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REPRODUCTION IN THE PORCUPINE

HYSTRIX AFRICAEAUSTRALIS PETERS

by

RUDOLPH JOHANNES VAN AARDE

Submitted in partial fulfilment of

the requirements for the degree of

D.Sc. (Zoology)

in the

Faculty of Science,

University of Pretoria,

PRETORIA

RSA

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REPRODUCTION IN THE PORCUPINE *HYSTRIX AFRICAEAUSTRALIS* PETERS

by

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ABSTRACT

The porcupine *Hystrix africaeaustralis* inhabits a wide range of habitat types throughout the Southern African Subregion and density in foraging areas in the Tussen-die-Riviere Game Farm (30°25' to 30°26'S/26°04' to 26°20'E) was estimated at 29,9 porcupines/km^2. Age of specimens collected during two culling operations could be determined reliably only for animals less than 24 months of age and ramifications of cementum lines, due to continual growth of the open-rooted molars, resulted in counts of these lines not being of use for age determination purposes.

Growth was approximately linear during the first 20 weeks of life and asymptotic body weight (11,7 ± 0,01 kg) given by the von Bertalanffy growth equation, was attained at the age of approximately 52 weeks. Males and females were similar in size.

Females ..... /iii

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The reproductive characteristics of the porcupine are similar to those of New World hystricomorph rodents and its life history strategy can be explained in terms of K-selection.

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To my Mother and Father

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The porcupine colony was established using animals donated by the Curators of the National Zoological Gardens (Dr D J Brand) and the Johannesburg Municipal Zoological Gardens (Mr W J Labuschagne). Mr G Visser and neighbouring farmers in the Loxton and Frazerburg districts kindly trapped and provided the free-ranging animals inclu= ded in the colony. All the feed for maintaining the animals was donated by Messrs L & S Gastaldi and clinical assistance was provided, when necessary, by Drs D G A Meltzer and H Ebedes.

The Director of the Nature Conservation Branch of the Orange Free State, Mr P G le Roux, kindly permitted the collection of study animals from the TdR Game Farm and Dr L P Stolz provided guidance and

assistance ..... /vii

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assistance in this respect. Messrs P Groenewald, F Marais, P J Botha, J Daymae, W Duke, P Matsobane, S Maypkiso, J Mpondo, P Motlohi and J Rakhokolotso assisted in collecting animals in the field. Further material was donated by Dr I G Gaiger.

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Prof G E Lamming of the School of Agriculture, University of Notting= ham, allowed me the use of his radioimmunoassay laboratory during two extended study visits. The guidance and assistance provided by Dr N B Haynes and Mrs Judith Bates during these visits enabled the establish= ment of a similar laboratory at the University of Pretoria.

Financial support was provided by the University of Pretoria, the Mammal Research Institute and the Council for Scientific and Indus= trial Research. I also gratefully acknowledge the award of the Senior Charles Astley Maberly Memorial Scholarship in consecutive years by the Transvaal branch of the Wildlife Society of Southern Africa.

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A special word of thanks to Patsy Skinner, Marthan Bester and Glenda Varrie for their encouragement and support through a difficult personal period during the course of this study.

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CHAPTER 1

INTRODUCTION AND MOTIVATION

The Cape porcupine *Hystrix africaeaustralis* is an Old World hystrico= morph* rodent and a member of the family Hystricidae which comprises four genera and 11 species. It is Africa's largest rodent and weighs 12,0 to 18,0 kg when adult. Porcupines apparently have a wide ecolo= gical tolerance and their natural habitats include tropical forests, woodlands, grassland savannas, semi-arid and arid environments throughout the Southern African Subregion (Smithers 1983). They have even been recently recorded on the gravel plains of the Central Namib Desert *(pers. obs.)*. Kingdon (1974) recorded *H. africaeaustralis* as far north as Kilimanjaro (south eastern Kenya) where they become sympatric with the crested porcupine *H. cristata*.

Although common and widespread, no comprehensive study has been undertaken as yet on the biology of *H. africaeaustralis*. Published information is limited to general accounts on distribution, breeding habits and feeding behaviour (de Graaff 1981, Kingdon 1974, Smithers 1971; 1983). Roth (1964) recorded the growth of a captive hand-raised porcupine and Thomson (1974) described tree-damage by the species in Southern Zimbabwe. Van Jaarsveld (1983) provided an account of

digestive ..... /

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* The term 'hystricomorph' is used for a group of rodents that are hystricognathous as well as hystricomorphous (see Lavocat 1974 and Wood 1974) and includes the South American Caviomorpha, the African Phiomorpha and the Old World Hystricidae.

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digestive capabilities and concluded that fibre is probably only included in the diet at times of food shortage. Related species have received some attention with Weir (1967; 1974), Thomè & Thomè (1980) and Gosling (1980) reporting on aspects of reproduction in captive *H. cristata*, *H. indica* and *H. hodgsoni* colonies respectively. Mohr (1965) documented aspects of the anatomy and the reproductive tract and general behaviour of *Hystrix* spp. kept in various zoological gardens in Germany. Ewer (1968) referred to their defence behaviour and Gutterman (1983) showed that Indian porcupines *H. indica*, through their habit of digging for food, contribute significantly to seed germination of plants in arid environments in Israel.

Motivated by the lack of scientific data on the biology of porcupines, the present study was directed at investigating reproductive and population characteristics of the Cape porcupine, thereby contributing to our understanding of the life-history tactics employed by African mammals.

Recent attempts to understand the significance of diverse life-history phenomena in terms of reproductive strategies have focussed on the concepts of r- and K-selection for which a number of correlates have been suggested (MacArthur & Wilson 1967; Pianka 1970; 1972). These concepts centred mainly on comparisons between the reproductive potential and reproductive effort of different species or of closely-related species. Other approaches have centred on evolutionary considerations of the optimal allocation of energy to the biological processes (maintenance, growth and reproduction) regarded as the most important in the life-history of an organism (Cody 1966; Gadgil &

Bossert ..... /

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Bossert 1970; Stenseth & Framstad 1980). The problem of a life-history strategy is considered here as the optimal allocation of resources towards maintenance, growth and reproduction.

In the survival of a species, reproduction, however, may be regarded as the most important of these three processes (Weir & Rowlands 1973). Bronson (1979) suggested that the way in which a species reproduces should be regarded as being the result of past selection for breeding success under environmental conditions imposed on the species. In response to environmental and biological cues, a species' reproductive features, however, will exhibit some degree of variation.

Variation due to biological cues can be associated either with the particular food chain within which the species operates, or it can be purely social, arising from variation in the interaction between individuals. Variation resulting from environmental forces can be cyclic and therefore predictable, or it can be aperiodic and therefore unpredictable. All this variation, however, can best be explained as being adaptive (Gadgil & Bossert 1970). All reproductive strategies observed furthermore should be considered as successful or they would not have been represented (Weir & Rowlands 1973).

The motivation for the present study furthermore arose as porcupines are often regarded as 'pests' of cereal and other crops and frequently are exterminated by farmers. During periods of population explosion they may also be responsible for the destruction of their natural environments (Thomson 1974). Without an understanding of the interaction between the species and its environment, the control of populations can neither be condemmed nor condoned. The study therefore also

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aimed at providing information to facilitate management policies for free-ranging porcupine populations. Furthermore it is believed that confusion existing about the relationship(s) between the New and Old World Hystricomorpha (Lavocat 1974; Wood 1974) may be elucidated by providing information on aspects of reproduction in the porcupine. Following Weir (1967) the terms Hystricomorpha and the nonadjective hystricomorph are used in their widest sense and the groups are distinguished by the prefixes 'New World' and 'Old World'.

Hystricomorph rodents are distributed throughout America, Africa and Asia, with 45 genera confined to South America, 14 to Africa, five to Asia and one occurring in northern America. The few hystricomorph rodents studied so far, appear to have more diversified patterns of reproduction than any other group of mammals (reviewed by Weir 1974).

Weir & Rowlands (1973) suggested that, in spite of relatively long zoogeographical isolation, species within this suborder still appear to be closely related. The reproductive processes in this group may therefore have been similar at one stage and differences observed today may be the result of exposure to different ecological conditions. My approach towards understanding the functional significance of reproductive features has been based on experimentation using captive animals, and 'adaptive correlation' which entailed a qualitative and quantitative description of the relations between reproductive parameters and between reproductive parameters and population and environmental variables. This approach should assist in relating trends in reproductive patterns to ecological influences.

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CHAPTER 2

STUDY AREA, MATERIALS AND METHODS

STUDY AREA

The Tussen-die-Riviere (TdR) Game Farm was established in 1967 after the cessation of farming activities in anticipation of inundation along the Caledon and Orange Rivers by filling the Hendrik Verwoerd Dam. This area was transferred to the Orange Free State Provincial Administration for development into a game farm and proclaimed as a nature reserve in 1972. The Game Farm extends over a triangular area of 22 000 ha, from 30°25' to 30°26'S/26°04' to 26°20'E on the peninsu= la at the confluence of these rivers (Fig. 1). Situated in the southern Orange Free State, RSA, it falls entirely in the False Upper Karoo Veld Type (Acocks 1953). The two river plains are separated from each other by high ridges underlined by sedimentary rocks of the Upper and Middle Beaufort series of the Karoo System and Karoo Dolori= ite. A large number of drainage lines run north and south from the main rivers.

Climate diagrams for Bethulie and Aliwal North, between which the Game Farm is situated (Fig. 1), are given by Werger (1973; 1980) who also described the climate of the area in detail. According to the Köppen System, this can be defined as arid, cold and dry, with a mean annual temperature less than 18°C (Werger 1973). The mean daily minimum temperature for the coldest month (July) and the maximum for the hottest month (January) are 0,1°C and 31,2°C respectively (Werger 1973). Winters are dry and the summer rainy season extends from

FIG. 1 ..... /
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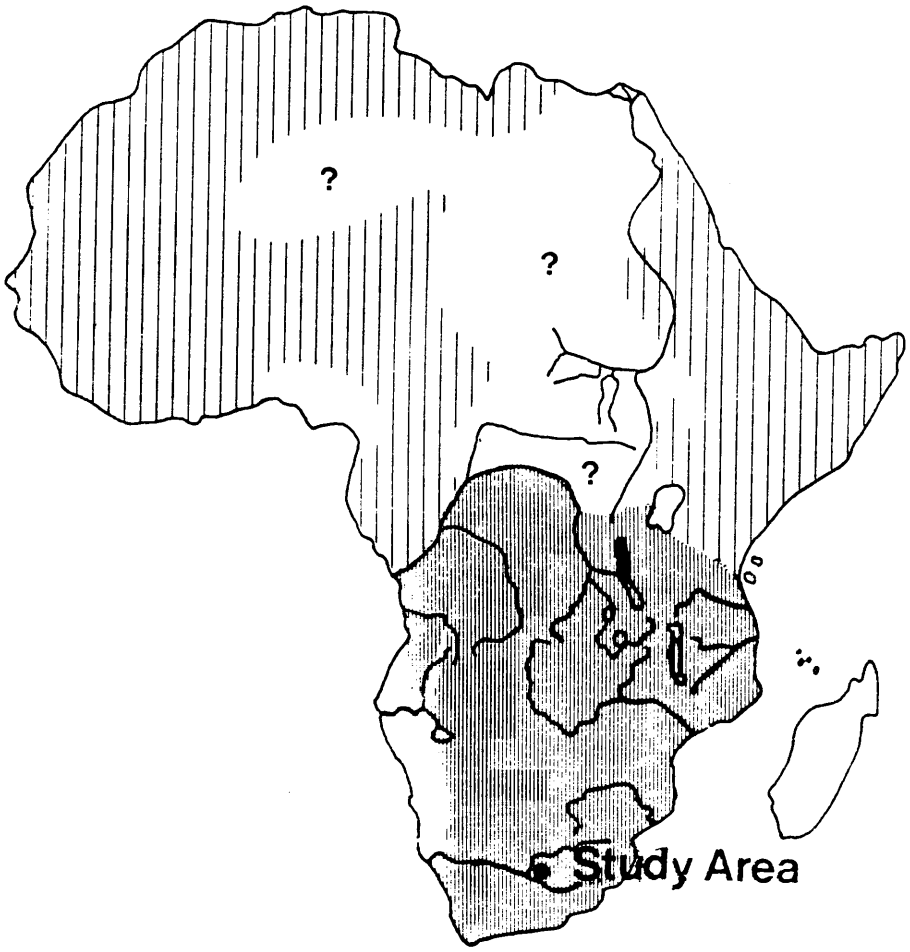

FIG. 1. Location of the Tussen-die-Riviere (TdR) Game Farm situated in the southern Orange Free State of the Republic of South Africa, in relation to the distribution of *Hystrix africaeaustralis* and *H. cristata*.

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November to April (maximum precipitation being recorded in March) with an average annual rainfall of 440 mm.

The bioclimatic map of UNESCO-FAO (1963) classifies the climate of this area as 'intermediate temperate tropical', indicating that the dry period coincides with the period of shortest daylight.

Information on the geology and geomorphology of the Game Farm as well as a detailed description of the plant communities in the area is provided by Werger (1973; 1980). Plant communities have been grouped into riverine communities, communities of the flats and gently-sloping terrain, and communities of the steep slopes; these being represented by one, four and three different communities respectively (Table 1).

Since 1967, small numbers of game were introduced gradually to the Game Farm from other nature reserves and since 1969 surplus game have been utilised by the public for sport hunting. Mammals occurring in the area include square-lipped rhinoceros *Ceratotherium simum*, kudu *Tragelaphus strepsiceros*, eland *Taurotragus oryx*, gemsbok *Oryx gazella* blue wildebeest *Connochaetes taurinus*, black wildebeest *C. gnou*, red hartebeest *Alcelaphus buselaphus*, impala *Aepyceros melampus*, blesbok *Damaliscus dorcas*, springbok *Antidorcas marsupialis*, mountain reedbuck *Redunca fulvorufula*, steenbok *Raphicerus campestris*, duiker *Sylvicapra grimmia*, rock-dassie *Procavia capensis*, aardvark *Orycteropus afer*, aardwolf *Proteles cristatus*, springhaas *Pedetes capensis*, Cape hare *Lepus capensis*, red-rock rabbit *Pronolagus rupestris*, Cape fox *Vulpes chama*, striped polecat *Ictonyx striatus*, yellow mongoose *Cynictis penicillata*, Cape wild cat *Felis lybica* and the small spotted cat *F. nigripes*.

TABLE 1 ..... /

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TABLE 1. Plant communities on the TdR Game Farm (Extracted from Werger 1973).

TYPE OF COMMUNITY	COMMUNITY
Riverine communities	*Acacia karroo - Celtis africana*
Communities of the flats and gently-sloping terrain	*Eragrostis lehmanniana - Chrysocoma tenuifolia* *Chrysocoma tenuifolia - Lessertia pauciflora* *Chrysocoma tenuifolia - Polygala leptophylla* *Chrysocoma tenuifolia - Nenax microphylla*
Communities of steep slopes	*Rhus erosa - Rhynchelytrum repens* *Rhus erosa - Stachys burchelliana* *Olea africana - Maytenus heterophylla*

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Caracal *Felis caracal* occur in limited numbers but irregular attempts have been made to eliminate all medium-sized carnivores from this area. No large carnivores occur within the boundaries of the Game Farm.

The porcupine's ability to cope and even flourish in agriculturally developed areas means that the present population within the Game Farm certainly originated from porcupines present within the area before its proclamation as a nature reserve.

MATERIALS AND METHODS

Husbandry of the captive porcupine colony

The study colony was established with porcupines donated by the Curators of the Johannesburg Municipal Zoological Gardens (n = 12), the National Zoological Gardens (n = 4), from porcupines caught and trapped in the Grahamstown (n = 5) and Loxton districts (n = 24) and the descendants of these animals.

The number of porcupines kept at any specific time during the study period (April 1980 - December 1983) varied from six to 45. Porcupines obtained from different sources were housed separately and intermingling was only allowed after a period of habituation, thereby limiting stress due to intercolony aggression. All porcupines were accommodated in groups of two to five at the University of Pretoria's Experimental Farm (25°45'S/28°12'E) in concrete enclosures. Each enclosure was surrounded by a one metre high brick wall and had an outdoor and roofed area with a concrete floor space of 7,2 m^2 and

11,3 m^2 ..... /

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11,3 m^2 respectively. Porcupines were allowed free access to the total area and were exposed to natural conditions of illumination, ventilation and temperature.

Following cleaning and disinfecting their enclosures, the porcupines were fed daily on a mixture of fresh fruit and vegetables. Their diet was intermittently supplemented by a commercial pelleted diet (Antelope Cubes, Epol (Pty) Ltd, Vereeniging, RSA). Fresh drinking water was available *ad libitum* and dry wood to gnaw on was occasionally placed in the enclosures. No bedding or additional shelters such as nest boxes, were provided.

The number of porcupines housed together and the age and sex composition of each group depended on the information to be obtained from the individuals within the group. The different combinations will be discussed later in the relevant chapters.

Individuals were identified by a system of holes and notches clipped into the left and right ear pinnae of males and females respectively, and by fitting colour-coded stercolite collars around the neck of each porcupine. Ear-clipping served as a back-up in cases where collars were lost, usually due to one porcupine nibbling on the collar of another.

Handling and immobilisation

Herding of porcupines within their enclosures during cleaning operations or when transferring them from one enclosure to another, or into a crush, was facilitated by holding a wooden board, approximately 60 x

80 cm ..... /

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80 cm, between the handler and the animal. Handling, except when weighing, was not possible without immobilisation. The administration of an intramascular injection of a combination of fentanyl citrate (Ethnor (Pty) Ltd, New Road, Halfway House, Transvaal, RSA) and xyla= zine hydrochloride (Rompun Bayer, Leverkusen, FRG) or ketamine hydro= chloride (Ketalar, Parke-Davis Laboratories (Pty) Ltd, Isando, RSA) and Rompun was effected by herding the porcupine intended for immobi= lisation into a crush box, 120 x 60 x 30 cm, designed for the purpose. Dosage rates (mg/kg), mean length of the induction period and the mean period to total recovery for female porcupines immobili= sed at two to seven-day intervals, are presented in Tables 2 & 3. Repetitive immobilisation did not affect induction time or time to recovery for a specific individual and was also similar for the two different combinations of immobilisation agents (Tables 2 & 3).

All porcupines were starved for a 12 h period before immobilisation, returned to their enclosures before recovery and were rewarded by providing food after recovery. Immobilised porcupines were weighed and temporal changes in body weight were taken as an indicator of their general condition. Captive-born porcupines were weighed without immobilisation by herding them into a hessian sack of known weight.

Collection of specimens from culled porcupines

Specimens were collected from 118 porcupines (64 males, 54 females) killed at bimonthly intervals on the Tussen-die-Riviere (TdR) Game Farm. The number of porcupines killed during each of six sampling periods from September 1981 to July 1982, is given in Table 4. Additional material collected by conservators of the Conservation

TABLE 2 ..... /

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TABLE 2. Dosage rates (mg/kg) and reaction times (min) for captive female porcupines immobilised with a mixture of fentanyl citrate (Ethnor (Pty) Ltd, New Road, Halfway House, Transvaal, RSA) and xylazine hydrochloride (Rompun, Bayer, Leverkusen, FRG). All values are given as means ± one standard deviation of the mean.

Animal's code number (sample size)	Dosage rate (mg/kg)			Mean time to recumbency (min)	Mean time to recovery (min)
	Body weight (kg)	Fentanyl citrate	Xylazine hydrochloride		
A (n = 16)	13,2 ± 0,6	0,20 ± 0,06	0,65 ± 0,12	7,5 ± 4,2	105,6 ± 33,3
B (n = 14)	12,9 ± 0,3	0,15 ± 0,06	0,64 ± 0,10	5,6 ± 2,7	94,6 ± 37,0
C (n = 19)	12,5 ± 0,4	0,15 ± 0,06	0,64 ± 0,10	3,7 ± 1,9	103,8 ± 43,1
D (n = 14)	11,1 ± 0,4	0,20 ± 0,07	0,74 ± 0,13	5,6 ± 2,0	145,8 ± 44,0
E (n = 10)	12,0 ± 0,9	0,19 ± 0,07	0,79 ± 0,12	4,0 ± 2,2	173,6 ± 69,8
F (n = 15)	10,9 ± 0,4	0,17 ± 0,06	0,72 ± 0,10	5,1 ± 1,5	159,3 ± 64,7
G (n = 12)	13,0 ± 0,8	0,20 ± 0,05	0,67 ± 0,11	5,2 ± 2,2	168,7 ± 52,6
H (n = 11)	12,1 ± 0,4	0,13 ± 0,04	0,61 ± 0,09	3,5 ± 1,0	84,0 ± 45,7
I (n = 19)	14,1 ± 0,9	0,15 ± 0,05	0,64 ± 0,16	4,8 ± 2,7	187,2 ± 54,0
J (n = 21)	13,0 ± 0,6	0,14 ± 0,04	0,60 ± 0,06	4,7 ± 2,4	135,8 ± 67,8
K (n = 16)	13,5 ± 0,5	0,16 ± 0,09	0,58 ± 0,05	5,0 ± 2,9	214,3 ± 18,0
All animals combined (n = 167)	12,4 ± 1,2	0,16 ± 0,06	0,66 ± 0,14	5,0 ± 2,7	135,8 ± 59,2

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TABLE 3. Dosage rates (mg/kg) and reaction times (min) for captive female porcupines immobilised with a combination of ketamine hydrochloride (Ketalar, Parke-Davis Laboratories (Pty) Ltd, Isando, RSA) and xylazine hydrochloride (Rompun, Bayer, Leverkusen, FRG). All values are given as means ± one standard deviation of the mean.

Animal's code number (Sample size)	Dosage rate (mg/kg)			Mean time to recumbency (min)	Mean time to recovery (min)
	Body weight (kg)	Ketamine hydrochloride	Xylazine hydrochloride		
A (n = 17)	14,1 ± 0,6	5,21 ± 0,06	1,42 ± 0,06	4,6 ± 1,9	105,8 ± 44,5
B (n = 14)	13,4 ± 0,7	5,71 ± 0,11	1,52 ± 0,11	4,5 ± 2,4	152,4 ± 41,4
C (n = 18)	14,9 ± 0,8	4,92 ± 0,07	1,35 ± 0,07	4,0 ± 1,5	106,8 ± 27,5
D (n = 14)	13,8 ± 0,3	5,75 ± 0,32	1,62 ± 0,32	4,8 ± 2,4	92,4 ± 37,9
E (n = 11)	13,9 ± 0,6	5,44 ± 0,20	1,51 ± 0,20	5,3 ± 2,1	187,5 ± 64,2
L (n = 6)	13,7 ± 0,9	5,20 ± 0,10	1,46 ± 0,10	3,7 ± 1,2	200,8 ± 70,0
M (n = 9)	14,3 ± 0,6	5,23 ± 0,48	1,61 ± 0,48	5,4 ± 1,3	144,6 ± 61,5
N (n = 14)	12,1 ± 0,6	5,75 ± 0,16	1,68 ± 0,16	5,3 ± 2,7	179,7 ± 57,7
K (n = 2)	14,3 ± 0,4	5,27 ± 0,04	1,41 ± 0,04	8,5 ± 0,7	Not recorded
O (n = 3)	14,1 ± 0,2	5,63 ± 0,13	1,51 ± 0,13	4,7 ± 2,1	Not recorded
All animals combined (n = 108)	13,9 ± 1,0	5,40 ± 0,64	1,51 ± 0,23	4,7 ± 2,1	147,2 ± 57,1

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TABLE 4. The number of porcupines of various age and sex classes killed during each of six sampling periods on the TdR Game Farm.

Sampling period	Adults*		Subadults**		Juveniles***	
	Males	Females	Males	Females	Males	Females
16 - 22 Sept. 1981	10	8	3	4	-	1
1 - 15 Dec. 1981	5	6	4	5	-	1
18 - 22 Jan. 1982	7	5	2	2	2	2
15 - 17 March 1982	8	5	5	5	-	-
18 - 22 May 1982	5	7	8	8	-	-
28 - 30 June 1982	2	2	3	3	-	-
TOTAL	37	33	25	17	2	4

* > 10,0 kg.
** < 4,0 < 10,0 kg.
*** < 4,0 kg.

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Management Subdivision of the Orange Free State Provincial Administra= tion during a cropping operation when 91 porcupines (56 males, 35 females) were killed on the TdR Game Farm between February 1977 and January 1978, were also included. Other sources of study material included 27 porcupines (16 males, 11 females) killed by officials of the Cape Department of Nature and Environmental Conservation as part of problem animal control operations, and those from four animals that died in captivity at the University of Pretoria's Experimental Farm.

All animals collected by the author were killed at night and a 20,0 ml heparanised blood sample was collected through cardiac puncture immediately thereafter. Following centrifugation, plasma fractions were stored at -20 °C until assayed for steroid hormone levels. All carcasses were weighed and processed within 4 h after being collec= ted. Standard morphometric data (body weight, body length, heart girth, shoulder height, pelvic height, hindfoot length) were collected and the reproductive status of each female was recorded.

Females were recorded as lactating when milk could be expressed from their teats. The condition of the vaginal closure membrane was recorded as either perforated or unperforated. All reproductive tracts were macroscopically inspected after evisceration and the number of implantations and/or uterine scars in each uterine horn was recorded. Fetuses were removed, weighed and their crownrump lengths measured following van Zyl & Skinner (1970). Ovaries, testes, epidi= dymides, vesiculae seminales, prostate glands and adrenals were weighed before fixation in AFA (mixture of 95% ethanol, 40% formalin, glacial acetic acid and distilled water; 3:1:1:5 by volume) or Bouin's

fluid ..... /

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fluid. Material fixed in Bouin's fluid was stored in 70% ethanol following 24 h of fixation.

Eyes were removed and stored in 10% formalin and skulls and humeruses were cleaned and stored dry. Kidneys, the surrounding kidney fat, spleens, stomachs and stomach contents were weighed after cleaning. The processing of all this material will be discussed during the relevant chapters.

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CHAPTER 3

AGE DETERMINATION AND GROWTH

INTRODUCTION

The importance of determining the ages of free-ranging animals and its relevance to studies of reproduction and population biology requires no motivation. The need to determine the absolute and/or relative age of all specimens included in the present investigation arose from attempts to define age at sexual maturity and senescence, age specific fecundity schedules and age specific reproductive values for free-ranging porcupines.

All ageing criteria applied during the present study are well-established (reviewed by Morris 1972) and included the sequential pattern of tooth eruption, tooth wear, counts of cementum annuli, counts of periosteal lines and the determination of age-related changes in dry eye lens weights.

Published accounts of techniques employed to determine the absolute ages of other hystricomorph rodents are limited and include that of Earle & Kramm (1980) for the Canadian porcupine *Erethizon dorsatum*, that by Willner, Dixon, Chapman & Stauffer (1980) for the coypu *Myocastor coypus* and that of Collett (1981) for the paca *Agouti paca*.

Studying the growth of porcupines was important because growth rate, age at weaning, period of parental dependence, age at sexual maturity and productivity are all important in determining the successful

survival ..... /

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survival of the species (Case 1978). In captive hystricomorphs growth has been documented for the brush-tailed porcupine *Atherurus africanus* (Rahm 1962), a hand-raised porcupine *Hystrix africaeaustralis* (Roth 1964), the green acouchi *Myoprocta pratti* (Kleiman 1970), plains viscacha *Lagostomus maximus* (Weir 1971a), casiragua *Proechimys guairae* (Weir 1973c) and paca (Collett 1981).

In this chapter attempts have been made to determine the age of porcupines based on morphometrics and histology of skeletal and dental material. Pre- and postnatal growth in free-ranging and captive animals have also been quantified.

MATERIALS AND METHODS

Age determination

Age determination has been based on tooth eruption and replacement, patterns of tooth attrition, counts of cementum annuli, counts of periosteal growth lines and dry eye lens weights following methods described by Klevezal' & Kleinenberg (1969), Morris (1972), Frylestam & von Scantz (1977) and Earle & Kramm (1980).

Tooth eruption and replacement

The sequence of eruption and replacement of teeth in the maxillary toothrow in porcupines of known age in captivity were determined during biweekly inspection of immobilised animals (see Chapter 2). A tooth was considered erupted when its occlusal surface was visible above the gum line.

Skulls ..... /

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Skulls of culled specimens collected on the TdR Game Farm were grouped into one of nine dental age groups (Fig. 2) with chronological ages being assigned to six of these.

Counts of cementum annuli

The left maxillar permanent premolar and/or first molar of all collected specimens and all teeth in the toothrow of nine porcupines were decalcified in a 5% nitric acid solution after being extracted from the alveolus, often by placing the cleaned skull into boiling water for 5 to 10 min. The nitric acid solution was changed every 24 h and complete decalcification required 48 to 140 h, depending on the size of the tooth. The lack of a white precipitate forming within 5 min after a 5% solution of ammonium-oxalate was added to the nitric acid solution was used as a criterion for complete decalcification (Earle & Kramm 1980).

Decalcified teeth were stored in water and their roots serially cross-sectioned at 20 m, either in a cryostat with a cooled blade or by using a microtome following routine embedding in paraffin wax. Fifteen to 20 cross-sections were mounted on glass microscope slides and stained for 20 to 25 min with Carazzi's haematoxylin. Stained sections were routinely dehydrated, and following clearing in two xylol baths, mounted with D.P.X. mountant (BDH Chemicals Ltd, Poole, UK). Sections were examined through a light microscope and the number of incremental lines in the cementum were counted at ten separate locations on these sections.

Counts ..... /

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Counts of periosteal lines

Cross-sections of a part of the shaft of the left humerus of each specimen were also prepared for microscopic examination. Decalcifi= cation in a nitric acid solution was usually complete within 48 h and 20 m sections, prepared on a slice microtome, were stained in Caraz= zi's haematoxylin after routine embedding in paraffin wax. Ten to 15 sections were examined and periosteal lines were counted at ten sepa= rate locations.

Eye lens weights

Eye lenses were removed from the eye balls after a 14 to 21 day fixa= tion period in 10% formalin (40% formaldehyde solution diluted 1:9 in water), cleaned, weighed and oven-dried at 80 °C to constant weight for eight weeks. Lenses were weighed at 14-day intervals during this period. Care was taken not to allow the hygroscopic dried lenses to absorb moisture by putting groups of dried lenses into a desiccator over anhydrous calcium chloride when taken out of the oven before weighing.

Tooth measurements

The length of permanent maxillar premolars of each culled porcupine was measured with a steel vernier caliper to the nearest 0,1 mm. The area of the occlusal surface of the same teeth was measured using an electronic planimeter (AAC-400, Hayashi Denkoh Co. Ltd, Tokyo) after a 12 X magnification drawing on cardboard with the aid of a drawing tube fitted to a stereoscopic dissecting microscope. The area (mm^2)

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was calculated as the mean of four consecutive readings corrected for magnification.

Growth

Prenatal

Fetuses removed from the uteruses of pregnant females culled on the TdR Game Farm were weighed and their crownrump lengths measured following van Zyl & Skinner (1970). Fetal age and specific fetal growth velocity were determined using the formula $\sqrt[3]{W} = a(t - t_o)$, where W = fetal weight, a = specific fetal growth velocity, t = gestation age in days, and t_o = the calculated intercept on the age axis (Huggett & Widdas 1951). The theoretical value for a was calculated using a birth weight of 351 g (see Chapter 4), where t = 93,5 days (see Chapter 4) and $t_o = t \times 0{,}3$ as suggested by Huggett & Widdas (1951).

Postnatal

Body weight for captive born porcupines (n = 18) was recorded at weekly intervals over the first two years of life and growth was described by fitting the theoretical von Bertalanffy curve to the data using the programme of Abramson (1965) as developed by Tomlinson & Abramson (1961). Age specific body weight was transformed to the third power and individual estimates for the curve were obtained through retransformation. The theoretical curve was derived from mean values of body weight for each age in weeks using the growth equation of Beverton & Holt (1957): $W_t = W_\infty [1 - e^{-k(t-t_o)}]^3$ where W_t =

coefficient .... /

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weight at age t in weeks, W_{∞} = asymptotic body weight, k = a coeffi= cient of catabolism, t = age in weeks, and t_o = the theoretical age at which the animal would have a zero body weight. All other curves were fitted through least square regression analyses and values are expres= sed as means $\pm$ one standard deviation of the mean.

Condition

The fat surrounding the kidneys and the kidneys were removed from each carcass after evisceration and the kidney fat and kidneys were weighed separately to the nearest 0,01 g. The Kidney Fat Index was calculated as the weight of the kidney fat/kidney weight x 100.

RESULTS

Age determination

Sequence of tooth eruption and replacement

Incisors were fully erupted at birth (n = 18) and the deciduous premo= lars started erupting at an age of approximately 14 days. Eruption of the first maxillar molars commenced 2,0 to 2,5 months (n = 8) after birth and the second molars were visible above the gumline at an age of five to six months (n = 7). The third maxillar molars erupted at an age of eight to 11 months (n = 8), with eruption being complete at an age of 12 months. Eruption of the permanent premolars was complete at the age of 23 to 25 months (n = 8) and the occlusal surfaces of the premolars were slightly worn 24 to 30 months (n = 6) after birth. All the flexi of the premolars were still distinct at this age. Descrip=

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tions and illustrations of the maxillary toothrow of these age classes are provided in Table 5 and Fig. 2.

Skulls of specimens collected on the TdR Game Farm were accordingly grouped into one of nine dental age groups (Fig. 2), with age groups I to III representing porcupines less than six months of age, age group IV animals eight to 12 months of age, age groups V and VI animals older than 12 months but less than 30 months of age, and age groups VII to IX porcupines older than 30 months of age.

Counts of cementum lines

Distinct annuli were visible in the cementum of all erupted teeth and no annulations were present in the cementum of newly erupted premolars and molars. Most cementum was deposited between the roots with cemen= tum lines being most discrete in the thick cementum pad forming at the proximal end of the roots. The degree of definition of the cementum lines and the distances between these lines varied considerably.

Ramification of the lines at lacunae in the cementum and the uneven deposition of cementum around roots (Fig. 3a) resulted in considerable variation in the number of lines counted. The coefficient of varia= tion for ten counts of cementum annuli conducted on four to eight sections of each tooth, varied from 0,0 to 117,0%, with the greatest variation recorded for the older dental age classes (VII - IX). Most coefficients of variation were larger than 20% but less than 50%.

In assuming that cementum lines may be formed on an annual basis and in considering the eruption interval of the permanent molars and the

TABLE 5 ..... /
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TABLE 5. Description of dental age classes based on the sequential eruption, replacement and wear of the occlusal surfaces of teeth in the maxillary toothrow of captive porcupines examined at bi-weekly intervals.

Dental age class	Absolute age (months)	Description of maxillary toothrow
I	Birth - 0,5	Deciduous premolar newly erupted
II	2,0 - 2,5	Deciduous premolar slightly worn with first molar newly erupted
III	5,0 - 6,0	Deciduous premolar and first molar slightly worn with second molar newly erupted
IV	8,0 - 11,0	Third molar erupted and deciduous premolar heavily worn
V	18,0 - 23,0	Permanent premolar erupting. Flexi of second and third molar still distinct and occlusal surface of first molar comprises of a number of 'dentine islands', defined as fosettes (see Maguire 1976)
VI	24,0 - 30,0	Permanent premolar fully erupted and slightly worn with paraflexus, mesoflexus, metaflexus, entoflexus and hypoflexus still distinct. Fosettes forming on occlusal surface of second molar and flexi still visible on third molar
VII	> 30,0	Fosettes distinct on all molars
VIII	> 30,0	Fosettes worn away on first molar
IX	> 30,0	Fosettes worn away on first and second molar

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FIG. 2. The maxillar toothrows of the nine dental age classes distinguished on the basis of the sequence of tooth eruption and replacement. A description of the toothrow of each of these age classes is presented in Table 5.

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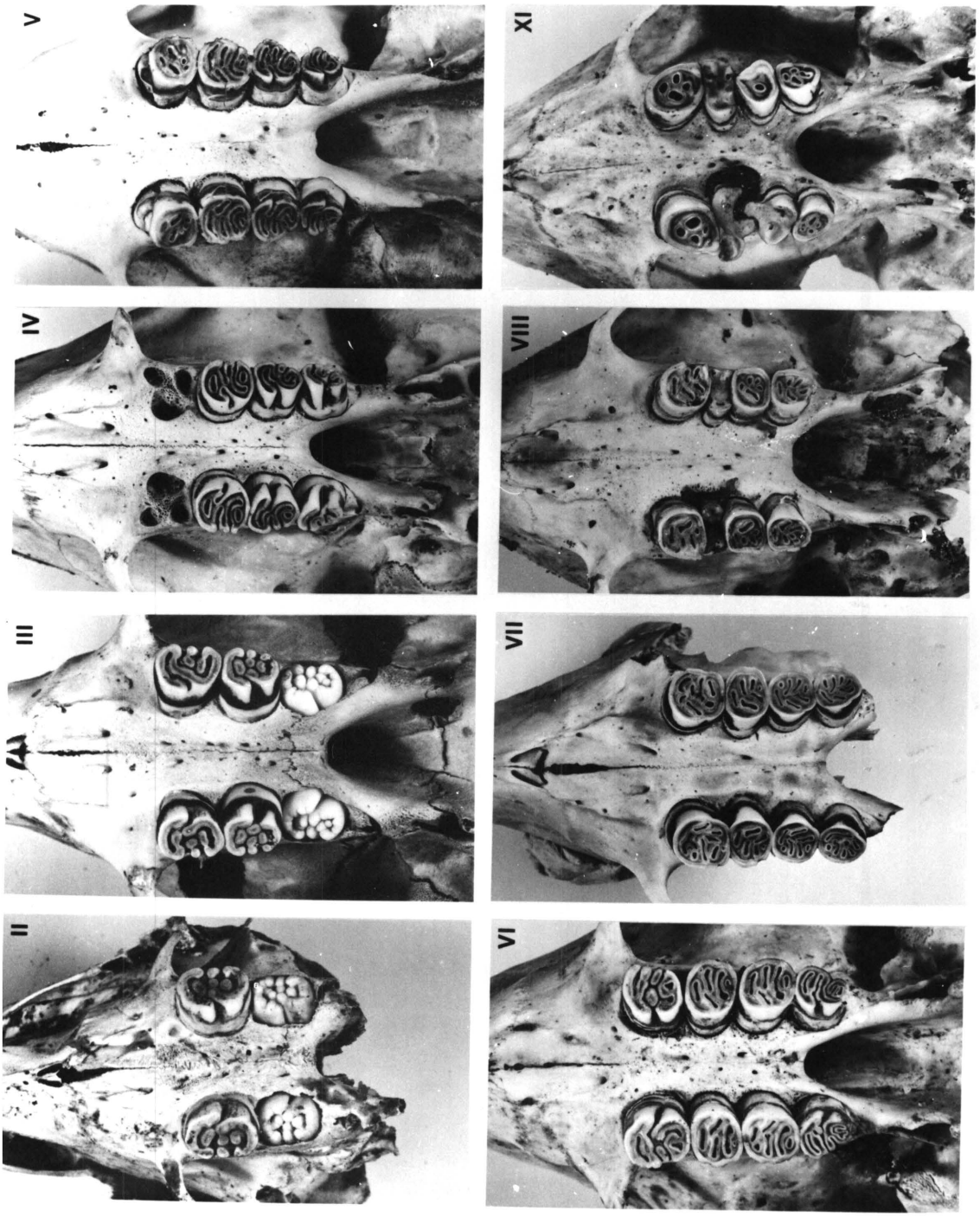

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FIG. 3a. Cross-section of the maxillar left premolar of an adult porcupine (dental age class VII) illustrating the ramification of cementum lines, probably as a result of the uneven deposition of cementum around the roots. (Haematoxylin, X 20).

FIG. 3b. Cross-section of the left humerus of an adult porcupine (dental age class VII) illustrating the ramification of lines in the periosteal zone (Haematoxylin, X 20).

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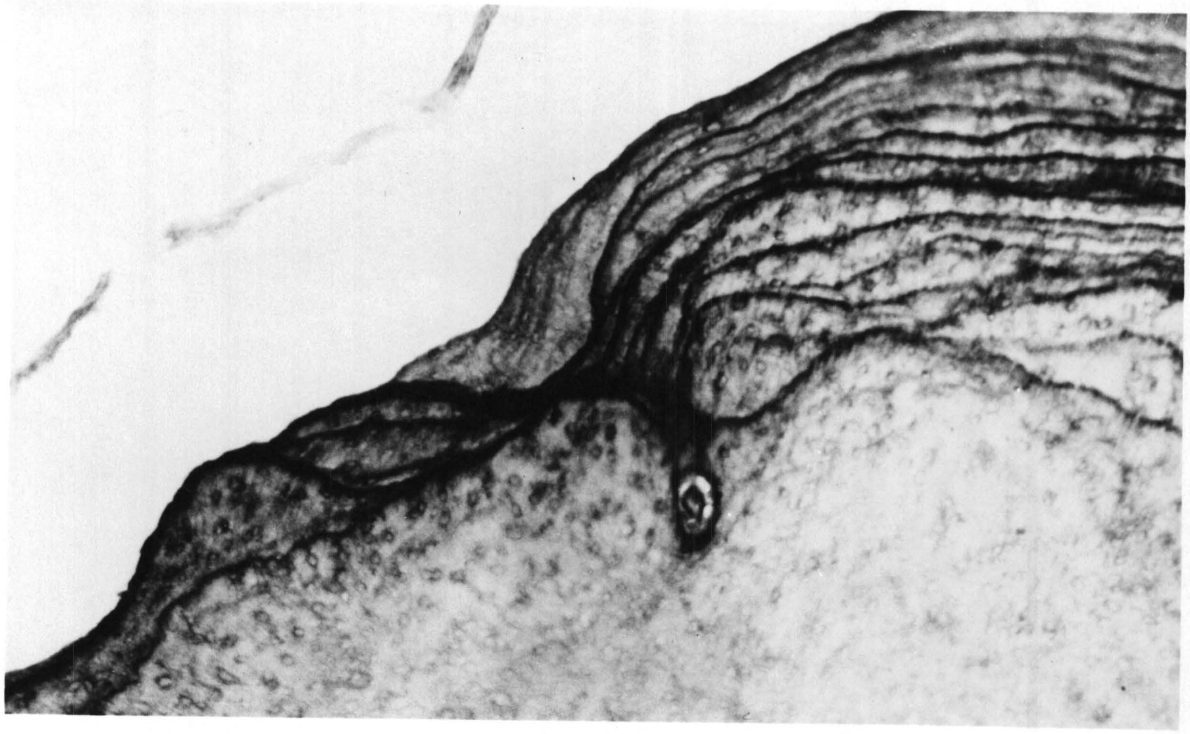

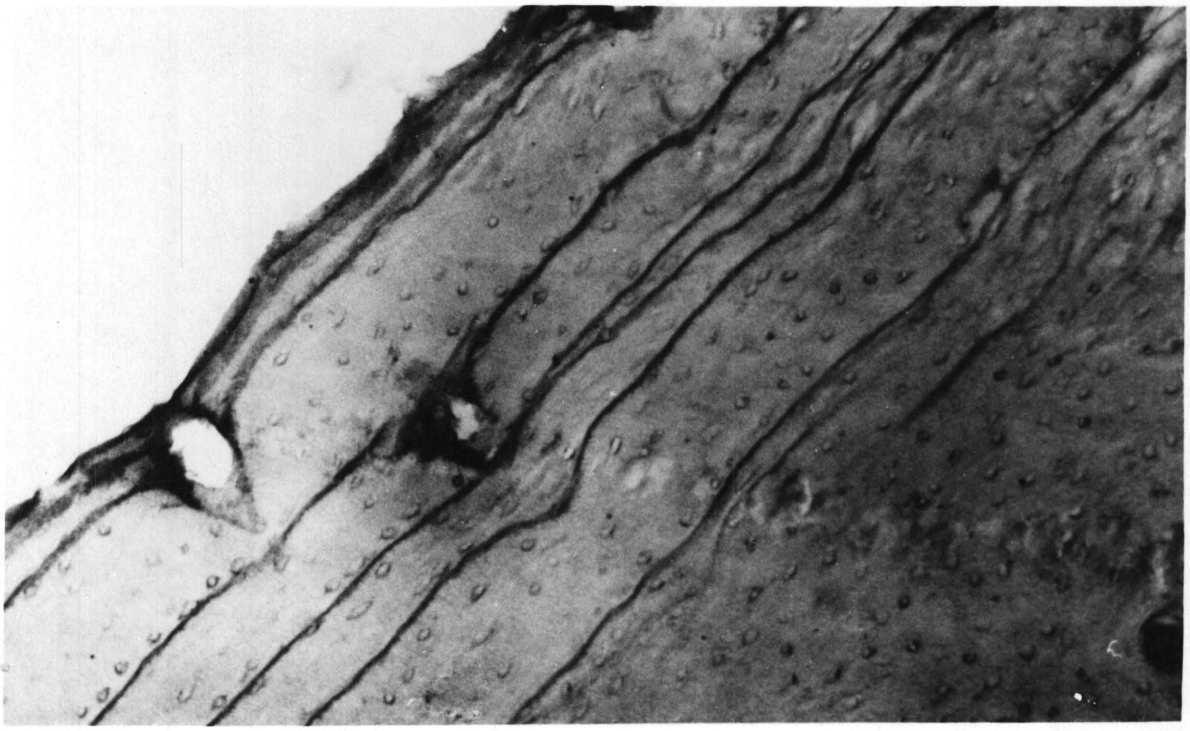

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premolars (Table 5), it is expected that the mean number of lines in the permanent premolar of a specific individual would be two less than in the first molar. The number of lines in the first molar should thus be one less than in the third molar.

