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THERMOREGULATION, HIBERNATION AND REPRODUCTION IN THE SOUTH AFRICAN HEDGEHOG ERINACEUS FRONTALIS

A SMITH

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Thermoregulation, hibernation and reproduction in the South African hedgehog **Erinaceus frontalis** A. Smith

by

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ABSTRACT

The relationship between oxygen consumption (Vo_2), ambient temperature (T_a) and body temperature (T_b) in the South African hedgehog **(Erinaceus frontalis)** was recorded in spring (September- October 1986), autumn (March-April 1987), winter (July-August 1987) and summer (November- December 1987). In spring the hedgehogs were unable to maintain their body temperature at an ambient temperature of 10 °C. At a temperature of 35 °C the body temperature was measured as 40 °C and the animals could not tolerate this high temperature. The lowest mean oxygen consumption measured during the different months ranged from 0.39 ± 0,03 ml $0_2(g.h.)^{-1}$ in autumn to 0,54 ± 0,08 ml $0_2(g.h.)^{-1}$ in summer.

The body mass of the hedgehogs reached a maximum in April and a minimum in August. It appears as if the South African hedgehog has the ability to hibernate. Non-shivering thermogenesis does occur in this species. During July when the ambient temperature dropped to 8 °C the frequency of activity was low. During the following sessions the frequency of activity became increasingly higher.

Aspects of maternal behaviour, growth and development of young from birth to weaning, and dispersal were recorded during three 24-hour observation sessions. The young of the two females studied, spent less time at huddling and suckling and more time alone in the nestbox and walking outside the nestbox with the mother when they reached the age of about 30 days. At an age of 44 days they were weaned. Litter size recorded during this study ranged from 1 - 11 (n = 6).

Seasonal changes in plasma testosterone and plasma progesterone levels during a one year period were determined. From September to January the arculating levels of testosterone were high while low levels were recorded from February to June. Testicular activity resumed at the end of winter when the hedgehogs were still hibernating. The existance of a substance that binds testosterone was confirmed. In the females, cylic ovarian activity started at the end of August. Plasma progesterone levels peaked during September and October. Aspects of the oestrous cycle of the female hedgehog were determined by progesterone levels in urine. These levels showed that the three females studied, had three or more oestrous cycles during the breeding season.

To my parents

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CHAPTER 1

INTRODUCTION AND MOTIVATION

The South African hedgehog **(Erinaceus frontalis)** belongs to the family Erinaceidae. It is distinguished from other families of the Order Insectivora, in that the body is densely covered by spines, by the presence of a vestigial tail, the presence of a relatively small brain cavity and a short pubic symphysis (Smithers 1983). The other families in the order found in the South African subregion, include the shrews (fam. Soricidae) and the moles (fam. Chrysochloridae). Five genera **(Erinaceus, Atelerix, Hemiechinus, Paraechinus, Aethechinus)** have been described in the subfamily Erinaceinae. In the past the status of these genera ranged from recognition of a single genus (**Erinaceus**, Dobson 1882), three genera (**Erinaceus, Hemiechinus and Paraechinus** - see Corbet 1974, 1978; Honacki, Kinman & Koeppl 1982), four genera (**Erinaceus, Hemiechinus, Paraechinus and Atelerix** - see Dorst & Dandelot 1972), to all five as valid genera (Thomas 1918; Cabrera 1925; Allen 1939; Simpson 1945). Robbins & Setzer (1985) compared population samples of the five genera using multivariate statistics on selected cranial measurements. The results of Robbins & Setzer's (1985) statistical analysis, as well as non-mensural characters, distribution, ecology and fossil history, suggest that all five genera are distinct and that all should be recognized.

In the past the single South African species **(frontalis)** has been placed in the genus **Aethechinus** (Allen 1939; Roberts 1951). Ellerman, Morris-Scott & Hyman (1953) placed it under **Atelerix** as a subgenus of **Erinaceus**. Robbins & Setzer (1985) regarded the African hedgehogs as generically distinct from **Erinaceus**. Smithers (1983) referred the South African species to **Erinaceus** but Meester, Rautenbach, Dippenaar & Baker (1986) refered it to **Atelerix**. According to them two subspecies of **Atelerix frontalis** are recognized namely **Atelerix frontalis frontalis** (A Smith, 1831) and **Atelerix frontalis angolae** (Thomas, 1918). Smithers (1971) indicated that neither size nor colouration of these subspecies differ sufficiently to justify the recognition of subspecies. According to Rautenbach (1978) the Namibian and Angolan population appears to be geographically isolated from the south eastern population since no hedgehogs have been recorded between 21° - 24°E. He thus argues that subspecific status are justifiable.

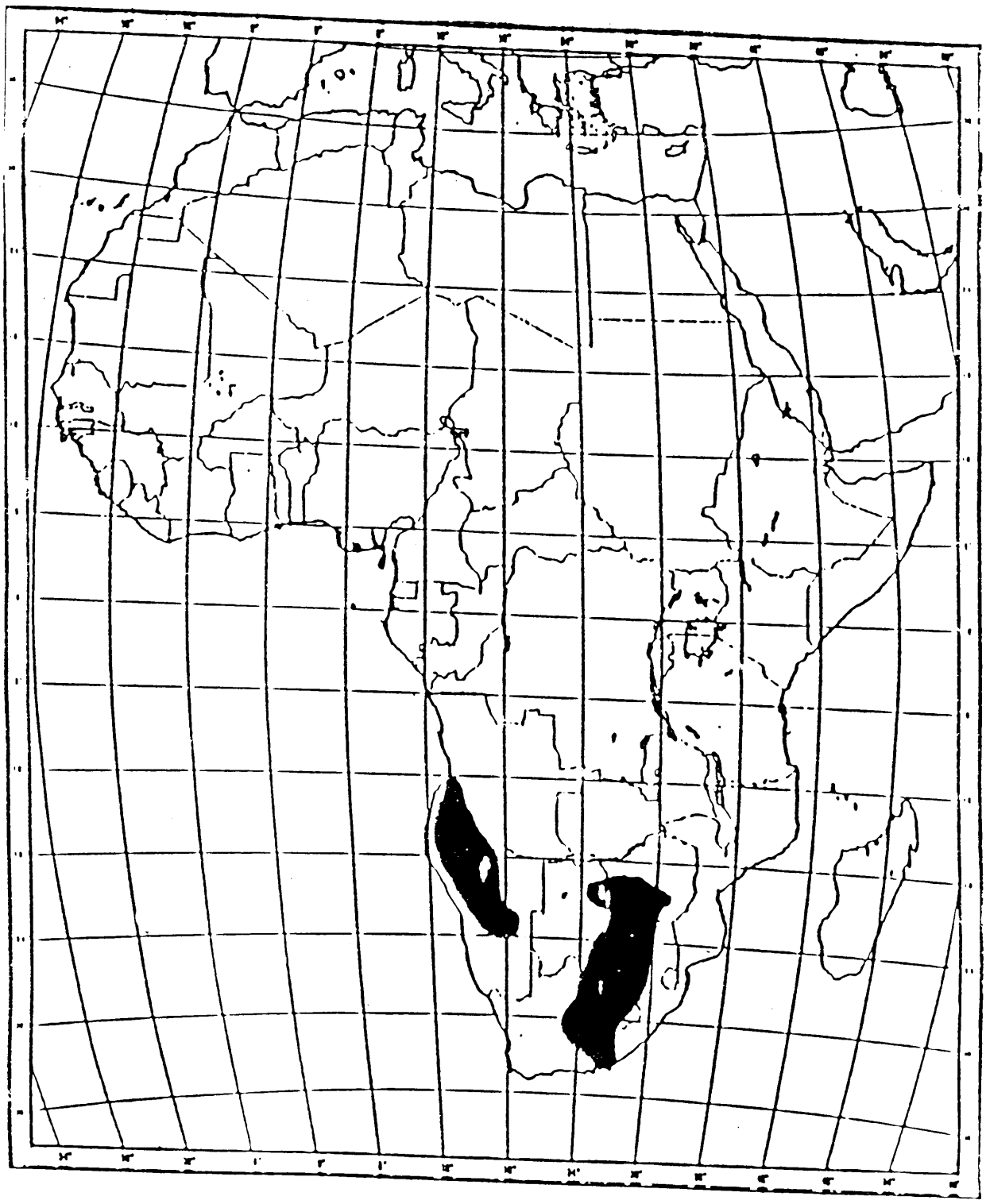

FIG. 1: The distribution of the South African hedgehog (Smithers 1983).

According to Smithers (1983) the South African species **(frontalis)** occurs in parts of the South African subregion and Angola (Fig. 1). In Namibia they occur in the north-western and central parts but not in the Namib desert and the coast. In Botswana they are limited to the eastern parts and in Zimbabwe they are distributed from the western border with Botswana and eastwards to Fort Victoria. In the Transvaal they are limited to the area west of 30°E longitude (Rautenbach 1978; Smithers 1983). They also occur in the Cape Province (except the south west), the Orange Free State, western Natal and the western parts of Lesotho. According to Rautenbach (1978) hedgehogs do not occur in the eastern Transvaal lowveld.

A peculiarity which hedgehogs share with only a few other mammals is their ability to hibernate (Herter 1965). He suggests that the requisite conditions for hibernation comprise a lowering of external temperatures and a physiological readiness to hibernate. The physiological readiness is probably determined principally by a rhythmic release of hormones into circulation (Herter 1965). Werner & Vens-Cappel's (1982) studies suggest an involvement of the hypothalamo-pituitary- adrenal axis in the control of nonshivering thermogenesis in euthermic European hedgehogs. Hoo-Paris & Sutter (1980 a; 1980 b) and Hoo-Paris Aina, Castex & Sutter(1984) experimented on aspects such as the control of plasma glucose levels during arousal and the role of cathecolamines in the regulation of insulin secretion during lethargy and arousal. Hoo-Paris & Sutter (1980 a) found that plasma insulin is necessary to control the normal development of plasma glucose during rewarming. The results of Hoo-Paris **et al.** (1984) suggest that, in hibernating animals there exists two pools of enzymes which are necessary to secrete pancreatic hormones: the cold adaptive enzymes should be more efficient in lowering activa tion energies than the homologous warm-adaptive enzyme.

According to Hoo-Paris & Sutter (1980 b), pancreatic inhibition during arousal seems to be due first to cold, then to effects of a blockage provoked by the stimulation of alpha-adrenergic receptors, which suggests a high increase in sympathetic activity during rewarming. No data however are available on aspects of energy metabolism, non-shivering thermogenesis, hiberna-tion and seasonal changes in the activity of the South African hedgehog.

Allanson (1934) histologically examined a large number of male European hedgehogs and provided information on the seasonal changes in the histology of the reproductive organs of the male hedgehog. Other studies on seasonal testicular activity of the European hedgehog have used different morphometric, histological and endocrinological parameters (Saure 1969; Wimsatt 1969; Saboureau 1981; Saboureau, Lauent & Boissin 1982 ; Saboureau & Boissin 1983a; Saboureau & Boissin 1983b; Saboureau, Castaing & Boissin 1984; Fowler 1982).

The oestrous cycle length and changes in hormone levels during the reproductive cycle of the female has not been investigated as extensively as the hormonal changes during the year and reproductive season of the male hedgehog. More recently Saboureau & Castaing (1986) determined the hibernation patterns of the female European hedgehog under natural environmental conditions in relation with age, food ability and changes in plasma hormone levels (oestradiol, progesterone, LH) during the year, and particularly, the reproductive season. Fowler (1986) investigated reproduction and heterothermy in the female European hedgehog. He attempted to determine if pregnant and lactating female hedgehogs are able to utilize adaptive hypothermia in order to avoid adverse conditions. Deanesly's (1934) data show that the females fail to mate at the first periods of estrous and to conceive after the first copulation. She ascribes it to a factor effecting the female.

