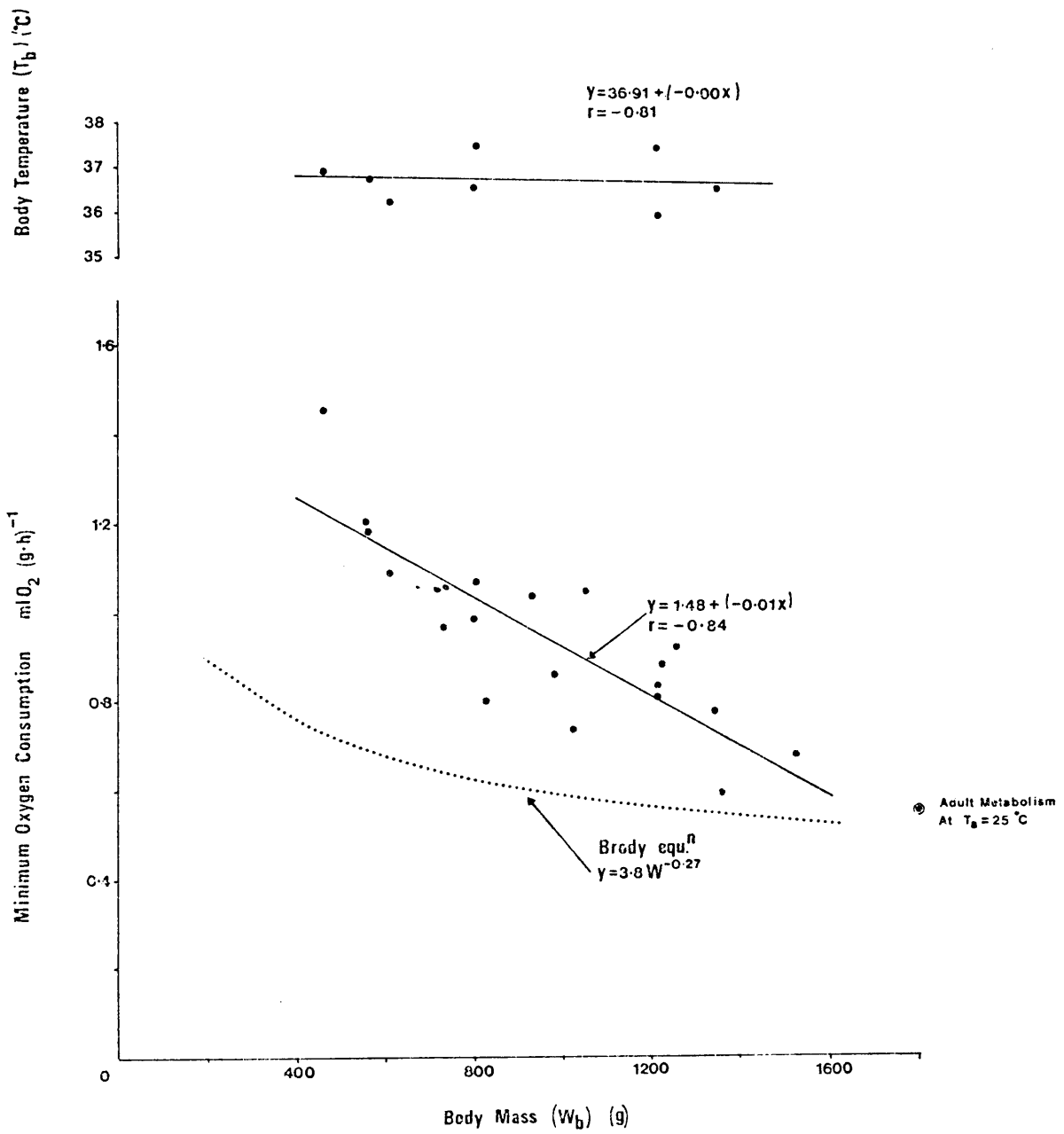
FIG. 27: Minimum oxygen consumption and body temperature
of growing griant rats at 25°C. N = 4.

averaged $36,65 \pm 0,05$ °C.

Evaporative water loss also decreased with an increase in body mass (Fig. 28). At 55 days old the EWL was $0,44 \pm 0,04$ mg H_2O $(g.h.)^{-1}$ and decreased to $0,12 \pm 0,07$ mg H_2O $(g.h.)^{-1}$ in giant rats 132 days old.

Making the same assumptions for calculating the conductance energy and MHE, an increase in body mass resulted in a decrease in total conductance energy from $2,13 \pm 0,28$ J $(g.h.°C)^{-1}$ in 55 day olds to $1,09$ J $(g.h.°C)^{-1}$ in 132 day old giant rats (Table 16). Over the same range of body masses the MHE declined from $49,2$ % to $27,8$ %.
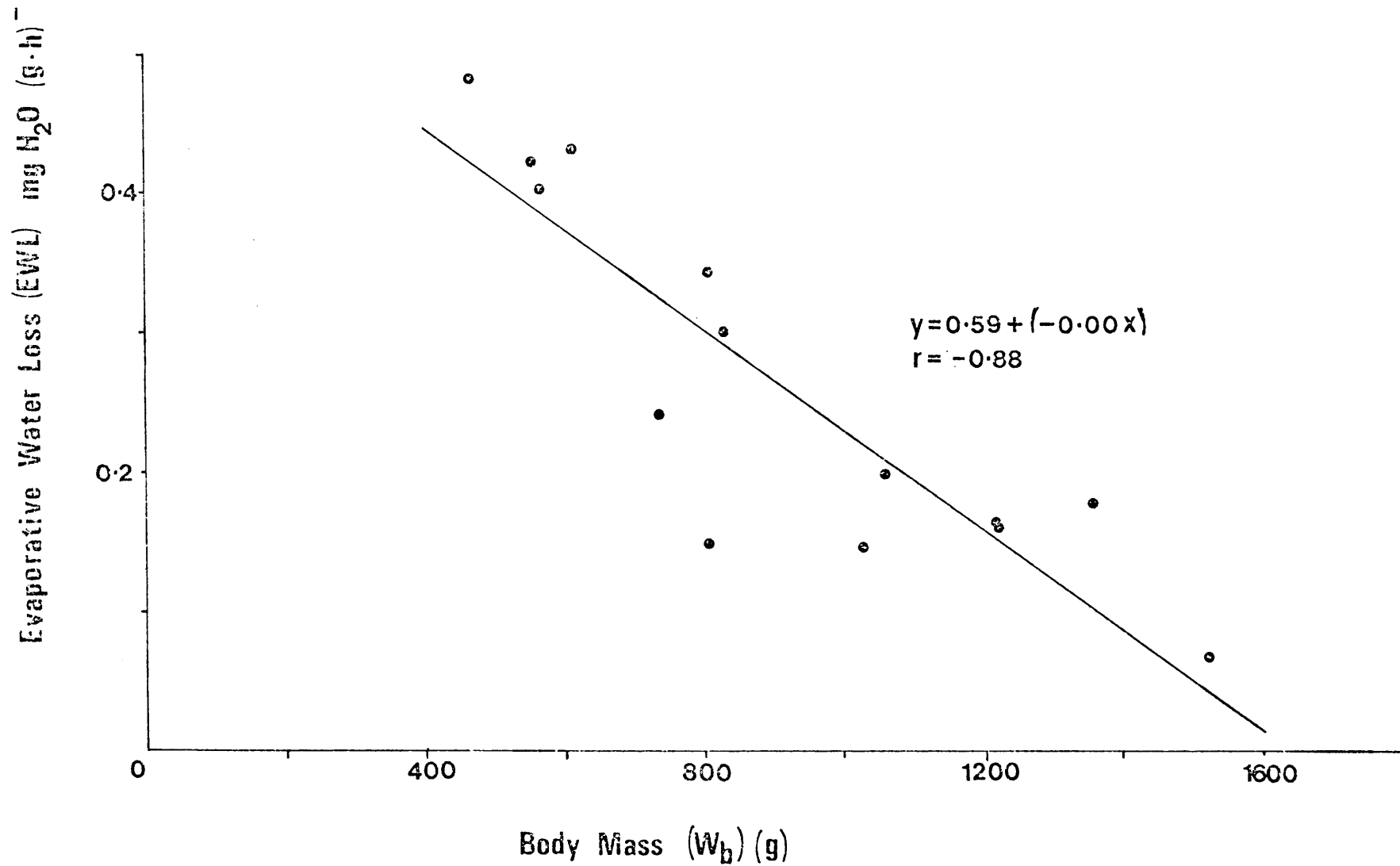
Fig. 28:   Evaporative water loss (EWL) of growing
            giant rats at 25°C.   N = 4.