The mean number of cementum lines counted in decalcified cross-sections of all teeth in the maxillary toothrow of nine porcupines, presented in Table 6, support this hypothesis, suggesting that at least some of the lines are formed on an annual basis.

The numbers of cementum lines in the premolars were consistently less than those in the first molar and more lines were deposited in the cementum of the first molar than the third molar (Table 6). These differences were not affected by age (Table 6) and were not within the expected limits for all animals (Table 7).

Periosteal lines

Definite lines were present in the periosteum of most humeruses cross-sectioned (Fig. 3b). The calculated coefficients of variation for ten counts conducted on four to six sections of each humerus varied, however, from 0,0 to 36,9% and precluded the reliable estimation of age based on counts of periosteal lines alone.

The minimum and maximum means calculated for individuals in each dental age class furthermore varied considerably and did not increase consistently with an increase in age (Table 8), thereby reducing confidence in counts of periosteal lines as a parameter to estimate ages of adult porcupines.

TABLE 6 ..... /

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TABLE 6. Mean (± S.D.) number of cementum lines counted at ten different locations on four to eight decalcified cross-sections of the maxillar premolar, first, second and third molars of nine porcupines culled on the TdR Game Farm.

Dental age class	Mean number of cementum lines			
	Premolar	First molar	Second molar	Third molar
IV	0,0*	1,8 ± 0,41	1,6 ± 0,53	0,0
V	0,0	1,4 ± 0,53	0,0	0,4 ± 0,55
VI	1,0 ± 0,00	3,8 ± 0,75	4,2 ± 0,41	3,0 ± 0,00
VI	1,4 ± 0,55	3,0 ± 0,00	2,0 ± 0,82	1,8 ± 0,45
VII	1,6 ± 0,53	3,8 ± 0,94	1,8 ± 0,44	2,2 ± 0,41
VII	1,7 ± 0,52	4,7 ± 0,49	3,6 ± 0,74	3,2 ± 0,41
VII	2,3 ± 0,52	4,0 ± 0,89	5,0 ± 1,00	2,4 ± 0,55
VII	2,4 ± 0,55	-	3,8 ± 0,41	2,5 ± 0,55
VIII	5,0 ± 0,00	6,5 ± 1,05	7,3 ± 0,52	5,0 ± 0,00

* Deciduous tooth.

TABLE 7. The difference between the mean number of cementum lines counted in the permanent premolar and the third molar and between the first and third molar of nine porcupines culled on the TdR Game Farm.

Dental age class	Difference between means	
	Premolar/First molar	First molar/Third molar
IV	1,83	1,83
V	2,00	1,03
VI	1,60	1,20
VI	2,82	0,82
VII	2,26	1,66
VII	3,04	1,64
VII	1,67	1,60
VII	1,60	1,50
VIII	1,50	1,50
Average difference	2,04	1,41

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Variation in the number of lines counted also resulted in a poor relationship between the number of periosteal and cementum lines (Fig. 4), with the number of periosteal lines tending to decrease with an increase in the number of cementum lines possibly resulting from periosteal lines being absorbed faster than cementum lines.

Eye lens weight

Mean combined dry eye lens weight increased linearly ($y = 0,04\ x + 0,019$; n = 55) and significantly ($r = 0,83$; $p < 0,001$) over the first 24 months of life (dental age classes II - V). The relationship between these variables for the adult age classes (VI - IX) was, however, not significant ($r = 0,41$; n = 57). The discontinuity in the relationship between dry eye lens weight and dental age class (Fig. 5) is ascribed to unequal age intervals being represented by each age class.

Tooth measurements

The hypsodontic open-rooted premolars of porcupines are conical in shape with the diameter at the crown of the newly erupted tooth being less than at the neck, where it is wider than at the roots. The area of the occlusal surface of the permanent premolars decreased slightly ($b = - 0,10$) with an increase in the length of the premolar (Fig. 6) but the relationship between the two variables was not significant ($r = 0,20$; n = 50).

The relationship between the area of the occlusal surface and dental age class was best described by a third degree polynomial curve

TABLE 8 ..... /

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TABLE 8. The minimum and maximum mean (± S.D.) number of periosteal lines calculated for individuals in each of the adult age classes.

Dental age class	Minimum and maximum mean (± S.D.) values calculated for individuals in age class	
	Minimum	Maximum
V	6,3 ± 1,37	-
VI	3,0 ± 0,00	3,7 ± 0,59
VII	4,0 ± 0,88	7,9 ± 2,09
VIII	3,2 ± 1,08	9,8 ± 2,59
IX	2,8 ± 0,50	6,0 ± 1,96

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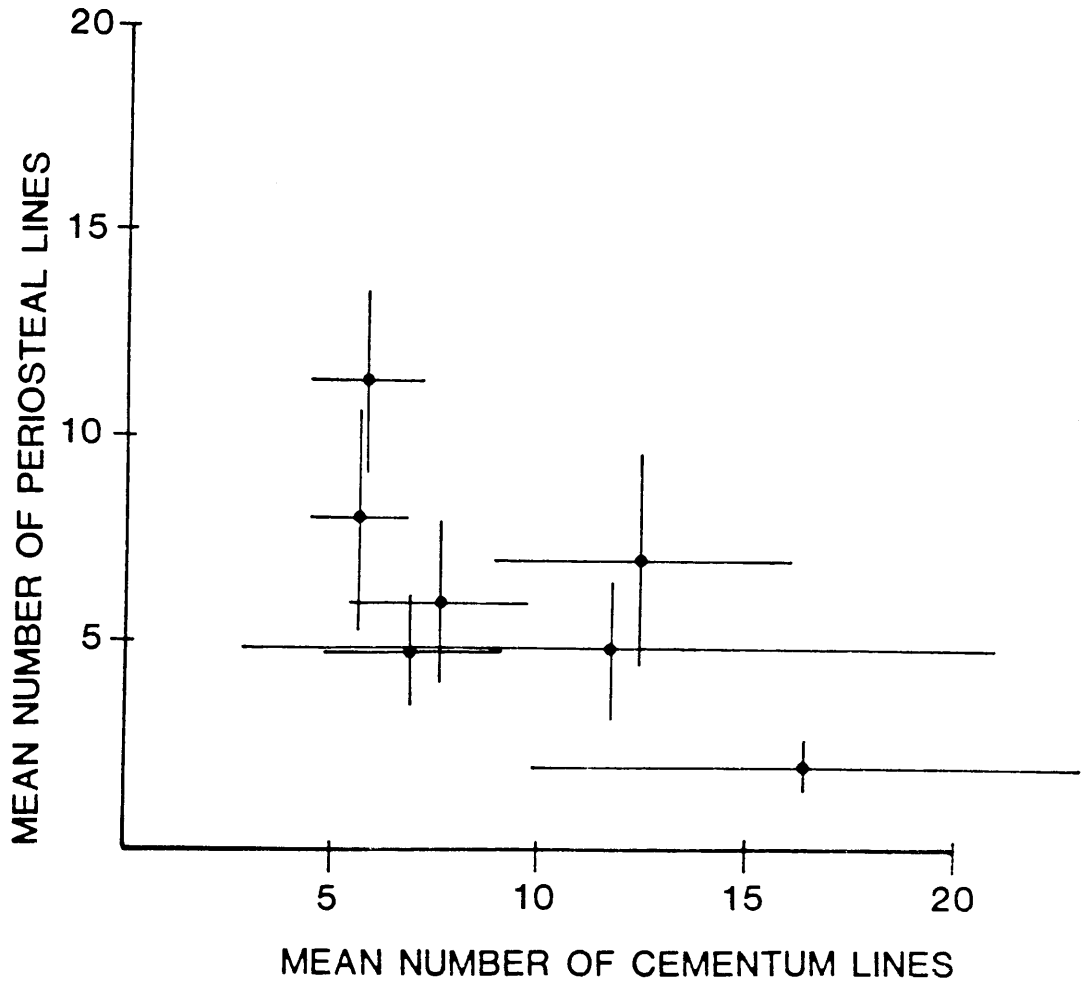

FIG. 4. The relationship between the mean number of periosteal lines and the mean number of cementum lines in the premolars of adult porcupines (dental age classes VII - IX). The horizontal and vertical lines represent one standard deviation of each mean.

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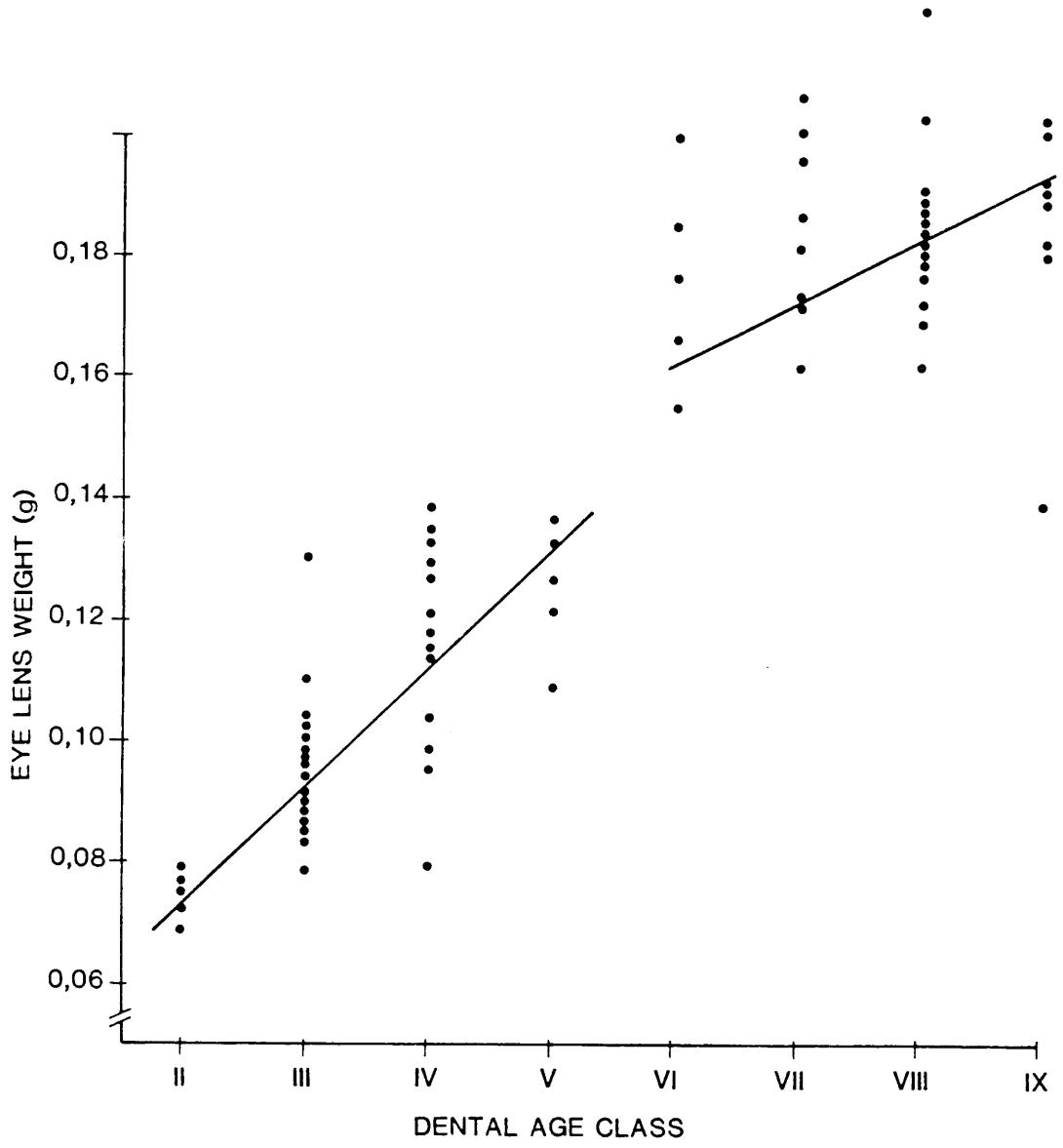

FIG. 5. The relationship between combined eye lens weight (g) and dental age class. The lines were fitted through least square regression analyses.

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following the equation $y = 73,07 - 39,76\ x + 7,24\ x^2 - 0,41\ x^3$ (r^2 = 0,72; n = 48) with occlusal surface as the dependent variable (Fig. 7). The area of the occlusal surface thus decreased from age classes VII to VIII after increasing exponentially between age classes IV and VII.

Growth

Prenatal

Using the equation of Huggett & Widdas (1951) and their approximation for t_o (t x 0,3), specific fetal growth velocity (a) was calculated at 0,1047 and the intercept at the age axis (t_o) at 28,1 days. The correction factor used to estimate t_o from t (gestation period) is, however, arbitrary and may introduce errors of up to 10% in specific fetal growth rates (a) of mammals with a gestation period longer than 50 days (Huggett & Widdas 1951). An analysis of the t_o values observed by Roberts & Perry (1974) for seven different New World hystricomorph rodent species indicated that they differed from + 19,9 to -36,6% from the theoretical values; these differences stemming from t_o being under- or overestimated, using the approximations of Huggett & Widdas (1951).

An evaluation of the data provided by Roberts & Perry (1974) indicated that these differences increase linearly and significantly (r = 0,93; $p < 0,01$) with an increase in gestation length.

By calculating t_o for hystricomorph rodents with a gestation period longer than 100 days as t x 0,3 (instead of t x0,2; Huggett & Widdas

FIG. 6 ..... /

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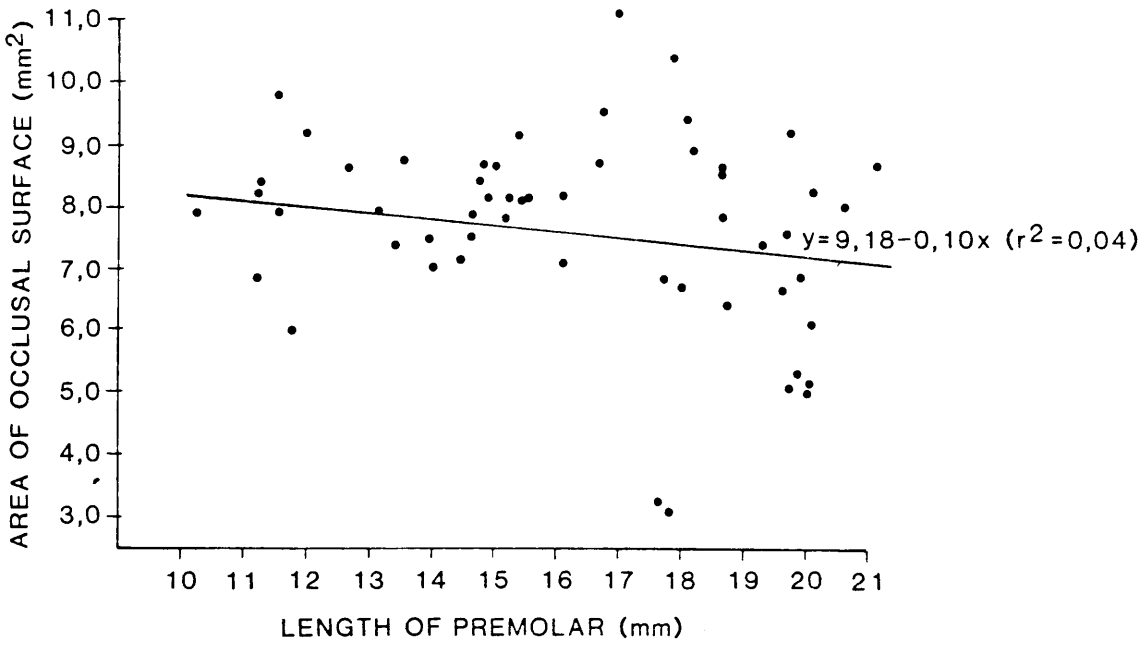

FIG. 6. Relationship between the length (mm) and the area of the occlusal surface (mm^2) of the premolars of adult porcupines. The line was fitted through least square linear regression analysis.

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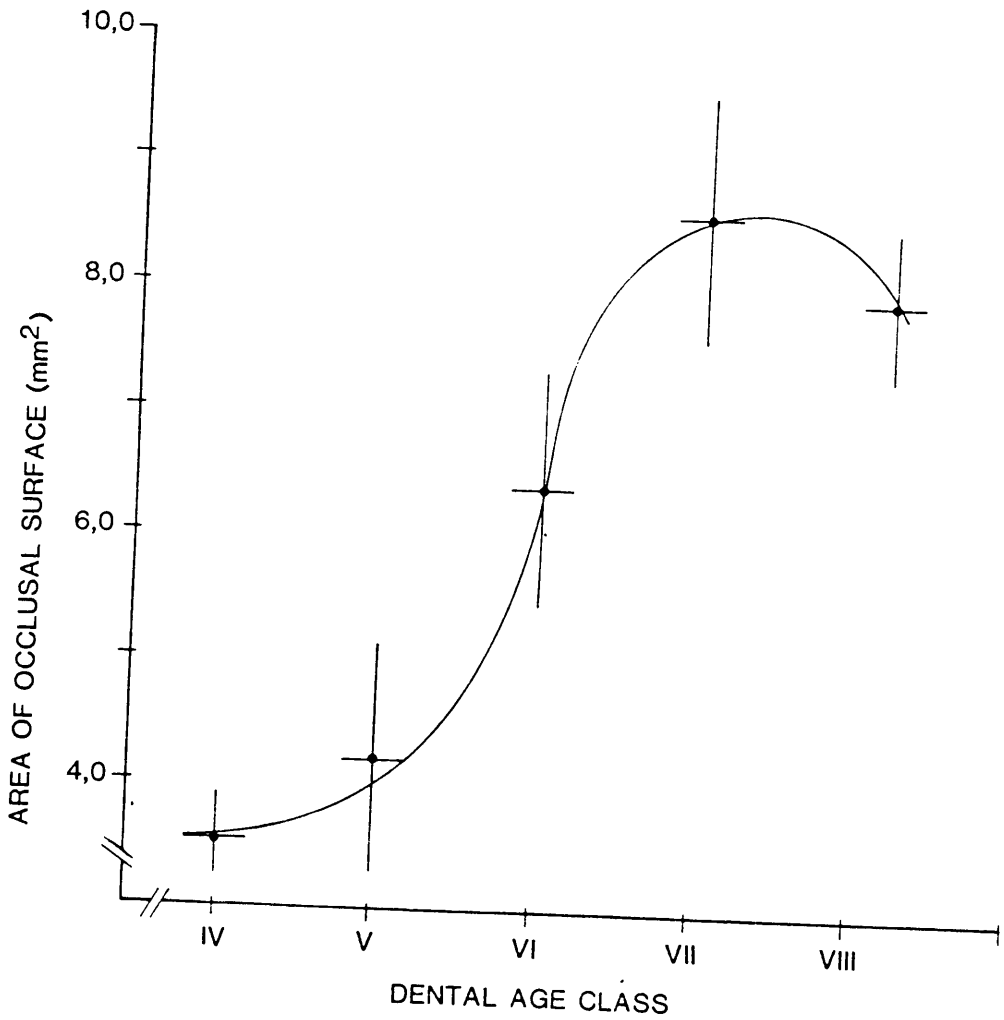

FIG. 7. The relationship between the area of the occlusal surface (mm^2) and dental age class. The third degree polynomial curve is described by the equation $y = 73,07 - 39,76\ x + 7,24\ x^2 - 0,41\ x^3$. Vertical lines present one standard deviation of the mean.

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1951), for those with a gestation period of 63 to 100 days as t x 0,4 (instead of t x 0,3), and for those with a gestation period less than 63 days as t x 0,25, the theoretical t_o and a values approximated those observed by Roberts & Perry (1974)(see Table 9). This procedure resulted in the specific fetal growth velocity for the porcupine being calculated at 0,1813 *cf.* 0,1047 using the approximation (t x 0,3) suggested by Huggett & Widdas (1951).

Postnatal

Age specific body weights for captive male and female porcupines did not differ significantly (Table 10) and the von Bertalanffy growth curve presented in Fig. 9, with its associated constant and coeffi= cients, describes growth in body weight for both sexes. Growth in body weight during the first 20 weeks of life was approximately linear and asymptotic weight (11,7 ± 0,01 kg) given by the growth equation, was attained at the age of approximately 52 weeks (Fig. 9).

Age (dental age class) specific body weights for free-ranging porcupi= ne males and females culled on the TdR Game Farm between Feburary 1977 and July 1982 did not differ significantly for most age classes (II - III, V, VI, VII, IX; Table 11). Differences in mean body weights of age classes IV and VIII (t_{32} = 3,12 and 2,85 respectively is ascri= bed to the presence of pregnant females within these classes, resul= ting in females being heavier than males.

The frequency distribution of males and females in specific weight classes, however did differ significantly (χ^2 = 12,67; p = < 0,01) with more females than males occurring in the heavier weight classes

FIG. 8 ..... /

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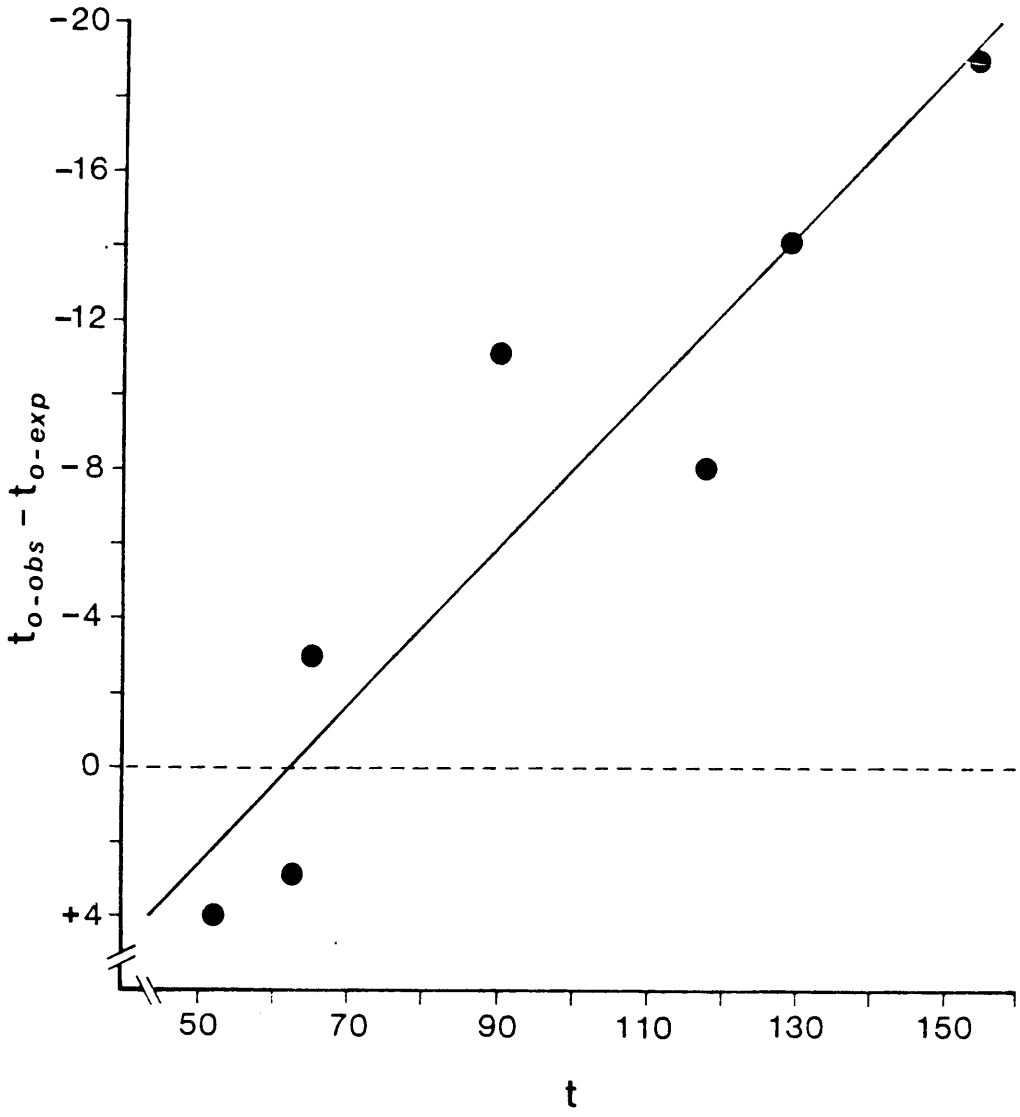

FIG. 8. Relationship between differences in the observed and theoretical values of t_o and gestation period for seven hystricomorph rodent species based on information published by Weir (1974) and Roberts & Perry (1974). The line was fitted through least square regression analysis.

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TABLE 9. Comparison between the observed and theoretical specific fetal growth velocities *(a)* for hystricomorph rodents based on various approximations of t_o.

Species	$\sqrt[3]{W}$ *	Observed values*		Theoretical values*		Theoretical values**		Mean gestation length (days)
		t_o	a	t_o	a	t_o	a	
Galea musteloides	3,405	12	0,0718	16	0,0896	13	0,0873	52,0
Proechimys semispinosus	2,466	22	0,0765	19	0,0560	26	0,0636	64,8
Octodon degus	2,422	38	0,0483	27	0,0384	36	0,0449	90,0
Chinchilla laniger	2,503	30	0,0436	22	0,0407	35	0,307	116,5
Lagostomus maximus	5,809	50	0,0641	31	0,0472	46	0,0539	153,7
Myocastor coypus	6,400	40	0,0595	26	0,0603	39	0,0711	129,0
Cavia porcellus	4,500	16	0,0900	19	0,0978	16	0,0970	62,4
Hystrix africaeaustralis	6,891	-	-	28	0,1047	38	0,1813	94,0

* From Roberts & Perry (1974).

** Values calculated using t x 0,25, t x 0,4 and t x 0,3 for animals with gestation periods < 63 days, $> 63 < 100$ and > 100 days respectively.

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TABLE 10. Age (weeks) and sex specific mean body weight (± S.D.) for porcupines born in captivity. Sample sizes are given in brackets.

Age weeks	Mean (± S.D.) body weight (kg)		t_{df} = value
	Males	Females	
5	1,80 ± 0,50 (8)	1,58 ± 0,50 (8)	$t_{14} = -1,11$
10	3,90 ± 1,11 (6)	3,37 ± 0,56 (8)	$t_{12} = 0,98$
15	4,98 ± 0,34 (6)	5,18 ± 1,08 (6)	$t_{10} = 0,37$
20	6,40 ± 0,61 (6)	6,06 ± 0,86 (8)	$t_{12} = -0,72$
25	7,26 ± 0,73 (6)	7,84 ± 1,25 (8)	$t_{12} = 0,81$
30	7,28 ± 1,11 (6)	8,12 ± 0,08 (6)	$t_{10} = 1,67$
35	8,75 ± 0,49 (6)	8,73 ± 0,64 (6)	$t_{10} = -0,05$
40	9,50 ± 0,69 (5)	10,22 ± 0,86 (5)	$t_{8} = 1,22$
45	9,65 ± 0,64 (5)	10,05 ± 0,60 (5)	$t_{8} = 0,76$
50	10,87 ± 1,02 (5)	10,90 ± 0,90 (5)	$t_{8} = 0,05$
60	11,15 ± 1,77 (5)	11,68 ± 1,09 (5)	$t_{8} = 0,51$

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TABLE 11. Age (dental age class) and sex specific mean (± S.D.) body weights for porcupines culled on the TdR Game Farm between February 1977 and July 1982. Sample sizes are given in brackets.

Dental age class	Mean (± S.D.) body weight (kg)		t_{df} = value
	Males	Females	
II	4,0 ± 1,43 (8)	4,1 ± 1,55 (9)	t_{15} = 0,89
III	6,9 ± 1,38 (19)	6,2 ± 2,06 (15)	t_{32} = 1,18
IV	9,1 ± 1,50 (22)	11,0 ± 1,94 (12)	t_{32} = -3,12*
V	10,8 ± 2,01 (6)	12,4 ± 2,05 (7)	t_{11} = -1,42
VI	11,5 ± 1,89 (15)	12,1 ± 1,19 (6)	t_{19} = -1,23
VII	11,9 ± 2,10 (18)	12,9 ± 2,22 (25)	t_{41} = -0,91
VIII	11,7 ± 1,42 (23)	13,2 ± 1,24 (11)	t_{32} = -2,85*
IX	11,0 ± 1,16 (3)	12,3 ± 2,25 (6)	t_{7} = -1,85

* Differences significant ($p < 0,05$).

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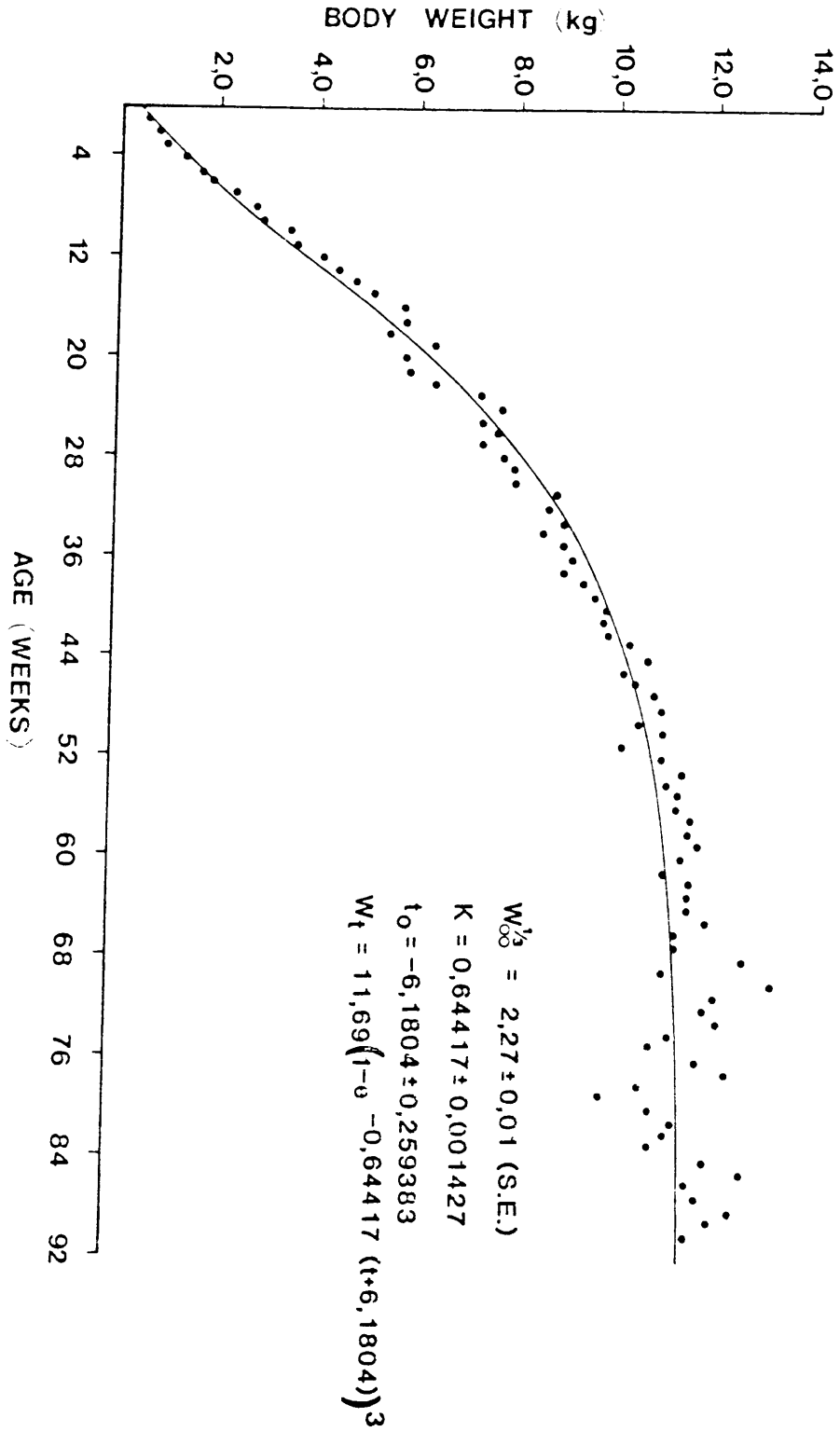

FIG. 9. The von Bertalanffy growth curve for porcupines (both sexes combined) born in captivity and weighed at weekly intervals over the first two years of life.

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TABLE 12. The number of males and females in each of nine weight classes. Data were collected from porcupines culled on the TdR Game Farm between February 1977 and July 1982.

Weight class (kg)	Number of porcupines	
	Males	Females
10,0 - 10,9	20	6
11,0 - 11,9	21	11
12,0 - 12,9	11	15
13,0 - 13,9	9	13
14,0 - 14,9	6	9
15,0 - 15,9	1	3
16,0 - 16,9	3	1
17,0 - 17,9	1	0
18,0 - 18,9	0	2
TOTAL	72	60

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TABLE 13. Age (dental age class) and sex specific mean (± S.D.) body weight, shoulder height, body length and curvilinear body length for porcupines killed on the TdR Game Farm between September 1981 and July 1982. Sample sizes are given in brackets.

Age class	Body weight (kg)		Shoulder height (cm)		Body length (cm) (Straight nose-tail)		Curvilinear body length (cm)		Heart girth (cm)	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
II	4,4 ± 1,11 (7)	4,2 ± 1,33 (5)	18,9 ± 2,23	20,8 ± 2,78	51,2 ± 4,73	51,6 ± 7,32	57,8 ± 5,63	56,6 ± 8,25	35,2 ± 4,25	33,0 ± 3,44
III	7,7 ± 1,36 (14)	6,9 ± 1,39 (13)	23,8 ± 1,49	22,8 ± 2,03	62,2 ± 4,08	61,8 ± 6,87	70,1 ± 4,29	68,1 ± 5,18	42,8 ± 3,22	42,1 ± 4,53
IV	9,4 ± 1,40 (9)	10,7 ± 2,08 (4)	25,6 ± 1,53	26,7 ± 1,91	68,3 ± 3,60	71,5 ± 3,09	76,9 ± 4,28	76,5 ± 1,99	47,2 ± 4,27	44,4 ± 4,95
V	9,5 ± 0,85 (2)	12,0 ± 2,06 (4)	25,8 ± 0,35	26,4 ± 1,61	66,5 ± 2,12	72,9 ± 4,80	73,8 ± 2,47	80,1 ± 5,06	45,0 ± 0,00	47,7 ± 2,30
VI	11,5 ± 0,75 (6)	13,7 ± 0,93 (5)	27,0 ± 0,98	29,0 ± 1,41	72,5 ± 2,26	78,0 ± 3,39	78,6 ± 1,50	83,6 ± 4,62	49,5 ± 3,38	52,4 ± 2,96
VII	11,7 ± 0,91 (7)	12,6 ± 1,45 (11)	27,9 ± 1,90	27,3 ± 1,49	72,4 ± 3,20	74,4 ± 2,76	80,7 ± 4,41	81,6 ± 1,95	50,9 ± 3,50	48,9 ± 5,78
VIII	12,4 ± 1,24 (17)	13,5 ± 0,93 (5)	28,4 ± 1,64	27,3 ± 1,24	75,1 ± 2,92	78,6 ± 1,07	82,6 ± 3,35	85,7 ± 3,96	49,2 ± 3,70	51,1 ± 3,86
IX	11,0 ± 1,16 (3)	12,3 ± 2,25 (6)	29,7 ± 1,15	28,1 ± 2,07	77,0 ± 3,61	74,1 ± 3,82	85,0 ± 5,00	81,1 ± 3,45	47,0 ± 4,58	48,4 ± 3,83

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TABLE 14. The effect of age on the Kidney Fat Index of porcupines culled on the TdR Game Farm between September 1981 and July 1982. Adult females were excluded from the calculations.

Dental age class	n	Kidney Fat Index (mean ± S.D.)
II	15	5,94 ± 6,46
III	25	8,02 ± 4,09
IV	13	12,89 ± 7,63
V	2	14,62 ± 7,91
VI	5	12,15 ± 8,25
VII	8	8,81 ± 5,96
VIII	13	11,72 ± 9,05
IX	4	10,06 ± 4,95

TABLE 15. The relationship between reproductive status and Kidney Fat Index in adult female porcupines culled on the TdR Game Farm between September 1981 and July 1982.

Reproductive status	n	Kidney Fat Index (mean ± S.D.)
Pregnant	12	25,60 ± 13,29
Lactating	9	10,98 ± 7,73
Non-active	10	11,51 ± 9,32

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(Table 12). Age specific body measurements for males and females confirm the lack of sexual dimorphic body sizes (Table 13).

Kidney Fat Index

Fat deposition, as reflected by the Kidney Fat Index was affected by age (Table 14) and attained peak values in age class V (18 - 23 months) with fluctuations during adulthood probably resulting from seasonal effects. The mean Kidney Fat Index calculated for adult males and adult, nonpregnant, nonlactating females (age classes V - IX) increased from a nadir in January to a peak in September. Values recorded throughout the breeding season (May - December) were higher than those recorded during the nonbreeding season (Fig. 10).

Mean Kidney Fat Index for pregnant females was significantly higher ($t_{19} = 2,94$; $p < 0,01$) than that recorded for lactating females, the latter being similar to the mean value recorded for nonpregnant, nonlactating adult females (Table 15).

DISCUSSION

Age determination

Using the parameters applied during the present investigation namely counts of cementum annuli or periosteal lines, chronological ages of porcupines could not be determined. Primary cementum lines however, are formed on an annual basis during the first few years of life, as suggested by the eruption interval of molars and permanent premolars and the differences between the number of lines in the cementum of

FIG. 10 ..... /

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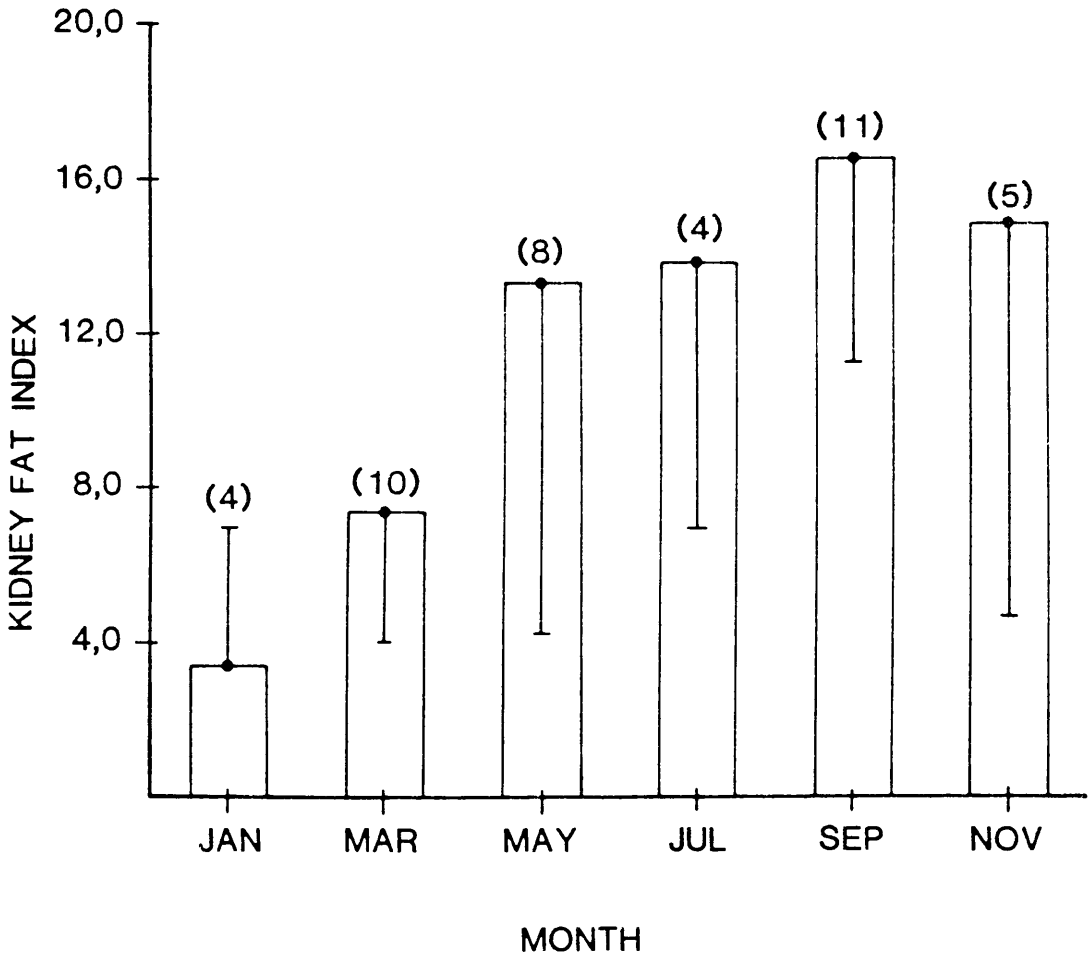

FIG. 10. Seasonal changes in the Kidney Fat Index of adult porcupines (age classes V - IX). Pregnant and lactating females were excluded when calculating monthly means. The vertical lines denote one standard deviation of the mean and sample sizes are given in brackets.

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these teeth (see Tables 6 & 7). Factors affecting the annular pattern of cementum growth have been the subject of much speculation but consideration of those is beyond the scope of the present study. However, it is generally accepted that the calcification rhythm in teeth may be disturbed by changes in the level of nutrition or periods of stress associated with reproduction (Klevezal' & Kleinenberg 1969; Morris 1972).

Ramification of cementum lines resulting from the uneven deposition of cementum due to continuous longitudinal growth of the open-rooted hypsodontic teeth of porcupines introduced variability beyond the levels of acceptance for the number of cementum lines counted. Similar problems have been encountered in other species, for example, bats (Philips, Steinberg & Kunz 1982), while Hall-Martin (1976), Gasaway, Harkness & Rausch (1978) and Leader-Williams (1979) all encountered problems in the interpretation of the layer structure of cementum of ungulates. Difficulties experienced in counting cementum lines accurately in porcupines, however, are not surprising since Klevezal' & Kleinenberg (1969) indicated that annual layers are not formed in teeth with permanent longitudinal growth.

Earle & Kramm's (1980) account of the use of this technique as a reliable indicator of real age in Canadian porcupines is surprising. Reliability in their study, however, was based on the differences between the number of cementum lines in the various teeth within the toothrow without accounting for the variability due to ramification and resorption. The shortcomings of such an approach are apparent and have been reviewed in detail by Dapson (1980). Well defined lines were present in the periosteal zone of the humeruses of all porcupines

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examined but resorption and ramification introduced variability beyond the level of acceptance for age determination purposes.