Estimates of the length of the gestation period in the European hedgehog vary between four and seven weeks, but the gestation period of the South African hedgehog has not been accurately determined. According to Smithers (1983) it appears that the gestation period of the South African hedgehog is about 35 days. The gestation length in mammals is thought to be largely controlled by the fetal genotype, maternal age (Racey 1981) and maternal body mass (McKeown, Marshall & Record 1976). Yet in hibernators estimates of gestation lengths are often variable because hibernators can become torpid under certain conditions. It is thus possible that depressed body temperature during gestation, with consequent reduction in the rate of fetal growth, is responsible for the variability in estimates of gestation length in heterotherms (Racey 1981). Fowler (1988) showed that hedgehogs have the ability to enter torpor readily, under approriate conditions, during the summer.

The gestation length is thus influenced by the environmental conditions which influence the metabolic rate and body temperature. Morris (1977) recorded the average litter size in England at an age of three to six weeks at 3,7. According to Kristiansson (1981) the mean litter size in Sweden is 5,2. The size of litters in South Africa varies between one and nine (Smithers 1983).

Most research on hedgehogs was done on the European hedgehog **(Erinaceus europaeus)** and information on the South African hedgehog is limited to a few checklists on South African mammals and observations by Smithers (1971; 1983), these contributing to our knowledge on taxonomy, distribution, habitat requirements, food and reproduction. As yet, no comprehensive study has been undertaken on the biology of the South African hedgehog. Motivated by the paucity of scienitific data available on the South African hedgehog, this study was undertaken to obtain information on thermoregulation, hibernation and specific aspects of reproduction. The following key questions were posed:

- What is the change in oxygen consumption of the South African hedgehog with the change in season?
- Does the phenomenon, non-shivering thermogenesis occur in the South African hedgehog?
- How does the frequency of activity of the hedgehogs change from winter to spring?
- What is the extend of parental care in the South African hedgehog?
- How does the testosterone levels of the male hedgehog change during the annual cycle?
- What is the characteristics of the female reproductive cycle with emphasis on changes in progesterone levels during the annual and the oestrous cycles?

Data for this study were mainly collected from a captive colony established on the Experimental farm of the University of Pretoria (25° 45'S/28° 12'E). Thirty hedgehogs were housed in concrete enclosures (3m x 2,5m). The concrete floors of the enclosures were covered with 5cm of soil and each enclosure was provided with a wooden nestbox filled with dried grass as nesting material. The hedgehogs were provided daily with food and water and their diet consisted of tinned dog food (Husky; Petz products (Pty) Ltd, N'Dabeni) and dried dog food (Epol meal; Epol (Pty) Ltd, P O Box 518, Isando, 1600) mixed with water. Supplementary to this, mealworms and raw eggs were supplied from time to time. The enclosures were cleaned every morning and the foodbowls were washed.

For anaesthezia, Fluothane (ICI South Africa [pharmaceuticals] Ltd) was used on a piece of cotton wool placed in a beaker that was held over the hedgehog's nose.

CHAPTER 2

THERMOREGULATION, HIBERNATION AND NON-SHIVERING THERMOGENESIS (NST)

INTRODUCTION

The hedgehog is a small mammal which have been shown to have the ability to hibernate, especially in countries which have winters where sub-zero temperatures are maintained for long periods. Energy metabolism studies during different seasons on this small hibernating mammal should yield interesting results.

Being a member of the Insectivora, the first eutherian order, this group may represent a link between the eutherian and reptilian levels of metabolism. Indeed Crompton, Taylor & Jagger (1978) (In Hudson 1973) showed that the three species of insectivora they studied, seem to have a "reptilian" level of metabolism. A characteristic of hibernators is that the major activities of their lives are limited to a relatively short spring-summer period of activity and hence biological and physiological processes are intensified in such animals (Gunderson 1972).

The second law of the thermodynamics insists that to maintain a constant body temperature at low ambient temperatures, without a change in body conductance, an animal must increase its heat production (Hulbert 1980). Heat generating mechanisms can be devided into two classes: non-shivering (NST) and shivering thermogenesis (ST). The physiology of both have been reviewed extensively by Jansky (1965, 1973). Shivering has been reported in all mammalian species while non-shivering thermogenesis has been reported in a small number of eutherian mammals (Hulbert 1980). Jansky (1973) reported that NST occurs not only during the exposure of animals to cold, but also during arousal from hibernation when it is necessary to produce the greatest amount of heat in the shortest possible time, in order to overcome a great temperature difference between body temperatures of hibernating and euthermic animals. The major site of heat production appears to be located in brown adipose tissue and muscle and is mediated by noradrenergic neurones (Jansky 1973). The actual mechanism of heat production is not known.

A method of lowering the cost of endothermy as well as increasing the temperature range in which a constant body temperature can be maintained, is to decrease body conductance (Hulbert 1980). In mammals this has been accomplished by the development of fur or subcutaneous fat reserves which reduces the radiation of heat into surroundings which is cooler than the animal (Herter 1965). The hedgehog, however, has a dorsal cover of sparsely placed spines which have been largely attributed to a defensive action rather than to that of insulation. Indeed, it is safe to assume that dorsal spines, which do not alter in length or density in different seasons, provide only minimal insulation to the hedgehog. Fat deposition or alternative physiological strategies (i.e. torpidity or hibernation) are conceivably important for effective thermoregulation in this species (Gunderson 1972). The hedgehog and some medium sized mammals, abandon homeothermy by daily or seasonal relaxation of body temperature homeostasis (Gunderson 1972). In these animals temperature changes can range from only a few degrees below euthermia, which may occur in daily torpor, to a pronounced drop in temperature that can be called hibernation (Hudson 1973). According to Hudson (1973) hibernation refers to an array of physiological changes including a drop in body temperature often to a few degrees above freezing which is maintained for several days of weeks before the animal spontaneously arouses. Gunderson (1972) listed other characteristics of hibernation namely markedly reduced oxygen consumption and arousal accompanied by the activation of major heat producing mechanisms.

In addition to extremes of cold mammals may also be confronted with heat loads, which they can either actively combat or tolerate. Hulbert (1980) states that virtually all mammals increase their body conductance by an increase in peripheral circulation in moderately hot environments.

The aim of this part of the study was to access the effects of season on physiological parameters of metabolism as determined from measures of oxygen consumption and body temperature at different ambient temperatures. In addition NST capacity was estimated as described by Heldmaier (1972).

MATERIALS AND METHODS

Six male hedgehogs were used in this study. They were housed in two seperate enclosures, each enclosure containing three hedgehogs. They were exposed here to natural conditions of light and temperature. Food and water were provided **ad libitum**.

The body masses of 24 hedgehogs (9 females and 15 males) were recorded monthly between February 1986 and January 1987. During July, August and September 1986, rectal temperatures were recorded while the animals were anaesthetized for the sampling of blood for other purposes (see Chapter 4).

Metabolism was measured by recording oxygen consumption (Vo_2) at temperatures ranging between 10 °C and 35 °C during all the seasons. These experiments were conducted during the day when hedgehogs are normally inactive. Oxygen consumption was determined in an open circuit system (see Depocas & Hart 1957). A custom built 2,8 ℓ perspex metabolic chamber was used. Compressed air was dried through columns of silica gel and flowed at a rate of 1000 ml/min through the chamber. Excurrent air was also passed through columns of silica gel before entering an AMetek 5-3A oxygen analyzer (Applied Electro Chemistry, Pittsburgh; Scientific Asociates, P O Box 262, Tokai, Cape Town, 7945).

The animals were individually tested at the different temperatures and before each experiment the body mass of each animal was determined. The hedgehog was placed in the chamber which was submerged in a temperature regulated water bath. The internal temperature of the chamber was determined with a copper-constantin thermocouple linked to a Fluke 52 K/J thermometer (Fluke, Everett; Protea Laboratory, P O Box 784978, Sandton, 2146). The animals were allowed to acclimate to the chamber temperature (T_a) for 1,5-2 h before Vo_2 was recorded. For determination of the resting metabolic rate (RMR) oxygen consumption was recorded every three minutes until five consecutive readings were obtained that did not differ by more than 0,3 %.

The results were corrected to standard temperature and pressure (STP) and the oxygen consumption was thus calculated, according to the laws of Boyle - Mariotte and Gay - Lussac, as follows:

$$Vo = \frac{V1\ P1\ To}{Po\ T1} \div Mb\ (g)$$

Where
- Vo = Oxygen consumption per body mass (ml O_2/g/h)
- V1 = Oxygen per minute (ml/h)
- Po = Standard pressure (760 mm Hg)
- P1 = Barometric pressure (mm Hg)
- To = Kelvin temperature (273 °C)
- T1 = Kelvin temperature + ambient temperature (°C)
- M_b = Body mass (g)

After measuring of oxygen consumption, the hedgehog was removed from the chamber and it's body temperature (T_b) measured by inserting a copper-constantin thermocouple (connected to a Fluke 52 K/J thermometer) 1 cm into the rectum of the hedgehog. The animals were not anaethetized for these measurements. All data are presented as means ($\bar{x}$) followed by one standard deviation of the mean (S.D.).

Minimal thermal conductance (C) was calculated at all temperatures for all the individuals using the formula $C = m(T_b - T_a)$, where m = metabolic rate, T_a = ambient temperatures and T_b = body temperature (Hart 1971).

The capacity for non-shivering thermogenesis was calculated as the ratio between the minimal Vo_2 and maximal Vo_2 following subcutanuous injection of 1,5mg/kg Noradrenaline (NA) (Sigma, Labretoria, P O Box 95777, Waterkloof, Pretoria, 0081) following Heldmaier (1971). The animal was placed in the metabolic chamber at 29 °C and Vo_2 was recorded every three minutes. Noradrenaline was injected only after five succesive similar readings of Vo_2 and recordings were made for one hour after the injection of noradrenaline.

RESULTS

The relationship between oxygen consumption (Vo_2), T_a and T_b in spring (September and October 1986), autumn (March and April 1987), winter (July and August 1987) and summer (November and December 1987) is presented in Figs 2a, 2b, 2c and 2d respectively.

In spring all six hedgehogs were unable to maintain their body temperature at an ambient temperature of 10 °C. The lowest body temperature then recorded at 10 °C was 29 °C. Body temperatures at T_a = 30 °C ranged between 32 - 34 °C ($\bar{x}$ = 33,8 ± 0,69 °C). During spring the hedgehogs apparently had a thermal neutral point rather than a thermal neutral zone (Fig. 2a).