Table 16   Total conductance and evaporative energy of growing giant rats at an ambient tempera= ture of 25°C. N = 4.

Age (Days)	Body Mass (W_b) (g)	Total Conductance (C) (ml $O_2 \cdot g^{-1} \cdot {}^\circ C^{-1}$)	Total energy Conductance (J $\cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}$)	Evaporative Energy (J $\cdot g^{-1} \cdot h^{-1}$)	Metabolic Heat Loss Evaporation (MHE) (%)
55	611,8	0,0945	1,879	1,040	55,3
55	553,1	0,103	2,078	1,008	48,3
56	565,0	0,101	2,036	0,963	47,3
56	465,5	0,126	2,528	1,161	45,9
77	800,8	0,084	1,693	0,826	48,8
77	829,4	0,069	1,378	0,816	59,3
78	734,0	0,083	1,658	0,576	34,7
92	1026,1	0,631	1,267	0,353	27,9
91	804,1	0,091	1,830	0,358	19,6
115	1219,0	0,071	1,431	0,379	26,5
115	1219,3	0,068	1,383	0,384	27,8
113	1258,5	0,079	1,578	0,329	20,9
114	1059,9	0,090	1,802	0,476	26,4
131	1361,2	0,051	1,016	0,422	41,6
133	1521,4	0,058	1,159	0,161	13,9

DISCUSSION

ADULTS

Metabolism

Giant rats were unable to cope with high ambient temperatures but they can adapt to temperatures as low as 10°C.

With a change in acclimation temperature from 10 to 24°C there was a subsequent shift of the thermoneutral zone (TNZ) from 18 - 30°C to 23,5 - 34°C respectively which would increase heat resistance. Such shifts in the TNZ are frequently found in other rodent species (Hart 1971; Wunder, Dobkin & Gettinger 1977). The fact that the minimal oxygen consumption values of the two groups did not differ significantly indicated that the two accli= mation temperatures lie within the thermal range of ambient tem= peratures at which giant rats can thermoregulate efficiently, without changing their thermoregulatory 'strategy'.

The resting metabolic rates (RMR) of giant rats acclimated to 10 and 24°C were found to be 7% and 22% greater respectively than the basal metabolic rate (BMR) predicted by the Brody equation:

$$\text{where} \quad M = 3,8 \ W^{-0,27}$$

$$M = \text{metabolism } (O_2 \text{ consumption})$$

$$W = \text{body mass (g)}$$

which predicts the metabolic rates of animals living in temperate

regions (Brody 1945; Hart 1971).   Since RMR and BMR only differ in the heat production of specific dynamic action within the TNZ it places estimates of the BMR of the giant rats in close agreement with those predicted.   Having a BMR close to or above the predicted metabolism is characteristic of animals living within temperate climates not exposed to high ambient temperatures (Hart 1971), frugivores (McNab 1969, 1980) and where there is no great need for water conservation (McNab 1979; Scheck 1982).   The giant rat fulfills all these requirements, being distributed with= in the moist tropical savannah where the rainfall ranges from 800 to 1400 mm per annum (Compare Fig. 1 with Fig. 2).   In their diet as found by Morris (1963), Rosevear (1969), Ajayi (1979) and, the present study (Tables 1 & 2) they showed a preference for soft, fleshy fruits which satisfy their water needs, reducing the importance of conserving water.   Consequently a reduction in metabolism and subsequent reduction in water loss is not essential for the survival of giant rats within their distributional range.

Giant rats acclimated to the two different temperatures showed different responses to high ambient temperatures.   Those accli= mated to 10°C showed a significant increase in metabolism beyond T_a = 30°C.   Unfortunately the body temperature (T_b) data are not complete but the fact that T_b rose to 38,4°C at T_a = 33°C from the normal T_b of 33,50 $\pm$ 0,18°C indicates a limited ability to control T_b at high ambient temperatures (Fig. 25).   Giant rats acclimated to 24°C showed a similar response in their T_b which rose beyond T_a = 30°C but their metabolism only rose sig=

significantly at a higher T_a = 34°C.   This indicates that limited hyperthermia could be withstood, before having to in= crease their metabolism.   From Fig. 24 a drop in the EWL is associated with this rise in body temperature indicating that water conservation is important at high ambient temperatures and that hyperthermia would be endured to save body water. The fact that the average T_b for those acclimated to 10°C was lower than that found for giant rats acclimated to 24°C is probably a result of the acclimation itself and the continuous= ly low T_a which would not be experienced in nature.   Therefore the T_b recorded for giant rats acclimated to 24°C may be a more realistic estimate of their actual field T_b's.