Combined eye lens weight increased with an increase in age but did not follow the pattern considered characteristic for mammals in general (Morris 1972); this discrepancy being ascribed to the dental age classes, based on eruption patterns, not representing chronological ages. The lines describing the relationship between lens weight and age nevertheless indicate an initial period of rapid growth from birth to 24 months of age, followed by a period of relatively slow growth (Fig. 5). The considerable overlap in lens weight within the sub= adult (II - IV) and adult (VI - IX) age classes is ascribed to the actual ages presented by each age class being continuous rather than discrete. Inequality in the ages represented by each class (see Table 5) contributed to the observed heteroscadasticity (see Dapson 1980) which rendered eye lens weight unsuitable as a criterion for age determination.

In addition, tooth measurements could not be used for age determina= tion as a result of the shape of the teeth and their continual longi= tudinal growth. The sequence of tooth eruption and replacement, how= ever, provided a ready means to determine the ages of porcupines less than 30 months of age. Chronological ages could be assigned to six of the nine dental age classes on the basis of age at eruption of the molars and replacement of the premolars as recorded in captive animals. The sequence of tooth eruption and replacement were also used by Corbet & Jones (1965) and Maguire (1976) to group porcupine skulls into relative age classes. These studies, however, were direc= ted at taxonomic aspects with no reference being made to the real ages

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represented by each age class.

Thus it is clear that without the availability of known age material representing most of the life-span of porcupines (20 years; Kingdon 1974), precise age determination of adult animals would not be feasible using established techniques.

Growth

Prenatal

Based on differences between calculated and observed values of specific fetal growth velocities for seven New World hystricomorph species, Roberts & Perry (1974) stated that the Huggett & Widdas equation is not applicable to hystricomorph rodents. They ascribed the observed differences to the fact that 'fetal growth rates of the hystricomorphs are extremely slow compared with those of other animals of similar birth weight'.

Huggett & Widdas (1951) clearly stated that t_o (intercept of the growth curve on the age axis) has no clear biological significance in fetal development but Roberts & Perry (1974) gave biological meaning to it by suggesting that the value of t_o is in good agreement with the time at which embryo development accelerates. In appreciating that calculated values for specific fetal growth velocity are drastically affected by t_o values and that the correction factors used to estimate t_o from gestation length are arbitrary and may introduce considerable error (Huggett & Widdas 1951), it would appear that the cor=

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rection factors used in the present study to estimate t_o, resulted in more realistic estimates for fetal growth rates and this being supported by the information in Table 9. The linear increase in differences between observed and theoretical t_o values with an increase in gestation length may, however, be interpreted as supporting Roberts & Perry's suggestion that differences in t_o values result from slow fetal development in hystricomorph rodents.

Frazer & Huggett (1974) use the same argument (slow early development) for rejecting the use of the Huggett & Widdas equation in describing prenatal growth rates in hystricomorph rodents. They based their argument on differences between observed and theoretical specific growth velocities for the chinchilla *Chinchilla laniger*, but did not consider that these differences actually resulted from totally different values (51 *cf.* 110 days) for gestation lengths being used to estimate t_o for the same species!

Therefore it is suggested that the equation of Huggett & Widdas (1951) may, in a modified form, be used to estimate specific fetal growth velocities for hystricomorph rodents, with the approximations used to estimate t_o being t x 0,25 for hystricomorphs with a gestation period less than 63 days, t x 0,4 for those with a gestation period between 63 and 100 days, and t x 0,3 for those with a gestation period longer than 100 days.

The calculated specific fetal growth velocities (0,1047 & 0,1813) using different approximations to estimate t_o (Table 9), for the porcupine, are higher than those reported for most other hystricomorph rodents (Asibey 1974; Frazer & Huggett 1974; Roberts & Perry 1974) but

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similar to the values estimated for the capybara *Hydrochoerus hydrochaeris* (Trapido 1949 in Frazer & Huggett 1974), paca *Agouti paca* (0,103; Collett 1981) and *Hystrix indica* (0,1021 - 0,1191; Thomè & Thomè (1980).

These relatively high values were all observed in larger (in terms of body size) species when compared to other hystricomorph rodents. The lack of a definite positive relationship between body size and gestation length in hystricomorph rodents (see Fig. 17; Chapter 4), however, suggests that gestation lengths in large hystricomorph rodent species are shorter than expected for the group, thereby possibly explaining the relatively high rate of fetal growth observed for them.

The relatively long gestation periods listed for hystricomorph rodents (Weir 1974) are the result, according to Roberts & Perry (1974), of the very slow early growth of the embryo. Nevertheless, the range of fetal growth velocities observed for hystricomorph rodents (0,04 - 0,18) is similar to those observed for most mammalian orders (Frazer & Huggett 1974), thus indicating that fetal development in hystricomorph rodents is not exceptional.

Postnatal

The von Bertalanffy equation has been applied to a large number of vertebrates and observed growth curves are sufficiently close to the empirical relationships to make the use of the equation an acceptable descriptive method for growth.

Figure 9 indicates that the von Bertalanffy growth curve describes

FIG. 9 ..... /

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postnatal growth in body weight of porcupines extremely well. Growth in captive porcupines was nearly linear up to the age of 20 weeks and asymptotic body weight was attained at the age of 52 weeks, the latter coinciding with the observed age at sexual maturity (see Chapters 4 & 5).

The extended lactation period observed in porcupines (see Chapter 4) and the protection and care afforded through intensive parental care (see Chapter 6) conceivably contribute to the relatively high rate of growth maintained during the first year of life. With sexual maturity attained during the second year of life and a life expectancy of approximately 20 years (Kingdon 1974), it is apparent that the relatively high rate of postnatal growth and development result in an extended reproductive period, thereby probably enhancing individual reproductive values by counteracting the slow reproductive rate due to seasonal breeding and a small litter size.

Furthermore it may be argued that this high rate of growth compensates for the small neonatal size of porcupines ($< 3,0\%$ of maternal body weight; see Chapter 4), which in turn may be ascribed to the relative short gestation period.

Asymptotic body weight predicted by the von Bertalanffy equation was slightly lower than the mean adult body weight attained by adult animals. However, the relatively short life-span for which data were included in the analysis of growth may have been a confounding factor. The calculated coefficient of catabolism ($k = 0,65$) was higher than those recorded for the dassie *Procavia capensis* (Fairall 1980; Steyn & Hanks 1983) and eland *Taurotragus oryx* (Jeffery & Hanks

1981) ..... /

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1981) but lower than that recorded for other ungulates (see Steyn & Hanks 1983 for references). This constant, however, has no biological or physiological significance (Roff 1980) and a comparison with other hystricomorph rodents, for which data are presently not available, would thus not have had any phylogenetic or biological meaning.

Case (1978) reported in a lengthy analysis on the adaptive signifi= cance of postnatal growth that growth rate is adapted to certain fea= tures of an animal's environment. He regarded feeding requirements, infant mortality rate and the availability of food to parents of particular importance in explaining interspecific differences in post= natal growth rates. The information available on hystricomorph rodents does not provide a basis for such an analysis. Case (1978), however, concluded that life-history attributes such as growth rate, precociality and relatively high birth weight, are in these rodents similar to those in ungulates. The three rodent subgroups (myomorphs, sciuromorphs and hystricomorphs) furthermore have very similar growth rates but differ markedly in other respects. Hystricomorphs in general, have long gestation periods, a small litter size and relati= vely high birth weights.

The growth rates of male and female porcupines and resulting asymp= totic body weights are similar. The form of paternal investment afforded by pairbond system of porcupines (see Chapter 6) limits the degree of sexual selection imposed on males, which favours a lack of sexual dimorphism, thus explaining the similarity in body size of the sexes.

Condition ..... /

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Condition

Seasonal changes in condition, as suggested by seasonality in the amount of fat reserves deposited around the kidneys of mammals living in temperate regions, have an adaptive significance in terms of survival (Leader-Williams & Ricketts 1981). Seasonal changes in fat deposition in adult male porcupines corresponded with changes in some of their reproductive parameters (i.e., testosterone levels; see Chapter 5) but, with the lack of information on their nutritional status, this cannot be explained in terms of seasonal environmental changes. Porcupines furthermore do not have a rutting season and the increased fat deposition before the extended breeding season cannot, as for the impala *Aepyceros melampus* (Hanks, Cumming, Orpen, Parry & Warren 1976), be explained in terms of the reproductive phenology of the species.

The effect of reproductive status on the fat reserves of adult females precluded a meaningful analysis of seasonality. The increased deposition of fat during pregnancy, probably resulting from increased circulating progesterone levels, may however prepare the female for the increase in energy demands posed during lactation. The lack of significance in difference in the Kidney Fat Index of non-reproducing and lactating females however suggests that these females are in general well-adapted to cope with the extra energy demands imposed by lactation.

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CHAPTER 4

FEMALE REPRODUCTIVE BIOLOGY

INTRODUCTION

Information on reproduction in the female porcupine is limited and includes the observations published by Weir (1967) on the crested porcupine *H. cristata*, Gosling (1980) on the Himalayan porcupine *H. hodgsoni*, and Thomè & Thomè (1980) on the Indian porcupine *H. indica*. Mohr (1965) published incidental but relevant observations on reproductive behaviour and litter sizes of various *Hystrix* species.

Information on the related New World species has been excellently reviewed by Weir (1974), who regarded the relative long gestation period, long oestrous cycle, the occurrence of a vaginal closure membrane and the lateral position of the nipples, as characteristic features of reproduction in this group of rodents. Published information on *Hystrix* species supports this notion since their gestation lengths have been recorded to vary from 112 days in *H. africaeaustralis* (Dekeyser 1955 in Weir 1974), to 105 days in *H. hodgsoni* (Gosling 1980) and 'approximately three months' in *H. indica* (Thomè & Thomè 1980). Mohr (1965) however recorded a minimum litter interval of 91 days for African porcupines (*H. cristata* and *H. africaeaustralis*). The length of the oestrous cycle has been reported to vary from 30 to 37 days in *H. cristata* (Weir 1974). Weir (1967) also confirmed the presence of a vaginal closure membrane and the lateral position of the nipples in this species.

Seasonal ..... /

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Seasonal breeding has been recorded for *H. brachyurus* and *H. hodgsoni* with two breeding seasons per year being reported for *H.africaeaustra=lis* and a lack of seasonality in *H.leucura* (Weir 1967). Gosling (1980), however, recorded *H.hodgsoni* as breeding throughout the year in captivity.

Weir (1967) illustrated the unusual appearance of the female genitalia of *H. cristata*, where the uretheral aperture is anterior to the small trilobed clitoris. The microscopic anatomy of the ovaries of this species was also described by Weir (1967) who indicated that luteinisation of the well-developed theca interna is prominent. Prominent vacuoles are present in the interstitial tissue and vascularity in the ovary of *Hystrix* was 'very striking' (Weir 1967). The nuclei of the basal layer of cells of the membrana granulosa is furthermore noticeably aligned (see Fig. 6 in Weir & Rowlands 1974). Accessory corpora lutea are also formed during infertile oestrous cycles (Weir & Rowlands 1974).

No information is as yet available on the functional activities of the ovary of *Hystrix*. Accessory corpora lutea in New World hystricomorphs are functionally equivalent to the corpora lutea of pregnancy and act as additional sources of progesterone (Heap & Illingworth 1974; Tam 1974). Follicles develop throughout pregnancy to a mature size and ovulation in the plains viscacha *Lagostomus maximus* (Weir 1967) and follicular cycles terminating in degeneration occur continually in the pregnant guinea-pig (Perry & Rowlands 1962). Modifications in the ovary and placenta enhance the synthesis of progesterone for the maintenance of gestation (Tam 1974). Peripheral levels of progeste=rone, as a result of the presence of progesterone-binding plasma

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proteins (PBPP), are higher than those reported in most other mammals (Heap, Ackland & Weir 1981).

In these rodents, progesterone requirements of pregnancy are apparently met by a mechanism adopted to ensure a substantial pool of steroid which can dissociate rapidly from its carrier rather than by a marked increase in progesterone production rate (Heap & Illingworth 1974). The function of high levels of progesterone-binding globulin, of which the synthesis is closely-related to plasma progesterone concentrations, is therefore probably to reduce the concentration of freely available progesterone in blood, and to provide a source of progesterone for binding components such as target cell receptors (Heap *et al*. 1981).

This chapter deals with aspects of reproduction in the female porcupine and is based on information obtained from captive animals and from free-ranging porcupines culled on a seasonal basis.

MATERIALS AND METHODS

Information and material were obtained from study colonies established at the University of Pretoria, from females culled on the TdR Game Farm (n = 89) and at various localities in the Cape Province (n = 14).

Females kept in captivity were examined after immobilisation (see Chapter 2) at two to seven day intervals for periods varying from 44 to 434 days (Table 16). Blood samples (5,0 ml) were collected in heparinised tubes through cardiac puncture between 10h00 and 12h00 and duplicate plasma fractions were stored at - 20 °C after separation

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through centrifugation. Females were also weighed, the condition of their vaginal closure membranes noted, and their teats palpated to determine if they were lactating. Following Weir (1974), the length of the oestrous cycle was taken as the interval from the first day of vaginal opening in one cycle, up to, but not including, the first day of opening in the following cycle. Enclosures where females were kept, were inspected daily for the presence of copulatory plugs.

The social context and reproductive status of each of 14 females at the onset and end of 28 observation periods, and the length of these periods, are presented in Table 16.

Age at first oestrus was determined for five females born in captivity and examined from the age of approximately eight months, as described earlier. Gestation length was calculated for four females as the interval between an observed copulation and parturition. These females were kept isolated from intact males after copulation and serial blood samples were collected from three of these at five to seven day intervals throughout pregnancy. Pseudopregnancies were monitored in a similar way. Age at first conception was recorded for nine females born in captivity, four of these were not immobilised until after parturition. All these females were housed with sexually experienced males (i.e., males that had sired offspring previously).

Three control groups, each comprising one parous female and one intact male, were not handled experimentally (therefore not immobilised) and provided additional information on the length of the litter interval.

Date of birth, birth weight and litter size were recorded for all

TABLE 16 ..... /

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TABLE 16. Periods of observation and serial blood sampling and the reproductive status of individual females kept in captivity for experimental purposes.

Female	Period	Days	Conspecifics present	Reproductive status at onset and end of observation periods	
				Onset	End
A	20/01/81 - 30/03/82	434	Intact Male/Female B/2 Offspring	Nulliparous, nonpregnant	Primiparous, nonpregnant, lactating
	30/03/82 - 16/06/82[2]	78	Intact Male/Female B	Parous, nonpregnant, lactating	Parous, nonpregnant
B	20/01/81 - 30/03/82	434	Intact Male/Female A/Offspring of A	Nulliparous	Nulliparous
	30/03/82 - 16/06/82[2]	78	Intact Male/Female A	Nulliparous	Nulliparous
C	07/01/81 - 28/04/81	111	Female D/Offspring	Parous, nonpregnant,lactating	Parous, nonpregnant
	28/04/81 - 30/10/81	185	Female D/Offspring/Intact Male	Parous,nonpregnant	Parous, pregnant
	30/10/81 - 25/03/82	146	Female D/Offspring/Vasectomised Male/Femal	Parous, pregnant	Parous, nonpregnant, lactating
	25/03/82 - 16/06/82[2]	83	Female D/Offspring/Vasectomised Male	Parous, nonpregnant,lactating	Parous, nonpregnant
D	07/01/81 - 28/04/81	111	Female C/Offspring of C	Parous, nonpregnant	Parous, nonpregnant
	28/04/81 - 30/10/81	185	Female C/Offspring of C/Intact Male	Parous, nonpregnant	Parous, nonpregnant
	30/10/81 - 25/03/82	146	Female C/Offspring of C/Vasectomised Male/	Parous, nonpregnant	Parous, nonpregnant
	25/03/82 - 16/06/82[2]	83	Female C/Offspring of C/Vasectomised Male	Parous, nonpregnant	Parous, nonpregnant
E	23/01-81 - 21/07/81	179	Female F/Intact Male	Parous, nonpregnant	Parous, nonpregnant
	21/07/81 - 13/01/82	176	Female F/Vasectomised Male	Parous, nonpregnant	Parous, nonpregnant
	18/03/82 - 16/06/82	90	Vasectomised Male/Offspring of F	Parous, nonpregnant	Parous, nonpregnant
F	23/01/81 - 21/07/81	179	Female E/Intact Male	Nulliparous, nonpregnant	Primiparous, pregnant
	21/07/81 - 29/12/82	161	Female E/Vasectomised Male/Offspring	Primiparous, pregnant	Parous, nonpregnant, lactating
G	23/01/81 - 29/09/81[1]	249	Female H/Intact Male	Parous, nonpregnant	Parous, nonpregnant
H	23/01/81 - 21/07/81	182	Female G/Intact Male	Parous, nonpregnant	Parous, nonpregnant
I	23/01/81 - 17/03/81[1]	853	Vasectomised Male	Nulliparous, nonpregnant	Primiparous, nonpregnant
J	21/01/81 - 09/06/81	139	Female K/Intact Male	Parous, nonpregnant	Parous, nonpregnant
K	21/01/81 - 23/06/81	153	Female J/Intact Male	Primiparous, nonpregnant	Primiparous, nonpregnant
L	13/08/81 - 12/03/82	211	Intact Male	Primiparous, nonpregnant	Primiparous, nonpregnant
	01/05/82 - 16/06/82[1]	46	Intact Male	Primiparous, nonpregnant	Primiparous, nonpregnant
M	10/11/81 - 22/03/82	132	Intact Male	Primiparous, pregnant	Parous, nonpregnant, lactating
	23/04/82 - 06/06/82[2]	44	Intact Male	Parous, nonpregnant,lactating	Parous, nonpregnant
N	26/05/81 - 30/10/81	157	Female C/Female D/Intact Male	Nulliparous, nonpregnant	Nulliparous, nonpregnant
	30/10/81 - 25/03/82	146	Female C/Female D/Vasectomised Male	Nulliparous, nonpregnant	Nulliparous, nonpregnant
		4 371	porcupine days		

[1] Died at end of period

[2] In contact with male only during stage encounters of 10 min. every 24 h.

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litters (n = 23) born in captivity. Additional information on the dates of birth and litter size were obtained from unpublished records kept by the National Zoological Gardens (n = 101) and the Johannesburg Municipal Zoological Gardens (n = 41). The mean dates of birth and standard errors of the means for each of these localities were calculated by using the method of Caughley (1977).

Reproductive tracts of 103 females of all reproductive and age classes were available for this part of the study. Fixed ovaries were weighed, serially sectioned at 5 μm along the longitudinal axis after routine dehydration and embedding in paraffin wax. Every tenth section was mounted on a glass microscope slide and stained, using haematoxylin and eosin. Diameters of antral follicles and corpora lutea were measured microscopically as the greatest length on any two perpendicular axes. These values (r_1 and r_2) were used to estimate volumes by means of the formula $\frac{4}{3}\pi r_1 r_2 \left(\frac{r_1 + r_2}{2}\right)$. Accessory corpora lutea were distinguished from primary corpora lutea by their smaller size and the presence of degenerating ova or remains of a zona pellucida (Rowlands, Tam & Kleiman 1970).

Date of conception and birth for each litter was calculated as the sampling date minus fetal age (see Chapter 3), and as the sampling date minus fetal age plus gestation period respectively. All values in this Chapter are expressed as means ($\bar{x}$) and one standard deviation of the mean ($\pm$ S.D.). Statistical significance in the text implies that $p \leq 0{,}01$.

Radioimmunoassay of steroid hormones

Reagents

Analytical ..... /

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Analytical grade light petroleum ether (distillation range 40 - 60 °C) and 'pro analysi' diethyl ether from Saarchem (Pty) Ltd (Krugersdorp, RSA) and Merck (Darmstadt, FRG) respectively were used without any further purification. The phosphate buffer (pH 7,0) comprised of the following in 200 ml deionised water:

Disodium hydrogen phosphate ($Na_2HPO_4.12H_2O$)	45,0 g
Sodium dihydrogen phosphate ($NaH_2PO_4.H_2O$)	10,8 g
Sodium chloride (NaCl)	18,0 g
Sodium azide (NaH_3)	02,0 g
Gelatin	02,0 g

The pH was corrected with NaOH when necessary.

Dextran-coated charcoal was used as a suspension of charcoal (Aktivo=le; 'pro-analysi', Merck, Darmstadt, FRG) in phosphate buffer (0,2 g/100 ml) containing 0,1 g dextran T-40 (Pharmacia, Uppsala, Sweden).

Scintillation fluid (Ready-Solve™ HB/b) and scintillation vials (Mini Poly-Q™ Vial) from Beckman Instruments (Pty) Ltd (Johannesburg, RSA) and crystallined progesterone (4-pregnene-3,20-dione) and oestra=diol-17β (1,3,5(10)-oestratriene 3,17β-diol) from Sigma Chemical Co. (Dorset, UK) were used. Radio-active steroids from Radiochemical Centre (Amersham, UK) had the following specific activities: [1,2,6,-7-^{3}H] progesterone (Code TRK 413), 308 mCi/mg; [2,4,6,7-^{3}H] oestra=diol-17β (Code TRK 322), 322 mCi/mg. These were used within six months and radio-chemical purity was not checked. Trivial names used in this chapter include progesterone for 4-pregnene-3,20-dione,

oestradiol-17β ...../

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oestradiol-17β for 1,3,5(10)-oestratriene-3,17β-diol, oestrone for 3-hydroxy-1,3,5(10)-oestratriene-17-one and oestriol for 1,3,5(10)-oestratriene3,16α,17β-triol.

Progesterone

The procedure used to measure plasma levels of progesterone was, with minor modifications, similar to that of Haresign, Foster, Haynes, Crighton & Lamming (1975).

Appropriate duplicate plasma samples from pregnant (10 or 50 µl) and non-pregnant females (50 or 100 µl) were transferred into 10 ml round-bottom glass tubes and progesterone was extracted with 2,0 ml petroleum ether. Sample volumes used for extraction depended on the expected concentration of progesterone and all volumes were made up to 100 µl with 0,1 M phosphate buffer (pH 7,0) containing 0,1% gelatin and sodium azide by weight. Due to the expected presence of high levels of progesterone-binding proteins (see Heap *et al.* 1981), 100 µl NaOH (0,6 mol/l) was added to plasma samples from pregnant females before extraction to denature progesterone-binding globulins. The same samples were also extracted without denaturation. The procedure of extraction involved thorough mixing of the plasma and ether on a vortex mixer for 1 min and freezing at -20 °C for 60 min. The organic phase was then decanted into a series of glass assay tubes (12 x 75 mm) and evaporated to dryness under a stream of nitrogen in a 37 °C water bath. The dried extracts were redissolved in 100 µl phosphate buffer. Four duplicate aliquots (50 - 100 µl) from plasma pools comprising samples from non-pregnant females were included in each assay for estimating the loss of steroid during extraction. Procedu-

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ral losses were estimated individually in all samples from pregnant females.

In all these cases, 100 µl [1,2,6,7-^{3}H] progesterone in ethanol (3 000 cpm) was added to each tube and dried down under a stream of nitrogen before addition of the plasma samples. After mixing on a vortex mixer for 1 min and incubation at 37 °C for 20 min, the samples for recovery estimates were extracted as above and dried down in scintillation vials.

A series of standards containing 7,8; 15,6; 31,2; 62,5; 125; 250; 500; 1 000 and 2 000 pg progesterone/100 µl phosphate buffer was prepared in duplicate and included in each assay. Two buffer blanks, containing 100 µl phosphate buffer as well as duplicate tubes containing the dried residue of the ether only, were also included in each assay. 100 µl of antiserum raised in a goat to progesterone-11-succinyl-bovine serum albumin as described by Furr (1973) and supplied by Specific Antisera Ltd (Wilmslow, UK) was added to plasma extracts, buffer blanks, ether blanks and standards at a 1:4 000 dilution in phosphate buffer.

The mixture was incubated at room temperature for 10 min and 100 µl [1,2,6,7-^{3}H] progesterone in phosphate buffer (20 000 cpm) was added. The contents of the tubes were then mixed for 1 min on a vortex mixer and incubated at 4 °C for at least 12 h (usually overnight).

Progesterone bound to the antibody was separated from the free steroid by the addition of 1,0 ml dextran-coated charcoal at 4 °C. The

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solutions were mixed for 30 sec, incubated at 4 °C for 15 min and centrifuged at the same temperature at 3 000 rpm for 15 min. The supernatants were decanted into scintillation vials and scintillation fluid (5,0 ml) was added to each vial. The vials were shaken properly and the radio-activity was counted at least 4 h later for 2 min, using a Beckman LS 5800 Scintillation Counter.

A standard curve of percentage radio-activity bound was plotted against the logarithm of the concentrations of progesterone over the range 7,8 to 2 000 pg/tube. The progesterone content of extracts was determined by interpolation on the standard curve. The concentrations in plasma samples were calculated, taking into account the original volume of plasma extracted and procedural losses during the extraction.

Progesterone concentrations for some samples were also determined at the University of Nottingham (Department of Physiology and Environmental Science, School of Agriculture). The procedure used at this laboratory was similar to that described above.

Oestradiol-17β

The protocol adapted for determining plasma levels of unconjugated oestradiol-17β was similar to that described by Abraham (1976) and Crosignani, Trojsi, Attanasio, Lombroso Finzi & Malvano (1975). Steroids were not purified and separated by chromatography after extraction.

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The recovery of known amounts of [2,4,6,7-^{3}H] oestradiol-17β (1 000 cpm) in absolute ethanol, dried under a stream of nitrogen, to which aliquots (1,0 ml) of pooled plasma from cyclic females were added, served to determine procedural losses incurred during extraction.

Plasma samples (1,0 ml), reagent blanks (phosphate buffer and diethyl ether) and tritiated steroid recovery samples were extracted with diethyl ether (4,0 ml) by shaking the mixtures thoroughly for 5 min on a multitube vortexer (Model 2601, Scientific Manufacturing Industries, Emeryville, USA). The aqueous phase was frozen at -20 °C for 60 min and the ether extract decanted into a set of clean glass assay tubes (12 x 75 mm). These were evaporated to dryness under a stream of nitrogen in a water bath at 37 °C. Dried extracts were resuspended in 100 µl phosphate buffer (pH 7,0) containing 0,1% gelatin and sodium azide by weight. A series of standards (0; 4,89; 9,75; 19,5; 39; 78; 156; 312; 625; 1 250 and 2 500 pg oestradiol-17β/100 µl phosphate buffer) was prepared in duplicate and included in each assay.

Antiserum in phosphate buffer (100 µl) at a dilution of 1:2 500 was added to standards, plasma extracts and reagent blanks, vortexed and left to incubate at room temperature (23 - 25 °C) for 10 min. The antiserum, supplied by R P Millar (Department of Chemical Pathology, University of Cape Town, RSA), bound 45 to 51% of [2,4,6,7-^{3}H] oestradiol-17β (10 000 cpm) in the absence of radio-inert oestradiol-17β. [2,4,6,7-^{3}H] oestradiol-17β (10 000 cpm) in 100 µl phosphate buffer was added to the contents of each tube which were vortexed again and left to incubate for approximately 12 h at 4 °C (usually overnight).

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The separation of antibody-bound and free steroid was performed at 4 °C by adding 1,0 ml dextran-coated charcoal suspension to each tube. The contents were agitated for 1 min, incubated for 10 min at 4 °C and centrifuged for 15 min at 4°C. Supernatants were decanted into scintillation vials and scintillation fluid was added to each vial. The contents of each vial were mixed thoroughly and radio-activity was measured in a liquid scintillation counter.

Duplicate samples (1,0 ml) from a pool of female porcupine plasma, and varying quantities (25, 50 & 100 pg/ml) of oestradiol-17β added to a male plasma pool, were analysed in each assay and served as internal controls.

Determination of progesterone-binding plasma proteins (PBPP)

The protocol adopted was similar to that described by Heap *et al.* (1981), with plasma samples diluted 20-fold with 10 mM-Tris-HCl buffer (pH 7,4) to a final protein concentration of $\sim$ 2 - 3 mg/ml. Duplicate aliquots (100 μl) of the diluted plasma were incubated with increasing amounts (0,125 - 4,0 nM) of [17α-methyl-^{3}H]-promegestone (New England Nuclear, Boston Massachussetts, USA) in the presence (to determine non-specific binding) or absence of a 100-fold excess promogestone (R5020; New England Nuclear, Boston Massachussetts, USA) for 15 min at 37 °C and overnight at 4 °C.

Dextran-coated charcoal (500 μl) was added and mixed thoroughly on a vortex mixer. After 15 min on ice, the tubes were centrifuged at 4 °C and 3 000 g for 15 min. Aliquots (500 μl) of the supernatant were decanted into scintillation vials and 4,0 ml of scintillation fluid

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was added. The amount of protein-bound radio-activity was measured in a scintillation counter. A duplicate set of blanks containing 100 µl ^{3}H-promegestone and 100 µl Tris-HCl buffer was also included in each assay. The quantities of bound and free steroid were estimated from the total of endogenous and added steroid and the results were plotted according to the method of Scatchard (1949). A single-point method was developed to permit the simultaneous analysis of a large number of samples (Heap *et al.* 1981). Plasma protein concentrations were determined as described by Lowry, Rosebrough, Farr & Randall (1951).

Milk intake

Determination of milk intake was based on the turnover of water by young as measured by tritium dilution following Green & Dunsmore (1978). Each of five captive-born porcupines was separated from their mothers, weighed and injected intraperitoneally with 500 µCi tritiated water containing 90 MBq activity (1,0 ml). They were deprived of food and water for a 6 h equilibration period and a blood sample (2,0 ml) was then collected from the femoral vein. Young were returned to their holding pens and subsequently weighed and bled at seven to eight day intervals over periods varying from 21 to 30 days.

Aliquots(100 µl) of water extracted from each blood sample were added to scintillation vials containing 5,0 ml scintillation fluid. Stan= dards were prepared by diluting tritiated water (1:1 000) and radio-activity of the samples and standards were counted on a Beckman LS 5800 Scintillation Counter. Milk consumption was estimated on the assumption that 1,0 ml milk contains 0,89 ml water (0,83 ml free water and 0,06 ml metabolic water; Green & Dunsmore 1978).

Milk ..... /

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Milk was collected from the mothers of the young on the day of bleeding. Young were separated from their mothers for approximately 6 h to allow the udders to distend with milk. Females were milked following immobilisation (see Chapter 2) and an intramuscular injection of approximately 0,1 1.U./kg oxytocin (Syntocinon, Basle, Switzerland).

RESULTS

Reliability criteria for assays

Progesterone

The procedure used in the newly-established Radioimmunoassay Laboratory at the University of Pretoria was similar to that applied to porcupine plasma samples during a study visit to the well-established laboratory at the University of Nottingham.

Antiserum from Specific Antisera Ltd (Wilmslow, UK) was used in both laboratories. The specificity of the antiserum has been described by Furr (1973) and cross-reactions of other steroids were: 11α-hydroxyprogesterone, 85%; 17α-hydroxyprogesterone, 12,5%; 5β-pregnane-3,20-dione, 12,5%; 5α-pregnane-3,20-dione, 3,0%; 5β-pregnane-3β-ol-20-one, 1,73%; 11-deoxycorticosterone, 1,1%; 5α-pregnane-3β-ol-20-one, 1,0%. Cross-reactions of 20α-hydroxypregn-4-ene-3-one, 20β-hydroxypregn-4-ene-3-one, 11-deoxycortisol, testosterone, androstenedione, pregnenolone, 5β-pregnane-3α,20α-diol and oestradiol-17β were less than 0,70%.

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The sensitivity of the assays, defined as twice the standard deviation of blank values, ranged from 0,16 to 0,73 ng/ml ($\bar{x}$ = 0,49 ± 0,21; n = 7). Ten buffer blanks measured during the assays contained 0,46 ± 0,26 ng progesterone equiv./ml.

Extraction efficiency was affected by plasma volume and plasma progesterone levels and decreased exponentially with an increase in progesterone levels (Fig. 11). Recovery estimates varied from 81,0 to 94,1% ($\bar{x}$ = 86,6 ± 4,85; n = 7) for samples containing 0,5 to 5,0 ng progesterone/ml and from 61,1 to 77,2% ($\bar{x}$ = 69,3 ± 4,43; n = 10) for samples containing $\nearrow$ 5,0 $\swarrow$ 15,0 ng progesterone/ml plasma. Recovery estimates for plasma samples containing $\geqslant$ 15,0 $\swarrow$ 160,0 ng progesterone/ml varied from 12,5 to 54,6% (n = 40) and was also affected by the volume of plasma extracted. All these samples originated from pregnant females and the low recovery estimates may be ascribed to the presence of progesterone-binding plasma proteins (Challis, Heap & Illingworth 1971; Heap *et al.* 1981). Heating of four plasma pools from pregnant females (30 min at 60 °C) in an attempt to denaturate proteins, did not improve recovery estimates (24,1 c.f. 24,7% for untreated samples) but the addition of 100 µl NaOH (0,6 mol/l) 10 min before extraction increased recovery estimates in the same samples to 69,6 ± 8,87%.

The intra- and interassay coefficients of variation calculated according to the method of Jeffcoate (1981) for the assays conducted at the University of Pretoria were 4,3 and 9,7% respectively. The interassay variation for a plasma sample containing 6,6 ng progesterone/ml included in all assays was 7,6%. The accuracy of the assays conducted at the University of Pretoria was tested by the recovery

FIG. 11 ..... /

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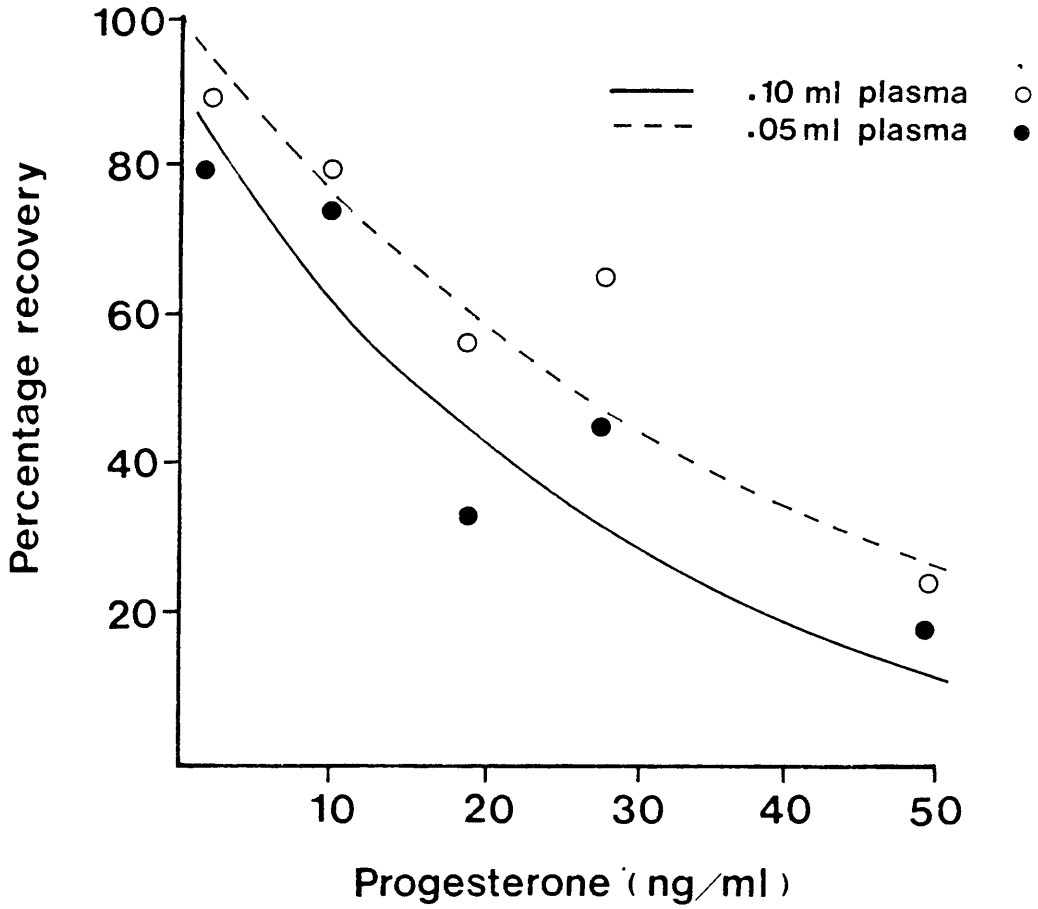

FIG. 11. The relationship between extraction efficiency and progesterone levels (ng/ml) in plasma pools from pregnant porcupine females. The curves were fitted through regression analyses.

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of progesterone added to a plasma pool. Amounts recovered did not differ significantly from that added (t_3 = 1,23; Table 17). The intra-assay coefficient of variation based on 20 duplicate samples assayed at the University of Nottingham was 9,0 and 14,0% for the range 40 to 60% and 60 to 80% bound respectively. Interassay variation based on a plasma sample containing 2,4 ± 0,13 ng/ml and included in all assays, was 14,2%. Addition of 125 and 500 pg progesterone to a plasma pool included in six assays conducted at the University of Nottingham gave recoveries of 94,0 ± 4,8 and 109 ± 4,2% respectively. The standard curve was highly reproducible.

Results obtained for ten plasma samples containing 0,5 to 15,0 ng progesterone/ml, and assayed at the University of Pretoria as well as at the University of Nottingham were significantly and linearly related; the relationship being described by $y = 0,93\ x + 0,70$ (r^2 = 0,97). Interlaboratory coefficient of variation was 20,2%.

Oestradiol-17β

The specificity of the antiserum raised in a rabbit has been quantified by the supplier and cross-reactions of other steroids were: oestrone, 0,01%; pregnanediol, corticosterone, de-oxy corticosterone, 17α-hydroxy pregnenolone, androstenedione, 20α-hydroxy progesterone, progesterone, testosterone and cortisol, 0,001%.

The sensitivity of the assays, defined as twice the standard deviation of values obtained from buffer blanks, ranged from 3,5 to 14,1 pg/tube ($\bar{x}$ = 10,6 ± 3,6) or 3,7 to 15,8 pg/ml ($\bar{x}$ = 11,7 ± 3,9). Buffer blanks

TABLE 17 ..... /

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TABLE 17. Estimates of progesterone concentration in a plasma pool from subadult females to which known amounts of progesterone were added. (No. of duplicate determinations in parenthesis).

Progesterone added (ng/ml)	Progesterone measured (ng/ml)
0	0,64 (2)
5	6,30 (2)
10	11,26 (2)
20	19,21 (2)

TABLE 18. Estimates of oestradiol-17β concentration in a pool of plasma from male porcupines to which known amounts of oestradiol-17β were added. (No. of duplicate determinations in parenthesis).

Oestradiol-17β added (pg/ml)	Oestradiol-17β measured (pg/ml)
25	27,77 ± 2,26 (6)
50	54,05 ± 8,75 (6)
100	91,75 ± 6,75 (4)

TABLE 19. The observed and expected number of oestrous cycles for the periods of decreasing and increasing daylight lengths in captive porcupine females. The periods when females were either pregnant or lactating were excluded in the calculation of the expected number of cycles.

Period	Number of cycles		χ^2 value
	Expected	Observed	
22 Jan. 1981 - 21 July 1981	29	22	1,69
22 July 1981 - 21 Jan. 1982	25	22	0,36

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measured in duplicate during eight assays contained 8,3 ± 2,8 pg oestradiol-17β equiv./ml. Extraction efficiency varied from 85,1 to 96,8% with a mean of 91,4 ± 4,3% for eight assays.

The accuracy of the assay was tested by the recovery of oestradiol-17 from male plasma pools. The amount recovered did not differ significantly ($t_{15} = -0,25$) from the amount added (Table 19). The intra- and interassay coefficients of variation calculated according to the method of Jeffcoate (1981) were 2,4 and 16,2% respectively. Interassay variation for a sample included in eight assays which contained 32,6 ± 3,1 pg/ml, was 9,4%. The standard curve was highly reproducible.

The oestrous cycle

Length and Seasonality

Females were polyoestrus and nonlactating adult females in captivity cycled throughout the year. Nine females examined systematically over a one year period, exhibited 81,5% of the expected (n = 54) oestrous cycles, and the number of cycles observed during the period of increasing daylight length as well as the period of decreasing daylight length did not differ significantly from that expected ($\chi^2 = 1,69$ and 0,36 respectively; Table 19).

The mean length of 43 oestrous cycles monitored in 12 females was 31,2 ± 6,5 (17 - 42) days, with most (60,5%) varying in length from 28 to 36 days (Fig. 12). Extreme deviations from the mean reflect cycle lengths in nulliparous females with the greatest variation (17 - 42

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days) occurring during the pubertal interval of two females. The mean length of six cycles monitored in two parous females housed with vasectomised males, did not differ significantly from that of parous females housed with intact males ($t_2 = 1,58$) and the data for the two groups were therefore combined. Similarly the mean cycle length of six nulliparous females (30,5 ± 7,3 days; n = 19) did not differ significantly ($t_{41} = 1,67$) from the mean observed in parous females (32,3 ± 6,2 days; n = 24).

The vaginal closure membrane remained perforated for a mean period of 8,8 ± 3,9 days (n = 34) and the copulatory plug was observed *in situ* on Days 3 to 8 ($\bar{x}$ = 6,0 ± 1,7; n = 8) after the day of vaginal opening. Copulation was observed two to eight days after vaginal opening ($\bar{x}$ = 5,0 ± 2,6; n = 8) and in two controlled observations, the copulatory plugs were expelled 45 and 48 h after copulation.

Progesterone and oestradiol-17β levels during the oestrous cycle

Temporal changes in concentrations of circulating progesterone and oestradiol-17β during 12 oestrous cycles monitored in six adult females are presented in Fig. 13. Cycles a, b, d, e and f were recorded in two parous females housed with a vasectomised male; Cycles c, g and j in two parous adult females, each housed with an intact male; Cycles h, i, k and l in two nulliparous adult females, each housed with an intact male. Periods between two consecutive vaginal openings and therefore the assumed length of these oestrous cycles plus one day, varied from 23 to 42 days ($\bar{x}$ = 34,0 ± 6,6; n = 12). The interval between oestradiol-17β surges for seven of these cycles (cycles associated and followed by oestradiol-17β surges), did not

FIG. 12 ..... /

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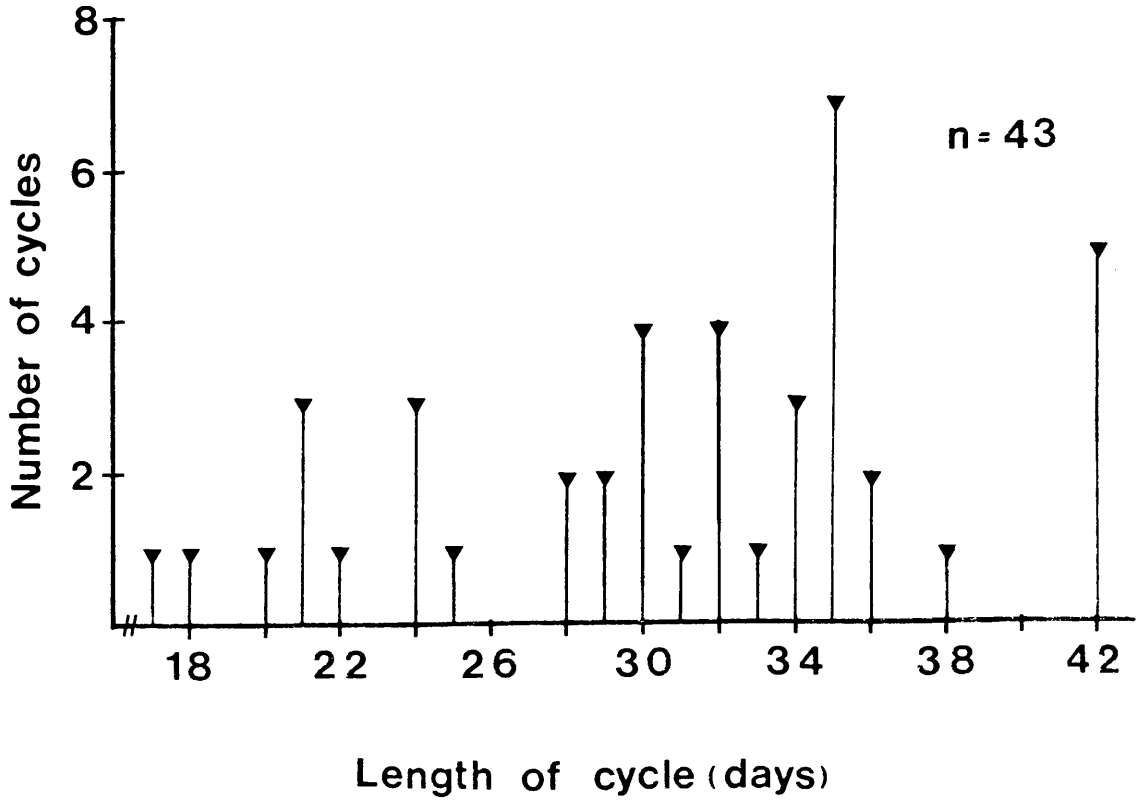

FIG. 12. The distribution of oestrous cycle lengths in parous and nulliparous female porcupines housed in captivity with males under conditions of natural illumination, ventilation and temperature, and a relatively constant food supply.