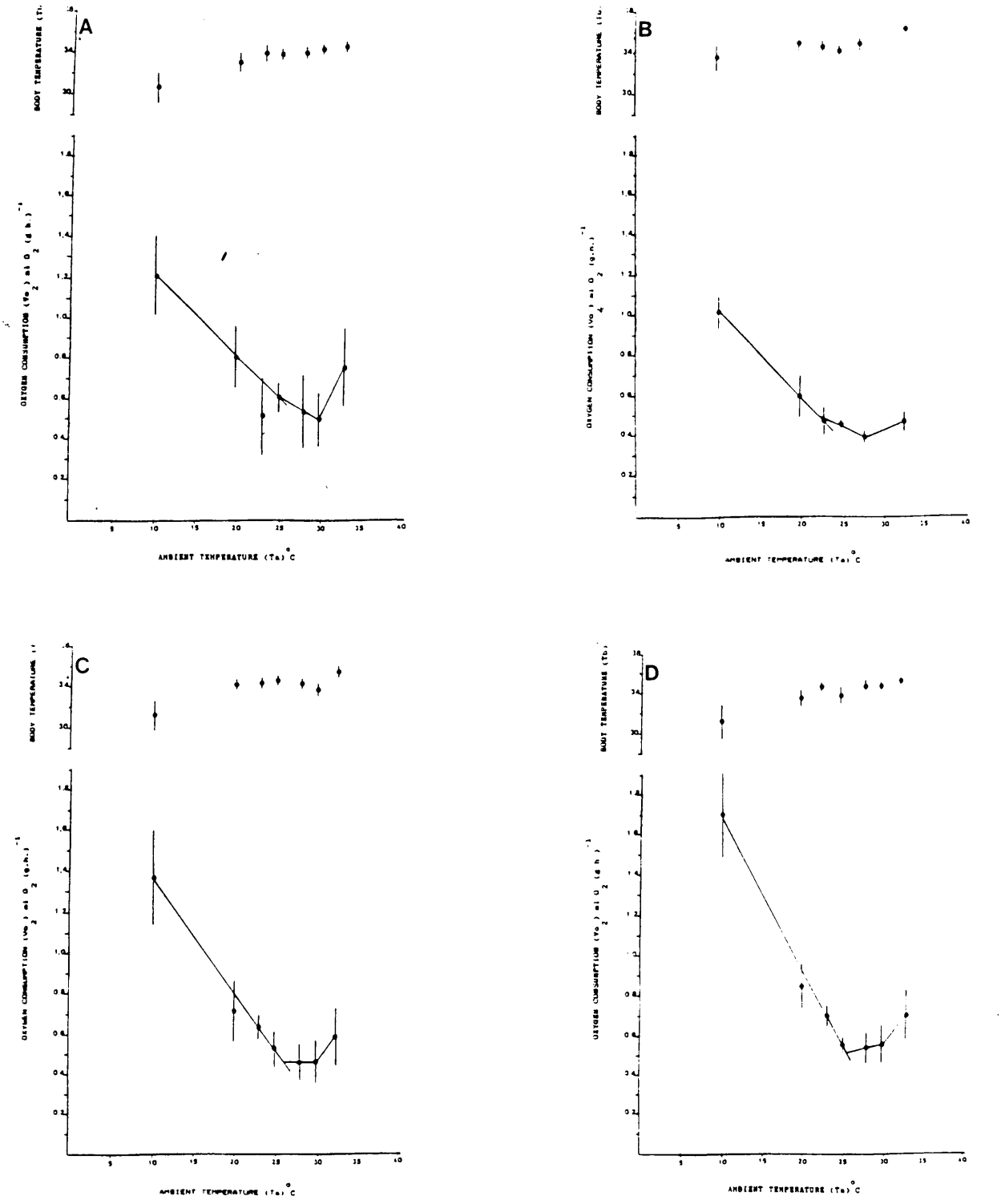

FIG. 2: Mean (S.D.) oxygen consumption (Vo_2) in ml $0_2(g.h.)^{-1}$ and body temperature (T_b) of **Erinaceus frontalis** at different ambient temperatures (T_a) during:

(a) spring (September and October 1986),

(b) autumn (March and April 1987),

(c) winter (July and August 1987) and

(d) summer (November and December 1987).

The lowest mean metabolic rate of 0,48 ± 0,13 ml 0_2(g.h.)$^{-1}$ was recorded at T_a = 30 °C. At temperatures higher than 30 °C the metabolic rate increased. Conductance below and above the thermal neutral point was 0,1 ± 0,04 ml 0_2/g.h. 1 °C at T_a = 28 °C and 0,17 ± 0,03 ml 0_2/g.h. 1 °C at T_a = 33 °C.

During autumn the lowest body temperature (31,6 °C) was recorded at T_a = 12 °C. The lowest mean metabolic rate (0,39 ± 0,03 ml 0_2(g.h.)$^{-1}$) was recorded at T_a = 28 °C and metabolic rate started increasing at temperatures higher than this. Only one recording was made at T_a = 35 °C and the oxygen consumption then was 1,42 ml 0_2(g.h.)$^{-1}$ and the body temperature 40 °C. Measuring of Vo_2 at this high temperature was not attempted with other animals for fear of loosing them. In contrast to spring, it appears that in autumn the hedgehogs had a thermal neutral zone between T_a = 28 °C and T_a = 33 °C. Conductance was 0,06 ± 0,01 ml 0_2/g.h. 1 °C at T_a = 28 °C and 0,15 ± 0,02 ml 0_2/g.h. 1 °C at Ta = 33 °C.

During winter the lowest body temperature recorded was 29 °C at T_a = 10 °C. The highest body temperature recorded at 33 °C was 36,2 °C. The lowest metabolic rate of (0,45 ± 0,11 ml 0_2(g.h.)$^{-1}$) was recorded at T_a = 30 °C. At T_a = 33 °C the metabolic rate increased to 0,58 ± 0,14 ml 0_2(g.h.)$^{-1}$. The thermal neutral zone for winter thus appears to be between 28 °C and 30 °C (Fig. 2c). Conductance at T_a = 28 °C was 0,08 ± 0,02 ml 0_2/g.h. 1 °C and at T_a = 33 °C 0,25 ± 0,01 ml 0_2/g.h. 1 °C.

During the summer experiments the lowest body temperature measured was 29,7 °C at T_a = 10 °C. Between T_a = 20 °C and T_a = 33 °C the body temperatures ranged between 32 - 35 °C. The lowest metabolic rate was recorded as 0,54 ± 0,08 ml 0_2(g.h.)$^{-1}$. In contrast to previous seasons the thermal neutral zone appears to be between 25 °C and 30 °C (Fig. 2d). Thermal conductance at T_a = 25 °C and T_a = 30 °C was 0,08 ± 0,02 ml 0_2/g.h. 1 °C and 0,38 ± 0,25 ml 0_2/g.h. 1 °C respectively.

The least square linear regression equations relating oxygen consumption to temperature during summer, winter, spring and autumn are $y = 2,31 - 0,06x$, $y = 1,77 - 0,05x$, $y = 1,58 - 0,04x$ and $y = 1,46 - 0,04x$ respectively. The lower critical points of winter ($0,45 \pm 0,11$; $T_a = 30$ °C) and summer ($0,54 \pm 0,08$; $T_a = 28$ °C) did not differ significantly ($t = 1,62$; $p < 0,05$). Thermal conductance at $T_a = 33$ °C was higher than at $T_a = 25$ °C during al seasons (Table 1). Below 25 °C the thermal conductance remained relatively constant. The mean minimum Vo_2 level measured before the noradrenaline injection was $0,53 \pm 0,08$ ml $0_2(g.h.)^{-1}$ in non-anaesthetized hedgehogs.

Table 1. Mean body mass (M_b) and body temperature (T_b °C) of hedgehogs during different seasons at three different temperatures (T_a) = 25, 28 and 33 °C. The calculated values of overall thermal conductance (C) are given using the equation $C = M (T_b - T_a)$.

Season	T_a(°C)	N	M_b (g)	T_b (°C)	$ml O_2/g.h./1$ °C
Spring	25	5	386,3 ± 34,6	33,4 ± 0,43	0,080 ± 0,010
	28	5	390,3 ± 35,5	33,5 ± 0,65	0,100 ± 0,040
	33	5	368,0 ± 36,5	34,0 ± 0,57	0,170 ± 0,030
Autumn	25	5	428,0 ± 40,3	34,32 ± 0,41	0,048 ± 0,008
	28	6	424,0 ± 38,3	35,5 ± 0,52	0,060 ± 0,011
	33	6	450,0 ± 34,9	36,1 ± 0,66	0,150 ± 0,020
Winter	25	5	409,0 ± 73,3	34,2 ± 0,59	0,058 ± 0,013
	28	5	407,0 ± 91,2	34,0 ± 0,29	0,076 ± 0,013
	33	5	401,0 ± 86,7	35,2 ± 0,50	0,245 ± 0,099
Summer	25	6	392,5 ± 40,4	33,6 ± 0,98	0,065 ± 0,012
	28	6	391,5 ± 66,3	34,6 ± 0,66	0,080 ± 0,014
	33	6	372,0 ± 68,8	34,6 ± 0,47	0,387 ± 0,200

Table 2. Maximal non-shivering thermogenesis (NST) in six male hedgehogs during summer, expressed as the ratio between maximal Vo_2 after noradrenaline injection and minimal Vo_2 before noradrenaline injection. Rectal temperature (T_b °C) was recorded before and after the injection of noradrenaline.

Vo_2 minimum ml $O_2(g.h.)^{-1}$	Vo_2 after NA/ Vo_2 minimum	T_b (°C) Before NA injection	T_b (°C) After NA injection
0,53 ± 0,08	1,42 ± 0,48	34,6 ± 0,62	36,7 ± 0,76

Table 3. Mean body mass (M_b) of 23 hedgehogs taken monthly from February 1986 to January 1987.

Month	M_b (g)	Month	M_b (g)
February	423,3 ± 26,4	August	362 ± 41,2
March	474,2 ± 34,3	September	387,5 ± 36,4
April	542,4 ± 46,1	November	375 ± 29,2
May	498,0 ± 69,7	December	398 ± 31,9
June	454 ± 54,2	January	427 ± 68,5

The mean maximal Vo_2 measured after the noradrenaline injection was 1,42 times higher than the Vo_2 measured before the noradrenaline injection (Table 2). The NST capasity was calculated as 2,6. After the noradrenalin injection mean body temperature increased from 34,6 ± 0,62 to 36,7 ± 0,76. Body temperatures measured during July ranged between 11 °C and 33 °C ($\bar{x}$ = 24,5 ± 6,87 °C; N = 25). In August body temperatures ranged between 15 °C and 34 °C ($\bar{x}$ = 27,55 ± 5,43 °C; N = 24) and in September the maximum body temperature was 39 °C with a minimum of 32 °C ($\bar{x}$ = 32,9 ± 4,39 °C; N = 15). Mean body mass peaked in April (542,4 ± 46,1g; n = 23) before the hibernation period and attained a minimum value in August (362 ± 41,2g), after the hibernation period (Table 3).

DISCUSSION

The cost and effectiveness of temperature regulation in endotherms can be described by parameters such as body mass, core temperature, basal rate of metabolism and minimal thermal conductance (McNab 1980). Oxygen consumption (Vo_2) at the lower critical point for winter (T_a = 30 °C), summer (T_a = 28 °C), spring (T_a = 30 °C) and autumn (T_a = 28 °C) is 10 % lower than the values expected from Kleibers' equation (Kleiber 1961) and during winter 8 % lower, during summer 9 % higher, during spring 2 % lower and during autumn 18 % lower than the values expected from McNab's equation (McNab 1988). According to McNab (1988) rate of metabolism scales proportionally to approximately $M^{0,75}$ for animals with a body mass (M) equal to or higher than 300g, which is the equation given by Kleiber (1961). This therefore was the equation used to calculate the expected values. The expected values from McNab was calculated using the equation $Vo_2 = a\ (\text{body mass in grams})^b$ with the constants a and b as given in the scaling equations for basal rate of metabolism in mammals and grouped by McNab according to feeding habits.

Kleiber (1961) did not include variables such as feeding habits and the taxonomic position of the animals into his calculations and it seems that the scaling equation given by McNab is a better estimate of the expected metabolic rate.