Conductance

As was found for the minimum oxygen consumption for giant rats acclimated to two different temperatures, the conductance values below thermoneutrality were not significantly different, even though that found for 10°C acclimated animals was only slightly lower than for the warm acclimated ones, as would be expected from a slight increase in insulation (Table 17.)   This indicates that the two acclimated temperatures made no appreciable change in their thermoregulatory 'strategy' and that they could cope with both efficiently.

The conductance values of giant rats acclimated to 10 and 24°C were found to be respectively 65% and 81% greater than those pre=

Table 17   Thermal conductances of giant rats acclimated to 10°C and 24°C compared to different estimates of conductance.

	10°C Acclimated (W_b = 1699,71 g)		24°C Acclimated (W_b = 1841,00 g)	
Conductance ml O_2 (g.h.°C)$^{-1}$		% Difference	Conductance ml O_2 (g.h.°C)$^{-1}$	% Difference
ACTUAL	0,038	---	0,040	---
PREDICTED$_a$	0,023	65	0,022	81
PREDICTED$_b$	0,023	65	0,022	81
PREDICTED$_c$	0,032	19	0,031	29
PREDICTED$_d$	0,033	15	0,032	27

a. $C = 1,00 \ W^{-0,50}$ (Kleiber 1961)

b. $C = 0,95 \ W^{-0,50}$ (Hart 1971)

c. $C = 0,76 \ W^{-0,43}$ (Bradley & Deavers 1980)

d. $C = 1,023 \ W^{-0,51}$ (Aschoff 1981)

dicted from body mass using Kleiber's equation (Kleiber 1961) (Table 17). The Kleiber equation was used because most metabolic data in the literature is compared to it.

Temperature differentials (Δ T_1) are also usually discussed in connection with conductance. It is defined as the tempera= ture differential between an animal and the environment at the lower limit of thermoneutrality:

$$\Delta T_1 \text{ (in °C)} = M/_C = 3,42 \text{ F W }^{0,25}$$

where F = fm/fc (McNab 1979a). The fm describes the mass - independent variations in basal rates [i.e. (measured basal rate)/ (Kleiber's basal rate)] and fc describes the same for conduc= tance [ie (measured minimal conductance)/(predicted conductance)]. Giant rats acclimated to 10 and 24°C had temperature differentials of 13,5 and 15.1°C respectively which were 1,0 and 1,7% respec= tively greater than that predicted. Resting metabolic rates were used in the calculation and therefore using basal rates would probably make the temperature differential less than predicted.

Since giant rats are large (Table 8) and have small surface to volume ratios, high metabolic rates and are burrowers, they there= fore need a high conductance to dissipate heat and reduce the probability of overheating. According to McNab (1979 a) animals living within burrows also have lower temperature differentials (ie. a low metabolism and high conductance) which would facili= tate heat loss but this was not found in giant rats. McNab (1979 a) found for large (greater than 80 g) burrowing mammals

such as the aardvark (<u>Orycteropus</u> <u>afer</u>), European badger (<u>Meles</u> <u>meles</u>) and armidillos (<u>Dasypus</u> <u>novemcinctus</u>) that they all have low metabolic rates, high conductances and low temperature diffe=rentials. How then can the giant rat which is a large burrowing rodent survive in its environment? The answer lies in the site of construction and depth of its burrow. Giant rat burrows are always constructed under plant cover to provide cool conditions and the bush temperature at 5 cm above ground level outside the burrow entrances was found to average 16,20 $\pm$ 4,62°C over a year (Table 3). The burrows themselves were large (45,67 $\pm$ 18,77cm in diameter and 25,64 $\pm$ 9,82 cm high) and were 72,71 $\pm$ 9,01 cm below the surface. Burrow temperatures at approximately this depth were found to be 16,00 $\pm$ 2,93°C and as this is less than 20°C, they are classified as 'cool' according to McNab (1979 a). It must be noted that these temperatures were not taken in the nest, where one would expect slightly higher temperatures. The entrances and tunnels were large averaging 19,60 $\pm$ 8,55 and 13,67 $\pm$ 3,83 cm respectively and probably enhanced ventilation, keeping the burrows cool as Vogel, Ellington & Kilgore (1973) found adequate ventilation within the burrows of prairie dogs (<u>Cynomys</u> <u>ludovicianus</u>). The fact that giant rats seal off their tunnels, probably as an antipredation measure, would make it more important to construct the burrows in cool environments. It therefore appears that giant rats can live comfortably, with=in burrows because of the cool surrounding environment and depth at which they construct them withoutneeding a low tempera=ture differential.

The tail in giant rats is 10,6% longer than the head body length (Table 8) and is probably an adaptation to aid climbing. Only rodents that are active climbers and are saltorial have tails longer than the head body length. The tail of the giant rat also probably acts as a thermal window to increase conductance at high ambient temperatures because it is thinly haired and becomes bright red with subcutaneous blood at ambient tempera= tures greater than 28 and 30°C in 10 and 24°C acclimated rats respectively. Tail licking was also noticed at these high ambient temperatures, emphasising the point that the tail plays an important role in releasing heat.

In recent years several attempts (Bradley & Deavers 1980; Aschoff 1981) have been made to develop a more accurate allometric de= scription of conductance. The trend has been to increase the amount of data from a wider range of mammalian species. The different equations and percentage differences of the actual conductances of the 10 and 24°C acclimated giant rats from the predicted values are presented in Table 17. The equation of Aschoff (1981) is the most accurate since it makes the closest estimate to the actual value but as mentioned previously, Klei= bers' formula (Kleiber 1961) was used in this study owing to its wide use.

Evaporative Water Loss (EWL)

Acclimation in giant rats had a dramatic effect upon the extent

of usage of evaporative cooling.   Giant rats acclimated to 10°C
were totally reliant upon their evaporative cooling at high
ambient temperatures and not upon dry thermal conductance.
This is emphasized by the 95% of metabolic heat lost at T_a = 20°C
by evaporative cooling (Fig. 26).   However giant rats acclima=
ted to 24°C showed better control of their EWL up to T_a = 28°C.
Beyond that more reliance was placed upon thermal conductance
and hyperthermia in order to save body water.   However since
EWL was again increased at ambient temperatures greater than
33°C this   means that only limited hyperthermia could be en=
dured.   This indicates that giant rats are not adapted to cope
with high ambient temperatures.   Salivation did not play ·an
important role in thermoregulation in the rats at high tempera=
tures as had been found in the hairy nosed wombat (Lasiorhinus
latifrons) (Wells'1972) and other rodents (Hart 1971).   Giant
rat chins were found to be damp at ambient temperatures greater
than 34°C.