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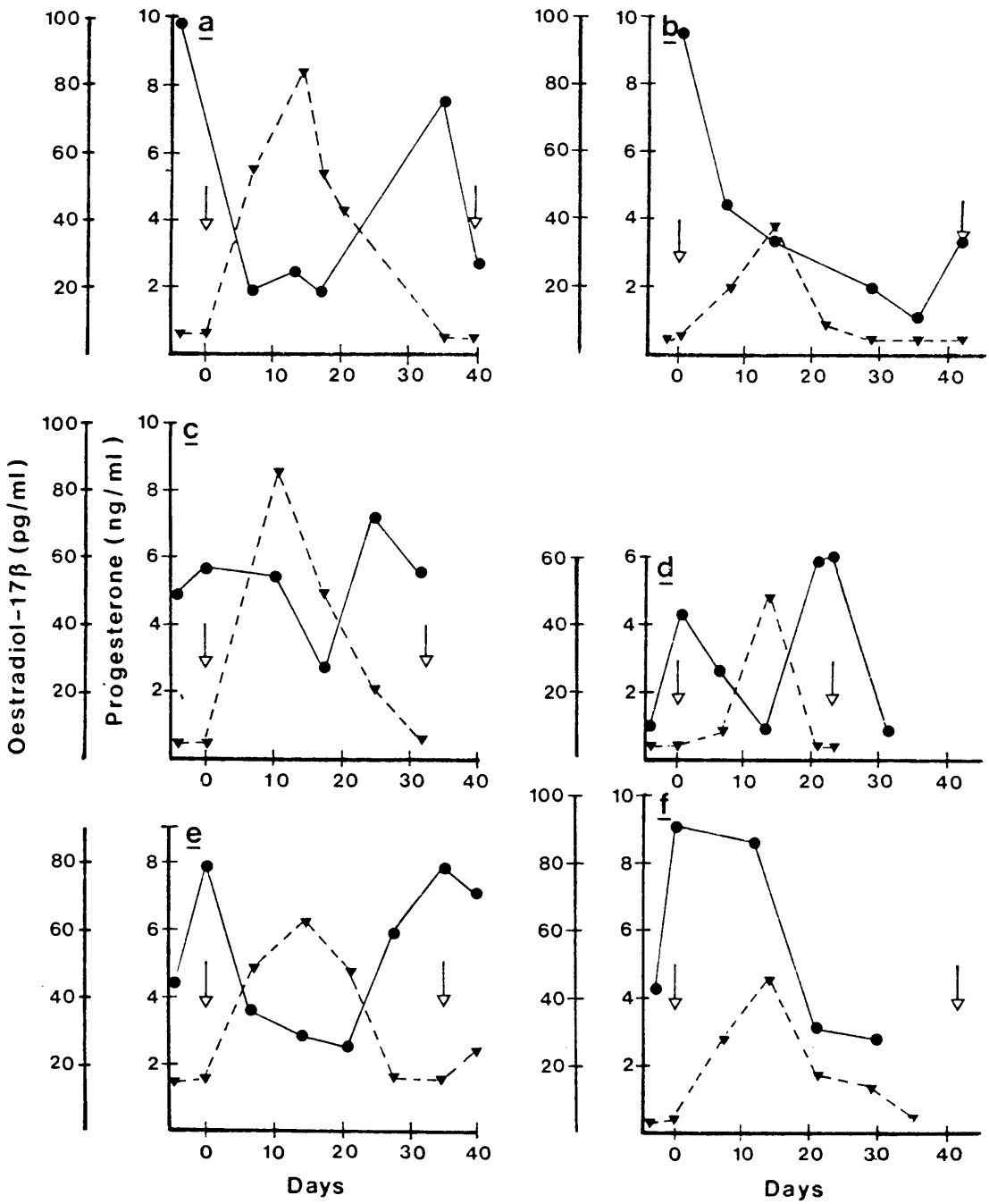

FIG. 13. Plasma progesterone (▼) and oestradiol-17β (●) levels throughout the oestrous cycle. The arrows indicate observed day of opening of the vaginal closure membrane.

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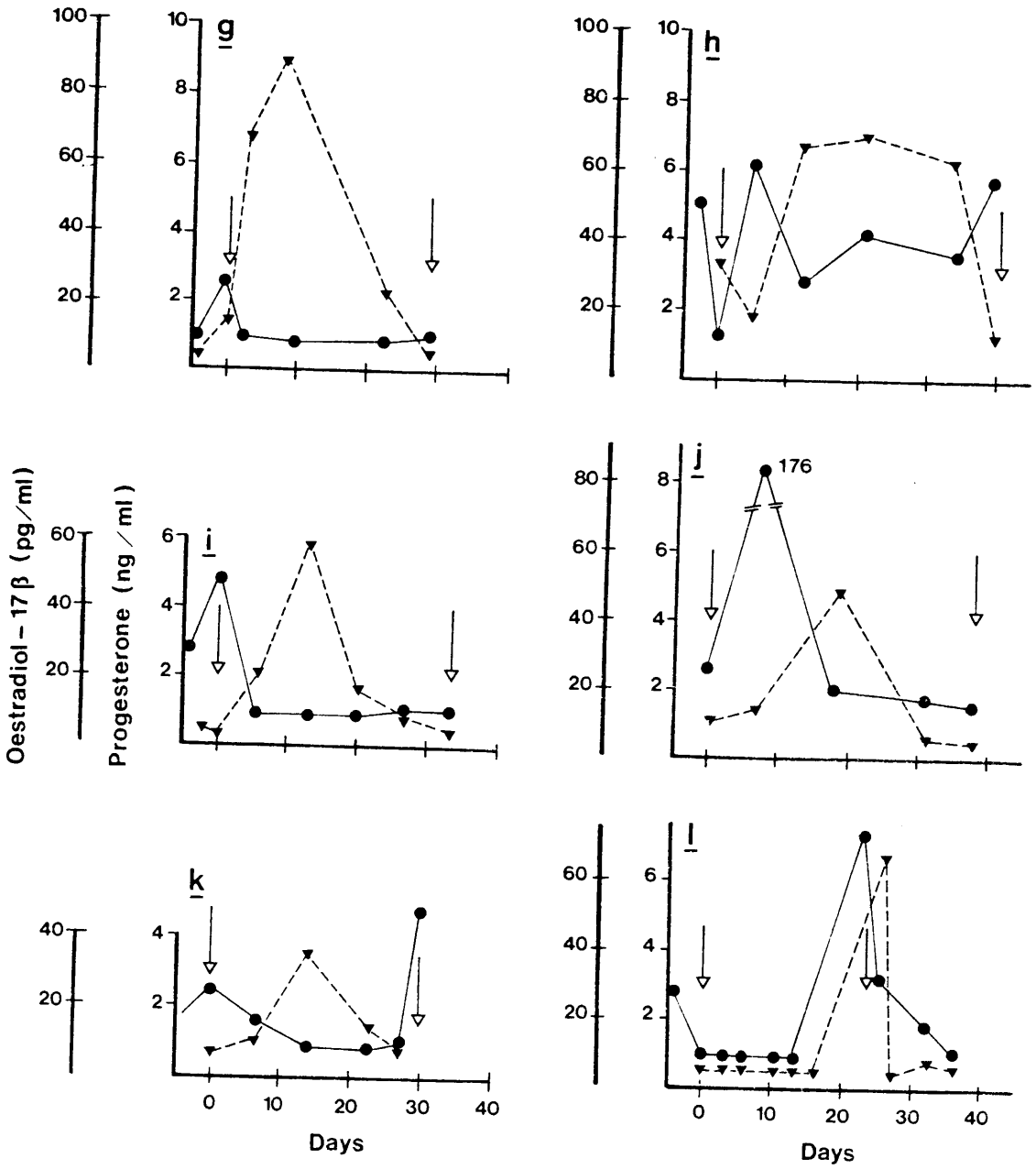

FIG. 13. Plasma progesterone (▼) and oestradiol-17β (●) levels throughout the oestrous cycle. The arrows indicate observed day of opening of the vaginal closure membrane.

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differ significantly from the interval between consecutive instances of vaginal opening (33,4 ± 7,98 *cf.* 34,6 ± 6,78 days; Paired- t_6 = 0,82). Oestradiol-17β surges coincided with vaginal opening and thus confirm earlier observations on other hystricomorph rodents that vaginal opening represents periods of oestrus (see Weir 1974).

Baseline and peak values of oestradiol-17β during the oestrous cycle varied within, as well as between animals, with baseline values varying from the limits of detection of the assay (10 pg/ml) to 40 pg/ml. Peak values varied from 25 to 176 pg/ml. Copulation occurred after the oestradiol-17β surge (Fig. 14).

Progesterone rose to detectable levels (>0,5 ng/ml) two to seven days after the observed day of vaginal opening and six to 12 days ($\bar{x}$ = 7,6 ± 1,8; n = 12; Fig. 13) after the observed peak in oestradiol-17β levels. Progesterone concentrations realised maximum values eight to 19 days ($\bar{x}$ = 13,8 ± 2,8; n = 12; Fig. 13) after vaginal opening with peak values varying from 3,2 to 9,0 ng/ml ($\bar{x}$ = 5,9 ± 2,1; n = 12). The length of the luteal phase, as suggested by the time in days when progesterone concentrations were higher than 0,5 ng/ml, varied from 21 to 35 days ($\bar{x}$ = 29,3 ± 4,7; n = 12).

The sequence of events occurring during the oestrous cycle can be summarised as follows: A rise in oestradiol-17β concentration is followed by the opening of the vaginal membrane, with the opening of the vaginal closure membrane coinciding with the peak in circulating oestradiol-17β levels.

FIG. 14 ..... /

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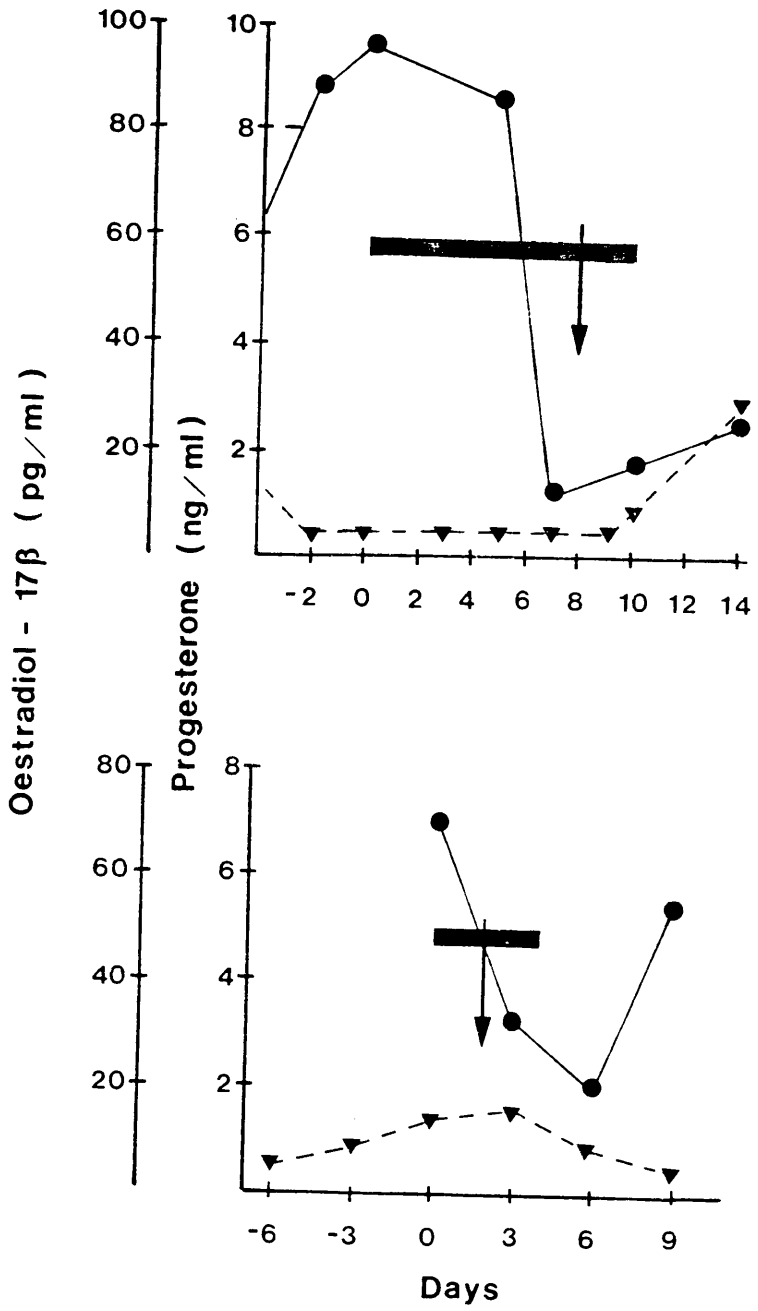

FIG. 14. Plasma progesterone (▼) and oestradiol-17β (●) levels in two parous females before, during and after the perforation of the vaginal closure membrane. Black bars indicate the periods of vaginal opening and arrows denote the day of copulation.

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Copulation occurs when oestradiol-17β levels decline and is followed by an increase in progesterone secretion, with progesterone levels attaining maximum values midway through the 31-day cycle, most of the cycle being occupied by the secretion of progesterone.

Figure 15 presents oestradiol-17β and progesterone profiles during and after 14 instances of vaginal opening where the lengths of the oestrous cycle either could either not be defined or where vaginal opening was not accompanied by a rise in circulating levels of oestradiol-17β. Cycles a to k were observed in parous females housed with intact males and Cycles l, m and n in nulliparous females housed under similar conditions.

Ten of the observed instances of vaginal opening (Figs 15b, c, e, f, h, i, j, l, m & n) were not preceded, accompanied or followed by an increase in oestradiol-17β levels, this representing 38,5% of all the cycles monitored (including those presented in Fig. 13). Luteal activity, as suggested by an increase in circulating progesterone levels, did not follow vaginal opening in five instances (Figs 15a, b, i, l & n), this presenting 19,2% of all the cycles monitored. Three of these occurred in two parous females and two in a nulliparous female. Some of the inconsistent profiles presented in Fig. 15 may be due to random sampling before, during or after opening of the vaginal closure membrane, while others (i.e., Figs 15b, h, i, l & n) may have resulted from 'anovulatory' cycles, early luteal regression or failure in the hormonal mechanisms responsible for the formation of the corpus luteum.

FIG. 15 ..... /

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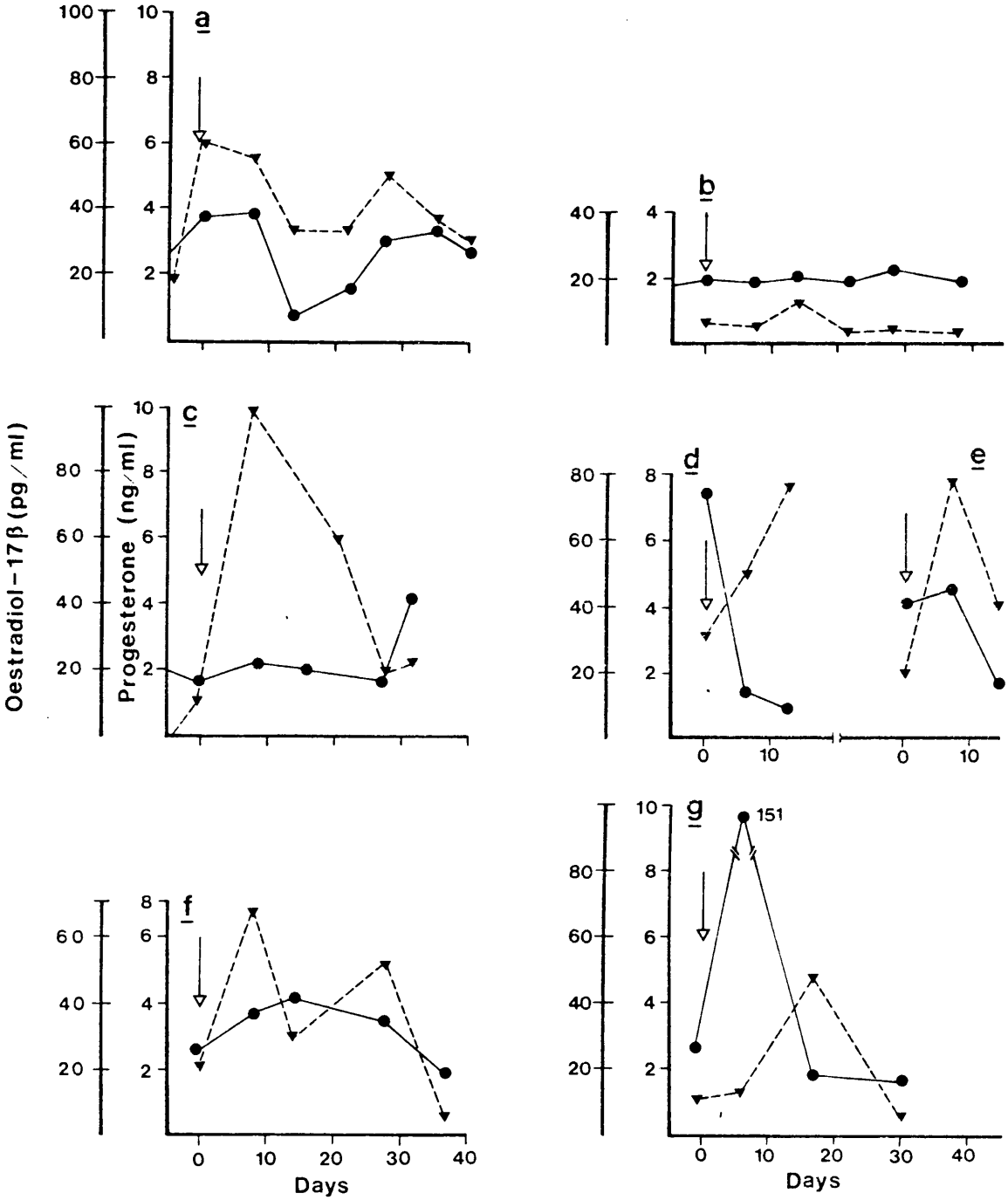

FIG. 15. Circulating progesterone (▼) and oestradiol-17β (●) levels during the period after opening of the vaginal closure membrane. Arrows indicate the day of observed vaginal opening.

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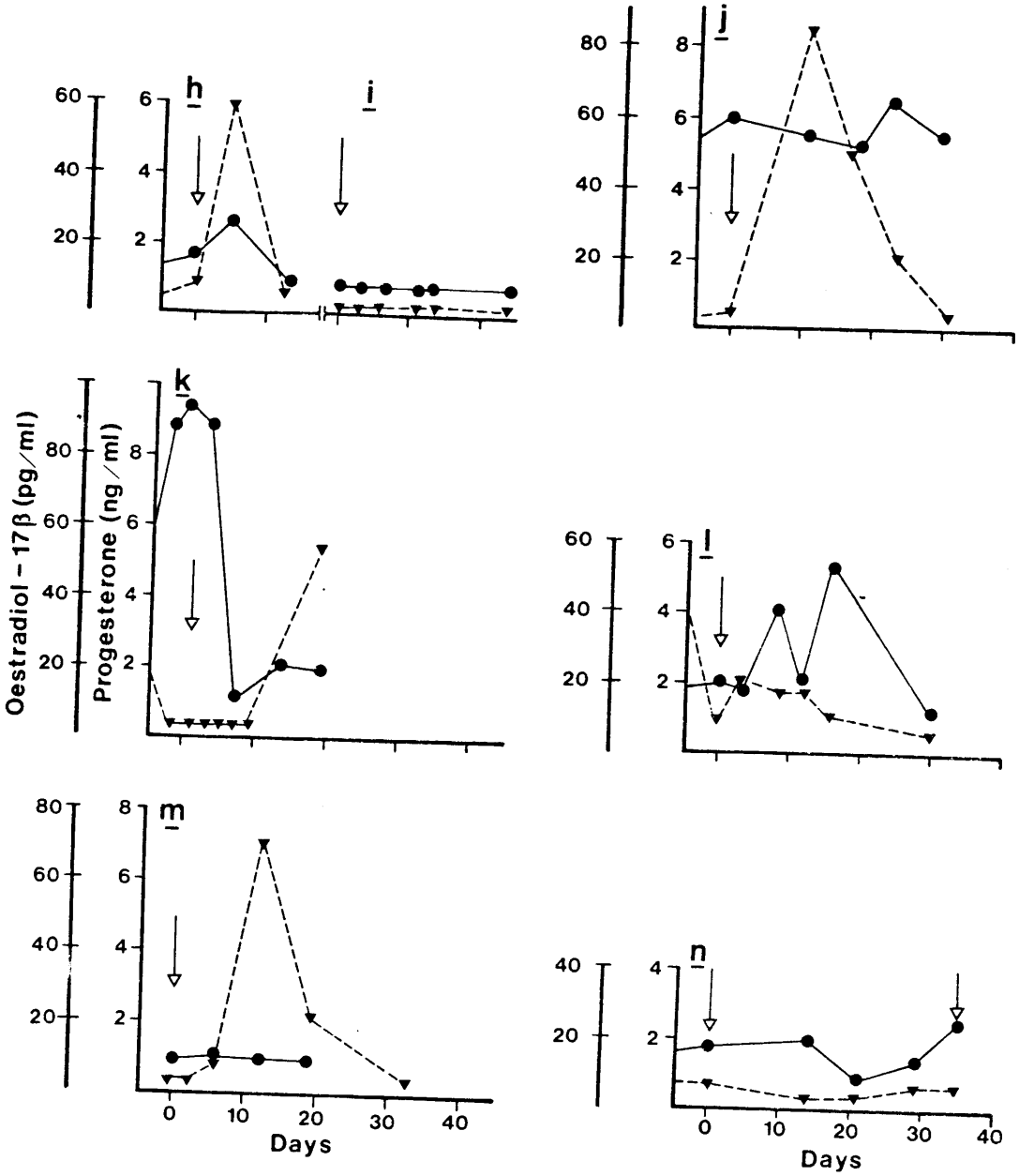

FIG. 15. Circulating progesterone (▼) and oestradiol-17β (●) levels during the period after opening of the vaginal closure membrane. Arrows indicate the day of observed vaginal opening.

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The effect of the male on oestrous activity

Three parous females housed isolated from males for a period of 111 to 120 days did not exhibit oestrous activity during that period, but opening of the vaginal membrane occurred five to 12 days after the introduction of males to their enclosures. Progesterone and oestradiol-17β concentration profiles for these females during these periods suggest that direct contact between male and female is required for the induction of cyclic ovarian activities.

Four of five females kept isolated from males except during stage encounters when they were in contact with a male for 10 min each day (24 h) for a period of 50 days, showed oestrous activity in the form of the opening of the vaginal closure membrane. Only four of the 11 periods of oestrus were followed by an increase in progesterone secretion, with three of these not preceded by copulation.

Age at sexual maturity

Age at first oestrus (vaginal opening) and conception for females born in captivity are summarised in Table 20. Age at first oestrus varied from 273 to 552 days ($\tilde{x}$ = 413,4 ± 118,4; n = 5). None of these females conceived during the first oestrus and age at first conception varied from 298 to 864 days ($\tilde{x}$ = 618,6 ± 172,3; n = 8). Females immobilised at irregular intervals before conception were significantly (t_6 = 2,64; $p < 0,05$) older (24,2 ± 3,8 months) when conceiving for the first time than those not immobilised (16,4 ± 4,5 months). Nulliparous females experienced three to seven ($\bar{x}$ = 5,8 ±

TABLE 20 ..... /

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TABLE 20. Age at first oestrus (perforation of the vaginal membrane) and first conception for porcupines born in captivity.

Females	First vaginal opening			First conception		
	Age		Weight (kg)	Age		Weight (kg)
	Days	Months		Days	Months	
A	510	16,74	10,5	755	24,80	12,9
B	325	10,67	11,0	864	28,40	12,1
F	407	13,36	10,5	586	19,24	11,3
L	552	18,14	13,5	741	24,33	14,1
M*	-	-	-	547	17,96	11,8
N	273	8,96	10,7	DID NOT CONCEIVE		
O*	-	-	-	609	19,99	11,9
P*	-	-	-	549	18,02	12,6
Q*	-	-	-	298	9,78	11,8
Mean ± S.D.	413 ± 118,4	13,57 ± 3,89	11,2 ± 1,28	618 ± 172,2	20,32 ± 5,67	12,3 ± 0,88

*Individuals not immobilised before conception.

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2,1; n = 4) periods of oestrus before conceiving, and age at first oestrus was apparently not affected by month of birth.

In regarding the presence of ovarian luteal tissue as indicative of sexual maturity, it became evident that 63,3 to 85,7% ($\bar{x}$ = 76,0%) of the females culled on the TdR Game Farm had cycled while between eight and 24 months of age. Ninety-four percent of those older than 24 months were sexually mature (Table 21).

Pregnancy

Length

The mean length of gestation for four females separated from males on the first day of copulation was 93,5 ± 0,6 (93 - (4) days (Table 22). The weight gain in these females during pregnancy is shown in Fig. 16 and varied from 10,0 to 21,0 g/day during the first half of pregnancy. Weight gain from Days 50 to 93 *post coitum* varied from 16,0 to 39,0 g/day and was significantly higher (Paired- t_2 = 3,56; $p < 0,05$) than during the first half of pregnancy.

The relationship between body weight ($\log_{10}$) and gestation length ($\log_{10}$) for 20 hystricomorph rodent species based on the information published by Weir (1974) is illustrated in Fig. 17. The slope of the line describing this relationship did not differ significantly from 0 and the increase in gestation length with an increase in body weight was not significant (r^2 = 0,34).

TABLE 22 ..... /

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TABLE 21. Age specific sexual maturity in free-ranging female porcupines culled on the TdR Game Farm during 1977/78 and 1981/82. Age determination was based on tooth eruption (see Chapter 3).

Age (months)	Number of females collected		Number with luteal activity in ovaries		Percentage sexually mature	
	1978	1981	1978	1981	1978	1981
8	3	16	0	0	0,0	0,0
8 24	11	14	7	12	63,6	85,7
24	17	19	15	19	88,2	100,0

TABLE 22. Gestation lengths in porcupines kept in captivity.

Reproductive status before conception	Observational conditions	Gestation length (days)
Parous	Mating and birth observed. Female isolated from male after mating.	93
Nulliparous	Mating and birth observed. Female isolated from male after mating.	94
Nulliparous	Mating and birth observed. Female isolated from male after copulatory plug was dropped.	93
Parous	Mating and birth observed. Vasectomised males two days after copulation; female housed in contact with male.	94
Mean ± S.D.		93,5 ± 0,58

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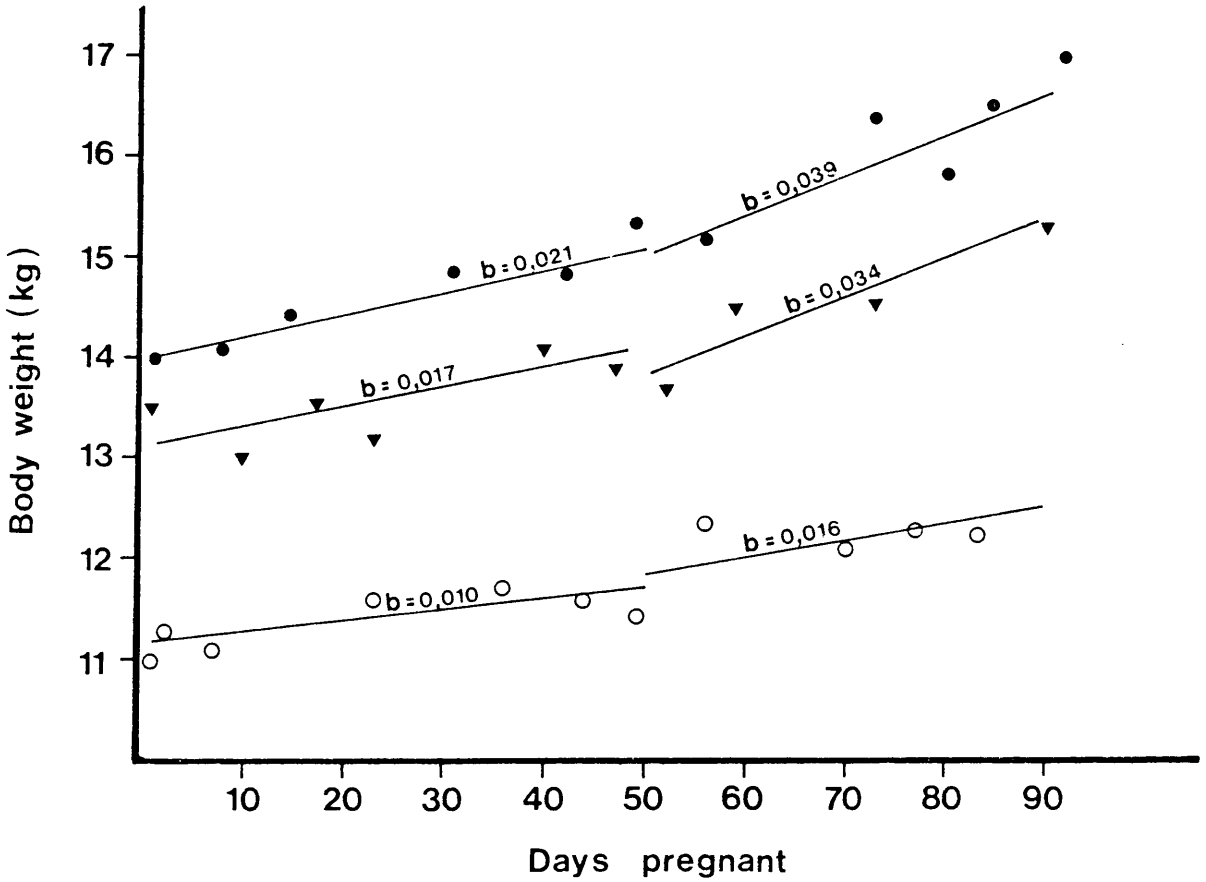

FIG. 16. Temporal changes in body weight (kg) of captive female porcupines weighed at irregular intervals throughout pregnancy. b = slopes of the lines fitted through linear regression analyses.

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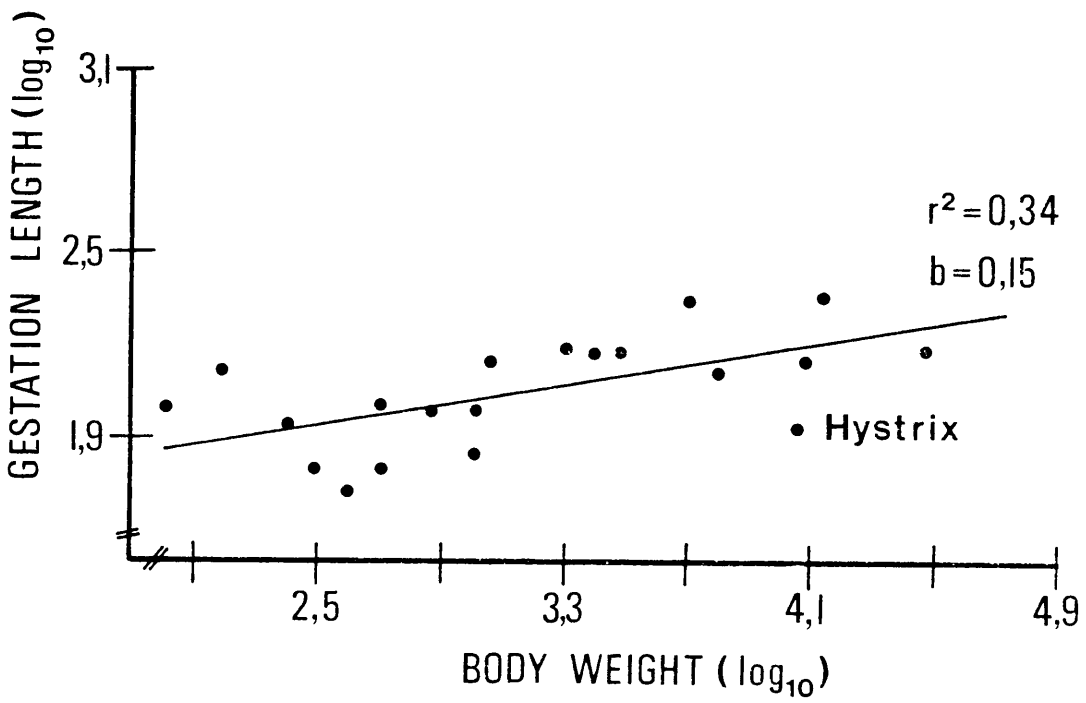

FIG. 17. The relationship between gestation length (log_{10}) and body weight (g log_{10}) in 20 hystricomorph rodent species. Original data from Weir (1974). r^2 = coefficient of determination and b = slope of the line fitted through linear regression analysis.

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Progesterone and oestradiol-17β levels during pregnancy

Circulating levels of progesterone in pregnant female porcupines remained relatively low (approximately 20 ng/ml) until Days 25 to 30 *post coitum*, increasing sharply thereafter to reach maximum values (102 - 180 ng/ml; n = 3), 42 to 60 days *post coitum* (Fig. 18). Progesterone concentration decreased gradually during the last thirty days of pregnancy and values on Day 85 *post coitum* (8 - 9 days *pre partum*) varied from 49,3 to 100 ng/ml ($\bar{x}$ = 77,3 ± 32,3; n = 4). Values in samples taken within six days after parturition varied from 0,5 to 7,1 ng/ml ($\bar{x}$ = 2,6 ± 3,1; n = 4). Progesterone concentrations during matings followed by conception varied from 2,0 to 4,1 ng/ml ($\bar{x}$ = 3,2 ± 1,0; n = 3) and were significantly higher ($t_7 = -4,73$; $p < 0,01$) than values observed (0,5 - 1,5 ng/ml; $\bar{x}$ = 0,9 ± 0,5; n = 6) on days of 'sterile' matings (matings with intact males which were not followed by pregnancy).

Oestradiol-17β levels at conception varied from 22,0 to 34,0 ng/ml ($\bar{x}$ = 25,3 ± 7,6; n = 3) and remained relatively low until Days 20 to 25 *post coitum* (Fig. 18). The rapid increase in oestradiol-17β concentrations approximated that of progesterone with peak values (170 - 210 pg/ml) being attained 60 to 85 days *post coitum* (Fig. 18). Oestradiol-17β levels on Day 85 *post coitum* varied from 185 to 210 pg/ml, decreasing to the limits of detection(< 10 pg/ml) within six days after parturition.

Progesterone-binding plasma proteins (PBPP)

Concentrations of PBPP for two pregnant females for which serial

FIG. 18 ..... /

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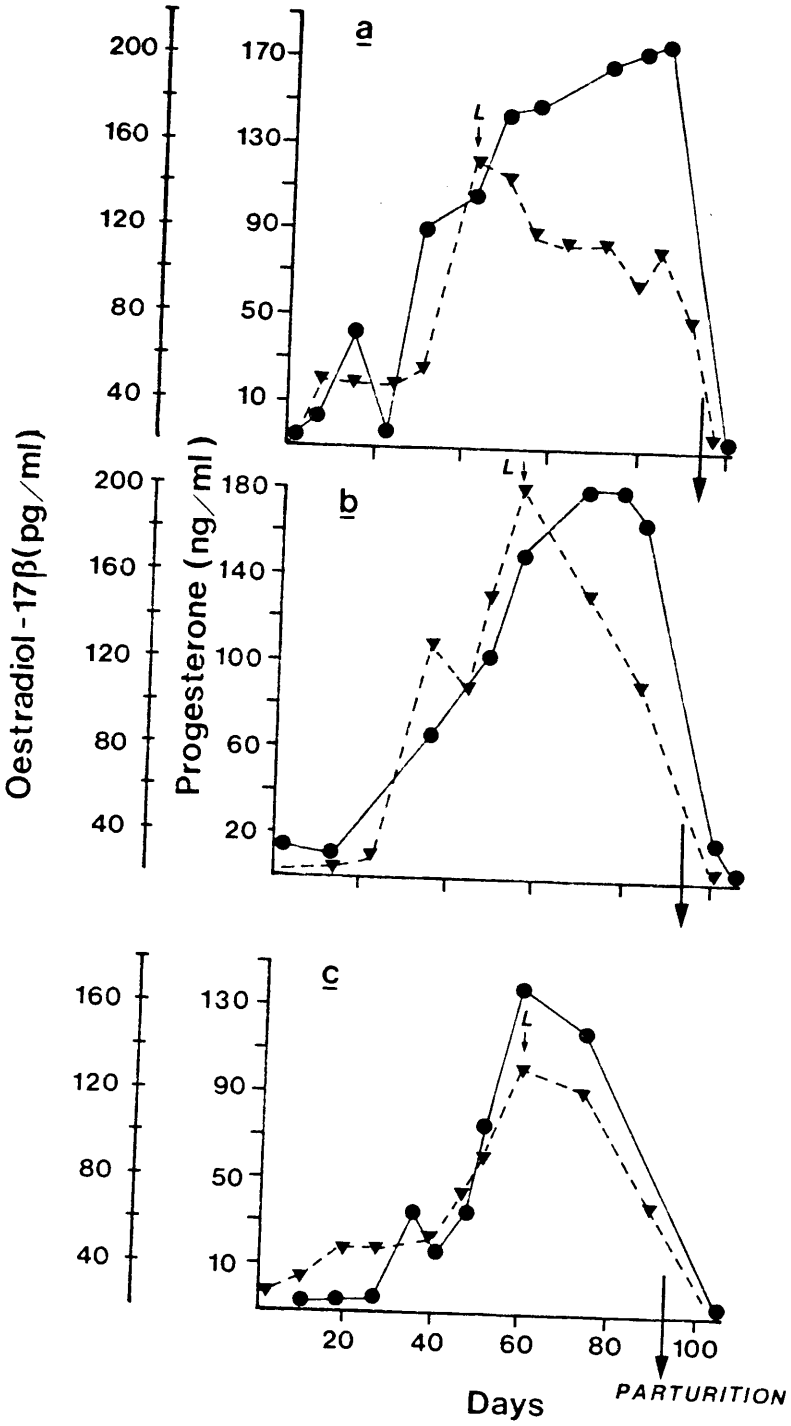

FIG. 18. Plasma progesterone (▼) and oestradiol-17β (●) levels throughout pregnancy in three captive female porcupines. *L* denotes the day from when milk could be expressed from the teats and the arrows indicate the day of parturition.

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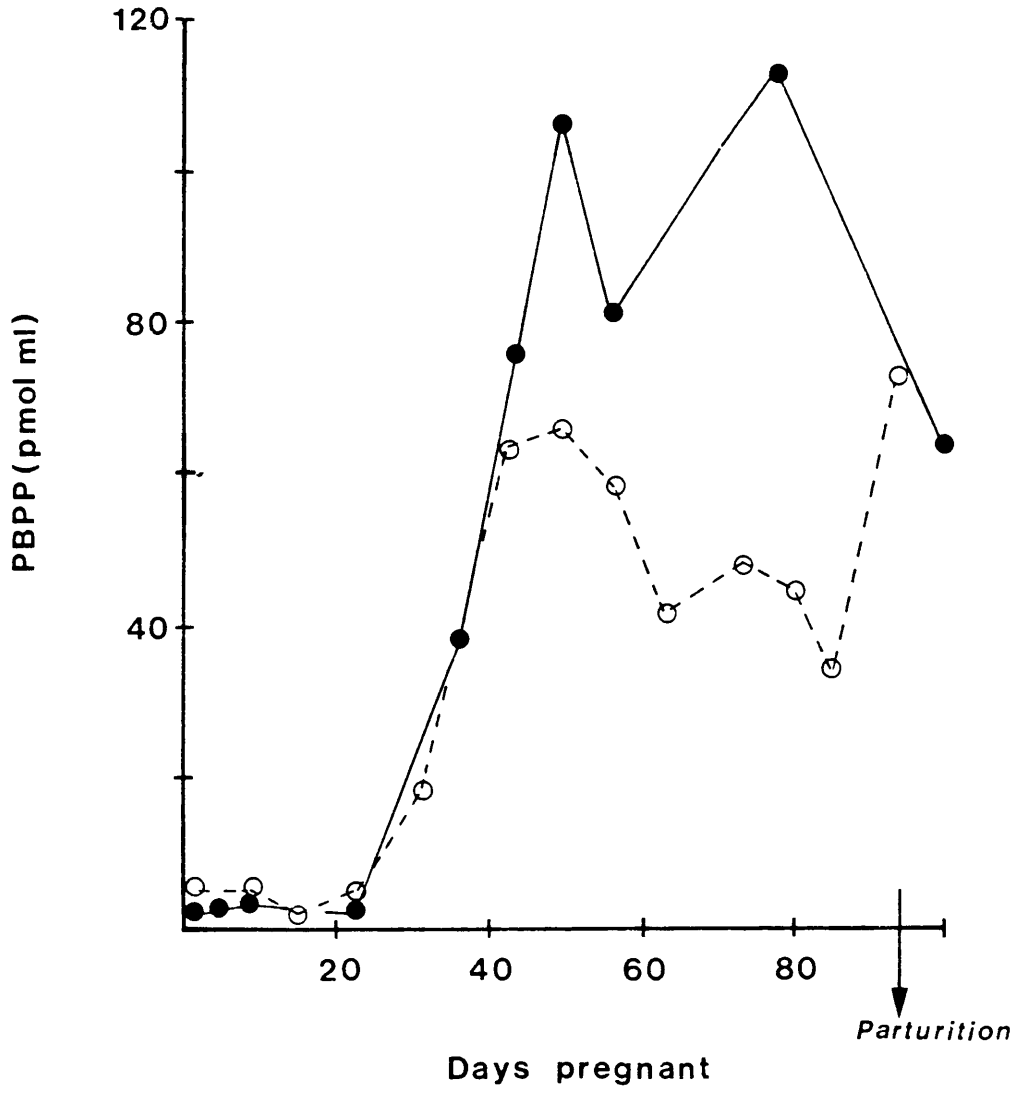

FIG. 19. Circulating levels of progesterone-binding plasma proteins (PBPP) (pmol/ml) in two pregnant porcupine females throughout pregnancy. The arrow denotes the day of parturition.

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plasma samples were available, showed a biphasic pattern, with peaks occurring between Days 50 to 56 and Days 73 to 77 *post coitum* (Fig. 19) but PBPP levels remained low ($\angle$20 pmol/ml; 319 fmol/mg protein) until Day 31 *post coitum*, thereafter increasing rapidly to the first (65,6 - 105,9 pmol/ml; 1 025 - 2 053 fmol/mg protein) and second (58,6 - 114,2 pmol/ml; 1 085 - 2 139 fmol/mg protein) peaks. Values remained relatively high (64,7 pmol/ml; 1 216 fmol/mg protein) until after parturition but were below 20,0 pmol/ml (342 fmol/mg protein) 16 days after birth (Fig. 19).

Progesterone values (ng/ml) increased linearly and significantly (r^2 = 0,81) with an increase in PBPP values (pmol/ml; Fig. 20). The molar ratio of plasma concentrations PBPP to progesterone remained below unity throughout pregnancy but increased approximately ten-fold after Day 31 *post coitum* and remained relatively high (0,164 - 0,222) throughout the remainder of pregnancy.