The difference between the metabolic rate measured in autumn and the expected value might be ascribed to climate (see McNab 1980). The peak in body mass during autumn can be ascribed to the accumulation of fat deposits in preparation for winter and possibly hibernation (Smithers 1983). In autumn they thus start to adjust their energetics to climate by modifying their insulation (Scholander, Hock, Walters & Irving 1950; Irving, Krog & Manson 1955). According to them this is the major means by which mammals adjust their energetics to climate.

The South African hedgehog maintained its body temperature at close to 34 °C at ambient temperatures of 25 to 33 °C during all seasons (Table 2). Shkolnik & Schmidt - Nielsen (1976) found a similar body temperature in three hedgehog species of different geographical areas that they compared under similar ambient temperatures. Results of the present study as well as that of Shkolnik & Schmidt - Nielsen (1976) is in accordance with Morrison & Ryser (1952) who found that hedgehogs regulate their body temperatures at about 3 to 4 °C below that of other mammals, which regulate there body temperatures in the range of 37 to 38 °C.

Thermal conductance is a measure of the ease with which heat is exchanged between the body and the environment (McNab 1980). It is a highly complex interaction of environmental factors with physiological and anatomical features such as fur thickness, pilo-erection, subcutaneous fat deposition and vasomotor changes (Herreid & Kessel 1967). The calculation of thermal conductance based on body temperature, resting metabolic rate, temperature and body mass have resulted in several interpretation problems. In the present study thermal conductance below 25 °C remained relatively constant, suggesting that at moderate temperatures physical thermoregulation plays a minor role in thermoregulation. This is true for most small mammals (Bradley & Deavers 1980). According to McNab (1980) a region of thermoneutrality is produced by a temperature- dependent variation in thermal conductance such that conductance decreases to a minimum as temperature falls and, as was seen in this study, increases when the T_a approaches the T_b. This increase facilitates heat loss and with hyperthermia, results in a saving in water that otherwise would have been required for evaporative cooling (Buffenstein & Jarvis 1985). In the present study the change in thermal conductivity is most obvious during the summer when the body weights are low and when hedgehogs have the least insulation.

Non-shivering thermogenesis (NST) is a heat-production mechanism liberating chemical energy due to processes which do not involve muscular contractions (Jansky 1973). In the present study the South African hedgehog had a NST capacity of 2,6 and the body temperature increased by 2,1 °C 30 min after injection with nor-adrenalin. The hedgehogs thus have the ability to use NST if they are exposed to cold or when awakening from hibernation.

According to Hudson (1980), hibernation is a type of torpor that is easily recognized. Hudson (1973) defines hibernation as the attainment of very low body temperatures, often only a few degrees above freezing, which is maintained for several weeks before the animal spontaneously arouses. Gunderson (1972) stated that hibernation is easier to characterize than to define. He says that some of the characteristics of hibernation are the decrease in body temperature and oxygen consumption, prolonged periods of apnea and an activation of the major heat-producing mechanisms when the animal arouses. Dmi'el & Schwarz (1984) showed that a continuous ambient temperature of 11 °C was the only condition required by **Hemiechinus auritus** and **Erinaceaus europaeus** to enter hibernation outdoors and in the laboratory. They state that the natural hibernation of the two species may be brought about by the combined effect of a continuous low temperature during winter and a decrease in food availability. Dmi'el & Schwarz (1984) believes that temperature is most probably the dominant factor inducing hibernation. In the South African hedgehog seasonal changes in body mass is clearly defined and is characteristic of hibernating mammals and the lowest body temperature (11,6 °C) was measured during winter. A further characteristic of these animals is that most of their reproductive activities are limited to a relatively short spring-summer period of activity (see Chapters 5 and 6). In Chapter 3 it is showed that the general locomotor activity is reduced during winter.

Although the seasonal changes in activity, body temperature and body mass suggest that the South African hedgehog does have the ability to hibernate, more extensive experimental work still has to be done to prove this.

CHAPTER 3

ACTIVITY PATTERNS AND SEXUAL BEHAVIOUR

INTRODUCTION

Hedgehogs are generally regarded as nocturnal animals. They remain in hiding and asleep during the day, become active at dusk and return to their nests at twilight before dawn (Herter 1965; Smithers 1983). Hedgehogs, however, are known to be active outside their asumed hours of activity and several authors (i.e Herter 1965; Meritt 1980; Smithers 1983) reported that hedgehogs are intermittently active during the day.

In spite of many statements to the contrary the hedgehog is not a silent animal (Gregory 1975). Gregory (1975) recorded high frequency twitters, hisses and snorts, screams and courtship sounds in the central African hedgehog **(Erinaceus albiventris)**. Burton (1969) and Poduschka (1969) described something similar to a scream in the European hedgehog. Little evidence is found amongst the earlier descriptions of hedgehog behaviour of a sound homologous to the courtship call in the repertoire of the European hedgehog (Gregory 1975).

The present study aimed to define seasonal changes in the activity patterns of the South African hedgehog and describe the sexual behaviour of the hedgehog.

METHODS

The six hedgehogs used for this study were housed in three different enclosures and maintained as described before (Chapter 1). The first enclosure had a female-male pair (hedgehogs numbers 1 and 2 respectively), the second, two males (hedgehogs numbers 3 and 4) and the third two females (hedgehogs numbers 5 and 6). To fascilitate individual identification an area on the spines of one of each pair was painted. Ambient temperatures were recorded at the start of each observational hour.

Observation procedures

An instantaneous scan, as outlined by Altman (1974), of the activity of the hedgehogs was carried out for 42 minutes at three minute intervals, starting on the hour. The activities recorded include running, walking, drinking, eating, grooming, courtship, presenting, mounting and copulation. The time spent in the nestbox and resting outside the nestbox were also recorded. Observations were undertaken on 1 and 2 July 1985, 18 and 19 August 1985 and 26 and 27 September 1985.

RESULTS

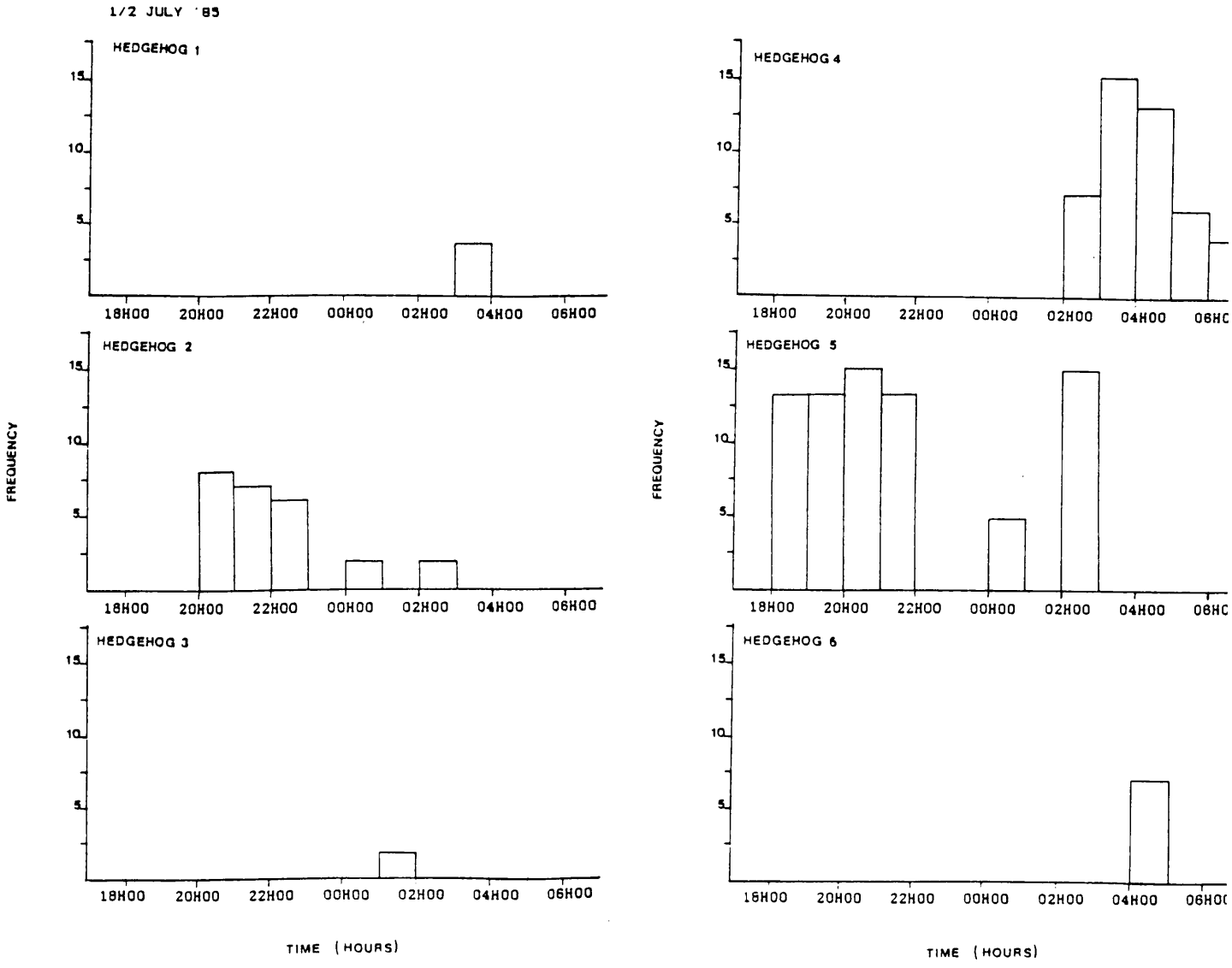

FIG.3: Activity profiles of six captive hedgehogs during 1 and 2 July 1985 18h00 - 06h00.