Therefore by remaining within the cool burrows during the day
and being nocturnally active at temperatures around 16.19 $^{\pm}$ 4.62°C
they are never exposed to high ambient temperatures.   Since their
food is predominantly soft fleshy fruits, water does not need to.
be conserved and evaporative cooling can be used in preference to
dry conductance in regulating body temperature.   Hudson & Rummel
(1966) also found that the burrow was important in body water
conservation, because two species of Liomys fed air - dried seeds
and exposed to high ambient temperatures lost body water but if
permitted to burrow, their weights remained constant.   Little

has been done on water regulation in rodents living within mesic en=
vironments but Heteromys, which inhabits tropical rainforests
of Central America appears very similar to giant rats by
having high metabolic rates and high conductances (McNab 1979 b)
but their water regulatory ability is quite well developed
which appears to be a family characteristic (MacMillen & Hinds
1983).   Therefore by being selective in burrow site and depth,
rodents with poor water conservatory abilities and average tem=
perature differentials may be able to penetrate into environ=
ments for which they are not physiologically adapted.

JUVENILES

With an increase in mass (over the studied range) in growing giant
rats there was a corresponding decrease in metabolism, conductance
and evaporating cooling.   For both metabolism and conductance
there was a reduction in the difference between the actual values
and that of predictions based on body mass.   Between 55 and 132
days the actual resting metabolic rates decreased from 78 to 32%
greater than the basal metabolic rates predicted from body mass
(Brody equation (Hart 1971)) (Fig. 27).   Over the same range the
conductance dropped from 146 to 101% greater than that predicted
using the Kleiber equation (Kleiber 1961).   These decreases in
the differences are a result of the growth of the animals, in
other words, the change in surface area to volume ratio and their
insulation.

McClure & Porter (1983) found there to be many properties such

as fur thickness, hair length and diameter of hair, involved in controlling heat loss through the insulation of neonatal cotton rats. They found in <u>Sigmodon</u> <u>hispidus</u> that the fur depth was the most important variable in controlling heat loss in nest= lings but in adults all the properties of the fur were important. In the 55 day old giant rats, the adult fur covered the entire body except the head and shoulders which were covered by fluffy juvenile fur and the thinly haired tail (Fig. 15). At this stage the hairs on both the dorsal and ventral sides were found to be 11 mm long (Fig. 12). By day 86 the adult fur had covered the head and shoulders completely, but the hair length reached that, found in adults after 129 days. Therefore changes within the insulation of growing giant rats were probably responsible for some of the decrease in conductance. With the increase in body mass there was also a decrease in total evaporative water loss (Fig. 28) which seems obvious with the decrease in mass specific metabolism. However, the metabolizable energy of evaporation (MHE) between 55 and 132 days decreased indicating that the relative importance of evaporative cooling in dissipa= ting heat decreased and dry thermal conductance increased. So by the time they reach adult size, dry thermal conductance could play a more prominent role in controlling heat loss. It must again be emphasized the possible important role played by the large tail in this function. It therefore appears that evapo= rative cooling and insulation change together in a complex manner regulating heat loss in growing rats similar to that found in adults.

How do these results relate to those measured in the field?
Only two young giant rats were caught during the entire field
study, one weighing 640 g (about 60 days old) and the other
990 g (about 98 days old). This means that either the young
are very cautious or do not leave the nest till a late age.
Ewer (1967) and in the present study (Fig. 15) recorded the
first foraging journeys of the young kept in captivity to be
when they were between 43 and 52 days of age, which corresponds
to the youngest rat found in the field. Interestingly, the
fur coats of these young were quite well developed, with the
adult fur covering the ventral and lateral sides and the fluffy
juvenile fur covering the dorsum. Probably the emergence of
the pups only takes place once thermoregulation is well developed
which coincides with the advent of weaning and development of
good insulation.

Giant rats probably then have a similar life history 'strategy'
as that found in the wood rat, Neotoma floridana, where develop=
ment is slow and the onset of active thermoregulation is deferred
to larger body masses when lower metabolic rates occur thereby
allowing more efficient growth in the earlier stages (McClure
& Randolph 1980). The food hoarding practised by giant rats,
as in wood rats, probably enhances the mothers' ability to give
increased maternal care to her pups thereby indirectly reducing
the chances of predation.

More research is required on the development of thermoregulatory

mechanisms coupled with physical and behavioural development to draw proper conclusions on the life history strategies of the giant rat, but all the signs indicate that giant rats have the 'slow' life history strategy characteristic of the larger rodents.

CHAPTER 8

CONCLUSIONS

The following can be concluded about giant rats relating their distribution, habits and habitat to their anatomy and physio= logy:

1. Giant rats show a general inability to withstand high ambient temperatures, greater than 30 - 33°C. They escape these conditions by being active outside their burrows nocturnally, occupying cool burrows in shaded environments and restricting their distribution to the moist savannah regions of Africa.

2. They spent little time (23,44% or 3,1 h) of the noctur= nal activity period active outside their burrows, there= by avoiding predation and saving energy by remaining in the burrow eating the hoarded food. Less exposure to the outside ambient temperatures would also reduce the costs of thermoregulation.

3. The home ranges of giant rats were smaller than those predicted for an omnivore according to the formula of Halstad & Bunnell (1979). This may result from either a productive habitat or efficient foraging behaviour or both of these factors. Restricting activity to a smaller area would also reduce the chances of predation. Home ranges calculated by the linked cell method (LC)

are more accurate in determining the actual area
utilized than those estimated by the minimum area
method (MAM). The latter method would equate more
with a territory.

The confinement of activity to habitats with cover is
also suggested as a possible means of avoiding pre=
dation which is probably why they exploit avocado
and macadamia orchards infrequently.

4. The altriciality and slow development of giant rat pups
   are also a characteristic of their burrowing habit.
   Since their birth and weaning masses and growth rates
   are lower than predicted, following Millar (1977), and
   the pups remain in parental care for a period after
   weaning, there appears to be a trade-off between mother
   and pups. During the ectothermic stage of development,
   the pups direct most of their energy into growth and
   delay thermoregulatory functions until they reach a
   larger body size. However, introduction of solid food
   at an early stage to the pups, through the mothers hoar=
   ding behaviour, would decrease the burden posed by lacta=
   tion on the mother, but she has to compensate by continued
   maternal care after weaning.

5. The preference for soft fruits and inefficiency in diges=
   tion of fibrous foods (Faturoti et al 1980; Tewe & Ajayi

1982) does not correlate well with the adaptations for om=
nivory and herbivory seen in the gut morphology of giant
rats.   This suggests flexibility in the morphology which
could be preadaptive should the diet change.   Phylogeny
may also play a rôle in determining gut morphology as
similarities in caecal structure were found in another
cricetid rodent, the dwarf hamster.