Litter size and weight at birth

Litter size at birth in captivity varied from one to three ($\bar{x}$ = 1,50 $\pm$ 0,66; n = 165) with most litters (58,8%) comprising singletons, while 32,1% comprised of twins and 9,1% of triplets (Table 23). Prenatal litter size in free-ranging porcupines (n = 18) varied from one to two, with 50% comprising singletons. Identification of uterine scars in lactating females was in agreement with litter sizes recorded in pregnant females, with one scar recorded in eight uteruses and two in two uteruses, suggesting a mean litter size of 1,39 $\pm$ 0,50 (n = 28) for free-ranging porcupines on the TdR Game Farm. Sex ratio at birth for 16 litters born in captivity at the University of Pretoria's Expe-

FIG. 20 ..... /

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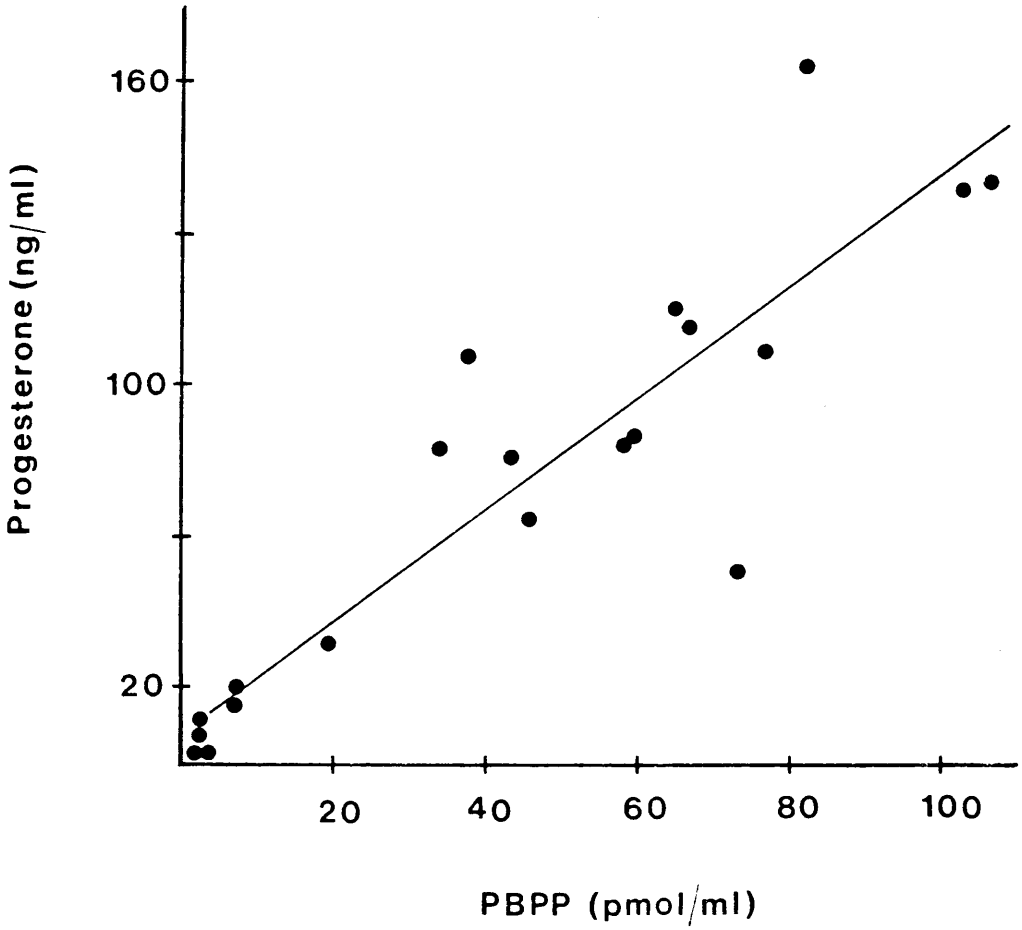

FIG. 20. The relationship between circulating levels of plasma progesterone (ng/ml) and circulating levels of progesterone-binding plasma proteins (pmol/ml. The line fitted through linear least square regression analysis is described by the equation $y = 29,27\ x + 9,70$.

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rimental Farm was 1:1,56 (male:female; n = 23) and did not deviate from unity (χ^2 = 0,55; $p < 0,05$).

Weight at birth for 19 porcupines weighed within 12 h following birth, varied from 300 to 440 g ($\bar{x}$ = 351,1 ± 47,4) and the mean weight of individual twins (354,7 ± 49,6g) did not differ significantly (t_{17} = 0,77) from that of singletons (331,7 ± 32,5g). The mean weight of eight twins born alive also did not differ significantly from each other (Paired- t_6 = -1,54). With the exception of two cases of fetal resorbtion, the weight of five twin fetuses also failed to differ significantly (Paired- t_3 = 1,34). Males were not significantly (t_{12} = 1,23) heavier than females at birth but males of heterosexual twins were significantly (Paired- t_3 = 6,67; $p < 0,001$) heavier than their sisters, the mean difference in weight being 85,0 ± 30,0 g. This however may be ascribed to insufficient sample size.

Individual weight at birth was 2,1% of that of mean adult female weight (12,9 ± 1,79 kg) and that of mean litter size, 4,1%, ranging from 2,7 to 8,2. The relationship between neonatal litter weight and maternal weight in 25 hystricomorph rodent species, based on information that has been published by Weir (1974), Gosling (1980) and Thome & Thome (1980), is presented in Fig. 21, indicating that neonatal litter weight increases significantly with an increase in maternal weight. Neonatal weight in *Hystrix*, however, was lower than that predicted by this relationship.

Lactation

The mammary glands have a triangular shape and are situated in a late-

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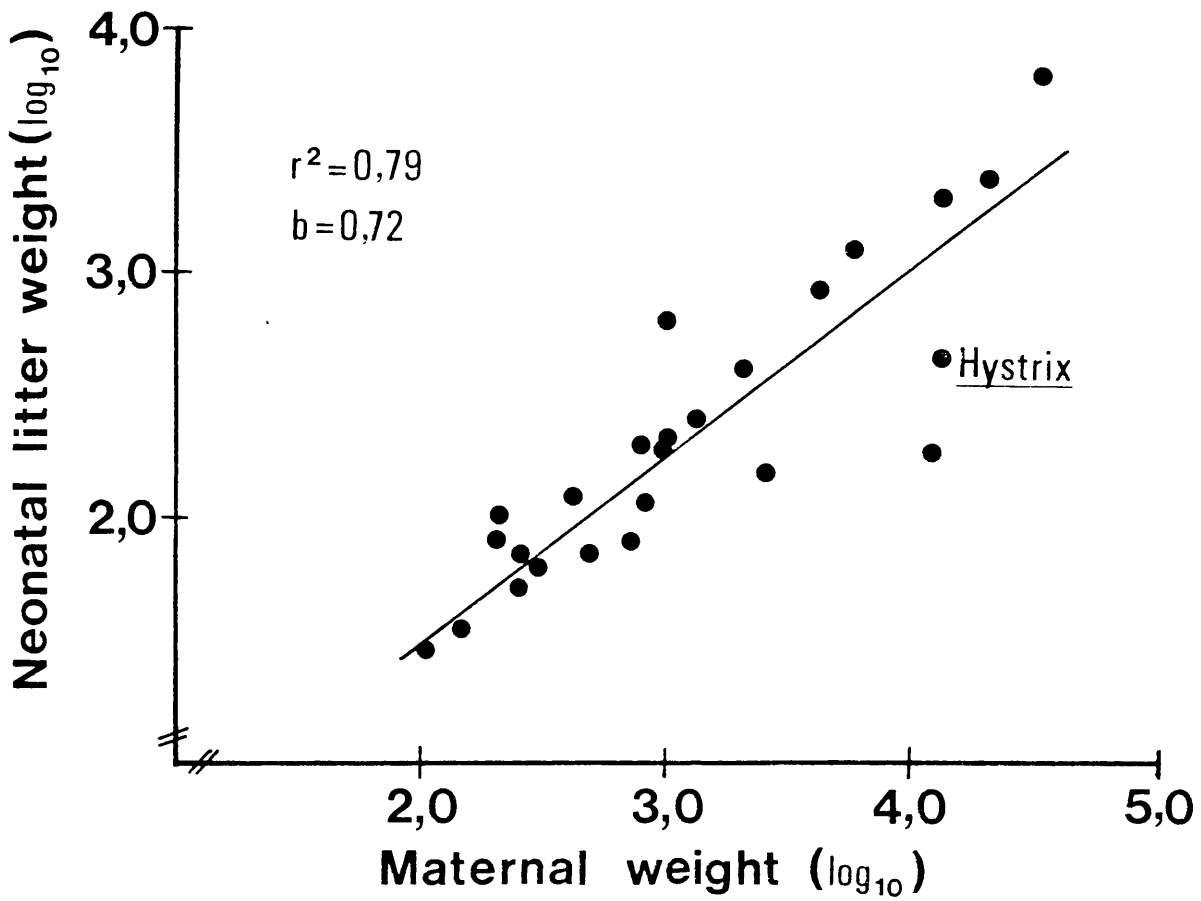

FIG. 21. The relationship betweeen neonatal litter weight (g log_{10}) and maternal weight (g log_{10}) in 25 hystricomorph rodent species. Original data from Weir (1974), Gosling (1980) and Thomè & Thomè (1980). The line was fitted through least square linear regression analysis, b representing the slope of the line.

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ral thoracic position posterior to the elbow of the forelimb. The two teats are placed centrally on each gland and no variation in teat number has been observed. Glands start to develop noticeably from 30 to 60 days after conception and milk could be expressed from the teats 42 to 60 days *post coitum* ($\bar{x}$ = 53,3 ± 9,87; n = 3), this coinciding with the observed peaks in progesterone levels during gestation (see Fig. 18). The combined weight of the two mammary glands of lactating females culled on the TdR Game Farm varied from 32,0 to 189,2 g (n = 10) with the heaviest gland measuring 10,0 x 3,0 x 19,0 x 0,5 cm.

Young suckled while their mothers were in a crouching position and twins always suckled from contra-lateral nipples. Near continuous teat contact during the first two weeks *post partum* was followed by intermittent contact up to 20 weeks of age.

Milk intake, based on the turnover of tritiated water in young and the assumption that 1,0 ml milk contains 0,89 ml water, varied from 217,6 to 219,0 ml/day in litter mates 22 days *post partum*, increasing to 323,4 ± 79,9 ml/day on Day 43 *post partum* (Fig. 22).

Daily milk intake in individual twins was similar (Paried- t_3 = -0,60) but significantly lower (t_2 = -11,12; p 0,001) than in singletons of comparable age. Intake per litter was, significantly higher (t_3 = -6,41; p 0,01) in twins than in singletons. Milk intake per unit body weight decreased slightly between Days 20 and 50 *post partum* (Fig. 22).

Change in maternal body weight during the first 60 days of lactation is presented in Fig. 23. Daily increase in body weight, as suggested

FIG. 22. ..... /

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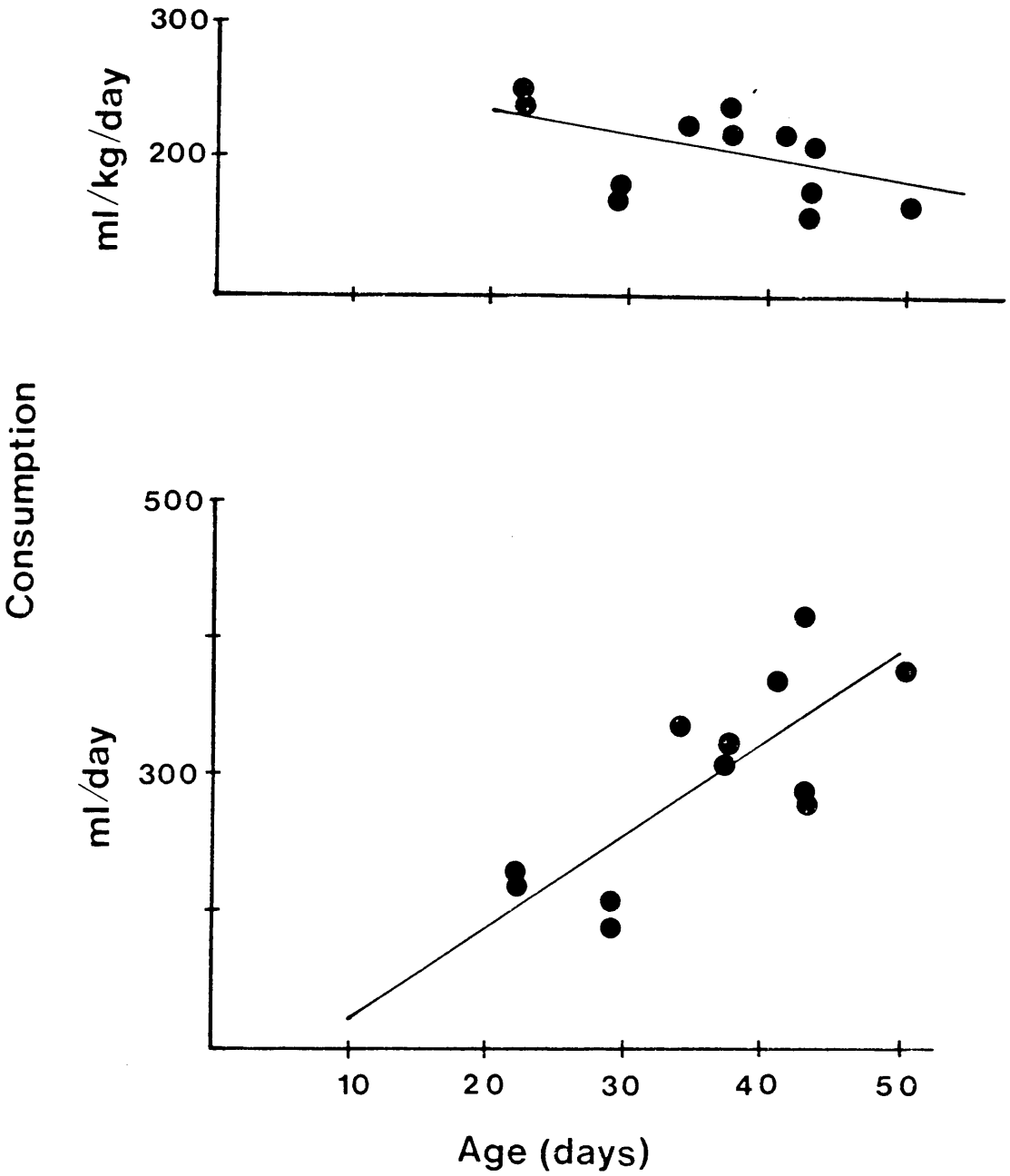

FIG. 22. The relationship between daily milk intake (ml/kg/day and (ml/day) and age (days) in porcupines born in captivity. Lines were fitted through least square linear regression analyses.

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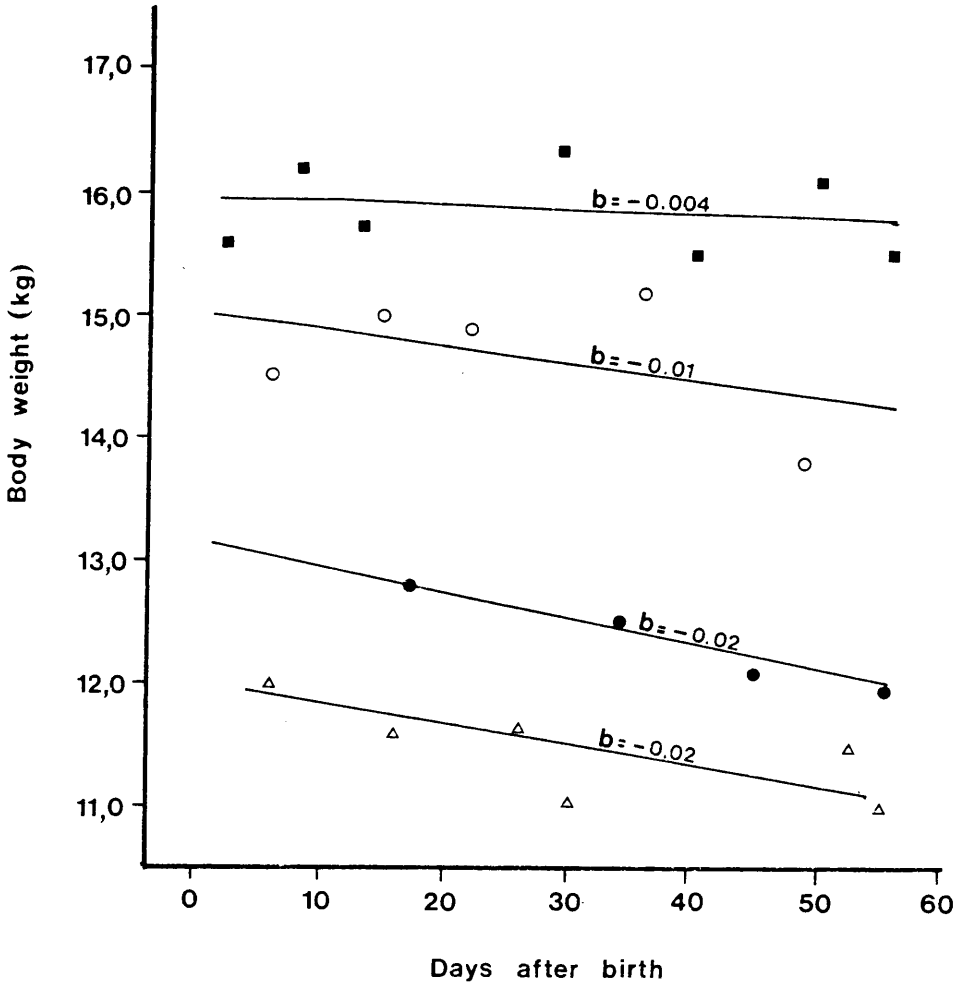

FIG. 23. Temporal changes in body weight (kg) of four captive female porcupines weighed at irregular intervals during the first 60 days of lactation. *b* = slopes of the lines fitted through least square linear regression anaylses.

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by linear regression analyses, varied from 4,0 to 20,0 g/day ($\bar{x}$ = 13,5 ± 7,90) and individual decreases were not related to litter size. In considering the *post partum* lactation period as the interval during which milk could be expressed manually from the nipples of immobilised females, the mean length of the lactation period was estimated at 100,6 ± 37,8 days (range 37 - 163; n = 9).

Progesterone and oestradiol-17β levels during lactation

In serial plasma samples from five lactating females housed with intact males, progesterone concentrations remained at the limits of detection throughout the period of lactation (37 - 163 days). Perforation of the vaginal closure membrane occurred twice during lactation (Days 87 & 138 *post partum)* in one of these females and was accompanied by increases in oestradiol-17β concentrations.

Vaginal opening also occurred in one of these females nine days *post partum* and although followed by copulation and the formation of a copulatory plug, was not preceded by a definite oestradiol-17β surge. Oestradiol-17β surges, accompanied by perforation of the vaginal closure membrane, followed by the copulation and increases in progesterone levels (thus normal cyclic activity) occurred, 39, 122 and 168 days after parturition and two, eight and 42 days after the cessation of lactation in three of these females.

Pseudopregnancy

Copulation with intact males occurred in both cases of pseudopregnancy monitored in captivity and was followed by periods (82 and 85 days)

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of fluctuating progesterone and oestradiol-17β levels (Fig. 24). Peak values in circulating progesterone concentration (6,0; 8,0 & 10,2 ng/ml) were similar to those observed in cyclic females but 10 to 15 times lower than in pregnant females. Oestradiol-17β levels fluctuated between 12,0 and 98,0 pg/ml (Fig 24) and were similar to those observed in cyclic (see Fig. 13) and pregnant females (see Fig. 18). No definite trend in the secretion of these steroids could be identified. Milk could be expressed from the teats of these females from Days 62 and 68 *post coitum* respectively but milk flow ceased before the onset of the following oestrus.

Body weight increased in both females at rates (20,0 g/day) similar to those observed in pregnant females over the first 50 days following copulation (Fig. 25), but decreased rapidly from Day 65 *post coitum*.

Litter interval

Litter interval calculated for ten intervals recorded in eight females housed continuously with intact males, varied from 296 to 500 days ($\bar{x}$ = 385,0 ± 60,4; Table 24) and was not affected by immobilisation, since the mean litter interval for experimental females was similar to that of control females (t_8 = 0,70).

FIG. 24

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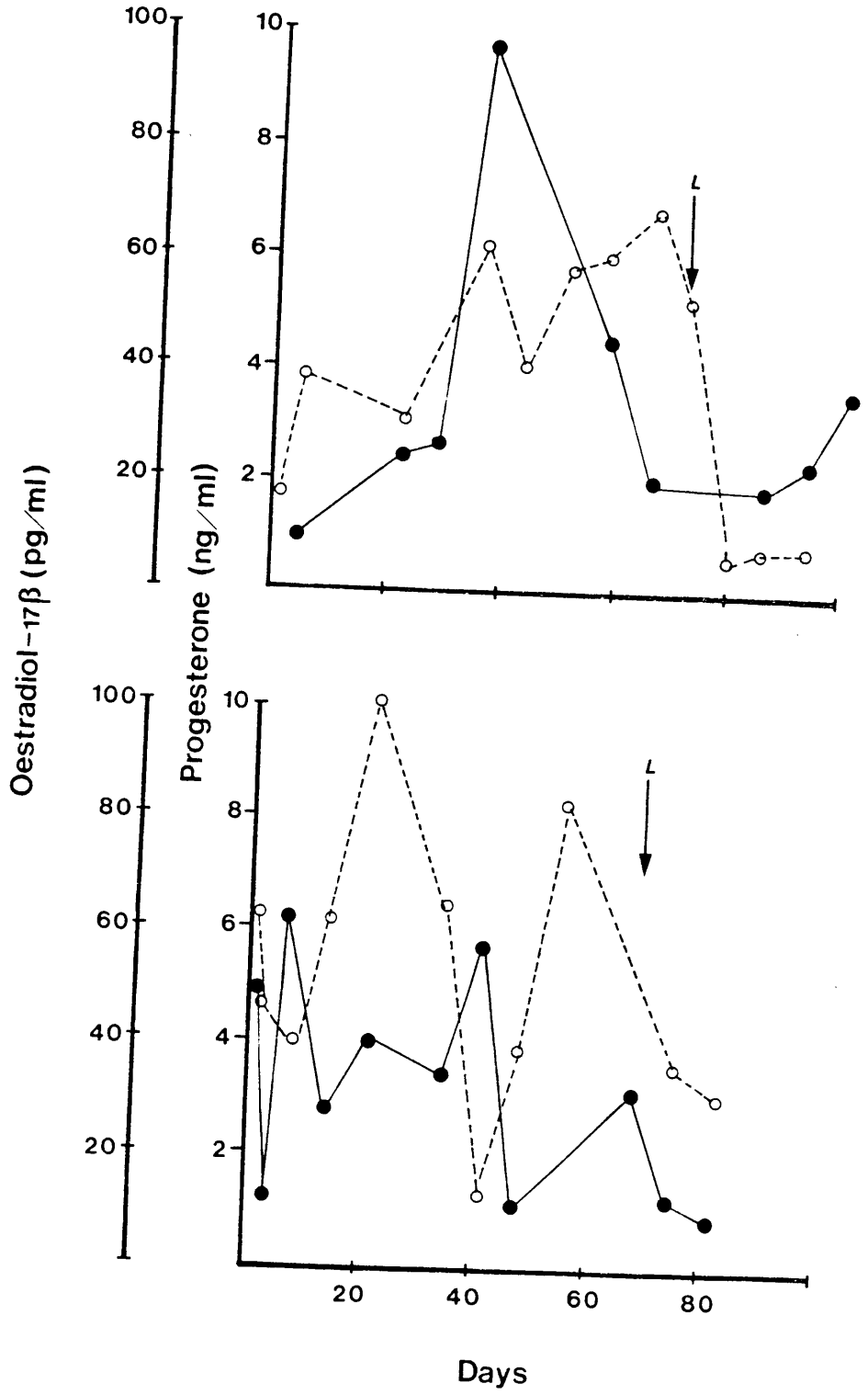

FIG. 24. Plasma progesterone (o) and oestradiol-17β (•) levels throughout periods of pseudopregnancy in two adult female porcupines housed in captivity. Arrows denote the day from when milk could be expressed from their teats.

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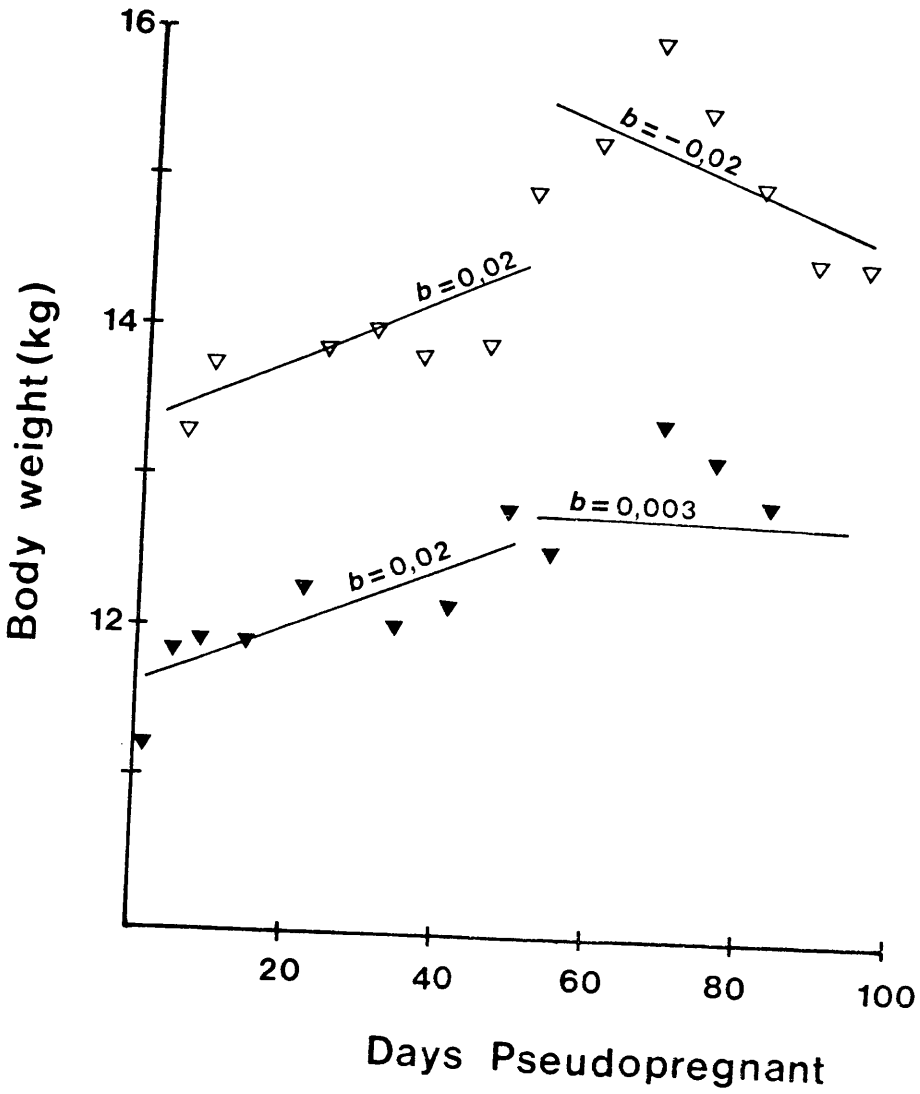

FIG. 25. Temporal changes in the body weight of two adult female porcupines throughout pseudopregnancy. Lines were fitted through least square linear regression analyses and *b* represents the slopes of these lines.

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TABLE 23. Frequency distribution of litter size for porcupines bred in captivity at the National Zoological Gardens (n = 101), the Johannesburg Municipal Zoological Gardens (n = 41) and the University of Pretoria (n = 23).

Litter size	Number of litters	Percentage
1	97	58,8
2	53	32,1
3	15	9,1
4	0	0

TABLE 24. Litter intervals recorded for female porcupines housed in captivity.

Female	Date of first birth	Date of following birth	Litter interval (days)
A	30 Dec 1981	11 Jan 1983	377
A	11 Jan 1983	27 Feb 1984	412
C	7 Nov 1981	1 Feb 1982	451
H*	7 Oct 1981	19 Feb 1982	500
K*	19 Dec 1982	6 Feb 1984	414
M*	25 Dec 1981	30 Dec 1982	370
M*	30 Dec 1982	21 Oct 1983	296
Q*	25 Jan 1982	27 Jan 1983	367
R*	22 Dec 1981	17 Nov 1982	331
R*	17 Nov 1982	19 Oct 1983	338
		Mean ± S.D. = 385,6 ± 60,4	

*Females not immobilised during litter interval.

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Seasonality

Captivity

The frequency distribution of births recorded in three captive groups indicates that porcupines breed throughout the year (Fig. 26) with most litters (78,7%; n = 165) being produced between August and March. This is significantly more than expected (χ^2 = 10,91; $p < 0,05$) for the period. The mean dates of birth (Caughley 1977) for these groups varied from 19 December to 8 January (Table 26) and the standard deviations of the birth dates (Caughley 1977) varied from 73,3 to 96,6 days (Table 25), thereby including 66,3 to 82,6% of the births recorded.

Free-ranging porcupines

Pregnant or lactating females were collected throughout the year with the percentage females pregnant or lactating during each sampling period varying from 14,3 to 100,0% (Table 26). The prolonged gestation and lactation period (total approximately 193 days) results in a summation of pregnant and lactating females during each sampling period not reflecting on the extent of seasonal breeding activities.

Extrapolation to the date of conception and birth using specific fetal growth rates (see Chapter 3) and fetal weights on the day of collec= tion, indicate that matings between May and December were successful, resulting in a birth season from August to March (Fig. 27). The mean date of birth was estimated at 21 December ± 66,9 days (Table 26) and the birth peak in January coincided with peaks in mean

FIG. 26 ..... /

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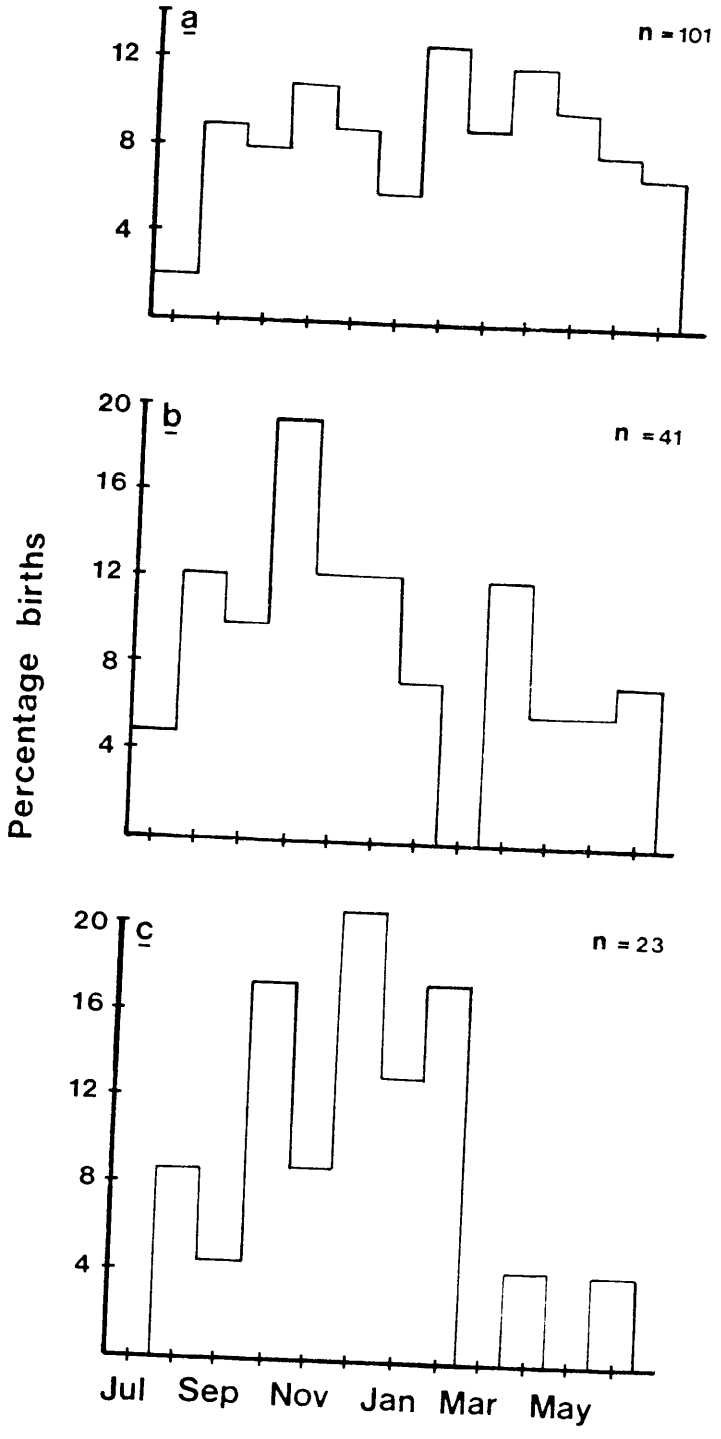

FIG. 26. The frequency distribution of births recorded in the National Zoological Gardens (a), the Johannesburg Municipal Zoological Gardens (b) and at the University of Pretoria (c).

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TABLE 25. The mean date of birth, standard deviation and standard error of the birth season for porcupines kept in captivity and for the population on the TdR Game Farm.

Locality	Number of births	Mean date of births	Standard deviation of season (days)	Standard error of season (days)
National Zoological Gardens of SA (Pretoria)*	101	8 January	96,6	9,6
Johannesburg Municipal Zoological Gardens**	41	19 December	91,5	14,3
University of Pretoria***	23	19 December	73,3	15,3
Tussen-die-Riviere Game Farm****	13	21 December	66,9	18,6

* Date of births recorded from 1926 to 1979.
** Date of births recorded from 1937 to 1979.
*** Own observations for 1979 to 1984.
**** Date of births extrapolated using fetal weights and fetal growth rate.

TABLE 26. The reproductive status of adult female porcupines collected on the TdR Game Farm during sampling periods between September 1981 and July 1982.

Sampling period	Number lactating	Number pregnant	Number of females collected	Percentage pregnant & lactating
16 - 22 Sep 1981	3	3	8	75,0
1 - 5 Dec 1981	3	3	6	100,0
18 - 20 Jan 1982	0	4	5	80,0
15 - 17 Mar 1982	2	1	5	60,0
18 - 22 May 1982	1	0	6	14,3
28 - 30 June 1982	0	1	2	50,0

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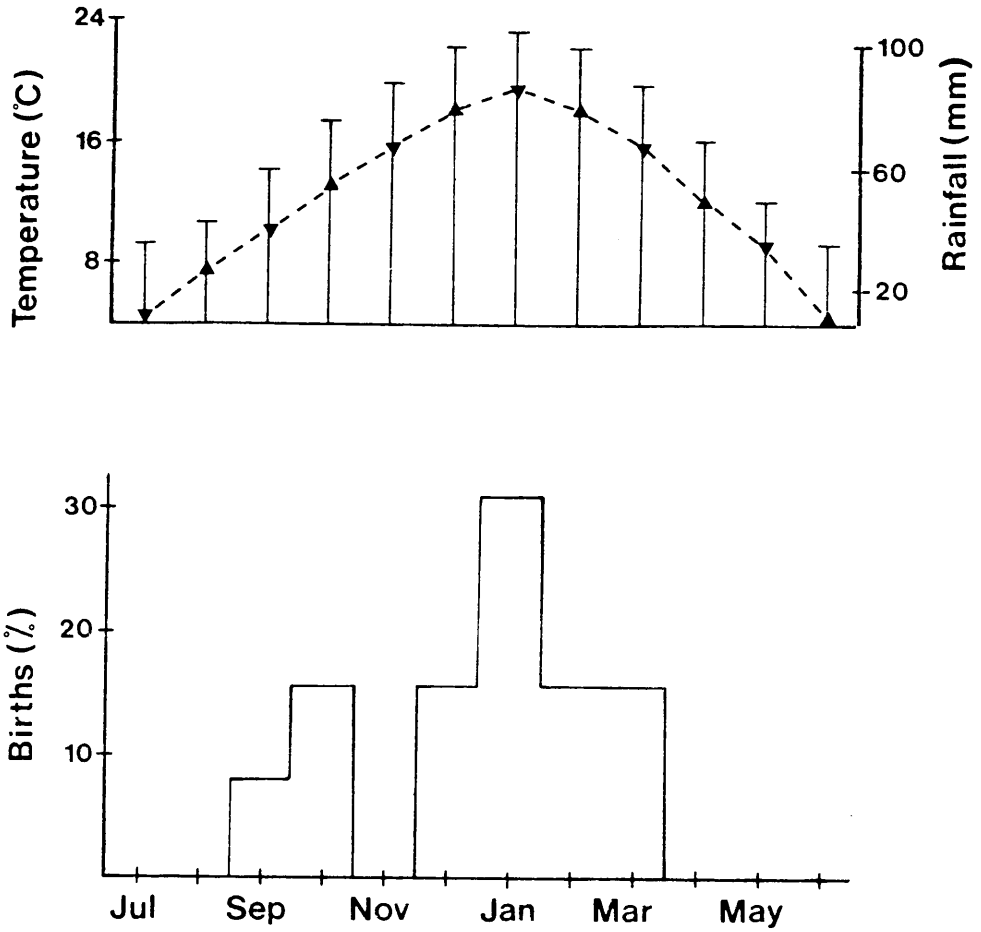

FIG. 27. Mean monthly temperature (T), average monthly rainfall (---) and frequency distribution of births of porcupines on the TdR Game Farm. Temperatures were taken from unpublished data recorded by the Weather Bureau, Department of Transport, Pretoria, RSA, for Bethulie between February 1981 and January 1982. Average monthly rainfall is that recorded at Bethulie between 1931 and 1960 (Weather Bureau, 1980). Frequency distribution of births is based on the projected date of birth from fetal age on the day of collection.

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monthly temperature (°C) and rainfall (mm)(Fig. 27).

Extrapolations through fetal growth rates for two pregnant females collected in the Cape Peninsula (winter rainfall area), suggested 15 May 1977 and 13 July 1978 as birth dates.

Description of the ovary

Macroscopic appearance

The ovoid, flattened ovaries were not enclosed by a bursa and had have a relatively smooth outer surface. Corpora lutea and follicles did not protrude above the surface and the latter may be visible as transparent bodies within the substance of the ovary. The ovary was attached to the mesovarium along its length. The fimbriated end of the Fallopian tube also extended over the total length of the ovary. The Fallopian tube had a well-developed cranial loop and was convoluted over its entire length.

The weight of the left and right ovaries did not differ significantly (Paired- $t_{47} = -0,75$) and combined ovarian weight of pregnant females ($\bar{x} = 0,78 \pm 0,25$ g; n = 9) did not differ significantly ($t_{14} = 0,59$) from that of lactating ($\bar{x} = 0,71 \pm 0,23$ g; n = 7) or reproductively inactive adults ($\bar{x} = 0,64 \pm 0,38$ g; n = 7; $t_{14} = 0,87$).

Microscopic anatomy

The constituent cell types of the ovary of the porcupine were similar to those described by Weir (1967), Weir & Rowlands (1974) and Harrison

& Weir ..... /

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& Weir (1977) for hystricomorph rodents in general. Rete ovaria and tubules of the epoöphoron have not been recorded.

Ovaries contained oocytes, follicles at various stages of development or atresia, corpora lutea, accessory corpora lutea, 'luteal bodies', interstitial tissue, connective tissue and a relatively well-developed vascular system.

Primary oocytes were situated in the cortex of the ovary below the tunica albuginea and primordial follicles occurred predominantly in the peripheral zone of the cortex. The formation of the antrum and maturation of follicles occurred throughout the cortex and medulla of the ovary. The largest follicles recorded were approximately 2,53 mm in diameter, most varying from 0,96 to 1,35 mm. Newly formed corpora lutea following ovulation, varied from 2,92 to 4,74 mm in diameter.

The nuclei of the basal layer of cells of the membrana granulosa of antral follicles were noticeably aligned (Fig. 28a) and the theca interna was well developed. The theca externa was less prominent. Transformation of follicles into accessory corpora lutea by luteinisation (Fig. 28b) or into interstitial tissue (Fig. 28c) occurred in all stages of follicular development, the latter being prominent in the ovaries of immature females. Primordial and antral follicles with more than one oocyte were common in the ovaries of immature females (Fig. 28d). Most of the volume of these ovaries consisted of developing and degenerating antral follicles of varying sizes (Fig. 28c).

Various types of corpora lutea have been recorded; these included the

FIG. 28 ..... /

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FIG. 28a. Follicle in the porcupine ovary showing the aligned nuclei of the basal layer of cells of the membrana granulosa and well-developed theca interna (TI). (AFA, Haematoxylin and Eosin, X 320).

FIG. 28b. Longitudinal section through the ovary of a pregnant female porcupine of 67 days *post coitum* illustrating the luteinisation of antral follicles, typical luteal bodies (LB) and two primary corpora lutea (CL). (AFA, Haematoxylin and Eosin, X 8).

FIG. 28c. Longitudinal sections of the ovaries of an immature porcupine illustrating follicles at various stages of development and degeneration, with most degenerating follicles being transformed to interstitial tissue. (AFA, Haematoxylin and Eosin, X 8,4).

FIG. 28d. Developing antral follicle with two oocytes in the ovary of an immature porcupine. (AFA, Haematoxylin and Eosin, X 320).

FIG. 28e. Longitudinal section through the ovary of a pregnant porcupine 33 days *post coitum* illustrating corpora lutea (CL), 'luteal bodies' (LB) and the formation of accessory corpora lutea (ACL) through luteinisation of the theca interna. (AFA, Haematoxylin and eosin, X 7).

FIG. 28f. Longitudinal section through the ovary of a pregnant porcupine 91 days *post coitum* illustrating the development of a large number of follilces. (AFA, Haematoxylin and Eosin, X 7).

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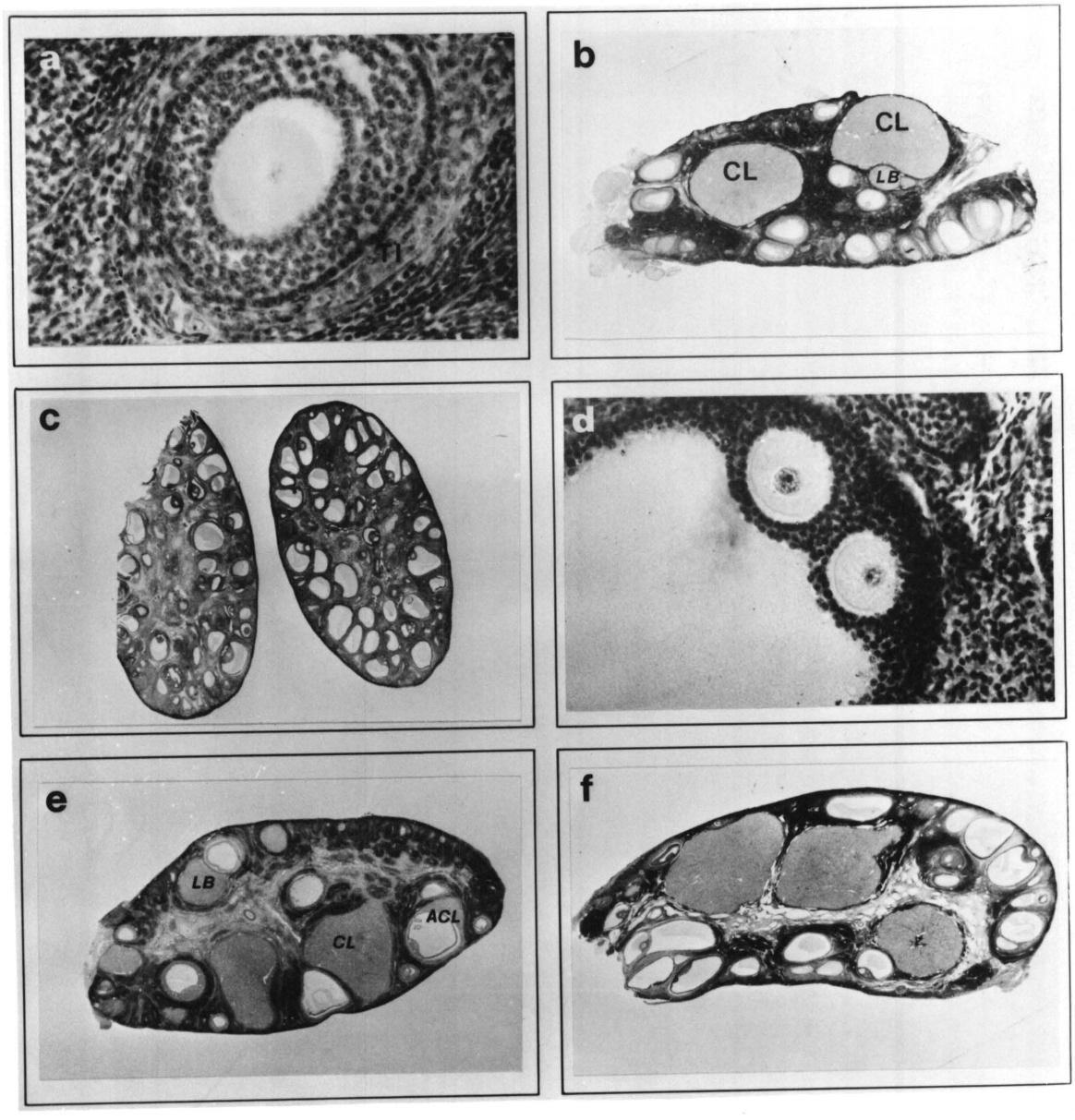

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so-called corpus luteum graviditatis (Fig. 28b), corpus haemorrhagicum, corpora lutea accessoria and 'luteal bodies' (Fig. 28b). Accessory corpora lutea and 'luteal bodies' were formed through luteinisation of the membrana granulosa or theca interna (Fig. 28b). Corpora lutea resulting from the luteinisation of ovulated follicles were usually larger than those formed from unovulated follicles (Fig. 28e). The lutein cells of all these 'luteal bodies' had the same histological appearance as primary corpora lutea.