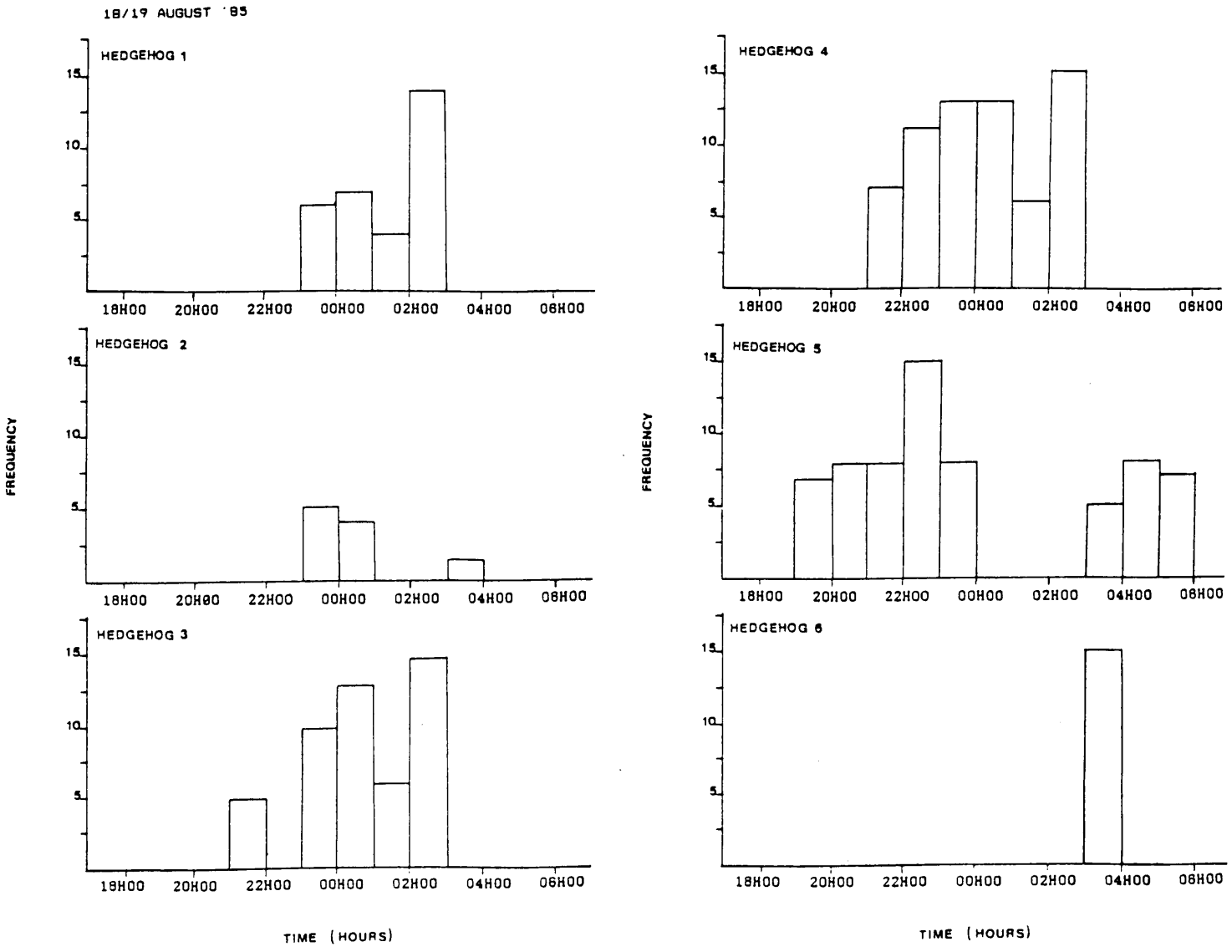

FIG. 4: Activity profiles of six captive hedgehogs during 18 and 19 August 1985 from 18h00 - 06h00.

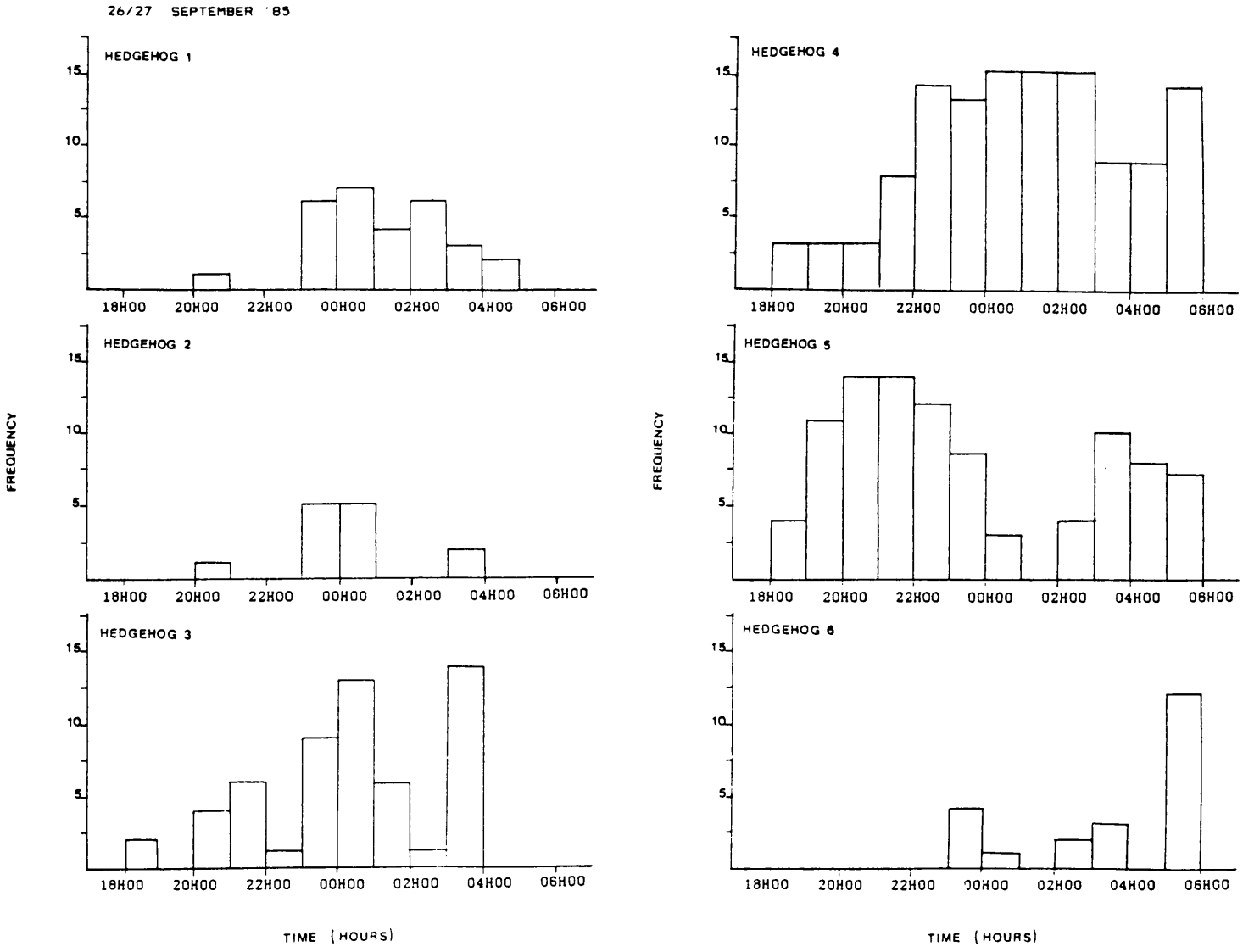

FIG. 5: Activity profiles of six captive hedgehogs during 26 and 27 September 1985 from 18h00 - 06h00.

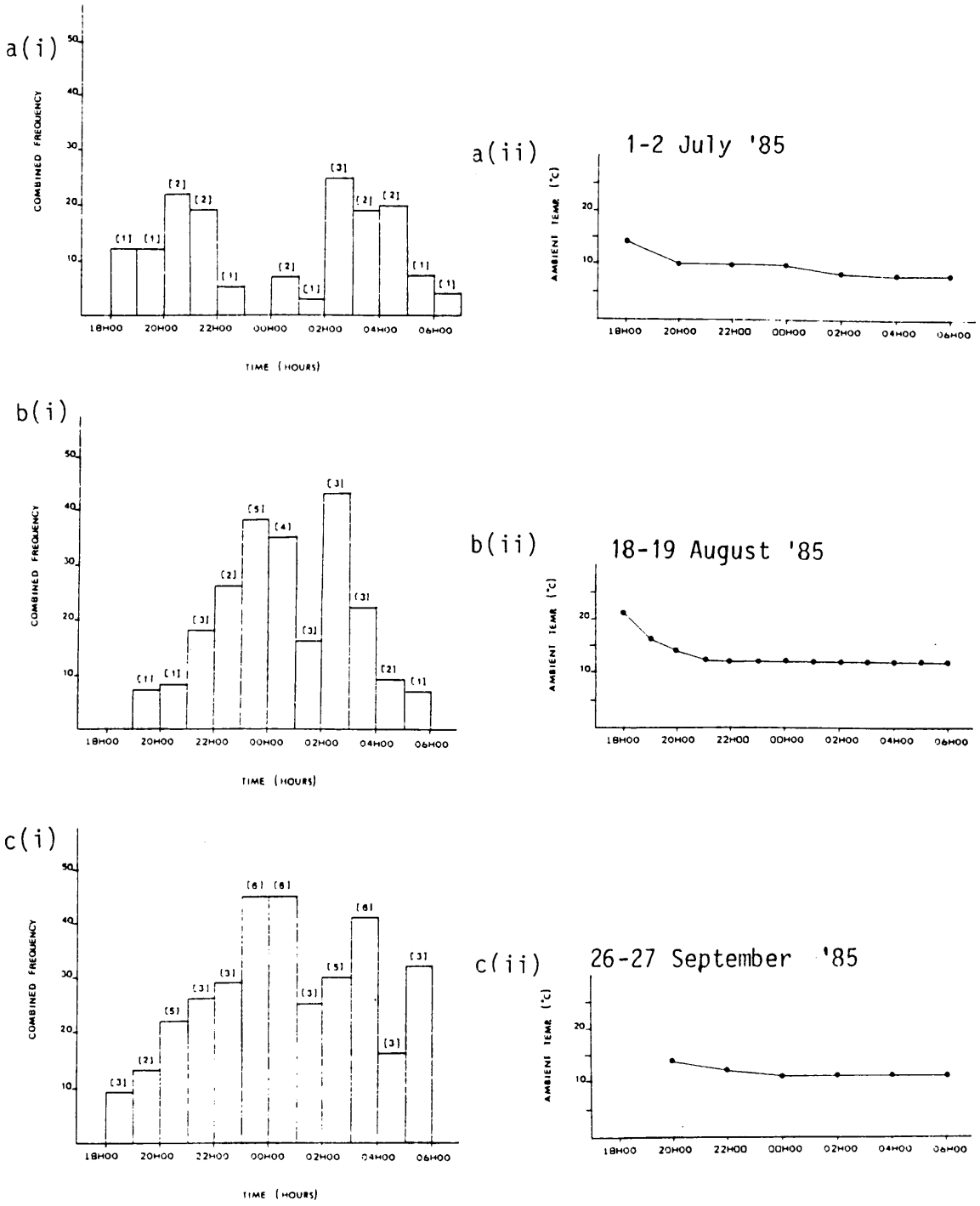

FIG. 6: The combined frequency of activity of six hedgehogs and the ambient temperature during the three observational sessions as recorded from 18h00 - 06h00 (Numbers in brackets represents the number of hedgehogs active during the different hours).

Activity patterns

The percentage of time that each of the six hedgehogs were active from 18h00-06h00 during the three observational sessions are presented in Figs 3, 4 & 5. These hedgehogs were not active from 06h00-18h00. During the first session (1 and 2 July 1985, Fig. 3) hedgehog number 5 was active from 18h00 until 21h00, at midnight and between 02h00-04h00. Females number 1 and 6 were active only between 03h00-04h00. Male number 2 was active from 19h00 until 21h00 and again around midnight. Male number 4 started his activity period at 01h00 and only returned to the nestbox after 05h00. The ambient temperature was 14 °C at 18h00 and dropped to 8 °C at 03h00 [Fig. 6(a)(ii)].

The hedgehogs were active for most of the observation period during the second session (18 and 19 August 1985; Fig. 4) except for female number 6 which was active only between 04h00 and 06h00. Female number 5 was active for almost the whole period except between 00h00-02h00, with the highest frequency of activity around 22h00. Males number 3 and 4 became active at 20h00 and maintained a high frequency of activity until 03h00, except between 00h00 and 02h00. Female number 2 showed low frequencies of activity between 22h00-00h00 and between 02h00-04h00. Female number 1 became active at 23h00 with a peak of activity at 03h00. The ambient temperature at 18h00 was 21 °C and it dropped to 12 °C at 03h00 [Fig. 6 (b)(ii)].

During the third session (26 and 27 September 1985, Fig. 5) hedgehogs number 1, 3, 4 and 5 were active through almost the whole observation period between 18h00 and 06h00. Hedgehogs number 4 and 5 were highly active with hedgehog number 4 having its peak activity period between 22h00 and 03h00 and again between 05h00 and 06h00. Hedgehog number 5 was very active from 19h00-23h00 and again from 02h00-06h00. Hedgehog number 1 had a low frequency activity period from 23h00-05h00. Hedgehog number 3 was active from 00h00-01h00 and 03h00-04h00. Hedgehogs number 2 and 6 were inactive during the largest part of this session. The ambient temperature changed from 14 °C at 20h00 to 11 °C at 04h00 [Fig. 6(c)(ii)].