The enlarged, papillated corpus and fornix ventricularis
of the stomach is associated with prolonged amylase acti=
vity and fermentation of glucose and not with fibre diges=
tion.   The average sized caecum showed structural adapta=
tions which probably aid retention and separation of the
digesta.   The Tunica mucosa of 'the caecum showed charac=
teristics associated with absorption which have been found
in other rodents (Snipes 1979a;   1979b).

The first colonic loop had large plique which are also thought
to facilitate absorption.

The slow passage rates of digesta in giant rats may facili=
tate efficient digestion of food, absorption of water, elec=
trolytes   and metabolites.   It could also enhance fibre
digestion.

6.   The slightly higher than predicted resting (RMR) and ave=
rage daily metabolic rates (ADMR) of giant rats can be

accounted for by their distribution in temperate, moist
environments, infrequent exposure to high ambient tempera=
tures and consumption of fruits.

Evaporative cooling is their most important mechanism
of heat loss at higher ambient temperatures. This depen=
dance on water is seen first in their restriction to regions
receiving 800 - 1400 mm of rain annually and second their
preference for soft, fleshy fruits and tubers in the wild.

The decrease in metabolism, conductance and metabolizable
heat of evaporation (MHE) with the increase in body mass
in growing giant rats were suggested to be associated with
the development of insulation in the young.

In conclusion the giant rats distribution, habits and habi=
tat selection are governed by thermoregulatory, energetic
and behavioural requirements. They require a cool, moist,
shaded environment to escape high ambient temperatures and
detection from predators and need moist foods to satisfy
their water demands.

SUMMARY

The burrows of giant rats were always located in cool, moist habitats. From burrow content analysis, giant rats were found to prefer soft, fleshy fruits.

The home ranges of giant rats were found to be smaller than predicted with more accurate estimates obtained using the linked cell method (LC) than from the widely used minimum area method (MAM), using convex polygons. Giant rats were found to be ac= tive only in the nocturnal period for 3,1 h and restricted their activity to areas providing cover.

The slow growth rates and behavioural development in giant rat pups is probably a result of their burrowing habit.

The gut morphology showed adaptations associated with omnivory and herbivory. The large papillated corpus probably prolongs activity of amylase and Bacillus. The caecum had features associated with digesta retention which may enhance the giant rats' limited ability to digest fibre.

The resting metabolic rate (RMR) and conductance (C) of giant rats acclimated to 10°C and 24°C were greater than predicted by body mass and their thermoneutral zone were 18 - 30°C and 23,5 - 34,0°C respectively. Evaporative water loss (EWL) was found to be the most important mechanism regulating heat loss

and with a decrease in EWL at ambient temperatures greater than 30°C, hyperthermia was noted.

With an increase in juvenile mass, corresponding reductions of RMR, C and EWL were noted.

OPSOMMING

Die gate van reuse rotte was altyd in koel en klam habitatte geleë. Van uit die gat inhoud analises kon afgelei word dat reuse rotte voorkeur gee aan sagte vlesige vrugte.

Die tuisgebiede van reuse rotte was kleiner as wat voorspel word en meer akkurate skattings is van die skakel sel metode (LC) as van die gebruikmaking van die gewone minimum area metode (MAM) met konvex polygone verkry. Dit is gevind dat reuse rotte al= leen snags aktrief is vir 3,1 h en slegs onder plant bedekking beweeg.

Die stadige groei tempo's en gedragsontwikkeling in jong reuse rotte is heelwaarskynlik 'n resultaat van hul grawende gedrag.

Die spysverteringskanaal morfologie van reuse rotte het aanpas= sings getoon geassosieer met omnivoor en herbivoor voedingswyses. Die groot papillae in die corpus is heelwaarskynlik 'n gevolg van aanhoudende amilase en <u>Bacillus</u> aktiwiteite. Die sekum het kenmerklike eienskappe getoon geassosieer met voedsel reten= sie. Die verhoogde voedsel retensie in die deel, kan 'n gevolg wees van die beperkte vesel verteringsvermoë van reuse rotte.

Reuse rotte geakklimatiseer by 10°C en 24°C het hoër rustende metaboliese tempo's (RMT) en liggaamsgeleidinge (C) getoon as wat voorspel word vir hul liggaamsmassa. Hul termoneutrale zones (TNZ) het gewissel tussen 18 - 30°C en 23,5 - 34,0°C res=

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pektiewelik.   Verdampende water verlies (EWL) was die belang=
rikste meganisme vir hitte verlies regulering verantwoordelik
was en het afgeneem by hoër temperature as 30°C waartydens
hiper termia in die rotte voorgekom het.

Die RMT, C en EWL het tegelykertyd afgeneem met die verhoging
in jong diere se massa.

REFERENCES

Acocks, J.P.H. 1975. Veld types of South Africa. 2nd
Edition. Memoirs of the Botanical Survey of South
Africa. No. 40. Dept. Agricultural Technical Services,
South Africa.

Ajayi, S.S. 1974. Giant rats for meat and some taboos.
Oryx 12: 379 - 380.

Ajayi, S.S. 1975a. Observations on the biology, domestication
and reproductive performance of the African giant rat,
Cricetomys gambianus Waterhouse in Nigeria. Mammalia
39: 343 - 364.

Ajayi, S.S. 1975b. Caging and breeding the African giant rat.
I. Inst. Animal Technicians Lond. 25(2): 75.

Ajayi, S.S. 1977. Field observations on the African giant rat
Cricetomys gambianus Waterhouse in Southern Nigeria.
E. Afr. Wildl. J. 15: 191 - 198.

Ajayi, S.S. & Tewe O.O. 1978. Distribution of burrows of
the African giant rat (Cricetomys gambianus Waterhouse)
in relation to soil characteristics. E. Afr. Wildl. J.
16: 105 - 111.

Ajayi, S.S., Tewe, O.O. & Faturoti, E.O. 1978. Behavioural changes in the African giant rat. (Cricetomys gambianus Waterhouse) under domestication E. Afr. Wildl. J. 16: 137 - 143.

Amlaner, C.J., Jr. 1980. The design of antennas for the use in radio telemetry. In: A Handbook on Biotelemetry and Radio Tracking, pp 251 - 261.(eds). Amlaner, C.J., Jr. & MacDonald, D.N. Pergamon Press, Oxford.

Aschoff, J. 1981. Mini review: Thermal conductance in mammals and birds: Its dependance on body size and circadian phase. Comp. Biochem. Physiol. 69A: 611 - 619.