Functional activity of the ovaries

During pregnancy

The ovaries of pregnant females consisted predominantly of primary corpora lutea and 'luteal bodies' of varying size (Figs 28 e & f). The number of 'luteal bodies' (including primary bodies) per ovary varied from one to 11 (Figs 28 b, e & f) and from five to 19 per animal, with the number of 'luteal bodies' per animal decreasing with an increase in fetal age (Fig. 29).

The number of positively identified primary corpora lutea per female varied from one to four with a mean ovulation rate of 2,5 ± 0,9 (n = 12). Primary corpora lutea persist throughout pregnancy with their numbers corresponding to the number of fetuses in seven (58,3%) of 12 females. Ovum mortality in the remainder as suggested by the difference between the number of primary 'luteal bodies' and fetuses, varied from one to two ($\bar{x}$ = 1,60 ± 0,55).

The volume of primary corpora lutea varied from 1,02 to 36,11 mm^3

FIG. 29 ..... /

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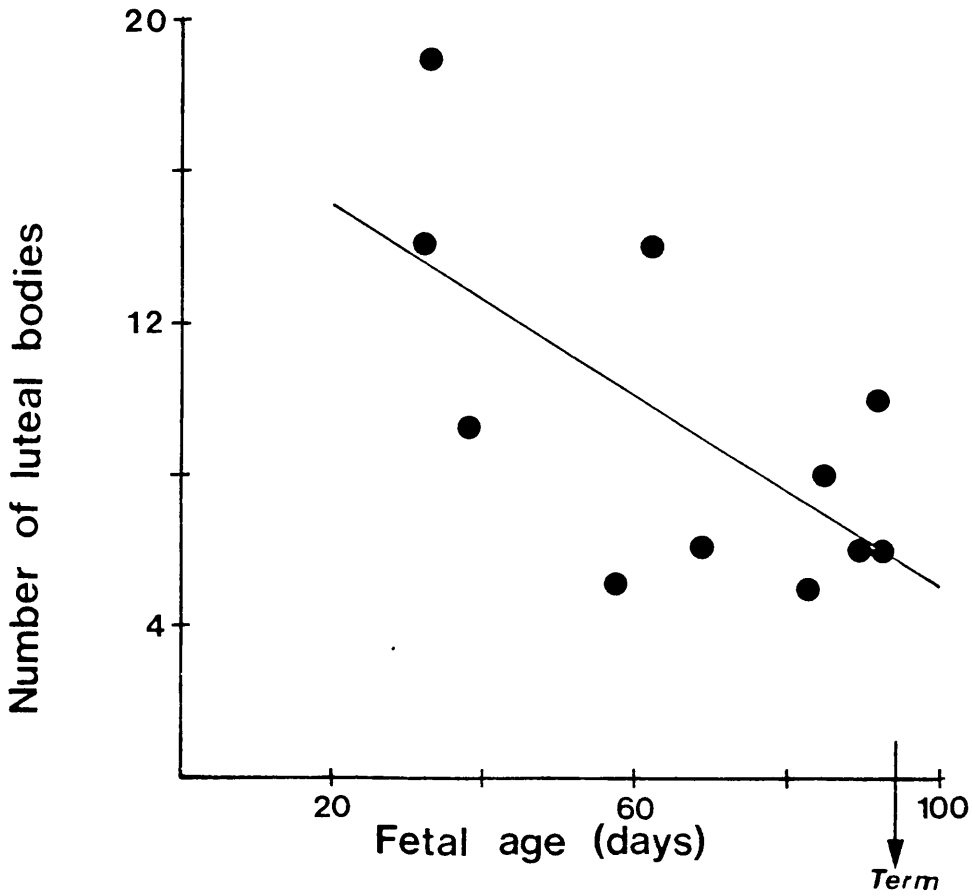

FIG. 29. The relationship between the total number of 'luteal bodies' in maternal ovaries and fetal age. The line has been fitted through linear regression analysis and is described by the equation y =17,75x-0,13 (r^2 = 0,45).

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($\bar{x}$ = 9,33 ± 7,39; n = 31) and were significantly (t_{102} = 9,17; $p < 0,001$) larger than other 'luteal bodies', these varying from 0,06 to 6,21 mm^3 ($\bar{x}$ = 1,07 ± 1,50); n = 73).

The total volume of luteal tissue per female apparently was not affected by fetal age (Fig. 30) and was also not related to circulating levels of plasma progesterone (ng/ml) measured in these females (Fig. 31). Maternal plasma progesterone levels were correlated however, with fetal age (Fig. 32) and followed a trend similar to those observed in captive pregnant females sampled at irregular intervals throughout pregnancy (see Fig. 18). The third degree polynomial function describing the curve relating maternal progesterone values to fetal age, suggested a peak (110,0 ng/ml) in progesterone concentrations 65 to 70 days *post coitum* (Fig. 32) which corresponds with observations on captive females.

Follicular activity, as suggested by the presence of varying numbers (13 - 31/female) of antral follicles in the ovaries of pregnant females, occurred throughout pregnancy (Fig. 28f). Most of these follicles were in the process of luteinisation or atresia and their numbers increased significantly with an increase in fetal age (Fig. 33).

The volume of the largest follicle in ovaries of pregnant females varied from 7,73 to 126,55 mm^3 with most (67,7%) varying from 10,0 to 30,0 mm^3. The size of the largest follicle in these females was not affected by fetal age (r^2 = 0,01) and also not related (r^2 = 0,09) to circulating plasma levels of oestradiol-17β. No definite relationship between circulating maternal oestradiol-17β levels and fetal

FIG. 30 ..... /

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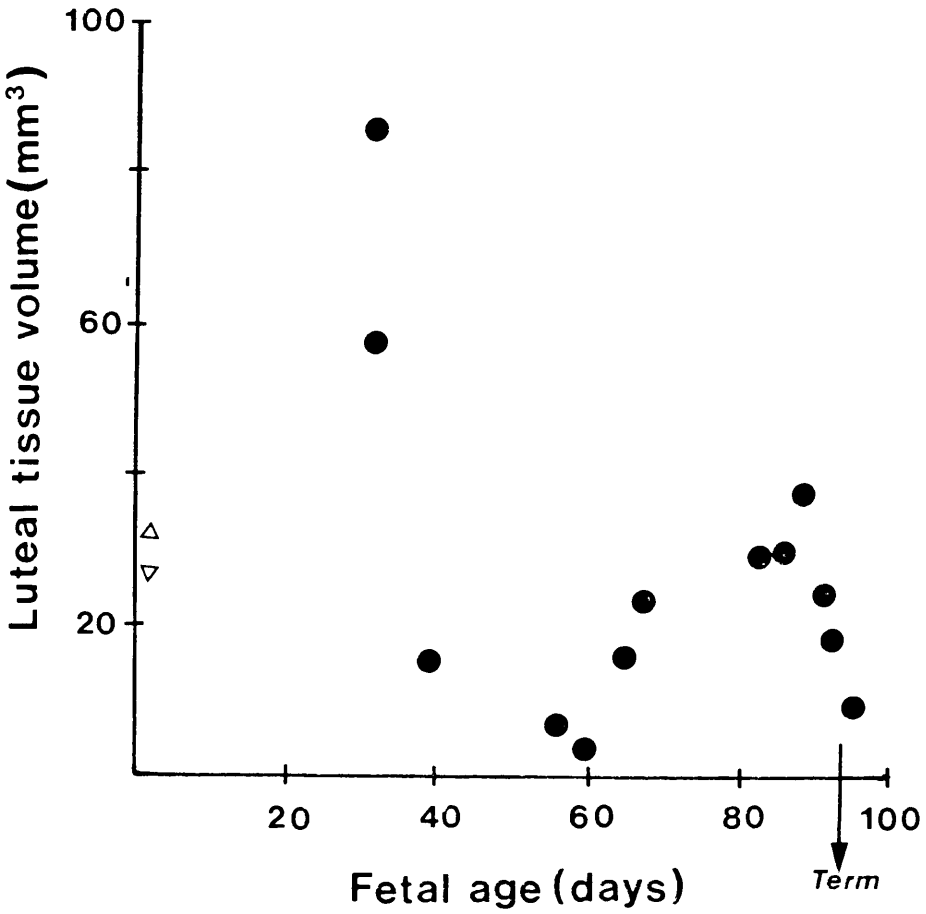

FIG. 30. The relationship between total luteal volume (mm^3) in maternal ovaries and fetal age. Δ- denotes volumes observed in ovaries of females with perforated vaginal membranes.

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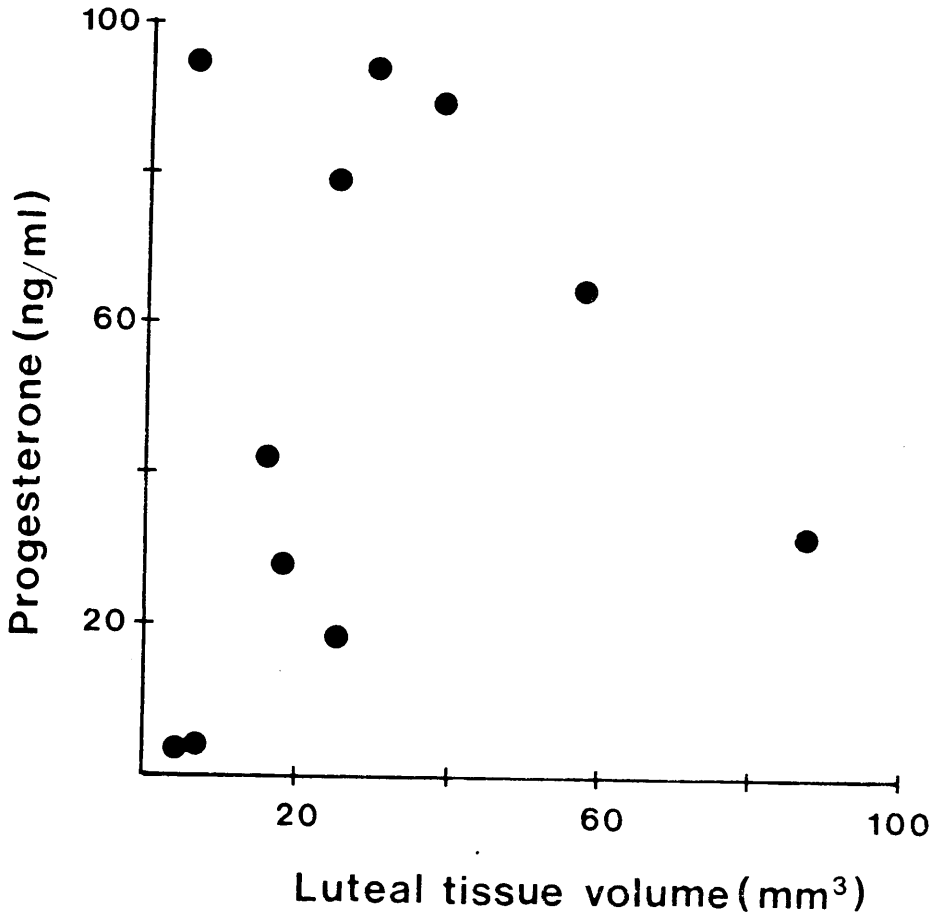

FIG. 31. The relationship between circulating levels of plasma progesterone (ng/ml) and the total volume (mm^3) of luteal tissue of pregnant porcupine females culled on the TdR Game Farm.

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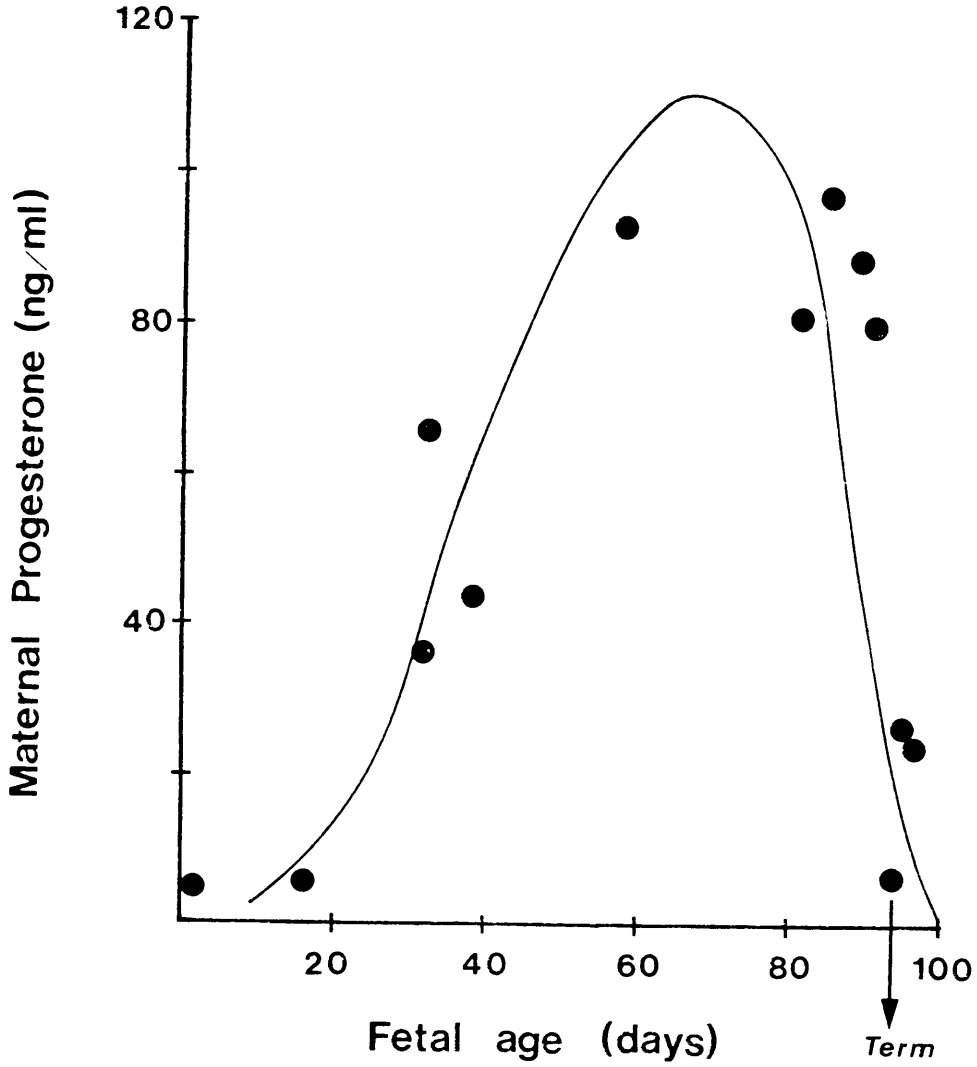

FIG. 32. The relationship between circulating maternal plasma levels of progesterone (ng/ml) and fetal age. The third degree polynomial curve relating these variables is described by the equation $y = 8{,}71 \pm 1{,}84\ x + 0{,}12\ x^2 + 0{,}0011\ x^3$ ($r^2 = 0{,}62$).

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FIG. 33. The relationship between the number of antral follicles in maternal ovaries and fetal age. The curve, relating these variables, is described by the equation $y = 1{,}88\ x^{0{,}59}$ ($r^2 = 0{,}80$).

FIG. 34. The relationship between circulating maternal plasma levels of oestradiol-17β and fetal age.

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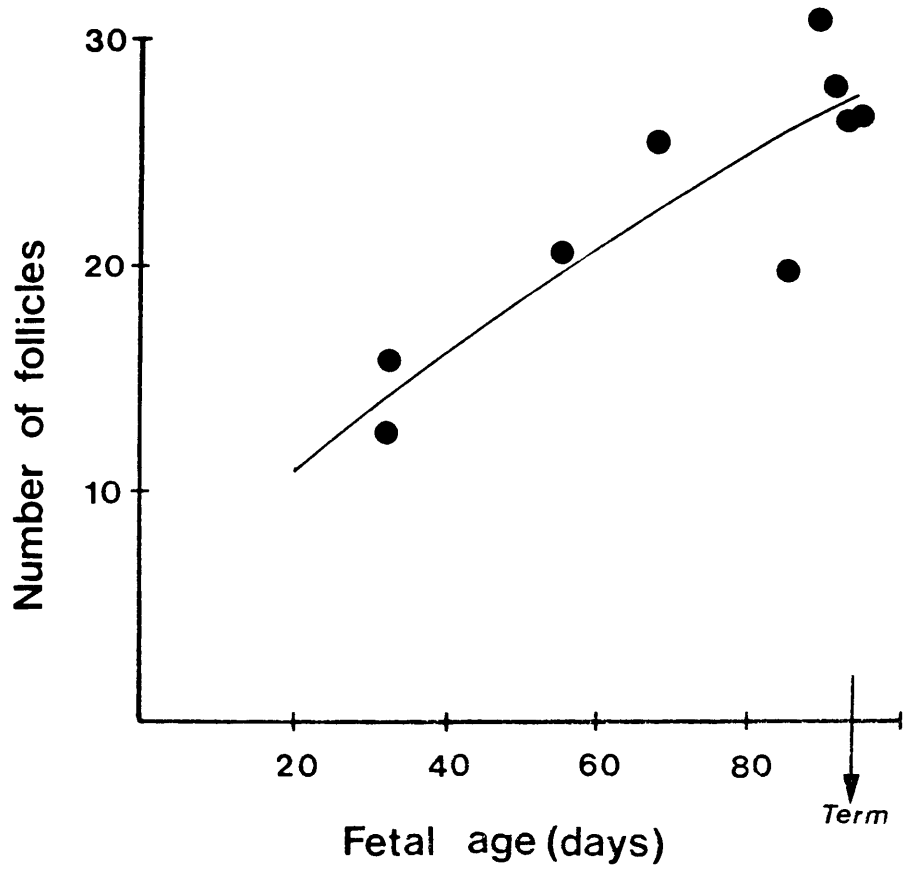

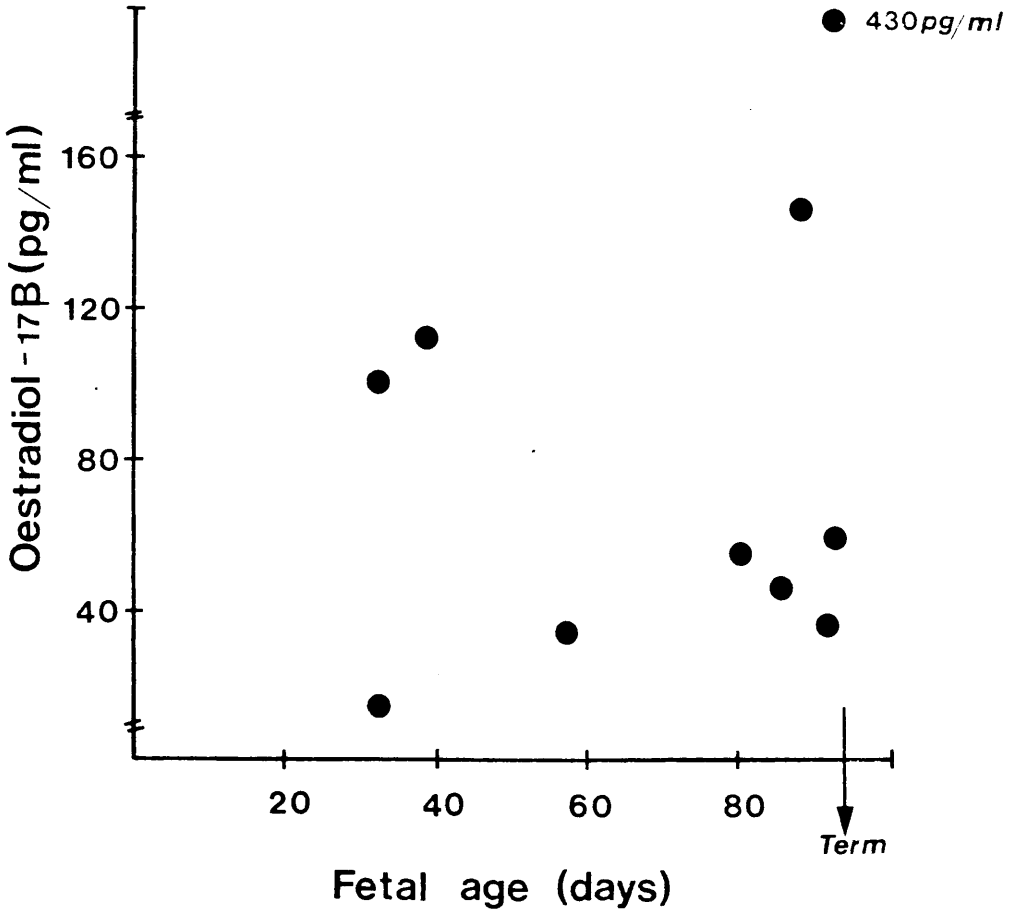

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age in culled females could be identified, probably as a result of large individual variation and limited sample size (Fig. 34). Oestradiol-17β levels in pregnant females varied from 14,2 to 430,0 pg/ml.

During lactation

The stage of lactation (i.e., days *post partum)* of lactating females from which ovaries were available (n = 9) could not be determined. These ovaries consisted predominantly of interstitial tissue and atretic antral follicles (7,47 - 20,67 mm^3 in volume) and varied in numbers from zero to 29 per ovary. Degenerating 'luteal bodies' occurred in most of these ovaries with the number of 'luteal bodies' varying from zero to five per ovary and one to eight per female. Total volume varied from 3,19 to 8,38 mm^3 and plasma progesterone values from 0,74 to 7,64 ng/ml.

Circulating levels of plasma oestradiol-17β in these samples varied from 20 to 170 pg/ml with the highest value being recorded for a female whose uterus still contained bloody fluid and which had not yet involuted following parturition.

DISCUSSION

Most research on hystricomorph rodents until now has been conducted on New World species and it is apparent that several unusual reproductive patterns occur within this group (Weir 1974; Weir & Rowlands 1974). Reproductive characteristics of the female porcupine are in agreement with those suggested as typical for the hystricomorph rodents as a

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group (see Weir 1974).

The oestrous cycle

The presence of a vaginal closure membrane which usually only perforates at oestrus and parturition, provides a ready means of determining periodicity of the reproductive cycle. This membrane has been recorded in all hystricomorph rodents studied so far, except the coypu *Myocastor coypus*, (Weir 1974). Rowlands & Weir (1977) regarded the perforation of this membrane as an 'external indicator of ovulation' and the synchronisation of perforation with regular oestradiol-17β surges in nine of the 26 cycles monitored (35,0%) in the porcupine, confirmed this. The absence of a definite oestradiol-17β surge at the onset of most of the cycles monitored is ascribed to relatively low intensity random sampling.

At oestrus, the vaginal orifice remained open for nearly nine days and the variation in recorded oestrous cycle lengths (17-42 days) may in part be ascribed to this. Perforation of the vaginal closure membrane, in accordance with the observations of Kleiman (1970) on the green acouchi *Myoprocta pratti*, has also been observed on occasion during pregnancy (Day 52 *post coitum)* in porcupine. This has also been recorded in pregnant guinea-pigs, degus *Octodon degus*, tuco-tucos *Ctenomys* spp. and plains viscachas *Lagostomus maximus* (Weir 1974).

Surges in oestradiol-17β levels were nearly always followed by variable increases in circulating progesterone levels (see Figs 13, 14 and 15). Failure of luteal activity in some cycles (i.e., Figs 13 1, 15a, b, f, i and 1) may be ascribed to intromission not always

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occurring during oestrus since copulation may, as in the rat, *Rattus norvegicus*, be required for maximal release of prolactin and thus for optimal function of the corpus luteum (see Herbert 1977).

Copulation always occurred after the peak in oestradiol-17β levels and the cyclic secretion of steroid hormones in females mated by vasectomised males (i.e., Figs 13a, b, d, e and f) were similar to those mated by intact males (i.e., Figs 13c, g and j). Cyclic activity in the porcupine is thus not an artifact in females isolated from fertile males in captivity. Factors responsible for 'sterile' matings with intact fertile males are still unknown and nulliparous and parous females experienced three to seven periods of oestrus before conceiving. The adaptive significance of this will be discussed later.

Basal levels of progesterone at the time of mating which culminated in pregnancies were significantly higher than those recorded during 'sterile' matings, thereby suggesting that priming of the reproductive tract by progesterone may be required for conception, either before, during or after the oestradiol-17β surge.

Copulation in the porcupine occurred two to eight days after the observed perforation of the vaginal closure membrane, with progesterone values increasing from basal levels two days after copulation. Increases in progesterone levels, probably resulting from the luteinisation of ruptured follicles following ovulation without copulation, occurred during three of the oestrous cycles monitored intensively, thus suggesting that coital stimulation is not always required to induce ovulation. Weir (1971b) proposed that ovulation in

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the plains viscacha is spontaneous but that luteinisation may be induced through copulation. Most other hystricomorph rodents ovulate spontaneously with a definite continuum existing between spontaneous and induced ovulators within the group (see Weir 1974). Some, however, (i.e. chinchilla) ovulate either in response to copulation or spontaneously (Weir 1973a).

Female porcupines isolated from males remained in anoestrus, but the introduction of a male resulted in the onset of oestrus within 12 days. These females were continuously exposed to the odours produced by males (males housed in pens next to the females), thus suggesting the actual physical contact between the sexes is required to initiate cyclic ovarian activity.

Most females (four out of five) kept isolated from males, except for daily stage encounters lasting 10 min, showed regular oestrous activity as suggested by the perforation of the vaginal closure membrane. Most female cuis *Galea musteloides*, also do not experience spontaneous cycles when isolated from males (Rood & Weir 1970) and behavioural as well as pheromonal mechanisms may be involved in initiating cyclic activity (Weir 1973b). The role of male pheromones in initiating cyclic ovarian activity in mice is well known from the experiments described by Whitten (1958). Oestrus and ovulation may also be stimulated in sheep and goats through the introduction of rams into flocks (Bruce 1970; Skinner & Hofmeyr 1969).

Porcupines are known to be sexually active throughout the oestrous cycle with females presenting to males and being mounted irrespective of the stage of their cycle. The behaviour elicited by the presence

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of the male followed by tactile stimuli through mounting may thus be involved in initiating and maintaining cyclic ovarian activity. Limited stimuli obtained during staged encounters may not have been sufficient to initiate and maintain full luteal activity, thus explaining why six (54,6%) of the 11 cycles monitored during staged encounters were not accompanied by a definite luteal phase. Obviously further research is required to explain the neuro-endocrine mechanisms involved here.

A lactation oestrus had been recorded in several New World hystricomorph rodents (see Weir 1974) and Weir & Rowlands (1974) suggested that all these rodents are capable of mating *post partum* but do not always conceive then. None of the five females inspected at short irregular intervals throughout the period of lactation experienced a characteristic oestrous cycle and perforation was not followed by luteal activity.

Examination of the ovaries of lactating females revealed limited follicular activity with most follicles in various stages of atresia, and luteal tissue limited to regressing bodies, probably residual from the previous pregnancy.

Normal cyclic activities in captive porcupines commenced 39 to 168 days *post partum* and two to 42 days after the cessation of lactation. Apparently lactation anoestrus is maintained by the action of oxytocin on the corpora lutea which prevents the growth of large follicles (Weir & Rowlands 1973). The suckling stimulus and high levels of proclatin associated with lactation have been implicated as causal agents resulting in infertility during lactation (McNeilly 1979).

Circulating ..... /

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Circulating levels of progesterone during the oestrous cycle varied from 0,5 to 9,0 ng/ml and varied within as well as between females. Peak values ($\bar{x}$ = 5,9 ± 2,1 ng/ml) were higher than those recorded in cyclic virgin guinea-pigs ($\bar{x}$ = 2,8 ± 0,3 ng/ml; Challis, Heap & Illingworth 1971) but lower than those recorded for nonpregnant cuis (17,9 ng/ml; Tam 1973). Hossain, Lee, Clarke & O'Shea (1979) recorded peak values of 3,66 ± 1,1 ng/ml in cyclic guinea-pigs.

Progesterone could be detected through most (approximately 93,0%) of the length of the cycle and attained maximum values midway through the cycle. Cyclic guinea-pigs attained maximum values on Day 12 of the 16-day cycle and declining luteal blood-flow did not initiate luteal regression (Hossain *et al.* 1979). The luteal phase of the oestrous cycle of the porcupine is thus similar to that of the guinea-pig and the extended period of progesterone secretion probably results in the cycle being relatively long. The length of the cycle and the observed variation is, however, in agreement with that observed in some New World hystricomorph species and in *Hystrix cristata* (see Weir 1974).

Peaks in unconjugated oestradiol-17β levels varied from 25 to 176 pg/ml and occurred before copulation when progesterone levels were relatively low. In spite of the observed variability the general pattern of steroid secretion during the oestrous cycle is a surge in oestradiol-17β secretion at the time of perforation of the vaginal closure membrane, with progesterone levels increasing from basal levels while or after oestradiol-17β levels decrease. Oestradiol-17β levels increase towards a peak when progesterone levels decrease and no evidence exists for a progesterone surge on the first day of the cycle as has been observed by Blatchley, Donovan & ter Haar (1976) in

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guinea-pigs. Progesterone levels at fertile matings were, however, significantly higher than basal levels recorded during sterile matings with intact males.

Pregnancy

Observations on the length of gestation are not in agreement with those reported earlier for African porcupines (i.e. Dekeyser 1955 in Weir 1974) who reported a gestation length of 112 days. Gestation lengths reported here (93 - 94 days) are correct since they were based on calculations of the interval between observed matings and normal parturition with pregnant females isolated from fertile males during that interval.

Gestation lengths in hystricomorphs vary considerably but are longer than those predicted for their body sizes (Weir 1974). No definite relationships between body size and gestation length could be identified during the present investigation. Except for one of the species studied (plains viscacha), long pregnancies are also not due to phenomena such as delayed fertilisation or delayed implantation (Roberts & Perry 1974).

Long gestation periods apparently are related rather to the extremely slow rate of prenatal growth, particularly in the early stages of pregnancy (see Chapter 3).

In the porcupine the initial period of pregnancy (zero - 25 days *post coitum*) is, as in the guinea-pig (Challis *et al.* 1971), cuis (Tam

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1973) and coypu (Rowlands & Heap 1966), characterised by relatively low levels of circulating progesterone when compared to levels during later stages of pregnancy. Progesterone values increased rapidly between days 25 and 40 *post coitum* and attained maximum values 50 to 60 days after mating. Peak values (102 - 180 ng/ml) were similar to those reported for guinea-pigs (approximately 200 ng/ml), lower than those reported in casiragua *Proechimys semispinosus* and cuis (approximately 250 ng/ml) and higher than those observed in the degu, viscacha and acouchi (50 - 60 ng/ml; Rowlands *et al.* 1970; Heap *et al.* 1981). These low levels are, however, higher than those recorded in hamsters, ewes and cows (see Tam 1974).

Two mechanisms have been suggested to be involved in supplementing the production of progesterone by the primary corpora lutea, these included the formation of accessory corpora lutea and the assumption of endocrine activity by the placenta (Tam 1974). The necessity for the development of excess luteal tissue in the chinchilla *Chinchilla laniger*, agouti *Dasyprocta* sp., acouchi, mountain viscacha and Canadian porcupine *Erethizon dorsatum*, is apparently caused by the long gestation period (Weir & Rowlands 1974).

In porcupines 'luteal bodies' are formed during pregnancy and primary corpora lutea and accessory luteal bodies are histologically similar (and thus presumably functionally similar) and persist throughout pregnancy with the number of 'luteal bodies' decreasing throughout gestation. The poor relationship between luteal activity, as suggested by volume, and circulating levels of progesterone may, however, be interpreted as suggesting extra-ovarian sources of steroid production. Amoroso & Perry (1977), however, warned against the

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assumption that endocrine activity can be adjudged from the histological appearance or size of the corpus luteum. Rowlands *et al.* (1970) concluded that changes in plasma progesterone levels in the acouchi closely follow the pattern of growth and decline in volume of the corpus luteum. Volumetric changes of the primary corpora lutea during pregnancies have been investigated by Rowlands (1956), Rowlands & Heap (1966) and Weir (1967, 1974) and differ from species to species but are similar in the guinea-pig and chinchilla, which differ from the coypu, and the cuis. In the chinchilla, agouti, acouchi and Canadian porcupine, primary corpora lutea are conspicuous for the first part of gestation and then the ovary becomes 'cluttered by histologically identical corpora lutea' (Weir & Rowlands 1974).

Rapid increases in progesterone levels in guinea-pigs after the fifteenth day of pregnancy are due to decreases in progesterone metabolic clearance rate (Illingworth, Heap & Perry 1970). Similar increases in the coypu have been ascribed to a 90% decrease in metabolic clearance rate accompanied by a three to six-fold increase in progesterone production (Heap & Illingworth 1974). Progesterone-binding globulins (PBG) are present in several pregnant hystricomorph rodent species (Heap *et al.* 1981) and in the guinea-pig sharp increases in PBG levels coincided with the time when the definite placenta is established (Heap *et al.* 1981). This is, however, not the case in pregnant casiragua, where progesterone-binding plasma proteins (PBPP) started to increase after the formation of the placenta. In the degu and viscacha, levels of these proteins increased before the formation of the placenta (Heap *et al.* 1981).

High-affinity progesterone-binding proteins in plasma of pregnant

porcupines ..... /

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porcupines were identified through the poor extraction of ^{3}H-progesterone from plasma pools. Binding was affected by the stage of pregnancy and was not identified in the plasma of cyclic females. PBPP have been identified in the plasma of pregnant porcupines through the technique described by Heap *et al.* (1981) and the pattern of PBG synthesis as suggested by circulating levels, was closely-related to the circulating levels of plasma progesterone.

The temporal pattern of PBPP concentration differs between species, with the biphasic pattern observed in pregnant porcupines being similar to that observed in guinea-pigs (Heap *et al.* 1981). Values in the porcupine were lower, however, throughout gestation than those recorded in pregnant guinea-pigs, casiragua, cuis, degu and viscacha (Heap *et al.* 1981). Enhanced synthesis of PBPP after day 31 may be associated with the formation of a definite placenta (see Heap *et al.* 1981) in the porcupine.

Thus it would appear that the production of PBPP during pregnancy in the porcupine provides a mechanism to conserve progesterone with the onset of production occurring 31 days *post coitum*, resulting in a sharp increase in circulating progesterone levels. Heap *et al.* (1981) suggest that in New World hystricomorph rodents progesterone requirements of pregnancy are met by a mechanism adopted to ensure a substantial pool of steroid which can dissociate rapidly from its carrier. This is then apparently also the case in the porcupine, an Old World hystricomorph rodent. PBPP may, however, also function to reduce the concentration of freely available progesterone in the blood and to provide a source of progesterone for target cell receptors.

Oestradiol-17 ..... /

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Oestradiol-17β profiles throughout pregnancy in hystricomorph rodents, until now, have been published only for the guinea-pig (Challis *et al.* 1971) and peak values (31,0 ± 5,2 pg/ml) were considerably lower than in the porcupine (170 - 210 pg/ml). Values for the porcupine remained low until days 20 to 25 *post coitum* and the rates of increase approximate those of progesterone and PBPP. Oestradiol-17β levels, however, remained high until before parturition while progesterone levels were decreasing. Oestradiol-17β levels in pregnant females were also higher than those recorded in cyclic females.

The observed pattern of oestradiol-17β secretion during pregnancy in the porcupine, as a result of its sharp increase during the first thirty days of pregnancy, is at variance with that observed in most mammals, but similar to the pattern observed in pregnant guinea-pigs. Plasma oestrogen concentration increases in most mammals during pregnancy (Bedford, Challis, Harrison & Heap 1972) and Austad, Lunde & Sjaastad (1976) recorded significaltly higher levels at mid-pregnancy in the bitch *Canis familiaris* than in the period following oestrus. The consistent changes of oestradiol in the pregnant porcupine are, however, at variance with their observations and may suggest that oestrogens are produced by the feto-placental system.

Oestradiol-17β is known as a major metabolite of progesterone in marmosets *Callithrix jacchus* (Shackleton 1974) and increases in circulating levels in porcupines may thus be ascribed to an increase in the metabolic breakdown of progesterone. However, this is at variance with the suggested decrease in progesterone metabolic clearance rate due to the increase in PBPP levels.

A follicular ..... /

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A follicular source is likely since antral follicles occurred in the ovaries of pregnant porcupines throughout gestation, with the number of large follicles increasing significantly with an increase in gestation period. In the plains viscacha, follicles develop throughout pregnancy to ovulatory size (Weir 1971b) and follicular cycles terminating in degeneration occur continually in pregnant guinea-pigs (Perry & Rowlands 1962). These may serve as a source of oestradiol-17β and thus explain the observed trend. Challis *et al.* (1971) suggested that ovarian oestrogen secretion may continue throughout gestation in guinea-pigs but ascribed the low levels of unconjugated oestrogens to a rapid rate of clearance.

The role of high levels of unconjugated oestradiol-17β in pregnant porcupines is not known. Circulating levels of hormones do not necessarily reflect their rates of secretion and as yet nothing is known about the metabolism or production of steroids and the relative contribution of the ovary, uterus, placenta and conceptus in the porcupine.

Concentrations of corticosteroid-binding globulin (CBG) or transcortin, with its high affinity for progesterone, occur at extremely high levels in pregnant guinea-pig plasma and are known to be related to high oestrogen levels in plasma (Heap & Illingworth 1974). Heating of plasma pools from pregnant porcupines at 60°C for 30 min which should destroy CBG binding of progesterone (Heap & Illingworth 1974), did not improve extraction efficiency of ^{3}H-progesterone, thus suggesting that progesterone in porcupines binds to PBG (Heap *et al.* 1981) and not to CBG, or that CBG, if occurring as a result of increasing oestradiol-17β levels, has functions other than binding progesterone.

Secreted ...../

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Secreted oestrogens have a luteotropic role in maintaining pregnancy, and luteal function can be enhanced through oestrogen administration in the last half of gestation (Amoroso & Perry 1977). It is also believed that oestrogens are essential in the control of luteal persistence and function in rodents (Amoroso & Perry 1977), thus explaining the functional role of high levels of oestradiol-17β in the porcupine.

Lactation

Milk could be expressed from the teats of pregnant porcupines 42 to 60 days *post coitum* and from pseudopregnant animals 60 to 72 days *post coitum*. In the case of pregnant females this coincided with observed peaks in progesterone levels when oestradiol-17β levels varied from 130 to 168 pg/ml (Fig. 18). Steroid levels of pseudopregnant females, however, were much lower, varying from 20 to 30 pg oestradiol-17β/ml and 5 to 6 ng progesterone/ml, suggesting that the absolute levels of these steroids are not of importance for mammary gland development. It is known that initial growth changes in the mammary gland during early pregnancy depends on the degree of lobulo-alveolar development attained during earlier oestrous cycles (Amoroso & Perry 1977), but the need for uterine priming for receptors may explain why porcupine females have to experience a number of oestrous periods before conceiving for the first time.

The inhibition of oestrous activity during the extended period of lactation has been confirmed by histological examination of ovaries from lactating females and the consistently low levels of progesterone

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during lactation. The persistence of small 'luteal bodies' in most ovaries of lactating porcupines may be due to the secretion of prolactin associated with lactation (see Perry 1971). Lactation anoestrus is not unusual for hystricomorph rodents and has been reported for the chinchilla (Weir 1967), the wild guinea-pig *Galea musteloides* Rood & Weir 1970), the green acouchi (Weir 1971c) and the plains viscacha (Weir 1971a). Milk intake of young increased with age but remained relatively constant per unit body weight. Relevant information, as far as known, is not available for other hystricomorph rodents.

Gosling (1980) recorded teat/infant contact up to the age of 20 weeks in the Himalayan porcupine *H. hodgsoni*, and Mohr (1965) recorded a period of 16 weeks in other members of the genus. Kleiman (1974) pointed out, however, that hystricomorphs sometimes suckle after lactation has ended and teat contact may thus have a social rather than a nutritional significance.

Neonatal porcupines are precocial (see Chapter 6) and although they may eat solids when 14 to 30 days old, are suckled for an extended period ($\bar{x}$ = 100,6 ± 37,8 days). The additional nourishment provided through the extended period of lactation apparently enhances survival and growth rate during the first few months of life, resulting in adult body weight being attained when approximately 12 months of age (see Fig. 9; Chapter 3). The high reproductive input through extended lactation, and the relative early age at sexual maturity results, in spite of relatively small litter size and an extended litter interval, in a high potential rate of population increase (see Chapter 6).

Pseudopregnancy ..... /

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Pseudopregnancy

Progesterone and oestradiol-17 values recorded during two incidences of pseudopregnancy fluctuated at levels similar to those observed during the oestrous cycle. Peak progesterone levels in pseudopregnant rabbits (10 - 15 ng/ml; Caillol, Dauphin-Vollemant & Martinet (1983) were, however, similar to those recorded in pregnant rabbits (17 - 19 ng/ml; Challis, Davies & Ryan 1973). The lack of a definite trend in progesterone secretion, the extended period of steroid secretion and observed development of the mammary glands, distinguished this condition from the oestrous cycle. Progesterone levels were furthermore ten to 15-fold lower than in pregnant females while changes in body weight, presumably as a result of fat deposition, were similar to those in pregnant females.

Pseudopregnancy has been documented in several mammals (i.e. rabbit, cat *Felis catus*, dog) and its duration is usually half of that of normal gestation (Amoroso & Perry 1977). However, it has not been documented for any other hystricomorph rodent. The condition defined as pseudopregnancy may however be interpretated as being due to successful conception followed by early resorption.

Litter size, neonatal weight, litter interval and age at sexual maturity.

Litter size in *Hystrix* varied from one to four (Mohr 1965, Weir 1974, Gosling 1980 and Thome & Thome 1980) but a maximum of three was recorded during the present study, with most litters comprising singletons and twins. Litter size in New World hystricomorphs varies considerably and no apparent correlation between gestation length and average litter size or maternal body weight could be detected (Weir

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1974). Litter size is also not related to adult body weight amongst all mammals (Millar 1977) and is in general regarded as a product of the resource budget of the reproducing individual (Tuomi 1980).