The activity profile for all six hedgehogs combined during the three different sessions are presented in Figs. 6 a, b & c. During the first session [1 and 2 July 1985, [Fig. 6(a)(i)] low frequency of activity occurred almost throughout the whole period between 18h00 and 06h00. During the following sessions the frequency of activity became increasingly higher [Figs. 6(b)(i) and 6(c)(i)] and during these sessions they were active throughout the whole period between 18h00 and 06h00. Activity peaked around midnight and again in the early morning.

Categories and descriptions of activity and behavioural patterns

Running was recorded when an individual started to run, usually in circles, or in a figure eight. On 19 August 1985, hedgehog number 4 started to run in a figure eight at 21h00 and kept on running until 03h00. He occasionally went off the tract to feed or pause in the nestbox before continuing to run. This behaviour was observed on two other occasions. The normal gait of the hedgehog, however, is a leisurely walk.

Grooming was recorded when the hedgehog was licking or scratching its head, flanks or forepaws. The hedgehogs in this study did not spend much time grooming themselves, nor did they groom each other. Grooming in this case was mostly a shaking and scratching of their bodies with their hindlegs.

Courtship was recorded as a continuous circling of the female by the male with the female keeping the male at bay by vocalizing, erecting her spines or trying to bite the male. This behaviour was recorded between hedgehogs number 1 and 2 during the third session between 23h00 and 01h00. During this period they occasionally returned to their nestbox. The male repeatedly emitted squeaking noises while following the female. She managed to get hold of the male on several occassions and bit him until he managed to free himself.

Presenting: The female adopted a special posture with the belly pressed flat to the ground and her back arched downwards so that her nose pointed skywards. Her spines then lay flat to the back.

Mounting was recorded when the male stood bipedally with his forepaws on the female's back, gripping the spines at the back of her head in his mouth. Mounting occurred at 24h12 between hedgehogs number 1 and 2. The female continued to walk around with the male following. Copulation lasted for seven minutes (24h16-24h23). She tried to bite the male after he withdrew. Both of them went into the nestbox after that.

Feeding and drinking: The hedgehogs did not feed immediately after leaving the nestbox. They ate food like earthworms and mealworms slowly by chewing or crushing them to death between the premolars. Not all the hedgehogs were observed drinking water and if they did, very little water was consumed, judging by the time they spent at the water bowls.

Defaecation and urination occurred mainly during the first few hours after wakening. The hedgehogs tended to defaecate and urinate in a particular spot in the enclosure. During the first session one of the hedgehogs ate its own faeces. This was the only time this kind of behaviour was observed.

Self-anointing, recorded when an animal produced spittle and then plastered it on its spines, was recorded on two occasions. Once it occurred briefly after a hedgehog had eaten a mealworm and once a male produced spittle while being held to be photographed. He, however, then did not smear it over its body.

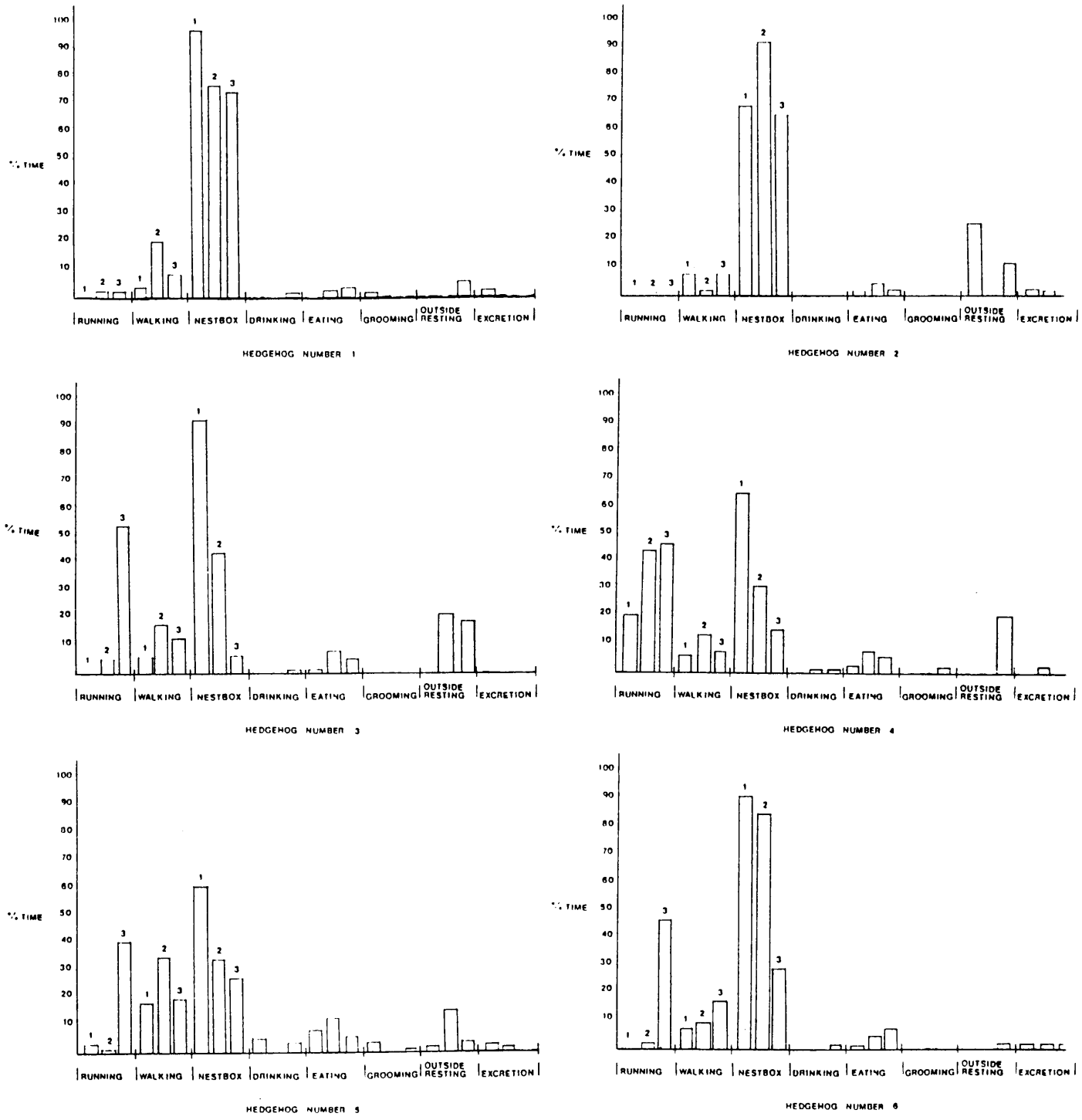

FIG. 7: Percentage of time spent on different behavioural and activity patterns by the six captive hedgehogs during the three observational sessions undertaken on (1) 1 and 2 July 1985, (2) 18 and 19 August 1985 and (3) 26 and 27 September 1985.

The percentage time each of the six hedgehogs spent at the different categories of behaviour and activity during the three sessions is given in Fig. 7(a-f). All six hedgehogs gradually spent less time resting in the nestbox and a higher percentage of time running, walking, eating and resting outside the nestbox as the seasons changed from winter to spring.

DISCUSSION

In this study the hedgehogs were active only between 18h00 and 06h00, except for the first session when they were inactive also between 23h00 and 24h00. Although they were active most of the night, activity peaked around midnight and again in the early morning between 02h00 and 05h00.

All hedgehogs did not become active at the same time, suggesting that the rythm of activity is not directly influenced by external factors (i.e daylight or temperature) but rather by an internal factor or factors (i.e body temperature). Herter (1965) found that European hedgehogs became active when their body temperatures attained a critical point. This critical point might be different for each individual hedgehog.

Courtship and mating behaviour observed during the present study was similar to that described by Herter (1965), Burton (1969), Morris (1983) and Poduschka (1977). Courtship can go on for several hours and mating can not be accomplished unless the female co-operates by adopting a special posture and flattening her spines.

Poduschka (1969, 1977) found that the male eastern European hedgehog **(Erinaceus europaeus roumanicus)** deposits numerous scent markings, consisting of fluid secretions from the urogenital opening, in the immediate vicinity and on the back of the female. He stated that this sexual scentmarking promotes mating readiness. This kind of behaviour was not mentioned by the other authors nor was it observed during the present study. Vocalisation during courtship and mating was however recorded in the present study. The male repeatedly emitted squeeking noises while following the female.

The female uttered only snorts and hisses as described by Herter (1965). Gregory (1975) refered to this sound, only heard from males, and in courtship, as the "serenade". Poduschka (1977) considers the acoustical signals with their ultrasound frequencies as stimulators for mating.

According to Meritt (1980) the West African hedgehog **(Erinaceus albiventris)** tend to defaecate and urinate in a particular corner of the enclosure and defaecation occurs in the early evening. This was also found during the present study. The West African hedgehog, however, placed their vent against the side of the cage, tail lifted, so that the faeces became plastered about 25 cm from the floor, and this was not found in the present study. In both species urination took place in the same area as defaecation.

Although not very extensive, captive South African hedgehogs did show the phenomenon of self-anointing. The hedgehog's habit of plastering itself with its own saliva was first recorded by Heck (1912). Since then Herter (1938, 1965), Burton (1969), Brockie (1976) and Morris (1983) have observed this behaviour and speculated on its function. Brockie (1976) and Morris (1983) disregarded most of the published explanations and stated that self-anointing is connected with scent which mainly serves as a form of sexual signaling. Most of the times self-anointing is used by young before weaning to make detection of lost young easy for the mother (Brockie 1976). According to Brockie (1976) self-anointing amongst adults occurs only during the breeding season. It has been suggested that the self-anointing reflex in captivity is triggered by novel objects or odours. It thus represents displacement activity, being inappropriate to the situation and seemingly purposeless (Brockie 1976).

Another interesting behaviour observed during this study, is the running in circles by one individual hedgehog for an hour or more. This was also reported by Morris (1983) and according to him, writers earlier than 1960 did not observe this behaviour pattern. He regards this activity as a symptom of poisoning caused by large quantities of diverse chemicals being used against garden pests. It is unlikely that it is caused by frustration as a result of captivity, as wild hedgehogs also exhibit this behaviour (Morris 1983).

CHAPTER 4

PARENTAL CARE AND POSTNATAL DEVELOPMENT

INTRODUCTION

Hedgehogs are solitary animals (Herter 1965). It is common knowledge that these animals do not form bonding pairs and the male does not play a part in the feeding of the young (Herter 1965). Little information is available on hedgehog litters born in South Africa. Smithers (1983) reported on the possible gestation length and the litter size. Jacobsen (1982) reported on neonate weight at birth and development within two days after birth of a litter of nine of which only four survived.

A variation in litter sizes amongst the European species were reported by different authors i.e. (Morris 1961, Herter 1965, Parkes 1975, Morris 1977 and Lienhardt 1979). Estimates of the length of the gestation period varies between four and seven weeks (Herter 1965). Racey (1981) and Fowler (1988) did studies explaining the variation in the gestation lengths.

The young are born with closed ears and eyes and shortly after birth the spines will protrude through the skin (Herter 1965). According to Jacobsen (1982) the quills protrude through the skin between one and three hours after birth. According to Herter (1965) the young can eat solid food at four weeks old. After the 40th day the mother usually drives the young away.