Balch, C.C. & Campling, R.C. 1965. Rate of passage of digesta through the ruminant digestive tract. In: Physiology of Digestion in the Ruminant (ed.) Dougherty, R.W. Butterworths, London.

Baker, C.M. & Meester, J. 1977. Postnatal, physical and behavioural development of Praomys (Mastomys) natalensis (a. Smith, 1834). Z. Saugetierk. 42: 295 - 306.

Batzli, G.O. & Cole, F.R. 1979. Nutritional ecology of microtine rodents: digestibility of forage. J. Mamm. 60: 740 - 750.

Behmann, H. (1973). Vergleichend - und funktionell- anatomische Untersuchungen am Caecum und Colon myomorpher Nagetiere. Z. Wiss. Zool. 186: 173 - 294.

Björnhag, G. 1972. Separation and delay of contents in the rabbit colon. Swedish J. agric. Res. 2: 125 - 136.

Bradley, S.R. & Deavers, D.R. 1980. A re-examination of the relationship between thermal conductance and body weight in mammals. Comp. Biochem. Physiol. 65A: 465 - 476.

Brody, S. 1945. Bioenergetics and Growth. Reinhold. New York.

Calhoun, J.B. & Casby, J.U. 1958. Calculation of home range and density of small mammals. Publ. Hlth Monogr. 55: 1 - 24.

Camain, R., Quenum, A., Kerrest, J. & Goueffans, S. 1960. Considerations sur l'estomac de Cricetomys gambianus Comp. R. Seanc. Soc. Biol., Paris 154: 1578 - 1579.

Carleton, M.D. 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia; Muroidea), with comments on functional interpretations. Mus. Zool. Univ. Michigan. 146: 1 - 42.

Carleton, M.D. 1981. A survey of gross stomach morphology in Microtinae (Rodentia: Muroidea). Z. Saugetierk. 46: 93 - 108.

Case, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in terrestrial vertebrates. Q. Rev.Biol. 58: 243 - 282.

Cass, T. 1973. Statistical methods in management. Cassell. London.

Chapin, J. 1932. The birds of the Belgian Congo. Bull. Am. Mus. nat. Hist. 65: 1 - 756.

Clemens, E.T. & Stevens, C.E. 1980. A comparison of gastro= intestinal transit time in ten species of mammal. J. agric. Sci., Camb. 94: 735 - 737.

Christian, D.P., Matson, J.O. & Rosenberg, S.G. 1978. Comparative water balance in two species of Liomys (Rodentia: Heteromyidae). Comp. Biochem. Physiol. 61: 589 - 594.

Cranford, J.A. 1977. Home range and habitat utilization by Neotoma fuscipes as determined by radiotelemetry. J. Mamm. 58: 165 - 177.

Dearden, L.C. 1969. Stomach and pyloric sphincter histo= logy in certain microtine rodents. J. Mamm. 50: 60 - 68.

Decopas, F. & Hart, J.S. 1957. Use of the Pauline oxygen analyser for measurement of oxygen consumption of ani= mals in open circuit system and in short-lag closed apparatus. J. appl. Physiol. 10: 388 - 392.

De Graaf, G. 1981. The Rodents of Southern Africa. Butterworths, Durban.

Drodz, A. 1975. Analysis of stomach contents of small mammals. In: Methods for Ecological Bioenergetics. pp. 325 - 333. (eds) Grodzinski, W., Klekowski, R.Z., & Duncan, A. Blackwell Scientific Publ., Oxford, London.

Ehle, F.R. & Warner, R.G. 1978. Nutritional implications of the hamster forestomach. J. Nutr. 108: 1047 - 1053.

Ellerman, J.R., Morrison-Scott, T.C.S. & Haymann, R.W. 1953. Southern African Mammals 1758 to 1951: a reclassification. British Museum (Nat. History) London.

Emmons, L.H. 1975. Ecology and behaviour of African rain= forest squirrels. Unpubl. Ph.D. thesis, Cornell University, Ithaca, 269 pp.

Emmons, L.H. 1981. Morphological, ecological and behavioural adaptations for arboreal browsing in Dactylomys dactylinus (Rodentia, Echimyidae). J. Mamm. 62: 183 - 189.

Emmons, L.H. 1983. A field study of the African brush=
tailed porcupine, Atherurus africanus by radiotelemetry.
Mammalia 47: 183 - 194.

Ewer, R.F. 1967. The behaviour of the African giant rat
Cricetomys gambianus. Z. Tierpsychol. 21: 6 - 79.

Faturoti, E.O., Tewe, O.O. & Ajayi, S.S. 1982. Crude fibre
tolerance by the African giant rat (Cricetomys gambianus
Waterhouse). Afr. J. Ecol. 20: 284 - 292.

Gargett, V. 1977. Mackinders eagle owl in the Matopos
Rhodesia. Proc. symp. African Predatory Birds. pp 46 -
61. Pretoria: Northern Transvaal Ornithological
Society.

Genest-Villard, H. 1967. Revision du genre Cricetomys
(Rongeuro, Cricetidae). Mammalia 31: 390 - 455.

Gessaman, J.A. 1973. Methods of estimating the energy
cost of free existence, pp. 3 - 31. In: Ecological
Energetics of Homeotherms (ed.) Gessaman, J.A.
Monograph Series Vol. 20, Utah State University Press,
Logan, Utah.

Getty, T. 1981. Analysis of central-place space use
patterns: the elastic disc revisited. Ecology 62:
907 - 914.

Gittleman, J.L. & Harvey, P.H. 1982. Carnivore home-range
size, metabolic needs and ecology. Behav. Ecol. Socio=
biol. 10: 57 - 63.

Gordon, M.S., Bartholomew, G.A., Grinnel, A.D. Jorgensen, C.B.
& White, F.N. 1977. Animal Physiology: Principles
and Adaptations. MacMillen Publ. Co., New York.

Gorgas, M. 1967. Vergleichend-anatomische Untersuchungen
am Magem-Darm-Kanal der Sciuromorpha, Hystricomorpha
und Caviomorpha (Rodentia). Z. Wiss. Zool. 175: 237 -
404.

Grodzinski, W. 1975. Energy flow through a vertebrate
population. In: Methods for Ecological Bioenergetics
pp. 65 - 94. (eds) Grodzinski, W., Klekowski, R.Z. &
Duncan, A. Blackwell Scientific Publ., Oxford.

Harestad, A.S. & Bunnell, F.L. 1980. Home range and body
weight - a re-evaluation. Ecology 60: 389 - 402.

Hart, J.S. 1971. Rodents. In: Physiology of Thermoregu=
lation pp. 2 - 130. (ed.) Whittow, G.E., Academic
Press, London.