Neonatal litter weight in hystricomorph rodents increases with an increase in maternal weight (Fig. 21) at a rate similar to that observed for 22 mammalian groups by Tuomi (1980). Neonatal weight in *H. africaeaustralis* ($\bar{x}$ = 351,1 ±.47,34 g) was within the limits (300 - 465 g) recorded by Mohr (1965) for the genus, but much lower than the 1 000 g listed for *H. cristata* by Weir (1974). Litter weight at birth, expressed as a percentage of maternal weight is high in New World hystricomorphs (11 - 60 %; Weir 1974).

Known neonatal litter weight in the Old World species, however, varied from 3,2% in *H. hodgsoni* (Gosling 1980) to 14,4% in the greater cane rat *Thryonomus swinderianus* (based on data in Smithers 1983) and is thus considerably lower than in New World species. The low values recorded for *Hystrix* are of interest and may be ascribed to their relatively short gestation period when compared to New World species of comparable size.

Litter intervals in *H. africaeausturalis* varied from 296 to 500 days and are thus significantly longer than those (91 days) recorded by Mohr (1965) for African porcupines and the 142 days recorded by Gosling (1980) for *H. hodgsoni*. Their observations suggest the occurrence of a *post partum* and/or lactation oestrus which does not occur in *H. africaeaustralis*. This discrepancy cannot be explained.

In spite of their apparent precocity at birth, most hystricomorph

rodents ..... /

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rodents appear to attain sexual maturity at a relatively old age. Puberty depends upon the time of the year when young are born and males are usually slower to mature than females (Weir 1974). The first oestrus may be induced by the presence of a male (i.e. in the cuis; Weir 1973b) and isolated females may experience first oestrus later than females living with males (i.e. in the casiragua; Weir 1974).

Among the Old World hystricomorphs vaginal opening may occur at the age of five months in the cane rat (Asibey 1974) and the first litter can be produced at the age of 12 months (Ewer 1969). Age at sexual maturity, however, appears to be a function of body size rather than age (Hogarth 1979). Vandenbergh, Drickamer & Colby (1972) proved that accelerated sexual development was not accompanied by accelerated body growth in female albino mice. They indicated that social factors (presence of males or their odour) and dietary protein were both factors regulating age at sexual maturation, with social factors contributing to 47,0% and dietary protein to 5,0% of the total variance at age of sexual maturation.

Sexual maturity in captive porcupines examined during the present investigation varied from nine to 18 months with the first successful conception at the age of ten months. Age at first conception was affected, however, by immobilisation but similar to that recorded for *H. indica* which starts reproducing at the age of two years (Thome & Thome 1980). Age at sexual maturity in free-ranging porcupines was similar to that recorded in captivity.

Seasonality ..... /

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Seasonality

The physiological mechanisms underlying seasonal breeding in African small mammals as an adaptation to long term survival are as yet not well understood. Nutritional demands when suckling, suggest that the time of birth is quite critical in order to ensure maximum opportunity for the offspring to survive. As a result of the relatively long gestation period, the reproductive events culminating in birth start under environmental conditions different from those prevailing when the young are born. Conceivably proximate factors should operate to ensure young are produced at the time most advantageous to their survival.

Free-ranging porcupines in the Karoo reproduce seasonally with the peak in their birth season coinciding with peaks in rainfall and presumably primary productivity (Fig 26). Birth dates deduced for two pregnant females collected in the winter rainfall area of South Africa confirm this, thereby suggesting that primary production may be an ultimate factor affecting reproductive activities. Underground rhizomes of grasses, bulbs and tubers are, however, apparently the most important food of porcupines and these are a relatively stable food source, thus not supporting this hypothesis. Moreover, the springhaas *Pedetes capensis*, which occupies a similar 'feeding niche', breeds in the wild throughout the year in the Highveld (Van der Merwe, Skinner & Millar 1980).

Seasonal breeding may be attributed to seasonal oestrus but captive porcupine females housed with intact males, do cycle throughout the year, with the intensity of cyclic activity not being affected by

daylength. ..... /

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daylength. Cyclic activities, however, are affected by lactation, which renders females anoestrous for approximately three to four months and is thus a limiting factor in female productivity. The social and physiological mechanisms underlying the three to seven infertile cycles following lactation are not known but, together with gestation and lactation periods, results in a litter interval of approximately one year ($\bar{x}$ = 385,0 ± 60,4 days). A hypothetical female conceiving at a specific time during a mating season will presumably therefore always conceive at about the same time during the following season. The length of the lactation period and the number of sterile cycles following lactation would serve as variables enhancing seasonality, with these probably being affected by temperature and rainfall (Skinner, van Aarde & van Jaarsveld 1984). The lack of seasonality in the three captive populations, which were maintained under natural conditions but which were provided with a relatively constant food supply, confirm this suggestion. It does not explain, however, the recurrence of sterile oestrous cycles.

The agreement in the estimated mean dates of birth for captive populations with those of the free-ranging population and the fact that births in captivity were unevenly distributed, with 78,8% recorded between August and March, suggest that other environmental factors also affect the reproductive cycle.

Seasonal as well as continuous breeding has been recorded in other *Hystrix* species kept in captivity (see Mohr 1965, Weir 1967, Gosling 1980, Thomè & Thomè 1980). Ewer (1969) referred to the lack of knowledge on the seasonal breeding activities of the cane rat while Asibey (1974) suggested that breeding in this species in Ghana is

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related to seasonality in rainfall. Plains viscacha in the southern part of their range, produce only one litter per year and in more favourable climates further north, two litters are produced (Weir 1974).

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CHAPTER 5

MALE REPRODUCTIVE BIOLOGY

INTRODUCTION

Male hystricomorph rodents have not been studied as extensively as females (Weir 1974) and published information on *Hystrix* species is limited to descriptions of the morphological (Thomè & Thomè 1981) and histological (Weir 1967) characteristics of the reproductive tract. Hystricomorph rodents do not have a true scrotum and the penis is directed posteriorly. The surface of the glans penis of most species is covered with spines or spicules (Pocock 1922 in Weir 1974) and the presence of a sacculus urethralis is considered characteristic of the suborder (Weir 1974). No hystricomorph males have been reported to be seasonal breeders and their gonads do not regress periodically.

This chapter deals with aspects of the reproductive biology of the male porcupine and is based on information obtained through direct observations on captive porcupines and material collected from males culled on the TdR Game Farm.

MATERIALS AND METHODS

Histology

Study material and relevant information were collected as described in Chapter 2. Testicular samples from all males and epididymides and samples from prostate glands of some males were later dehydrated,

embedded ..... /

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embedded in paraffin wax, sectioned at 5 µm and routinely stained in Delafield's haematoxylin, using eosin as a counterstain. The stained sections were microscopically examined for the stage of spermatogenesis and the mean seminiferous tubule diameter for each male was calculated from 25 tubules in cross-section using a calibrated micrometer eyepiece and a 10 X objective.

Radioimmunoassay of testosterone

Reagents

'Pro-analysi' diethyl ether from Merck (Darmstadt, FRG) was used for the extraction of testosterone from plasma samples without any further purification. The phosphate buffer (pH 7,0) comprised the following, in 100 ml deionised water:

Disodium hydrogen phosphate ($Na_2HPO_4.12H_2O$)	22,5 g
Sodium dihydrogen phosphate ($NaH_2PO_4.H_2O$)	5,4 g
Sodium chloride (NaCl)	9,0 g
Sodium azide (NaN_3)	1,0 g

The pH was corrected with NaOH when necessary. The assay buffer consisted of a 0,1% (w/v) gelatin solution in the above phosphate buffer and the buffer used to reconstitute dried extracts consisted of 1,0% (v/v) methanol in phosphate buffer.

Dextran-coated charcoal consisted of a suspension of charcoal (Aktivole; 'pro-analysi', Merck, Darmstad, FRG) in assay buffer (0,25 g/100 ml) containing 0,025 g dextran T-40 (Pharmacia, Uppsala, Sweden).

Scintillation ..... /

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Scintillation fluid (Ready-Solve™ CP) and scintillation vials (Mini Poly-Q™) from Beckman Instruments (Pty) Ltd (Johannesburg, RSA) and crystallised testosterone (Δ^4-androsten-17β-ol-3-one) from Sigma Chemical Co. (Dorset, UK) were used. [1,2,6,7-^{3}H] testosterone, Code TRK 402, with a specific activity of 349 mCi/mg was purchased from Radiochemical Centre (Amersham, UK).

Assay

Duplicate plasma samples (50 or 100 µl) were transferred into 10 ml round-bottom glass tubes and testosterone was extracted with 4,0 ml diethyl ether. The extraction procedure involved thorough mixing for 5 min on a multitube vortexer (Model 2601, Scientific Manufacturing Industries, Emeryville, USA). The organic phase was poured off into clean assay tubes (12 x 75 mm) after freezing the plasma fraction at -20 °C for 60 min. The dried extracts were dissolved in 100 µl phosphate buffer containing 1,0% methanol. Standards (3,9; 7,8; 15,6; 31,2; 62,5; 125; 250; 500 and 1 000 pg testosterone/100 µl phosphate buffer with 1,0% methanol) were prepared in duplicate and included in each assay.

Antiserum in phosphate buffer (100 µl) at a dilution of 1:800 was added to standards, plasma extracts and reagent blanks. [1,2,6,7-^{3}H] testosterone in 100 µl assay buffer (approximately 10 000 cpm) was then added to the contents of each tube which were mixed thoroughly and left to incubate for 60 min in a water bath at 37 °C.

After incubation the separation of antibody-bound and free steroid was carried out at 4 °C by adding 0,5 ml dextran-coated charcoal

suspension ..... /

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suspension to the contents of each tube. These solutions were mixed gently for 30 sec, incubated at 4 °C for 10 min and centrifuged at the same temperature at 3 000 rpm for 10 min. The supernatants were decanted into scintillation vials and scintillation fluid (4,0 ml) was added to each vial. The contents of the vials were mixed properly and radio-activity was measured at least 4 h later for 2 min, using a Beckman LS 5800 Scintillation Counter.

A standard curve of percentage radio-activity-bound was plotted against the logarithm of the concentrations of testosterone over the range 3,9 to 1 000 pg/tube. The testosterone contents of each tube were determined by interpolation on the standard curve.

The recovery of known amounts of [1,2,6,7-^{3}H] testosterone (1 000 cpm) in phosphate buffer containing 0,1% methanol to which aliquots (50 or 100 μl) of pooled plasma from adult males were added, served to determine procedural losses incurred during extraction.

Extraction efficiency and the original volume of plasma extracted were taken into account when calculating the concentrations of testosterone in plasma samples.

RESULTS

Reliability criteria for the testosterone assay

The specificity of the antiserum raised in a rabbit and provided by R P Millar (Department of Chemical Pathology, University of Cape Town, RSA) was determined by the supplier and cross-reactions with other

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steroids were: 5α-dehydrotestosterone 5,1%; adrostenedione, dehydroepiandrosterone, etiocholanolone, androsterone, progesterone and oestradiol-17β, 0,008%.

The sensitivity of the assays defined as twice the standard deviation of the blank values (Jeffcoate 1981), ranged from 10,6 to 33,9 pg/tube ($\bar{x}$ = 18,4 ± 13,5; n = 3) or 237,6 to 370,6 pg/ml ($\bar{x}$ = 290,7 ± 70,4; n = 3). Six buffer blanks included in three assays contained 205,7 ± 49,7 pg testosterone equiv./ml.

Recovery estimates varied from 89,1 to 92,8% ($\bar{x}$ = 91,2 ± 1,9; n = 3) and were not affected by volume over the range 50 to 100 l plasma. Intra-assay coefficient of variation calculated according to the method of Jeffcoate (1981) was 5,3%. Interassay coefficient of variation for a plasma sample containing 730 ± 46,7 pg testosterone/ml was 6,4% and for a sample containing 6 283 ± 757,0 pg/ml, 13,6%. Addition of 1 000 pg testosterone/ml to a plasma pool included in all assays resulted in a recovery of 102 ± 1,0%.

Morphology of the reproductive tract

The appearance of the external genitilia of *Hystrix africaeaustralis* is similar to that described for *Hystrix* species by Mohr (1965), for-*H. cristata* by Weir (1967) and for *H. indica* by Thomè & Thomè (1981)-The S-shaped penis is posteriorly directed when not erected and the subcutaneous testes are not suspended in a scrotum. The surface of the glans penis of the adult male is covered with inconspicuous spicules and the well-developed sacculus urethralis is only pronounced when the penis is fully erect.

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The accessory glands (vesicular gland, prostate and Cowper's glands) are well developed in the adult with the prostate being macroscopically divisible into a left and right lobe. The fluid of the diverticulated vesicular gland forms a gel when mixed with that of the prostate and presumably forms the copulatory plug after copulation. The microscopic appearance of the testes, epididymides and prostate was similar to that illustrated of *H. cristata* (see Weir 1967).

Age-related characteristics

Age-related mean combined testes, epididymides, prostate and vesicular gland weights, mean seminiferous tubule diameter and mean plasma levels of testosterone are summarised in Table 27. Maximum mean testes, epididymides, prostate and vesicular gland weights were recorded for males in age classes VII and VIII (older than 30 months). Mean testes weight (6,56 ± 2,05 g; n = 17; Table 27) recorded for age class VI (23,1 - 30,0 months) did not differ significantly (t_{37} =0,51) from that recorded for age classes VII ($\bar{x}$ = 6,81 ± 2,12 g; n =22) and VIII ($\bar{x}$ = 7,56 ± 1,61 g; n = 21; t_{36} = 1,73) implying that asymptotic testes weight was attained at an age of 23 to 30 months.

Seminiferous tubule diameter peaked in age class VIII ($\bar{x}$ = 0,148 ± 0,015 mm; n = 21) but this value did not differ significantly from the mean recorded for age classes VI (t_{34} = 0,82) and VII (t_{41} =1,54). This suggests that asymptotic seminiferous tubule diameter ($\bar{x}$ =0,144 ± 0,012 mm; n = 15) may be attained at an age of 23 to 30 months.

None of the males in age class III (5,1 - 8,0 months) exhibited spermatogenic activity, while 73,3% of the 15 males in age class IV

TABLE 27 ...../

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TABLE 27. Age specific mean (± S.D.) testes weight, epididymides weight, prostate weight, vesiculae seminales weight, seminiferous tubuli diameter and plasma testosterone levels in free-ranging porcupines culled on the TdR Game Farm. Sample sizes are given in parenthesis.

Age class	Age interval (months)	Testes weight (g)	Epididymides weight (g)	Prostate weight (g)	Vesiculae seminalis weight (g)	Seminiferous tubule diameter (mm)	Testosterone levels (ng/ml)
II	2,0 - 5,0	0,89 ± 0,41 (10)	0,54 ± 0,27 (7)	7,89 ± 3,77 (9)	0,77 ± 0,72 (4)	0,074 ± 0,012 (10)	3,38 ± 3,36 (7)
III	5,1 - 8,0	1,98 ± 1,13 (19)	1,04 ± 0,37 (12)	10,34 ± 8,79 (11)	2,25 ± 1,98 (12)	0,095 ± 0,030 (20)	3,89 ± 2,99 (11)
IV	8,1 - 18,0	4,32 ± 1,93 (15)	1,26 ± 0,29 (7)	30,97 ± 16,88 (9)	5,19 ± 2,77 (6)	0,123 ± 0,030 (16)	2,72 ± 2,05 (6)
V	18,1 - 23,0	4,20 ± 1,49 (5)	1,41 ± 0,75 (3)	16,15 ± 2,43 (2)	1,48 ± 1,48 (2)	0,132 ± 0,021 (6)	6,91 ± 1,20 (3)
VI	23,1 - 30,0	6,56 ± 2,05 (17)	1,79 ± 0,67 (6)	43,85 ± 12,37 (5)	3,43 ± 3,56 (4)	0,144 ± 0,012 (15)	2,09 ± 0,94 (3)
VII	30	6,81 ± 2,12 (22)	2,09 ± 0,76 (7)	33,98 ± 9,33 (7)	6,54 ± 3,40 (5)	0,143 ± 0,017 (22)	2,36 ± 2,10 (7)
VIII	30	7,56 ± 1,61 (21)	2,19 ± 0,55 (15)	39,38 ± 18,15 (15)	5,81 ± 1,58 (10)	0,148 ± 0,015 (21)	2,49 ± 1,64 (16)
IX	30	4,87 ± 1,12 (5)	1,69 ± 0,31 (4)	27,96 ± 16,55 (4)	4,80 ± 2,45 (4)	0,137 ± 0,012 (5)	1,52 ± 0,96 (5)

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(8,1 - 18,0 months) were undergoing spermatogenesis. Gonocytic elements (spermatogonia, spermatocytes and spermatids) were present in the seminiferous tubules of all males in age classes V to IX (older than 18 months).

Plasma testosterone levels for males in age class IV varied from 0,43 to 4,48 ng/ml ($\bar{x}$ = 2,72 ± 2,05; n = 6) and did not differ significantly (t_{15} = 0,84) from those recorded in younger males. Mean seminiferous tubule diameter for males in this age group ($\bar{x}$ = 0,123 ± 0,030 mm; n = 16) was, however, significantly (t_{25} =3,45; $p < 0,001$) larger than that found in younger males, but significantly smaller (t_{21} = -3,00; $p < 0,001$) than values recorded for males 18 to 30 months old (age classes V and VII). The mean testosterone value recorded for males 18 to 23 months old, (6,91 ±1,20 ng/ml) was, significantly higher than that recorded for older males (Table 28; t_{27} = 5,06; $p < 0,001$).

A captive born male fertilised a parous female when ten months old and mounting accompanied by thrusting was recorded in males at a minimum age of eight months (n = 3).

The relationship between paired testes weight (g) and body weight (kg is presented in Fig. 35. Separate lines were fitted for sexually immature (age classes II - IV) and mature males (age classes V - IX). The line for the first group was described by the equation $y = 0,56 - 1,5x$ and that for the latter by $y = 2,52x + 0,35$; with testes weight as the dependent variable. The increase in testes weight with body weight was significant (r = 0,73; $p < 0,001$; n = 50) only for the immature group.

FIG. 35 ...../

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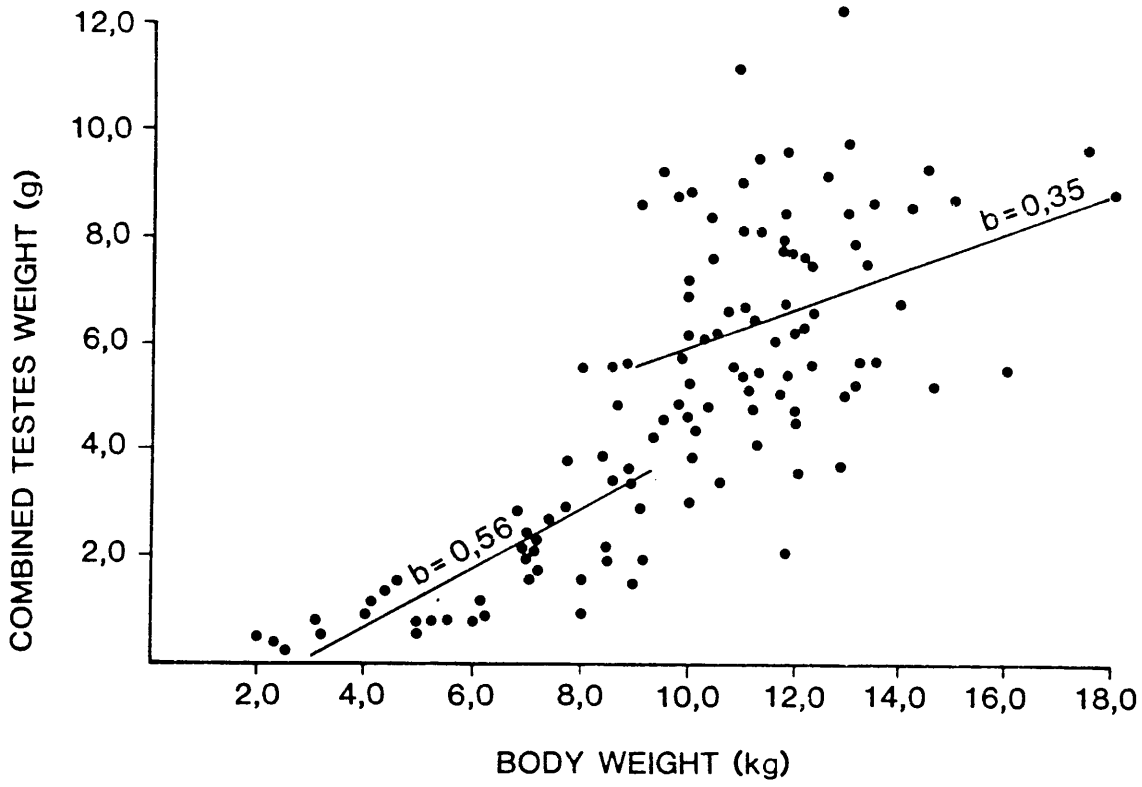

FIG. 35. The relationship between combined testes weight and body weight for porcupines (n = 124) culled on the TdR Game Farm between February 1977 and July 1982. Separate lines were fitted through least square regression analyses for males in age classes II to IV and V to IX, the latter presenting sexually matured males.

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Mean seminiferous tubule diameter increased linearly ($y = 0,085x + 0,008$) and significantly ($r = 0,73$; $p < 0,001$) with an increase in paired testes weight, but heteroscadasticity due to an increase in residual variance with an increase in testes weight, rendered the equation unreliable for predictive purposes.

Seasonality

Spermatogenesis, as suggested by the presence of spermatogonia, spermatocytes and spermatids in the seminiferous tubules of adult males (older than 18 months of age) occurred throughout the year. Combined testes weight and epididymides weight for adult males did not change seasonally (Figs 36a & b), while mean vesicular and prostate gland weights increased from May to July, with the mean values recorded for the period January to May being lower than those recorded from July to December (Figs 36d & e). These differences were significant ($t_{23} = -4,96$ and $t_{32} = -5,50$ for prostate and vesicular gland weights respectively; $p < 0,001$).

The increase in mean seminiferous tubule diameter from July to September, followed by a decrease from September to December (Fig. 36f) was, however, not statistically significant ($t_9 = 1,43$ and $t_{11} = -0,13$ respectively).

Mean plasma testosterone levels increased from a nadir of 0,98 ± 0,44 ng/ml in January to 3,31 ± 2,11 ng/ml in March, with mean values remaining above 3,0 ng/ml up to July, decreasing thereafter until December. However, these changes were not statistically significant ($t_{11} = -2,04$ and $t_8 = 0,99$ respectively) and the mean values recorded

FIG. 36 ..... /

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FIG. 36. Seasonal changes in mean testes weight, epididymides weight, prostate weight, vesicular gland weight and mean testosterone levels in adult porcupines culled on the TdR Game Farm between September 1981 and July 1982. Sample sizes are given above the means and vertical lines present one standard deviation. Horizontal bars denote the observed period of successful conceptions as suggested by fetal age.

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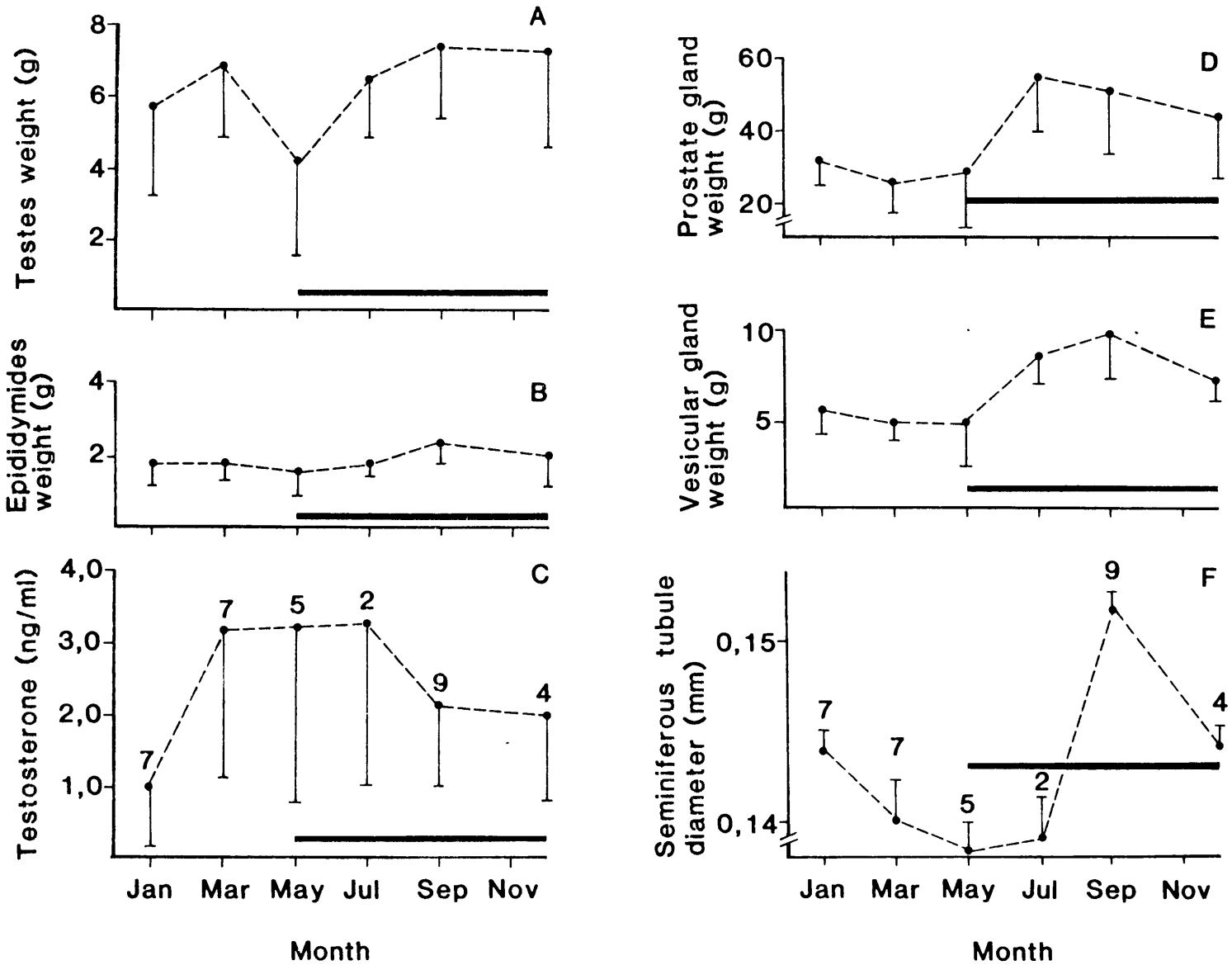

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from September to January were similar to those recorded between March and July (t_{33} = -2,27).

DISCUSSION

Circulating levels of testosterone in porcupines varied from 400 pg/ml to 10,92 ng/ml and the highest value was recorded for a male five to eight months of age. The values recorded for adult males varied from 400 pg/ml to 5,81 ng/ml and were similar to those recorded for adult guinea-pigs, but lower than those recorded for the rabbit, bull, monkey and man (Rigaudiere, Pelardy, Robert & Delost 1976 for references). Rigaudiere *et al.* (1976) ascribed the relatively low levels of testosterone in the plasma of guinea-pigs to the absence of testosterone-binding globulin, resulting in a high metabolic clearance rate of testosterone. The high efficiency of extraction of testosterone from porcupine plasma without the prior denaturation of proteins might be considered indicative of the absence of testosterone-binding proteins and thus explain the relatively low levels recorded.

Testosterone levels in pubertal porcupine males were significantly higher than those recorded in sexually mature males. This is in agreement with observations on guinea-pig, mice, rats (Rigaudiere *et al.* 1976) and rabbits (Berger, Chazaud, Jean-Faucher, de Turkheim, Veyssiere & Jean 1976).

The relatively high levels of testosterone in pubertal males may partly be due to modified testicular sensitivity to gonadotrophins (Odell, Swerdloff, Bain, Wollesen & Grover 1974). Lee, Bremner, Cumming, de Kretser & Findlay (1981) indicated, however, that it is

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not clear whether changes in sensitivity to gonadotrophins play a role in the initiation of the pubertal process in the rams. Pituitary testicular relationships in porcupines, however, need to be investiga= ted to explain the mechanisms involved in pubertal development.

Minimum age at fecundity in captivity (ten months) was similar to the age recorded (eight - 18 months) when full spermatogenic activity commenced in free-ranging porcupines. The pairbond social system in porcupines (see Chapter 6) may however prevent young sexually mature males from breeding before being socially established. Males, eight to ten months old, were observed to mount females (even their mothers), this may be an artifact of captivity, as males were housed with their natal family groups for extended periods.

Porcupines in captivity breed throughout the year while free-ranging animals breed seasonally, with the period of successful conceptions on the TdR Game Farm lasting eight months, from May to December (see Chapter 4). The full spermatogenic cycle observed in seminiferous tubules of all adult males suggests that males, in general, have the ability to fertilise ova throughout the year. The increased circula= ting levels of testosterone (although not significant) before the breeding season and the statistically significant heavier weights of prostate and vesicular glands (Figs 36 d & e), probably in response to the increased testosterone secretion, may be indicative of some degree of reproductive seasonality in males. This is however not supported by the trends in testes weight, epididymides weight and seminiferous tubule diameters (Figs 36 a, b & f). The seasonal trend in testoste= rone secretion and the weights of the accessory glands producing the copulatory plug can not be explained in terms of environmental or

physiological ...../

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physiological variables, as yet.

Captive males provided with a constant supply of food and exposed to relatively natural environmental conditions (photoperiod, temperature and ventilation), are fertile throughout the year and seasonal breeding in porcupines may with the information available, best be explained in terms of factors (physiological through the environment) affecting the female (see Chapter 4). The inability to form a copulatory plug as a result of a decrease in accessory gland activity may, however, play a role in successful seasonal fertilisation.

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CHAPTER 6

POPULATION BIOLOGY

INTRODUCTION

Information on the population biology of hystricomorph rodents is limited and a detailed analysis of the demographic parameters has been published only for the paca *Agouti paca* (Collett 1981).

The motivation for culling a large number of porcupines on the TdR Game farm originated from the reported destruction of the habitat due to the ringbarking of trees and rare aloe species (L.P. Stolz *pers. comm.)*. During the first intense culling operation (February 1977 - January 1978) 91 porcupines were killed and during the second (July 1981 - July 1982) another 118, resulting in 209 porcupines being accounted for over the five year period. The relatively large numbers of porcupines on the Game Farm at the time of culling probably result= ed from the absence of large carnivores for which porcupines are known to be an important food source, particularly in arid environments (Smithers 1983).

The two separate data sets originating from material and information collected during these culling operations form the basis of the analyses presented in this chapter. The analyses of the demographic characteristics of the population are important for understanding the reproductive strategy of the species and in planning control program= mes. An opportunity is also provided to evaluate the reaction of the porcupine population to an artificial reduction in density.

MATERIALS ..... /

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MATERIALS AND METHODS

Distribution patterns and estimates of population density were inferred from information collected at night during six sampling periods between September 1981 and July 1982. Right-angle distances (m) from the route followed to all porcupines encountered in the beam of a spotlight (Q-beam, 200 000 c.p., Saetra (Pty) Ltd, Pretoria, RSA), held at right-angles on both sides of the vehicle while driving at 20 to 25 km/h along a fixed route of 57,7 km through all major habitat types on the Game Farm, were recorded. Only individuals killed were included in the analyses of density and all distances were recorded by the same observer. The number of observers per sampling period varied from six to eight. Data obtained during these surveys were treated as described by Caughley (1977) for transects of indefinite width and for the nonselective removal of animals.

Information related to the age structure of the 1977/78 and 1981/82 population and age-related demographic parameters, based on the age determination techniques described in Chapter 3, was analysed as suggested by Caughley (1977) and Elseth & Baumgardner (1981). These analyses were based on the assumption that the standing age distribution (the number of animals relative to the number of newborn, in each age class at the time of culling) represented a stable age distribution.

The inability to assign chronological ages to specimens older than 24 months of age required the development of a method to estimate adult survival rates independently from the age structure. The model used to estimate survival rates was based on the following assumptions:

1. Age ..... /

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1. Age specific probability of survival (l_x) decreases logarithmically with an increase in age (x).

2. Longevity is approximately ten years and l_{10} equals 0,000. (Kingdon 1974 reported that porcupines kept in captivity may live up to 20 years, suggesting that it is not unreasonable to assume a longevity of ten yers under natural conditions.)

3. Fecundity rate (m_x) for porcupines older than 24 months remained constant. (According to Caughley (1977) deviation from a constant rate of adult fecundity is only slight in large mammals and may, for the purpose of population analyses, be expressed as a mean value.)

The l_x values, calculated independently from the age structure of the population, were used accordingly to estimate population growth rate (r_s) from survival and fecundity schedules, nett productive rate (R_o) and age specific mortality rates (q_x) as described by Caughley (1977) and Elseth & Baumgardner (1981).

RESULTS

Distribution and Density

Porcupines were encountered during the night only and most occurred in the *Crysocoma tenuifolia - Lessertia pauciflora* and *C. tennuifolia - Polygala leptophylla* communities of the flat and gently sloping terrain (Table 28). Only a few animals were seen on steep slopes (mainly in *Rhus erosa - Rhynchelytrum repens* grassland; (Table 28)

TABLE 28 ..... /

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TABLE 28. Number of porcupines culled in each of the plant communities on the TdR Game Farm. Sample sizes are given in parenthesis. (See Werger 1973 for a description of the communities).

Type of community	Community	Number of porcupines (%)
Riverine	*Acacia karroo - Celtis africana*	0,0 (0)
		Subtotal 0,0 (0)
Flats and gentle slopes	*Eragrostis lehmaniana - Chrysocoma tenuifolia*	4,6 (4)
	C. tenuifolia - Lessertia pauciflora	39,8 (35)
	C. tenuifolia - Nenax microphylla	13,6 (12)
	C. tenuifolia - Polygala leptophylla	31,8 (28)
		Subtotal 89,8 (79)
Steep slopes	*Rhus erosa - Rhynchelytrum repens*	8,0 (7)
	R. erosa - Stachys burchelliana	1,1 (1)
	Olea africana - Maytenus heterophylla	1,1 (1)
		Subtotal 10,2 (9)

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and no porcupines were recorded within the riverine communities.

Application of DeLury's method (Caughley 1977) to the standardised data set on the number of porcupines killed per unit effort resulted in a density of 176,6 porcupines/km^2 (Table 29). This high estimate was due to the poor relationship (r^2 = 0,31) between the variables used to estimate catchability (see Table 29).

Density was estimated at 29,9 porcupines/km^2 in foraging areas when using the method described by Caughley (1977) for transects of indefinite width and data obtained during transect surveys conducted between September 1981 and July 1982. The applicability of this method of analysis to the data set was ascertained by the significant (r^2 = -0,82; $p < 0,001$) linear relationship between the number of porcupines seen ($\log_{10}$) per distance interval and the midpoints of these intervals (Fig. 37).

The probability of seeing a porcupine within the beam of a spotlight while driving at 20 to 25 km/h decreased exponentially with an increase in distance from the transect line (Fig. 38). Mean sighting distance was 23,9 m and maximum sighting distance, calculated through regression analysis as suggested by Caughley (1977) was 87,6 m.

Social organisation

Free-ranging porcupines

Most (89,3%; n = 95) porcupines encountered on the TdR Game farm while

foraging ..... /

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TABLE 29. Estimating the size of the porcupine population on the TdR Game Farm by Delury's method.

Sampling period	Previous effort (km)	Number of porcupines killed/km (x 100)	$\log_{10}$ porcupines killed/km (x 100)
1	0	7,83	0,89
2	332,0	9,36	0,97
3	556,4	8,51	0,93
4	779,7	10,16	1,01
5	996,3	8,04	0,91
6	1 270,1	2,44	0,39

b = -0,00030.

$1 - p$ = 0,99931.

C = 118

N = 176,6 porcupines/km^2.

Population size was estimated as $(N) = \frac{C}{1 - (1 - p)} n$ where $1-p$ = antilog$_{10}$ b and b = the slope of the linear regression line relating porcupines killed/km to effort expended prior to a given sampling period. n = the number of units of effort and C = the total number of porcupines killed/km x 100 (See Caughley 1977).

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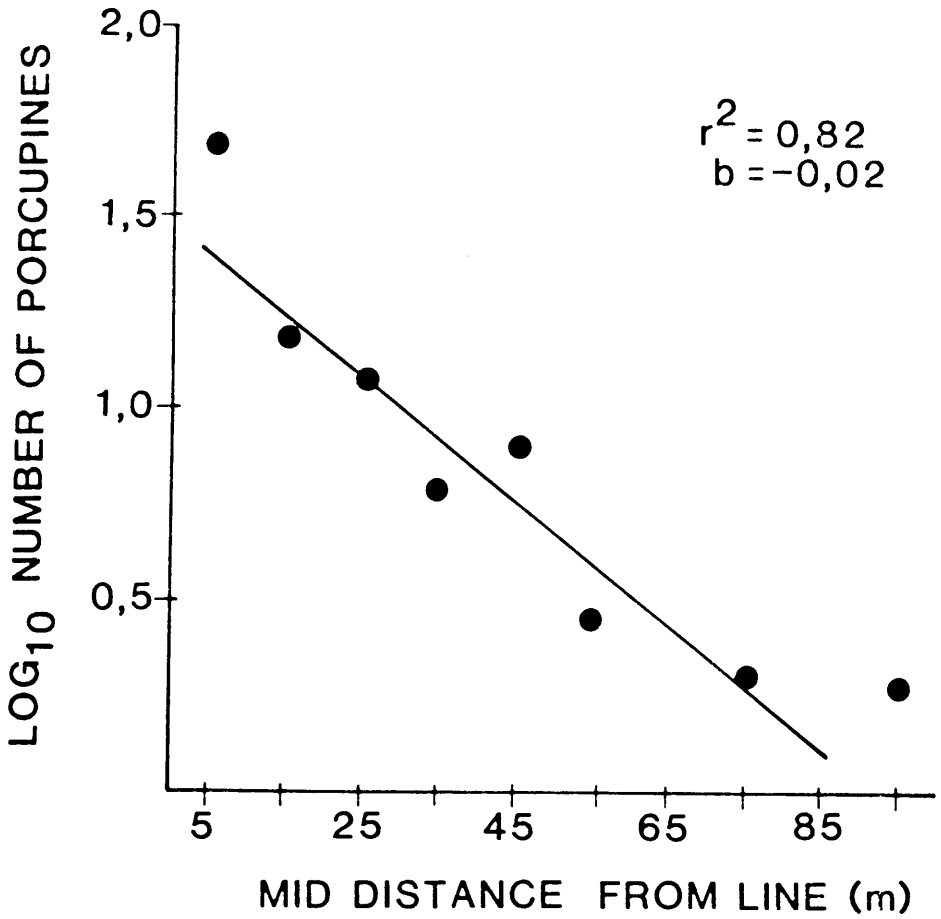

FIG. 37. The relationship between the number of porcupines seen (log_{10}) and the distance from the route followed at 20 to 25 km/h on the TdR Game Farm. The line was fitted through least square regression analysis.

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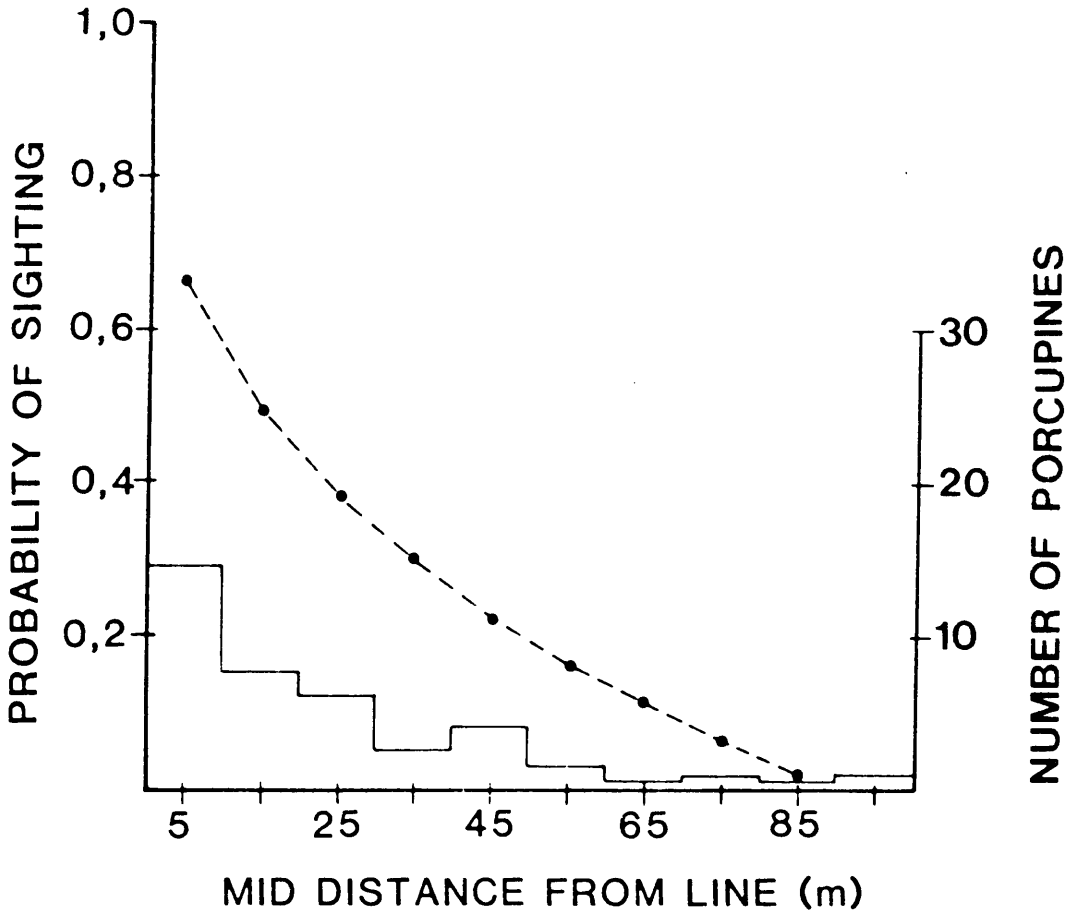

FIG. 38. The probability of seeing a porcupine at varying distances from a route driven at 20 to 25 km/h on the TdR Game Farm.

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foraging were solitary. Groups comprising two individuals were seen on seven occasions while three individuals foraging together were seen twice only. Three of the seven pairs comprised of one adult male and one adult female (three of these being pregnant) while other pairs comprised an adult male and a juvenile 2,5 to 5,5 months of age as estimated by the relationship between body weight and age (see Fig. 9; Chapter 3). Both groups of three comprised an adult male, adult female and one juvenile and all males encountered in these groups were at least 24 months of age (dental age class VII - VIII; see Chapter 3). Juveniles, however, were encountered alone at a minimum age of 2,5 months (body weight 3,1 - 3,2 kg).

Groups of porcupines trapped together at the same burrow system elsewhere comprised an adult male and adult female (n = 4), an adult male and juvenile (n = 3), juveniles only (n = 2) and an adult male, adult female and juvenile (n = 2).

Captive porcupines

Only one of the two females housed with an intact male in the same group (n = 4) reproduced over a two-year period of observation. This was also the case where three females were kept with one intact adult male (n = 2). In two cases where two adult females were kept with two adult males, both females reproduced. All these females cycled regularly and the number of reproducing females within a group was related to the number of adult males present within the group.

None of the three females kept in their natal groups up to the age of three years reproduced, in spite of regular cyclic ovarian activity.

Two ..... /

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Two of them reproduced within six months after being separated from their natal group.

Fecundity

Based on extrapolated information obtained by determining fetal age, the birth season was defined as the eight month period from August to March with a peak in January. Mean date of birth was calculated as 21 December with a standard error of 18,6 days.

Litter size at birth for the free-ranging population on the TdR Game Farm was unknown but prenatal litter size for this population was similar to that recorded for litter size at birth in the captive population ($\bar{x}$ = 1,50 ± 0,66; n = 165; see Chapter 4). Sex ratio at birth did not deviate from unity (see Chapter 4). Juvenile, subadult and adult sex ratios also did not differ from unity (χ^2 = 0,67; 1,52; 0,23 respectively).

The mean annual incidence of pregnancy (Caughley 1977) for the population on the TdR Game Farm was 1,19 suggesting that free-ranging adult females produce one litter per year (n = 12).