The young grow rapidly because they have to reach a weight that would help them survive the winter. To hibernate during the winter, European hedgehogs must accumulate sufficient fat reserves by late autumn to support themselves during the subsequent winter torpor and occasional bouts of activity (Morris 1984). He implies that the animals must reach a critical minimum body weight before hibernation. This may also be the case in the South African hedgehog.

This chapter deals with maternal behaviour and reports on the growth and development of the young from birth to weaning, and dispersal. Information is also provided on litter size, the gestation period, age at weaning and sexual maturity.

MATERIALS AND METHODS

Study animals

Information on parental care and posnatal development were obtained from hedgehogs provided by Mr Carl Tomaschko (Kyalami, Johannesburg). They were kept at his home in a semi-natural enclosure surrounded by a brick wall. Two wooden nestboxes with lids that could be opened from the side were provided. The nestboxes were lined with dried grass as nestbuilding material. The hedgehogs (1 male, 2 females) were fed on tinned dog food [Husky, Petz Products (Pty) Ltd, N'Dabeni] and from time to time milk was provided. One of the females (Female A) gave birth to three male pups on 13 October 1985 and the other (Female B) gave birth to three female pups on 5 October 1985. Female B had a second litter of four young (2 males, 2 females) on 22 November 1985. Additional information also was obtained from a pregnant hedgehog (Female C), caught on 25 November 1985 which had a litter of eleven on 1 January 1986. Only two males and two females survived.

Observation procedures

Three 24 hour observation sessions were undertaken on the young of females A and B to access:

1) The changes in the frequency of huddling against the female by the young during a 24 hour period.

2) Changes in the frequency of suckling during a 24 hour period.

3) Daily changes in the frequency of being alone.

4) The percentage time allocated to huddling, suckling and being alone by the young.

During each observation session the young were observed for 42 minutes of each hour. An instantaneous scan (Altman 1974) of their behaviour was carried out at three minute intervals, starting on the hour. Observations were made on 24 October 1985, 7 November 1985 and 18 November 1985. The young of Female A were 11, 25 and 37 days old when studied while the young of Female B were then 19, 33 and 44 days old.

RESULTS

Behavioural patterns

Suckling was recorded whenever the young sucked on the teat of the mother or another female. It was not possible to distinguish between suckling and teatholding, but suckling was recorded while the mother lie in a position to make suckling possible. On 24 October 1985 (Fig. 11a), the young of Female B suckled intermittently through the largest part of the afternoon, from 13h00-17h00 and during the early evening from 18h00-19h00. Suckling occurred again between 01h00 and 02h00 at a low frequency and at a high frequency from 05h00. On 7 November 1985 suckling occurred at a high frequency between about 17h00 and 20h00 and at a low frequency between 22h00 and 01h00 (Fig. 11b). Between 02h00 and 04h00 the young of Female B were suckled by Female A. The young of Female B did not suckle during the last observations on 18 November 1985. On 24 October 1985 the young of Female A were suckled between 13h00 and 18h00 and again between 01h00 and 04h00 (Fig. 8a). During the second session they suckled during the early afternoon, around 22h00 and again between 01h00 and 02h00 (Fig. 8b). During the third session they suckled during the early afternoon, from 23h00 to 01h00 and again from 03h00 to 04h00 (Fig. 8c).

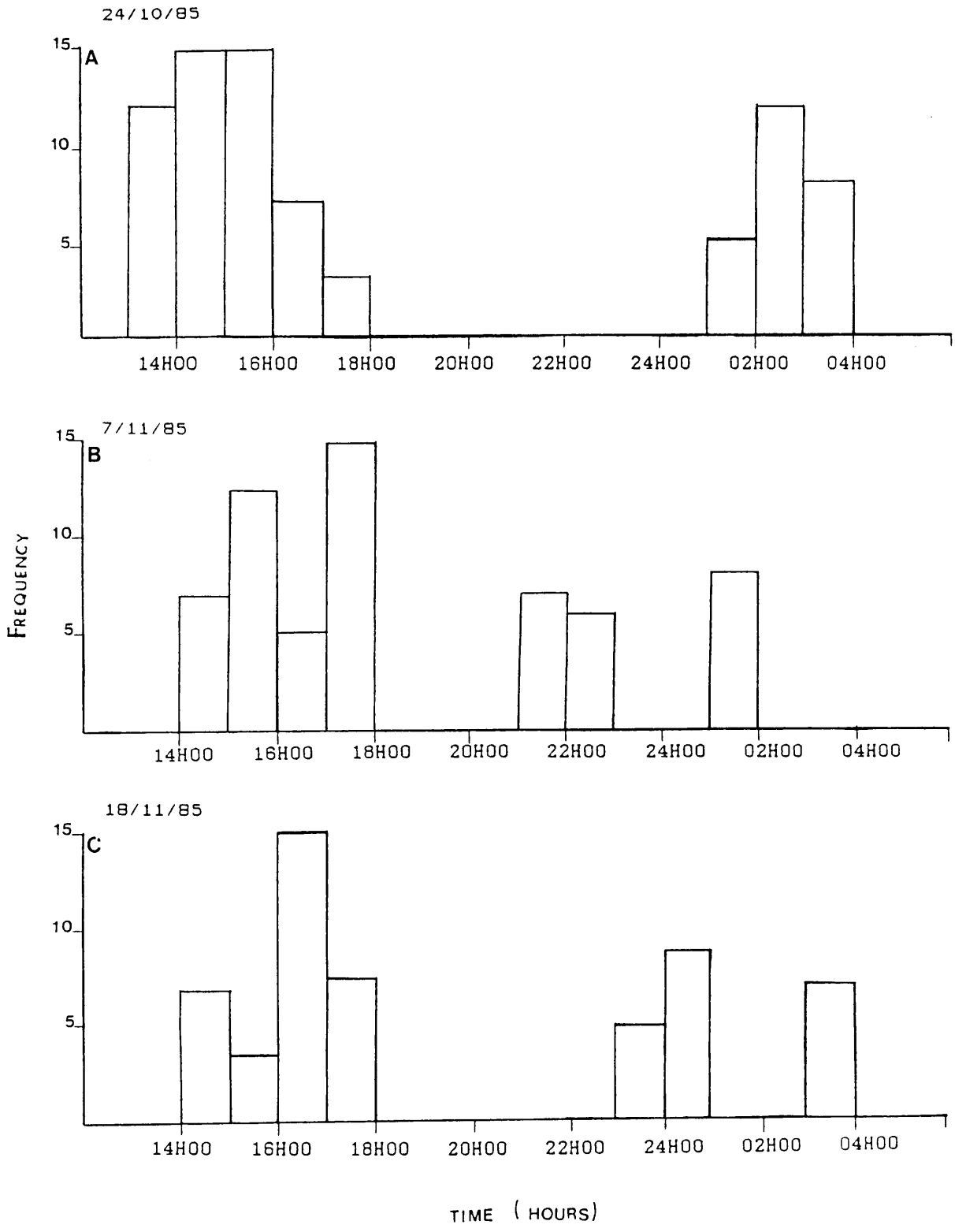

FIG. 8: Changes in frequency of suckling by young of Female A between 13h00 - 06h00 during

(a) 24 October 1985,

(b) 7 November 1985 and

(c) 18 November 1985.

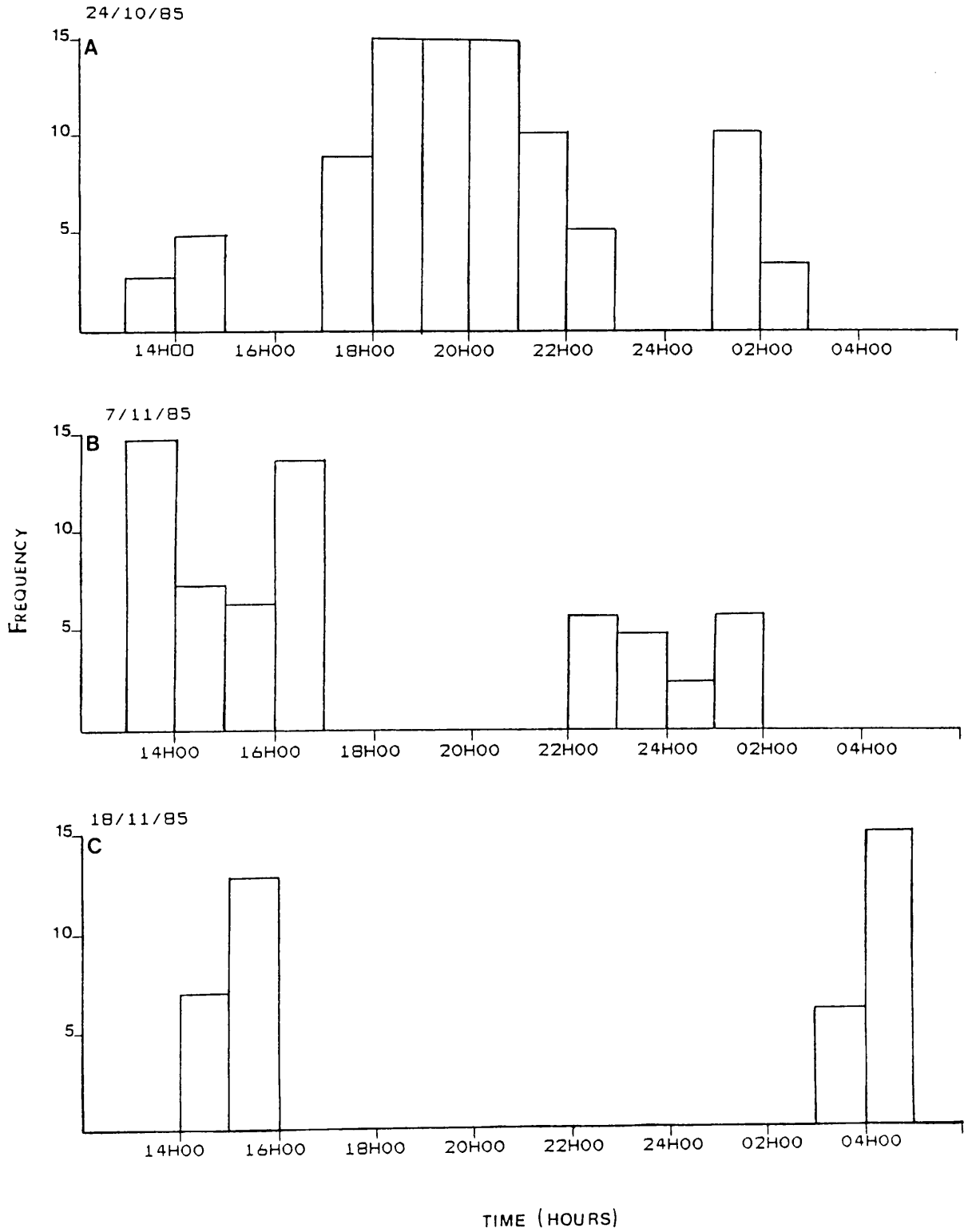

FIG. 9: Changes in frequency of huddling against female by young of Female A between 13h00 - 06h00 during:

(a) 24 October 1985,

(b) 7 November 1985 and

(c) 18 November 1985.