Hudson, J.W. & Rummel, J.A. 1966. Water metabolism and
temperature regulation of primitive Heteromyids, Liomys
salvani and Liomys irroratus. Ecology 47: 345 - 354.

Humason, G.L. 1962. Animal Tissue Techniques. W.H. Freeman & Co., San Francisco.

Hume, I.D. & Warner, A.C.I. 1980. Evolution of microbial digestion in mammals. In: Digestive Physiology and Metabolism in Ruminants, (eds) Ruckerbusch, Y.X. Trivend, P., M.T.P. Press, Lancaster.

Iwuala, M.O.E., Braide, E.I. & Maduka, N. 1980. Observations on the food habits of some African rodents. Rev. Biol. Trop. 28: 227 - 236.

Kenagy, G.J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54: 1201 - 1219.

Kleiber, M. 1961. The Fire of Life. Wiley, New York.

Knight, M.H. & Skinner, J.D. 1981. Thermoregulatory, re= productive and behavioural adaptations of the big eared desert mouse, Malacothrix typica to its arid environment. J. Arid. Environ. 4: 137 - 145.

Kokkin, M.J. 1981. Stomach morphology of the giant rat Cricetomys gambianus Waterhouse (1840). Unpubl. B.Sc. (Hons) thesis, Rhodes University, Grahamstown.

Kostelecka- Myrcha, A. & Myrcha, A. 1964. The rate of passage of food stuffs through the alimentary tract of certain Microtidae under laboratory conditions. Acta theriol. 9: 37 - 53.

Kramer, D.L. & Nowell, W. 1980. Central place foraging in the eastern chipmunk Tamias striatus. Anim. Behav. 28: 772 - 778.

Krebs, J.R. 1980. Optimal foraging, predation risk and territory defence. Ardea 60: 83 - 90.

Layne, J.N. 1968. Ontogeny. In: Biology of Peromyscus (Rodentia), pp. 148 - 248 ,(ed.) King, J.A. American Society of Mammalogists, U.S.A.

Mace, G.M. & Harvey, P.H. 1983. Energetic constraints on home range size. Am. Nat. 121: 120 - 132.

MacDonald, D.W., Ball, F.G. & Hough, N.G. 1980. The evalu= ation of home range size and configuration using radio tracking data. In: A Handbook on Biotelemetry and Radio Tracking, pp. 405 - 424 ,(eds) Amlaner, C.J. Jr & MacDonald, D.W. Pergamon Press, Oxford.

MacMillen, R.E. & Hinds, O.S. 1983. Water regulatory effi= ciency in heteromyid rodents: a model and its application. Ecology 64: 152 - 164.

Maddock, A.H. 1981. Gastric morphology of the white-tailed
    rat Mystromys albicaudatus (A. Smith 1834) and preliminary
    investigations of its digestive processes. Unpubl.
    M.Sc. thesis, Rhodes University, Grahamstown.

Maddock, A.H. & Perrin, M.R. 1981. A microscopical exami=
    nation of gastric morphology of the white-tailed rat
    Mystromys albicaudatus (Smith 1834). S. Afr. J. Zool.
    16: 237 - 247.

Majer, J.D. 1973. Observations on the activity patterns of
    the forest giant rat Cricetomys emini (Mammalia: Crice=
    tidae) Mammalia 37: 390 - 393.

Maxwell, C.S. & Morton, M.L. 1975. Comparative thermoregu=
    latory capabilities of neonatal ground squirrels. J.
    Mamm. 56: 821 - 828.

McBee, R.H. 1977. Fermentation in the hindgut. In: Micro=
    bial Ecology of the Gut, pp. 185 - 217 (eds) Clarke,
    R.T.J. & Bauchop, T., Academic Press, London.

McClure, P.A. & Porter, W.P. 1983. Development of insula=
    tion in neonatal cotton rats (Sigmodon hispidus).
    Physiol. Zoöl. 56: 18 - 32.

MacClure, P.A. & Randolph, J.C. 1980. Relative allocation of energy to growth and development of homeothermy in the eastern woodrat (Neotoma floridana) and hispid cotton rat (Sigmodon hispidus). Ecol. Monogr. 50: 199 - 219.

McManus, J.J. 1971. Early postnatal growth and the develop= ment of temperature regulation in the Mongolian gerbil Meriones unguiculatus. J. Mamm. 52: 782 - 792

McNab, B.K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97: 133 - 140.

McNab, B.K. 1969. The economics of temperature regulations in neotropical bats. Comp. Biochem. Physiol. 31: 227 - 268.

McNab, B.K. 1979a. The influence of body size on the ener= getics and distribution of fossorial and burrowing mammals. Ecology 60: 1010 - 1021.

McNab, B.K. 1979b. Climatic adaptation in the energetics of heteromyid rodents. Comp. Biochem. Physiol. 62A: 813 - 820.

McNab, B.K. 1980. Food habits, energetics and the population biology of mammals. Am. Nat. 116: 106 - 124.

Meester, J. & Hallett, A.F. 1970. Notes on the early post=
natal development in certain southern African Muridae
and Cricetidae. J. Mamm. 51: 703 - 711.

Millar, J.S. 1977. Adaptive features of mammalian
reproduction. Evolution, Lancaster, Pa. 31: 370 - 386.

Montgomery, G.G. & Sunquist, M.E. 1978. Habitat selection
and use by two-toed and three-toed sloths. In: The
Ecology of Arboreal Folivores. pp. 329 - 359. (ed.)
Montgomery, G.G. Smithsonian Institution Press, Washington.
D.C.

Morris, B. 1963. Notes on the giant rat (Cricetomys gam=
bianus) in Nyasaland. Afr. wildLife 17: 103 - 108.

Palgrave, K.C. 1977. Trees of Southern Africa. C. Struik
Publishers, Cape Town.

Panagis, K. & Nel, J.A.J. 1981. Growth and behavioral
development in Thamnomys dolichurus. Acta theriol.
26: 381 - 392.

Parra, R. 1978. Comparison of foregut and hindgut
fermentation in herbivores. In: The Ecology of Arboreal
Foliveres. pp. 205 - 229. (ed.) Montgomery, G.G.,
Smithsonian Institution Press, Washington, D.C.

Perrin, M.R. & Curtis, B.A. 1980. Comparative morphology of the digestive system of 19 species of Southern African myomorph rodents in relation to diet and evolution. S. Afr. J. Zool. 15: 22 - 33.

Perrin, M.R. & Maddock, A.H. 1983. Anatomical and nutri= tional adaptations in African Rodents. S. Afr. J. Anim. Sci. 13: 23 - 25.