Age specific fecundity schedules (m_x) based on the information given above and the frequency of occurrence of reproductively active (pregnant or lactating) females differed because fewer young females (< 24 months of age) were reproductively active during 1977/78 than during 1981/82 (Table 30). None of the females > 6 months < 12 months collected during 1977/78 were reproductively active while 75,0% of these females reproduced during 1981/82. The calculated number of

TABLE 31 ..... /

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TABLE 30. Age specific fecundity schedules for the porcupine population on the TdR Game Farm based on the assumption that litter size at birth equals litter size in captivity.

Age (months)	Percentage reproductive activity during breeding season		Female births per female per season (m_x)	
	1977/78	1981/82	1977/78	1981/82
>0 ≤ 6	0,00	0,00	0,00	0,00
>6 ≤ 12	0,00	75,00	0,00	0,56
>12 ≤ 24	63,60	88,90	0,48	0,67
>24	88,20	95,70	0,66	0,72

TABLE 31. Sex specific age structures for the 1977/78 and 1981/82 porcupine populations as reflected by subsamples culled on the TdR Game Farm.

Age (months)	Number of porcupines culled			
	1977/78		1981/82	
	Males	Females	Males	Females
>0 ≤ 6	6	5	22	18
>6 ≤ 12	11	5	9	4
>12 ≤ 24	10	5	8	9
>24	23	15	26	22
	$\frac{2}{3} = 0,74$		$\frac{2}{3} = 1,51$	

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female births per female for females > 12 months of age was also higher during 1981/82 than during 1977/78 (Table 30).

In considering the age structures of the female segment of the popula= tion (see Table 32) and age specific fecundity schedules (Table 31) it became evident that during 1977/78 females older than six months produced 0,49 female offspring per female per year while the 1981/82 population produced 0,69 female offspring per female per year.

Age structure

The standing age distribution for male and female segments of the 1977/78 as well as the 1981/82 populations did not differ significant= ly from each other (χ^2_3 = 0,74 & 1,51 respectively; Table 31). The data for the sexes therefore were combined, these indicating that the standing age distribution, based on the nine dental age classes distinguished (see Chapter 3) for the 1977/78 population, differed significantly (χ^2_7 = 21,48; $p < 0,001$) from that of the 1981/82 population.

A reduction of these dental age classes to four chronological age classes, based on the sequential pattern of tooth replacement and wear (see Chapter 3), substantiated the significance in difference between the age structures of these subsamples (χ^2_3 = 10,77; $p < 0,05$). A reduction to year classes (0 - 12, 12 - 24, 24 months) however, masked this difference, suggesting that the age structures of the two subsamples were similar (χ^2_2 = 1,89). This implies that the differences outlined above may be due to sampling bias resulting from differences in time specific sampling intensity, enhanced by the

effects ..... /

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effects of seasonal breeding on the standing age distribution.

Age composition of the 1977/78 and 1981/82 population changed seasonally and differed considerably for each period, with the biphasic pattern in the presence of porcupines less than 12 months of age during 1977/78 not being evident during 1981/82 (Fig. 39). Percentage contribution of the first year age class ($>2 \leq 12$ months) varied from 14,3 to 56,5% ($\bar{x}$ = 32 ± 16,9%; n = 6) during 1977/78 and from 42,0 to 55,5% ($\bar{x}$ = 46,2 ± 8,5%; n = 6) during 1981/82. The 1977/78 population thus tended to be 'older' than the 1981/82 population as a result of the presence of more young animals ($>0 < 6$ months) in the latter, perhaps due to sampling in the previous period.

Survival and Mortality

Age specific probability of survival (l_x), probability of dying (d_x) and mortality rates (q_x) for the first two years of life were calculated following Caughley (1977). Based on the assumption of a stable age distribution, this analysis suggests that mortality rate of newborn porcupines up to the age of two months, was higher during 1977/78 than during 1981/82 (Table 32; body weight for age data suggests that porcupines entering the second age class were all older than two months).

Mortality rate during the first year of life, however, was higher during 1981/82 than during 1977/78. Considering the median age of each age class, these mortality figures (see Table 32) reflect mortality during the first six months of life.

FIG. 39 ...../

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FIG. 39. Seasonal changes in the age structures of the porcupine population on the TdR Game Farm as reflected by subsamples collected between February 1977 and January 1978 (n = 82) and between September 1981 and July 1982 (n = 118).

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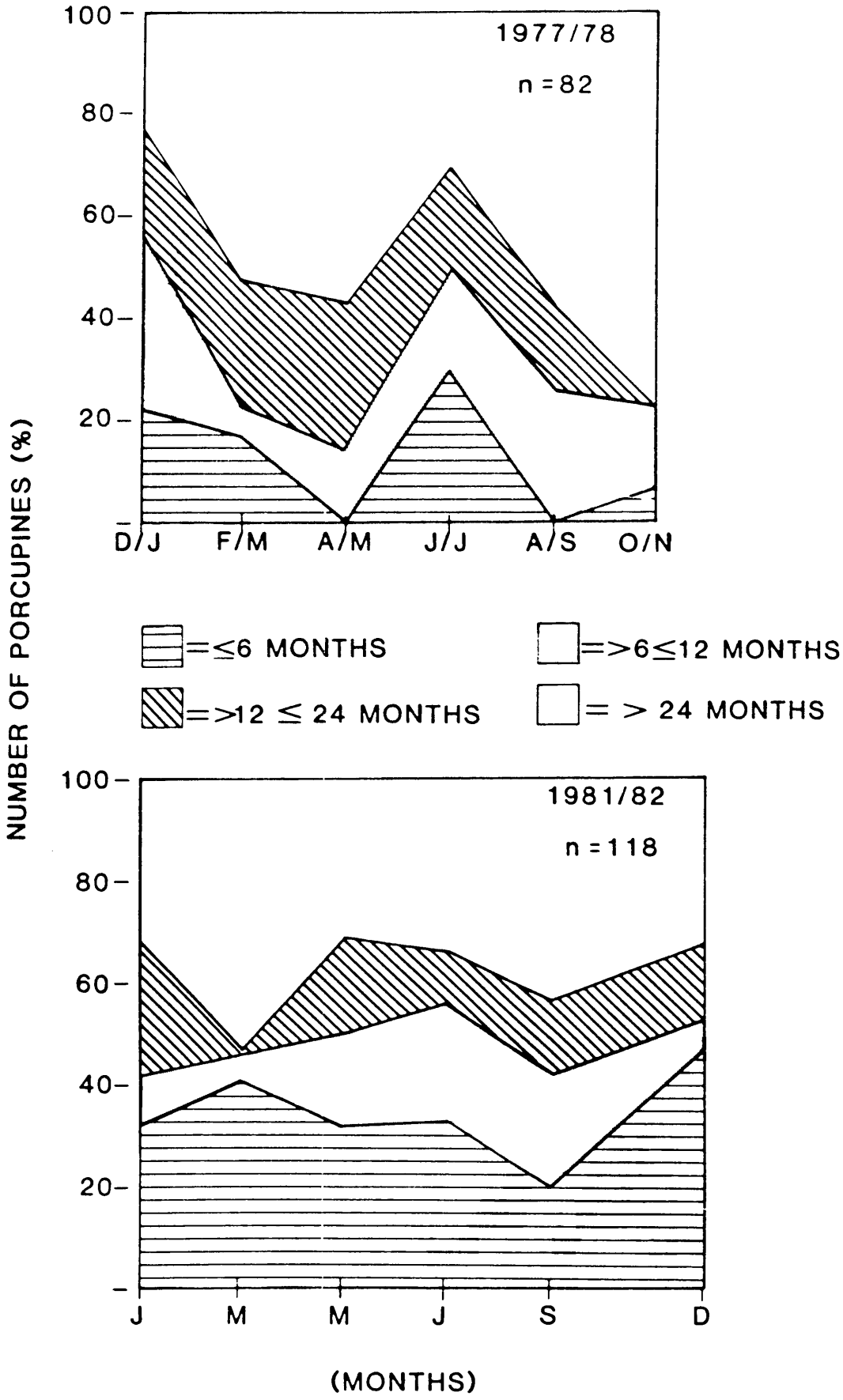

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TABLE 32. Age specific probability of surviving (1_x), dying (d_x) and mortality rate (q_x) for the 1977/78 and 1981/82 porcupine populations based on the assumption that the standing age distribution equals temporal age distribution and that the rate of increase (r) equals 0. (See Caughley 1977 for definitions).

Age (months) (x)	Median age (months) ($x + x + 1/2$)	Frequency* (f_x)		Probability of surviving (1_x)		Probability of dying (d_x)		Mortality rate (q_x)	
		1977/78	1981/82	1977/78	1981/82	1977/78	1981/82	1977/78	1981/82
Newborn	0	32,3**	51,4**	1,000	1,000****	0,164	0,000	0,164	0,000
> 0 ≤ 12	6	27,0	53,0***	0,836	1,000	0,372	0,669	0,445	0,669
>12 ≤ 24	18	15,0	17,0	0,464	0,331	-	-	-	-
>24	24	38,0	48,0	-	-	-	-	-	-

* Age specific sex ratios did not differ significantly and data for males and females therefore were combined.

** Estimated from age specific fecundity schedules and presents the expected number of newborn females within the subsamples.

*** 13,64% of females in this class were reproductively active and m_x thus 0,102.

**** f_x at $x + 1$ larger than at x and 1_x thus 1,000.

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The logarithmic functions described the relationship between the probability of survival (l_x) and age (x) extremely well (r^2 = 0,97 & 0,84 for the 1977/78 and 1981/82 subsamples respectively) and the suggested constant adult survivorship is in agreement with that illustrated for a variety of longlived species (Collett 1981; Silver 1979). Age specific l_x values for the 1977/78 and 1981/82 populations inferred through interpolation from these curves on the assumption that l_{10} equals 0,000, are presented in Figs 40a and b. Probability of survival, based on the assumptions of a stable age distribution, is also presented and the values for the coefficients of determination suggest that the inferred l_x values can be regarded as representative of the real values.

Population growth

Estimation of age specific probabilities of survival did not depend on the age structure; instantaneous growth rates (r_s) based on the survival and fecundity schedules, using the equation $\Sigma l_x e^{-rx} m_x = 1$ and the method described by Caughley (1977), were calculated at 0,0438 (4,38%year) and 0,0977 (9,77%/year) for the 1977/78 and 1981/82 populations respectively.

Calculation of theoretical life tables

Stable age distribution (S_x) and the resulting mortality schedules of the populations were calculated as suggested by Caughley (1977), where $S_x = l_x e^{-rx}$, $d_x = S_x - S_{x+1}$, and $q_x = d_x/S_x$. Age specific probability of survival (l_x), as suggested by the logarithmic models, and as corrected (S_x) considering growth rates, probability of dying (d_x)

FIG. 40 ..... /

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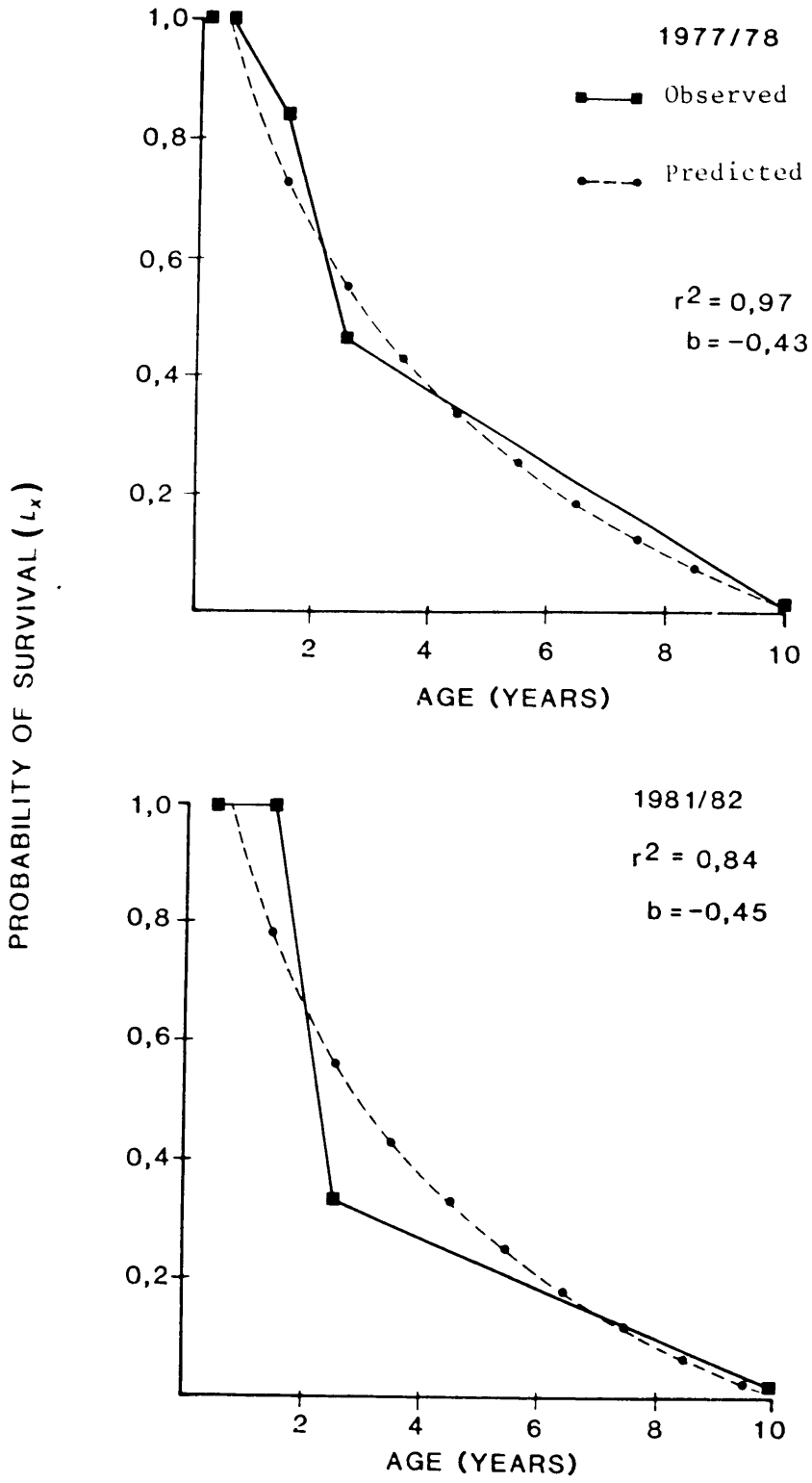

FIG. 40. Age specific probability of surviving (l_x) for the 1977/78 and 1981/82 porcupine population on the TdR Game Farm based on the assumption that r =0 and l_{10} = 0,00. Curves were fitted through nonlinear least square regression analyses.

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and age specific mortality rates (q_x) for the 1977/78 and 1981/82 populations are presented in Table 33.

It is important to note that in spite of differences in growth rate age specific mortality rates (q_x) were very similar for the two subsamples, being relatively low during the first five years of life, thereafter increasing rapidly to attain peak values at the age of ten years.

Nett reproductive rate

Nett reproductive rate (measurement of the average number of female offspring produced by each female during her entire life-span) was calculated at 1,21 and 1,43 using the equation $R_O = \Sigma l_x m_x$ (Elseth& Baumgardner 1981) and the m_x equals values given in Table 31, assuming that m_3 to m_{10} equals 0,66 and 0,72 for the 1977/78 and 1981/82 subsamples respectively.

A graphic presentation of age specific $l_x m_x$ schedules for these two subsamples suggests that the difference in nett reproductive rates results from an earlier age at first reproduction in the 1981/82 subsample. Reproductive rate furthermore is a function of survival rather than a change in fertility (Fig. 41).

Generation time

In considering $T_c = \frac{1}{R_o} \Sigma x m_x l_x$ as a measure of generation time which represents the average reproductive age of females (Elseth & Baum= gardner 1981), this statistic has been calculated as 4,14 and 3,73 for

TABLE 34 ..... /

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TABLE 33. Theoretical age specific probability of survival (1_x), corrected age specific probability of survival (S_x), probability of dying (d_x) and mortality rate (q_x) for the 1977/78 and 1981/82 porcupine populations inhabiting the TdR Game Farm. (See text for explanations).

	Probability of survival (1_x)		Corrected probability of survival (S_x)		Probability of dying (d_x)		Mortality rate (q_x)	
Age (x)	1977/78	1981/82	1977/78	1981/82	1977/78	1981/82	1977/78	1981/82
0	1,000	1,000	1,000	1,000	0,303	0,325	0,303	0,325
1	0,728	0,744	0,697	0,675	0,190	0,215	0,273	0,319
2	0,553	0,559	0,507	0,460	0,132	0,140	0,260	0,304
3	0,428	0,429	0,375	0,320	0,096	0,098	0,256	0,306
4	0,332	0,328	0,279	0,222	0,076	0,072	0,272	0,324
5	0,253	0,245	0,203	0,150	0,060	0,053	0,296	0,353
6	0,186	0,175	0,143	0,097	0,049	0,039	0,343	0,402
7	0,128	0,114	0,094	0,058	0,040	0,030	0,426	0,517
8	0,077	0,061	0,054	0,028	0,032	0,023	0,593	0,821
9	0,032	0,013	0,022	0,005	0,022	0,005	1,000	1,000
10	0,000	0,000	0,000	0,000	-	-	-	-

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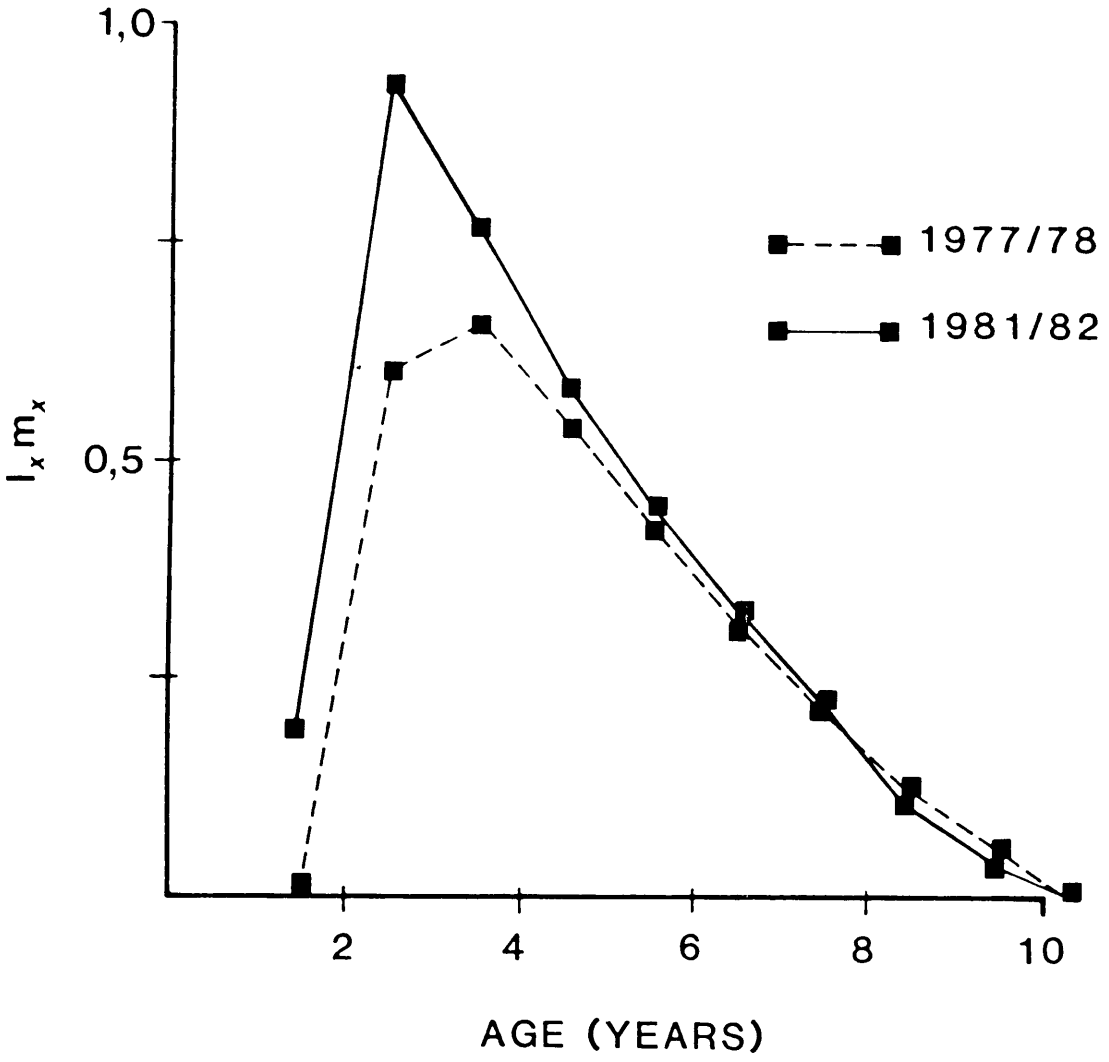

FIG. 41. Age specific changes in $l_x m_x$ values for the porcupine population on the TdR Game Farm, illustrating that adult reproductive rate is a factor of survival rather than a change in fecundity rate. (See Elseth & Baumgardner 1981).

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the 1977/78 and 1981/82 populations respectively. This confirms that the average reproductive age in 1981/82 was less than during 1977/78.

DISCUSSION

Porcupines are widely distributed over the Southern African Subregion (Smithers 1983) and in being nocturnal and apparently catholic in their feeding habits, have a wide ecological tolerance. Under natural conditions they are known to shelter and breed in rock crevices, caves and abandoned aardvark *Orycteropus afer* burrows which they may modify through further active burrowing.

Constraints on the use of 'nonselective removal methods' to estimate density have been outlined by Caughley (1977) and the lack of linearity in the regressions used to estimate catchability indicates that the probability of encountering porcupines during each sampling period was not constant. This lack of constancy is probably due to the effects of climatic factors, such as temperature on foraging activities.

Application of DeLury's method to the data set available for density estimates resulted in a relatively high estimate (176,6 porcupines/ km^2) which, as a result of the time interval (ten months) between the first and last sampling period and inconsistencies in catchability, cannot be regarded as reliable.

The application of methods designed to estimate density from data sets collected during transect surveys of indefinite width, resulted in density being estimated at 29,9 porcupines/km^2 in foraging areas

(predominantly ...../

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(predominantly *Chrysocoma tenuifolia - Lessertia pauciflora* and *C. tenuifolia - Polygala leptophylla* communities). This estimate should be treated as an index of density and the available information precludes speculation on its accuracy. It is however of interest to note that in terms of biomass (350 kg/km^2) this estimate is very similar to that reported for the paca (New World hystricomorph) in Colombia (340 kg/km^2; Collett 1981).

The inability to group individuals older than 24 months into discrete chronological age classes hampered the calculation of a full life table on the basis of the age structure of the population. The need to estimate population statistics (based on demographic parameters) of importance in understanding the reproductive strategy of the porcupine and to set management policies for the population, required the development of a method to assign survival rates to all age classes.

The development of such a method or model, either for descriptive or predictive purposes based on real data and realistic assumptions, obviously would have shortcomings but would permit predictions and conclusions which cannot, as stated by Elseth & Baumgardner (1981) 'be equalled by mere verbalisation'.

In spite of several shortcomings in the original data set, the calcu= lation of age specific fecundity and survival rates for porcupines less than 24 months of age, based on the assumption of stability in age structure, also assisted in explaining the reaction(s) of the porcupine population towards an artificial reduction in density. This is complimented by the statistics derived independently from the frequency distribution of ages in the population.

Before ..... /

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Before considering the interrelationship between the calculated population statistics, the environment and the social organisation of porcupines, it should be recalled that a change in survival rates or age specific fecundity schedules will affect the prevailing stable age distribution, which would then converge to another stable form, the latter being appropriate to the 'new' survival and fecundity schedules. Obviously this would affect the population's rate of increase when defined in terms of age specific probability of survival and fecundity.

Thus it is assumed that the age structure of the 1981/82 population reflects an age distribution converted to a stable form different from that of the 1977/78 population, due to disturbances inflicted by the artificial reduction of the population during 1977/78. Differences in age specific probability of dying and mortality rates (Table 32) for subadult porcupines thus are attributed directly to the culling operation between February 1977 and January 1978, with the probability of subadult mortality during 1981/82 being higher than during 1977/78. The higher first year mortality rate during 1981/82 than during 1977/78 can not be explained from the information presently available.

Age specific fecundity rates apparently were affected also by the artificial reduction in density (see Table 30) with reproductive activity commencing at an earlier age during 1981/82 than during 1977/78. Reproductive activity in captivity is limited by social factors with the number of reproducing females per group being a factor of the number of adult males present in the group. No females kept within their natal group, even up to the age of three years,

reproduced ..... /

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reproduced, and an inability to disperse as a result of high density may conceivably explain the earlier age at first reproduction following the artificial reduction in density. Difference in adult fecundity rate is a factor of more reproductively active females in the 1981/82 subsample than in the 1977/78 subsample, a difference which may also be explained in terms of an inability to disperse due to high densities.

These differences in fecundity rates resulted in the estimated rates of population increase differing considerably, this being approximately 9,8% per year during 1981/82, compared to 4,4% per year during 1977/78. This reaction is reflected also in the differences in the nett reproductive rate and generation intervals calculated for the two subsamples as substantiated by the presence of more young porcupines in the 1981/82 than in the 1977/78 subsample (see Fig. 39).

To summarise this analysis it is possible that one of the most important reactions of this population towards a reduction in density was an increase in growth rate through a change in reproductive rate. This resulted primarily from shortening the age to puberty probably due to a relaxation of social factors which usually inhibit reproductive activity.

Although the exact values of these statistics may not be reliable, it is believed that the differences observed for the two independent subsamples through equal treatment, provide an insight into the reaction(s) of individuals within a population towards changes in their environment.

Porcupines ...../

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Porcupines live in extended family groups where each group comprises at least an adult male, one adult reproducing female and a varying number of siblings, all of these contributing to the postnatal care of the youngest litter. Observations on captive porcupines indicate that they are monogamous, with the pairbond system being enhanced through the independence of sexual behaviour on the female's reproductive condition. Males actively protect young against intruders and the protection afforded through accompanying the young during foraging excursions during the first five months of life conceivably enhances survival of juveniles. This is reflected in the high juvenile survival rate up to the age of six months with 33,1 to 55,5% of newborn individuals attaining an age of 12 months. (These estimates were based on fecundity schedules and may therefore be underestimates of actual survival rates.)

High first year survival, as a result of the dependence of growth rate on survival and fecundity schedules, would counteract the effect(s) of low fecundity rates and thus would enable porcupines to maintain a relatively high population growth rate when required (i.e., high predation pressure on artificially induced mortality).

Considering the calculated population statistics it would appear that the life-history strategy of the porcupine can be explained in terms of a low fecundity rate, low age at first reproduction, an extended period of reproductive activity and high first year survival, these being in agreement with observations on ungulates in general but different from observations on most rodent species (Collett 1981).

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CHAPTER 7

CONCLUSIONS

LIFE-HISTORY STRATEGIES

The relationship between habitat, ecological strategies and population parameters can be explained in terms of r- and K-selection (Pianka 1970; 1972) and this approach features prominently in the analysis of life-history tactics (Stearns 1976). K-selection is geared towards the efficient use of environmental resources and favours interoparity, an extended life-span, delayed sexual maturity, small litters, large body size and intensive parental care (Pianka 1970).

Many life-history parameters arise as a consequence of body size (such as gestation length, growth rate, life-span and litter weight) and according to Western (1979)should be distinguished from those varying between populations and according to environmental circumstances.

In being a relatively large rodent (largest in Africa) with a long gestation period, small litter size and a long life-span (see Chapter 4), porcupines may be considered K-strategists. This is supported by the analysis of the demographic characteristics of the free-ranging population studied during the present investigation (see Chapter 6), which suggests that density is regulated by the dependence of repro= ductive activity on social factors. Other reproductive attributes, such as the extended lactation period, low offspring adult weight ratio and intensive parental care, suggest a reproductive strategy that involves a large parental investment in a small number of

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offspring (see Chapter 4), predicting a high chance of survival of each offspring, which may also be considered indicative of K-selection. (The high probability of first year survival is supported by the information in Chapter 6).

This life-history strategy is in agreement with the strategies described for other porcupines (Gosling 1980) and for the paca (Collett 1981) but differs from that of the capybara *Hydrochoerus hydrochaeris* (Ojasti 1973 in Collett 1981) and the cane rat (Asibey 1974), with both species producing large litters and experiencing a high infant mortality rate.

COMPARISON WITH OTHER HYSTRICOMORPHS

The outstanding reproductive features of the porcupine (long gestation period, long oestrous cycle, the presence of a vaginal closure membrane, the lateral position of the nipples, inguinal testes, the presence of a sacculus urethralis) are similar to those regarded as diagnostic of hystricomorph rodents (Weir 1974) and thus provides additional evidence that the Old World hystricomorphs and New World caviomorphs are related through a common ancestor. This is also supported by the presence of accessory luteal bodies and the high levels of progesterone-binding plasma proteins during pregnancy, which, as has been reported for New World species (Heap *et al.* 1981), results in extremely high levels of circulating progesterone during pregnancy. Furthermore, this supports the hypothesis of Weir & Rowlands (1973) that the suborder Hystricomorpha is homogenous and should not be subdivided into Hystricomorpha (Old World species) and Caviomorpha (New World species).

MANAGEMENT ..... /

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MANAGEMENT IMPLICATIONS

Porcupines survive in spite of intensive modifications of their natural habitats throughout the Southern Africa Subregion. Their catholic feeding habits result in their being regarded as agricultural pests and their habit of ringbarking a variety of tree species has resulted, as was motivated for culling in the present study, in the decision to artificially reduce their numbers.

The data and analysis presented here, however, suggest that porcupine numbers are regulated through social factors affecting reproductive activity and that an artificial reduction in density results in an earlier age at first reproduction, which will promote an increase in population growth rate.

This reaction of a K-selected species conceivably operates to maintain numbers at an asymptotic level. Thus it should be appreciated that an attempt to reduce population numbers artificially, would be followed by a relatively rapid recovery in numbers through an increase in the nett reproductive rate of the young component of the population (see Chapter 6), which through continual attempts to reduce density, will result in a destabilisation of the age structure of the population. This conceivably would favour an even higher rate of population increase, which, when attempts to reduce density are culminated, will result in the population exceeding the carrying capacity of its habitat, with subsequent degradation.

Problems of the kind encountered on the TdR Game Farm may be ascribed to the absence of natural predators of porcupines, but it is believed

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that the age structure established without disturbing density and lowered fecundity maintained through the effects of social factors on reproductive activity, favoured a stabilised population growth rate. It has been shown that porcupine activity, through their habit of digging for food, benefits seed germination (Gutterman 1983) and that their presence may thus be required to maintain stability within an ecosystem.

The high density of porcupines in agriculturally developed areas may also be ascribed to the absence of natural predation but an artificial increase in carrying capacity through the cultivation of cereal and other crops may be of greater importance. High densities may also be due to continual 'low-key' nonselective artificial predation through incidental hunting which can stimulate reproductive rate. Alkon *(in litt.)* recently illustrated that Indian porcupines *H. indica* damage less than 1,0% of potato crops and concentrate their activities on the outer rows of potato fields, thus not being as destructive as believed by local inhabitants.

All this confirms that a specific artificial change to a natural system will affect components of that system, often detrimental to the ecosystem as a whole, and that decisions, for instance, to reduce porcupine numbers, should be based on research results rather than 'abdominal biology'.

It is believed that the porcupine population on the TdR Game Farm should be allowed to reach an asymptote which would be self-regulating for density. If this is undesirable, reduction in density should not be based on incidental hunting but on properly planned culling

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operations based on principles of harvesting (Caughley 1977) and the information presented in this thesis.

SUMMARY ...../

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SUMMARY

The study was based on information obtained from porcupines *Hystrix africaeaustralis* kept in captivity at the University of Pretoria and on material and data collected during culling operations on the Tussen-die-Riviere (TdR) Game Farm.

Porcupines on this Game Farm foraged predominantly in the *Chrysocoma tenuifolia - Lessertia pauciflora* and *C. tenuifolia - Polygala leptophylla* communities of the flat and gently sloping areas and density during 1981/82 was estimated at 29,9 porcupines/km^2. Established age determination techniques such as counts of cementum lines, counts of periosteal lines, age-related changes in eye lens weight, and changes in tooth dimensions due to attrition, were not applicable to the study material as a result of variability. Consistency in the age at which maxillar molars erupted and premolars were replaced as well as the pattern of attrition of the occlusal surfaces of teeth in the maxillar toothrow, provided a method for distinguishing nine dental age classes. Chronological age, based on observations on captive porcupines, could be assigned to six of these.

Prenatal growth rate, based on a modification of the Huggett & Widdas (1951) equation, was higher (specific fetal growth velocity = 0,1047) than that recorded for several other hystricomorph rodents but within the limits recorded for this suborder as a whole. Postnatal growth has been described by fitting a von Bertalanffy growth curve to information collected from captive porcupines over the first two years of life. Porcupines were fully furred and precocial at birth and then weighed 300 to 440 g ($\bar{x}$ = 351,1 ± 47,3 g; n = 19). Growth over the

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first 20 weeks of life was approximately linear and asymptotic body weight ($\bar{x}$ = 11,7 ± 0,01 (S.E.) kg) was attained at an age of 52 weeks. Lack of sexual dimorphism in body dimensions could be explained on the grounds of the mating system and intensive parental care provided by both parents. The high rate of postnatal growth was ascribed to the extended lactation period ($\bar{x}$ = 100,6 ± 37,8 days; n = 9).

Age at sexual maturity of captive females varied from 9,0 to 18,1 months ($\bar{x}$ = 13,6 ± 3,9; n = 5) and were affected by immobilisation. Females held in captivity were polyoestrous and those kept in contact with an adult male cycled throughout the year. Direct contact between males and females was required to maintain cyclic ovarian activity, and sexual activity, occurring throughout the cycle, is apparently of importance in maintaining the pairbond.

The length of the oestrous cycle varied from 17 to 42 days ($\bar{x}$ = 31,2 ± 6,5; n = 43) and oestrus was characterised by the perforation of the vaginal closure membrane, which coincided with a peak in oestradiol-17β secretion, with values then ranging from 25 to 176 pg/ml plasma. The oestradiol-17β surge was followed by copulation two to eight days after perforation of the vaginal closure membrane. Circulating levels of plasma progesterone increased slowly thereafter and attained peak values (3,2 - 9,0 ng/ml) midway through the cycle. The long cycle is ascribed to the extended luteal phase, varying from 21 to 35 days in length.

Lactation suppressed cyclic ovarian activity and adult females experienced three to seven cycles after the end of lactation before conceiving, with progesterone levels at oestrus followed by conception

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($\bar{x}$ = 3,2 ± 1,0 ng/ml; n = 3) being significantly (t_7 = -4,73; $p <$ 0,01) higher than those during 'sterile' oestrous periods.

The relatively long gestation period (93 - 94 days) was characterised by low levels of progesterone (approximately 20 ng/ml) until Days 25 to 30 *post coitum* and the rapid increase until Days 42 to 60 *post coitum* to peak values ranging from 102 to 108 ng/ml was accompanied by an increase in progesterone-binding plasma protein (PBPP) and oestradiol-17β levels. The latter attained higher values then than during the oestrous cycle. Steroid hormone levels fluctuated widely during pseudopregnancy.

Litter size in captivity varied from one to three ($\bar{x}$ = 1,50 ± 0,66; n = 165) and milk consumption increased from 218 ml/day on Day 22 *post partum* to 323 ml/day on Day 43 *post partum*.

The tendency towards seasonal breeding in captivity reduced the role of nutrition as a mediator on reproductive activity and seasonal breeding in the free-ranging population on the TdR Game Farm has been influenced in all probability by the extended lactation period followed by sterile oestrous cycles for which the underlying physiological mechanisms are still unclear. This was confirmed by the litter interval ($\bar{x}$ = 385 ± 160,4 days; n = 10) observed in females held in contact with adult males in captivity.

Males were reproductively active throughout the year and attained physiological sexual maturity at an age of 8,1 to 18,0 months. A tendency towards seasonality in the activity of accessory glands, preceded and accompanied by an increase in plasma testosterone levels,

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may be implied as enforcing seasonal breeding in females.

Age specific fecundity schedules and juvenile survival in the population on the TdR Game Farm was affected apparently by the artificial reduction in density during the 1977/78 culling operation,resulting in a doubling (4,3 *viz.* 9,8% per year) in the estimated rate of population increase. Considering the social organisation of porcupines, it is suggested that porcupine numbers are regulated through density dependent factors affecting age specific reproductive and survival rates.

The reproductive characteristics of the porcupine are similar to those described as diagnostic of the New World caviomorphs, and their life-history strategy can be described in terms of K-selection. Artificial reduction in density through its effect(s) on population demographic variables is considered undesirable and a plea is made to allow populations to be regulated by density dependent factors.

OPSOMMING ..... /

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OPSOMMING

Die studie is gebaseer op inligting en materiaal wat verkry is van ystervarke *Hystrix africaeaustralis* wat in gevangeskap by die Universiteit van Pretoria aangehou is en van wilde ystervarke wat gedurende twee uitdunningsprogramme op die Tussen-die-Riviere (TdR) Wildsplaas versamel is.

Ystervarke op die Wildsplaas voed hoofsaaklik in die *Crysocoma tenuifolia - Lessertia pauciflora* en *C. tenuifolia - Polygala leptophylla* gemeenskappe van plat en effens skuins gebiede, en digtheid gedurende 1981/82 was beraam op 29,9 ystervarke/km^2.

Bekende ouderdomsbepalingstegnieke soos tellings van sementlyne, tellings van periosteale lyne, ouderdomspesifieke veranderinge in ooglensgewig en veranderinge in tandafmetings weens slytasie, was as gevolg van variasie nie toepasbaar op die studiemateriaal nie. Die konstante ouderdom wanneer die maksilêre kiestande sny en die premolares verplaas word, sowel as die verweringspatroon van die maal= oppervlakte van die kiestande, het 'n metode gebied om nege dentale ouderdomsklasse te onderskei. Gebaseer op waarnemings op ystervarke wat in gevangeskap aangehou is, kon werklike ouderdom aan ses van hierdie klasse toegeskryf word.

Prenatale groeitempo is bepaal deur 'n aanpassing van die Huggett & Widdas (1951) formule en was hoër (spesifieke fetale groeitempo = 0,1047) as die waarde bepaal vir meeste ander hystricomorphe knaagdiersoorte, maar binne die beperkinge bepaal vir die suborde as 'n geheel.

Postnatale ..... /

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Postnatale groei is beskryf deur die Von Bertalanffy-groeikromme deur gebruik te maak van inligting wat van ystervarke vanaf geboorte tot op 'n ouderdom van twee jaar verkry is. Ystervarke is ten volle behaard en prekosiaal met geboorte wanneer hulle 300 tot 400 g ($\bar{x}$ = 351,1 ± 47,3; n = 19) weeg.

Groei gedurende die eerste 20 weke na geboorte is byna liniêr en asimptotiese liggaamsgewig (11,7 ± 0,01 (standaard fout) kg) is op 'n ouderdom van 52 weke bereik. Die afwesigheid van geslagsdimorfisme het bygedra tot die verklaring van die paringsisteem en die intense ouerlike versorging waaraan beide ouers deelneem. Die hoë tempo van postnatale groei word, onder andere aan die verlengde laktasie tydperk ($\bar{x}$ = 100,6 ± 37,8 dae; n = 9) toegeskryf.

Wyfies wat in gevangeskap gebore is, het geslagsrypheid op 'n ouderdom van 9,0 tot 18,1 maande ($\bar{x}$ = 13,6 ± 3,9; n = 5) bereik en geslagsrypheid was deur immobilisering beïnvloed. Wyfies wat in gevangeskap aangehou is, was poli-estrus en die wat in kontak met volwasse mannetjies aangehou is, het estrus regdeur die jaar ondervind. Direkte kontak tussen mannetjies en wyfies was noodsaaklik vir die onderhoud van sikliese ovariale aktiwiteite. Geslagsgedrag was nie afhanklik van die voortplantingstatus van die wyfie nie en is waarskynlik van belang vir die onderhoud van die paringsisteem.

Die lengte van die estrussiklus het vanaf 17 tot 42 dae ($\bar{x}$ = 31,2 ± 6,5; n = 43) gevarieer en perforering van die vaginale membraan, met 'n piek in estradiol-17β sekresie (25 - 176 pg/ml plasma) was kenmerkend van estrus. Die estradiol-17β piek is deur paring twee tot agt dae na die opening van die vagina gevolg. Progesteroonvlakke het

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daarna geleidelik toegeneem en maksimum waardes (3,2 - 9,0 ng/ml) halfpad deur die siklus bereik.

Die lengte van die siklus was 'n faktor van die lengte van die luteale fase wat vanaf 21 tot 35 dae geduur het. Die aktiwiteite van die ovariums is deur laktasie onderdruk en wyfies het na die laktasie tydperk drie tot sewe estrusperiodes beleef voor suksesvolle bevrugting plaasgevind het. Progesteroonvlakke gedurende vrugbare estrustydperke ($\bar{x}$ = 3,2 ± 1,0 ng/ml; n = 3) was betekenisvol (t =-4,73; $p < 0,001$) hoër as gedurende steriele estrustydperke.

Die relatiewe lang dragtigheidstydperk (93 - 94 dae) is gekenmerk deur relatiewe lae progesteroonvlakke (ongeveer 20 ng/ml) tot en met Dag 25 tot Dag 30 *post coitum* en die vinnige toename tot Dag 42 tot Dag 60 *post coitum*, met piekwaardes wat vanaf 102 tot 180 ng/ml gevarieer het, was met 'n toename in progesteroonbindende plasma proteïene en estradiol-17 vlakke vergesel. Hormoonvlakke het baie gevarieer gedurende skyndragtigheid. Werpselgrootte het in gevangeskap van een tot drie ($\bar{x}$ = 1,50 ± 0,66; n = 165) gevarieer en melkinname het vanaf 218 ml/dag op 'n ouderdom van 22 dae, tot 323 ml/dag op 'n ouderdom van 43 dae toegeneem.

Die neiging tot seisoenale teling in gevangeskap stel voor dat die seisoensverskynsel nie aan voeding toegeskryf kan word nie. Seisoenale teling in wilde ystervarke is gedeeltelik toe te skryf aan die lang soogtydperk wat deur 'n aantal steriele estrussiklusse gevolg word. Die fisiologiese meganismes wat hierby betrokke is, is nog nie bekend nie. Die lengte van die werpsel interval ($\bar{x}$ = 385 ± 60,4 dae; n = 10) wat by diere in gevangeskap waargeneem is, onderskraag hierdie

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stelling.

Volwasse mannetjies was regdeur die jaar reproduktief aktief en het fisiologiese geslagsrypheid op 'n ouderdom van 8,1 tot 18,0 maande bereik. Die neiging tot seisoenale veranderinge in die aktiwiteite van bygaande kliere, wat voorafgegaan is en geassosieer was met 'n toename in testosteroonvlakke, kan betrokke wees by die verklaring van seisoenale teling in wyfies.

Ouderdomspesifieke vrugbaarheid en die oorlewing van jongelinge in die bevolking wat die TdR Wildsplaas bewoon, is deur die kunsmatige vermindering van digtheid gedurende 1977/78 beïnvloed en het aanleiding gegee tot 'n verdubbeling (4,3 *viz.* 9,7% per jaar) in die groeitempo van die bevolking. Met inagneming van die sosiale stelsel van ystervarke blyk dit dat bevolkingsgetalle deur digtheidsafhanklike faktore gereguleer word weens die invloed van digtheid op ouderdom=spesifieke voortplantings- en oorlewingstempo's.

Die voortplantingskenmerke van die ystervark stem ooreen met die wat as diagnosties vir die Nuwe Wêreld caviomorphe knaagdiere beskou word en die lewenstrategie van die ystervark kan in terme van K-seleksie omskryf word. Die kunsmatige vermindering van digtheid word weens die invloed van digtheid op bevolkingsdemografiese veranderlikes nie ondersteun nie en 'n pleidooi word gelewer om bevolkings toe te laat om hulle getalle self te reguleer.

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