Pitman, C.R.S. & Adamson, J. 1978. Notes on the ecology and ethology of the Giant Eagle Owl Bubo lacteus (Temminck). Pt. 2. Honeyguide 96: 25 - 52.

Popenoe, W. 1920. Manual of Tropical and Subtropical Fruits. MacMillen Co., New York.

Pyke, G.H., Pullram, H.R. & Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52: 137 - 154.

Randolph, P.A., Randolph, J.C., Mattingly, K. & Foster, M.M. 1977. Energy costs of reproduction in the cotton rat Sigmodon hispidus. Ecology 58: 31 - 45.

Rautenbach, I.L. 1978. The Mammals of the Transvaal. Ph.D. thesis, University of Natal, Pietermaritzburg.

Rérat, A.   1978.   Digestion and absorption of carbonhydrates
    and nitrogenous matters in the hindgut of the omnivorous
    nonruminant animal.   J. Anim. Sci. 46: 1808 - 1837.

Roberts, A.R.   1951.   The Mammals of South Africa.   Trustees
    of the Mammals of S.A. Book Fund, Central News Agency,
    Johannesburg.

Rodale, J.I.   1961.   Complete Book of Food and Nutrition
    Rodale Book Inc.   Emmaus, Pennsylvannia.

Rosevear, D.R.   1969.   The Rodents of West Africa.   Trustees
    of the British Museum (Nat. History).   London.

Sampson, R.J.   1973.   Surface II   Graphics System.   Kansas
    Geological Survey,   Lawrence, Kansas.

Scheck, S.H.   1982.   A comparison of thermoregulation and
    evaporative water loss is hispid cotton rat Sigmodon
    hispidus texianus from northern Kansas and south-central
    Texas.   Ecology 63:   361 - 369.

Schoener, T.W.   1971.   Theory of feeding strategies.   Ann.
    Rev. Ecol. Syst. 11:   369 - 404.

Scott, E.D.   1979.   A comparison of postnatal development in
    South African myomorph rodents.   Unpubl. MSc. thesis
    University of Natal, Pietermaritzburg.

Siegel, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill, Kogakusha, Tokyo, Düsseldorf.

Smithers, R.H.N. 1966. The Mammals of Rhodesia, Zambia and Malawi. Collins, London.

Smithers, R.H.N. 1975. Guide to the rats and mice of Rhodesia. Nat. Mus. Monum. Rhod. Salisbury, Rhodesia.

Smithers, R.H.N. 1983. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.

Smithers, R.H.N. & Wilson, V.J. 1979. Checklist of Rhodesian Mammals. Mus. Mem. Nat. Mus. Monum. Rhod.; No 9 Salisbury, Zimbabwe-Rhodesia.

Snipes R.L. 1979a. Anatomy of the caecum of the dwarf hamster (Phodopus sungorus). Anat. Embryol. 157: 329 - 346.

Snipes R.L. 1979b. Anatomy of the caecum of the vole Microtus agrestis. Anat. Embryol. 157: 181 - 203.

Snipes R.L. 1981. Anatomy of the caecum of laboratory mouse and rat. Anat. Embryol. 162: 455 - 474.

Snipes R.L., Clauss, W, Weber, A. & Hörnicke, H.   1982.
Structural and functional differences in various divi=
sions of the rabbit colon.   Cell Tissue Res.   225!
331 - 346.

Suída, S. & Szymanska, Z.   1961.   Comparative investigations
of the salivary glands of small rodents.   Acta theriol.
5:   141 - 151.

Taylor, K.D. & Quy, R.J.   1978.   Long distance movements
of a common rat (Rathus norvegieus)' revealed by radio
tracking.   Mammalia   42:   63 - 71.

Taylor, C.R., Schmidt-Nielsen, K. & Ruab, J.L.   1970.
Scaling of the energetic cost of running to body size
in mammals.   Am. J. Physiol.   219:   1104 - 1107.

Tewe, O.O. & Ajayi, S.S.   1979.   Utilization of some common
tropical foodstuffs by the African giant rat (Cricetomys
gambianus Waterhouse).   Afr. J. Ecol.   17: 165 - 173.

Tewe, O.O. & Ajayi, S.S.   1982.   Performance and nutrient
utilization by the African giant rat (Cricetomys gambianus)
on household wastes of some local foodstuffs.   Afr. J.
Ecol. 20:   37 - 41.

Thompson, S.D.   1982.   Spatial utilization and foraging
behaviour of the desert wood rat, Neotcma lepida lepida.
J. Mamm. 63: 570 - 581.

Van Soest, P.J., Uden, P. & Wrick, K.F. 1983. Critique
and evaluation of markers for use in nutrition of humans
and farm and laboratory animals. Nutr. Rep. Int.
27: 17 - 28.

Vogel, S., Ellington, C.P. & Kilgore, V.L. 1973. Wind
induced ventilation of the burrow of prairie-dogs
Cynomys ludovicanus. J. Comp. Physiol. 85: 1 - 14.

Voigt, D.R. & Tinline, R.R. 1980. Strategies for analyzing radio
tracking data. In: A Handbook on Biotelemetry and
Radio Tracking, pp. 387 - 404 (eds) Amlaner, C.J. Jr &
MacDonald, D.W. Pergamon Press, Oxford.

Vorontsov, N. 1962. The ways of food specialization and
evolution of the alimentary system in Muroidea. In:
Symposium Theriologicum. Publ. House Czeck. acad.
Sci.: 360 - 377.

Vorontsov, N. 1967. Evolution of the alimentary system
of myomorph rodents. Publ. House Nauka: 235 pp.

Walter, H. & Leith, H. 1960. Klimadiagram - Weltatlas. Gustav
Fischer Verlag, Jena.

Wellard, G.A. & Hume, I.D. 1981. Digestion and digesta
passage rate in the brushtailed possum, Trichosurus
valpecula (Kerr). Aust. J. Zool. 29: 157 - 166.

Wells, R.T. 1978. Thermoregulation and activity rhythms
in the hairy-nosed wombat, Lasiorhinus latifrons
(Owen), (Vombatidae). Aust. J. Zool. 26: 639 -
651.

Williams, E. & Scott, J.P. 1953. The development of
social behaviour patterns in the mouse, in relation
to natural periods. Behaviour 6: 35 - 64.

Wunder, B.A. 1975. A model for estimating metabolic rate
of active or resting mammals. J. Theor. Biol. 49:
345 - 354.

Wunder, B.A., Dobkin, D.S. & Gettinger, R. 1977. Shifts
in thermogenesis in the Prairie vole (Microtus ochro=
gaster) Oecologia 29: 11 - 26.