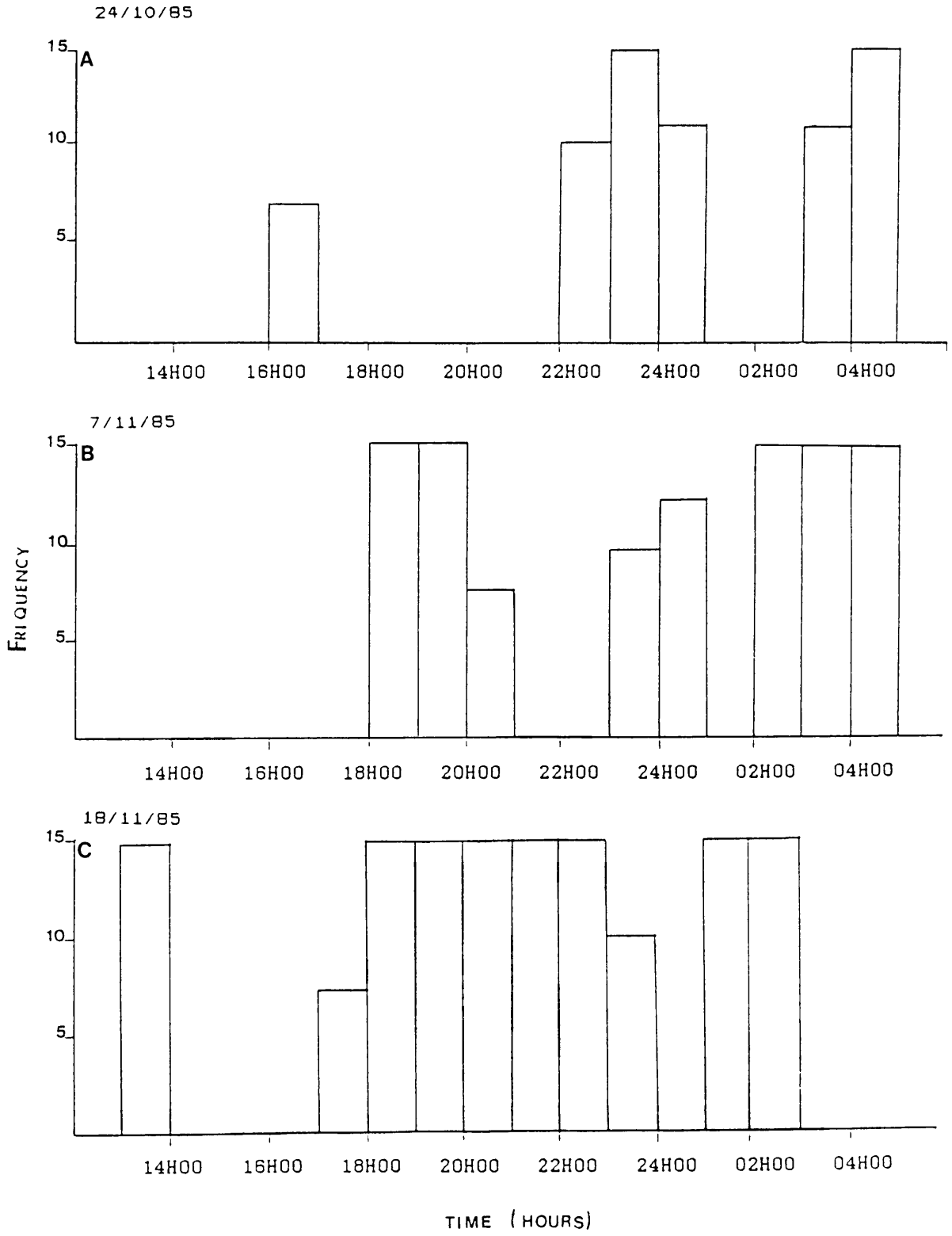

FIG. 10: Changes in frequency of being alone by young of Female A between 13h00 and 06h00 during:

(a) 24 October 1985,

(b) 7 November 1985 and

(c) 18 November 1985.

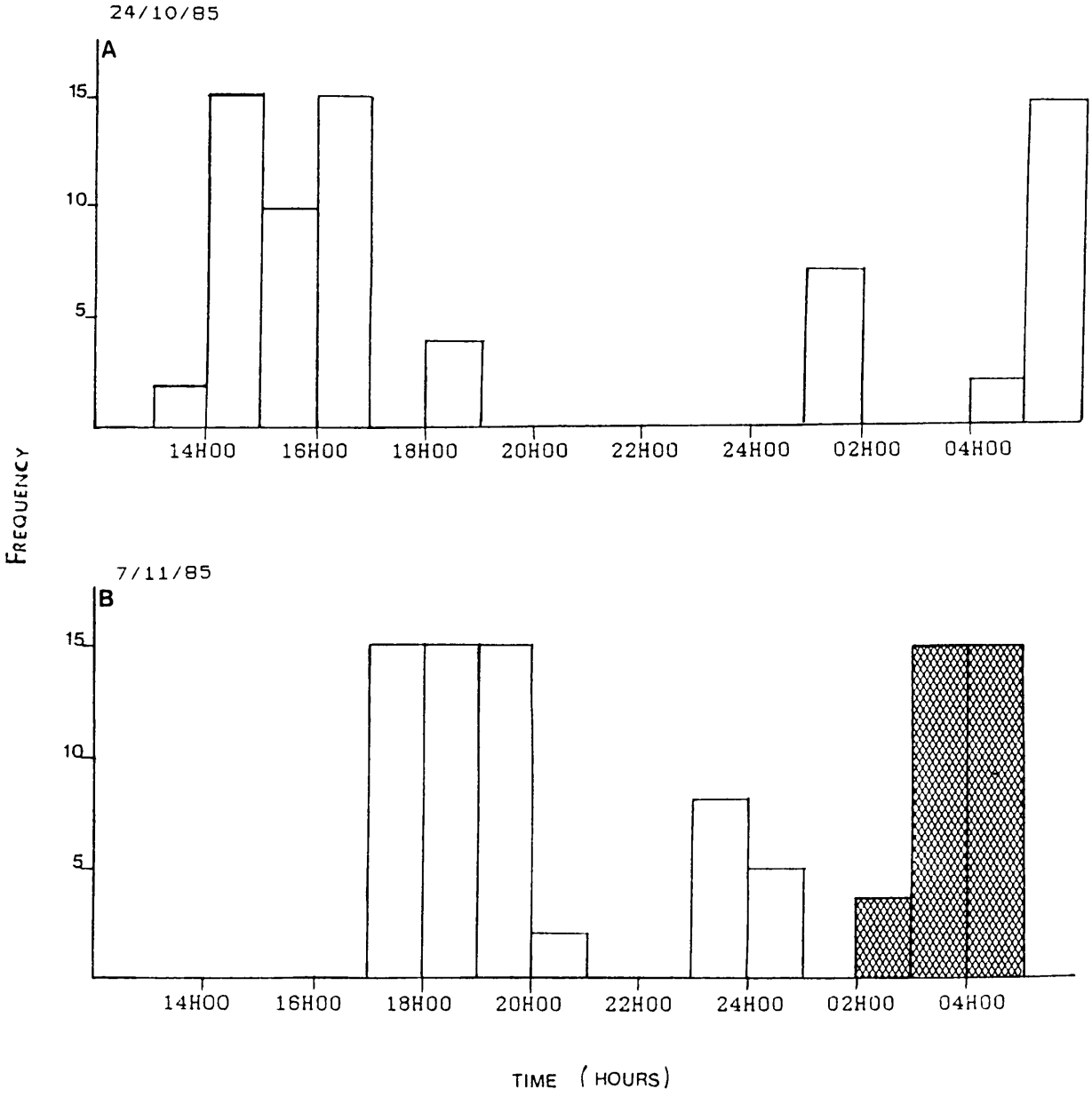

FIG. 11: Changes in frequency of suckling by young of Female B between 13h00 and 06h00 during:

(a) 24 October 1985 and

(b) 7 November 1985.

The shaded area represents the time period during which the young of Female B was suckled by Female A.

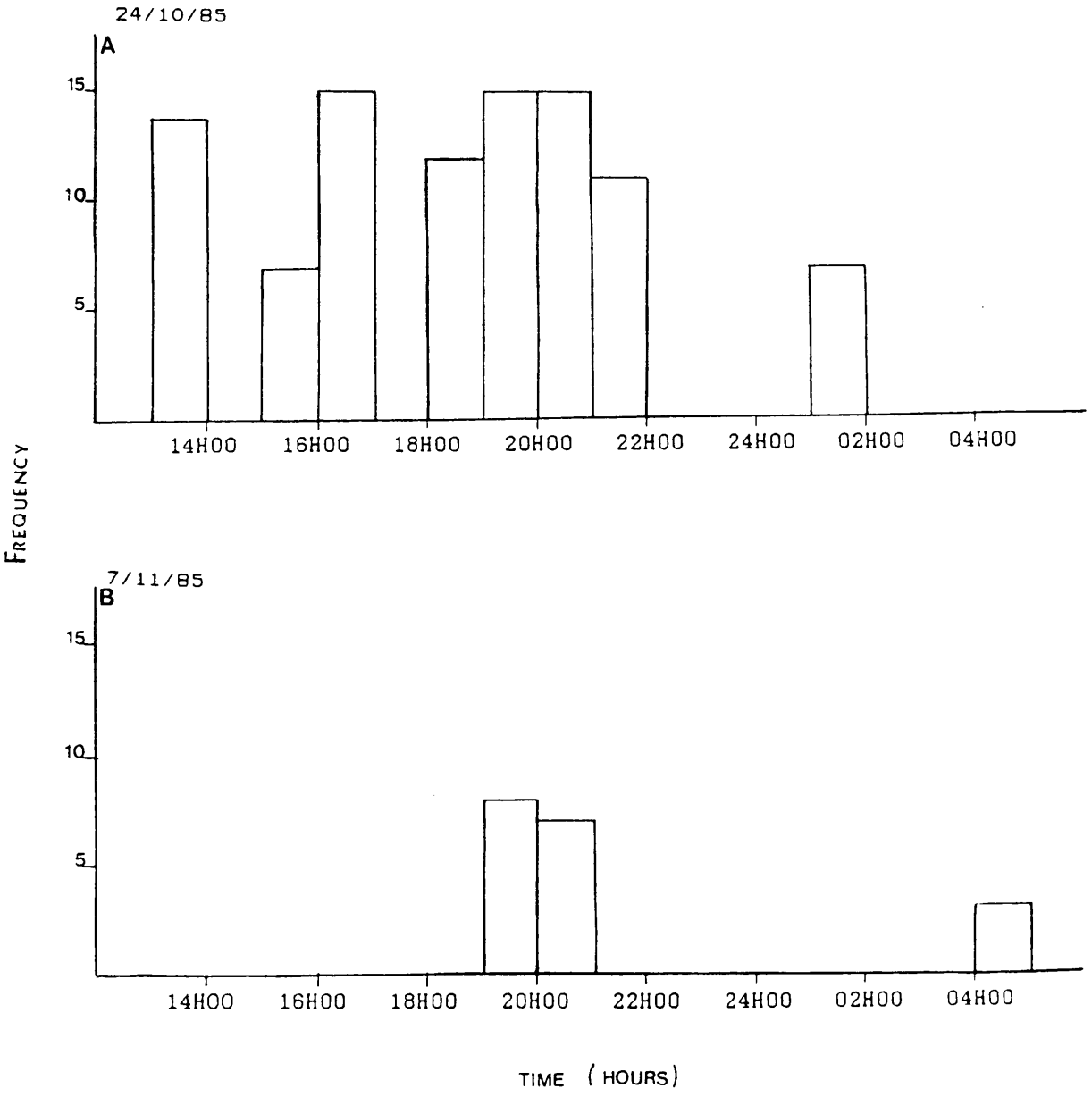

FIG. 12: Changes in frequency of huddling against female by young of Female B between 13h00 - 06h00 during:

(a) 24 October 1985 and

(b) 7 November 1985.

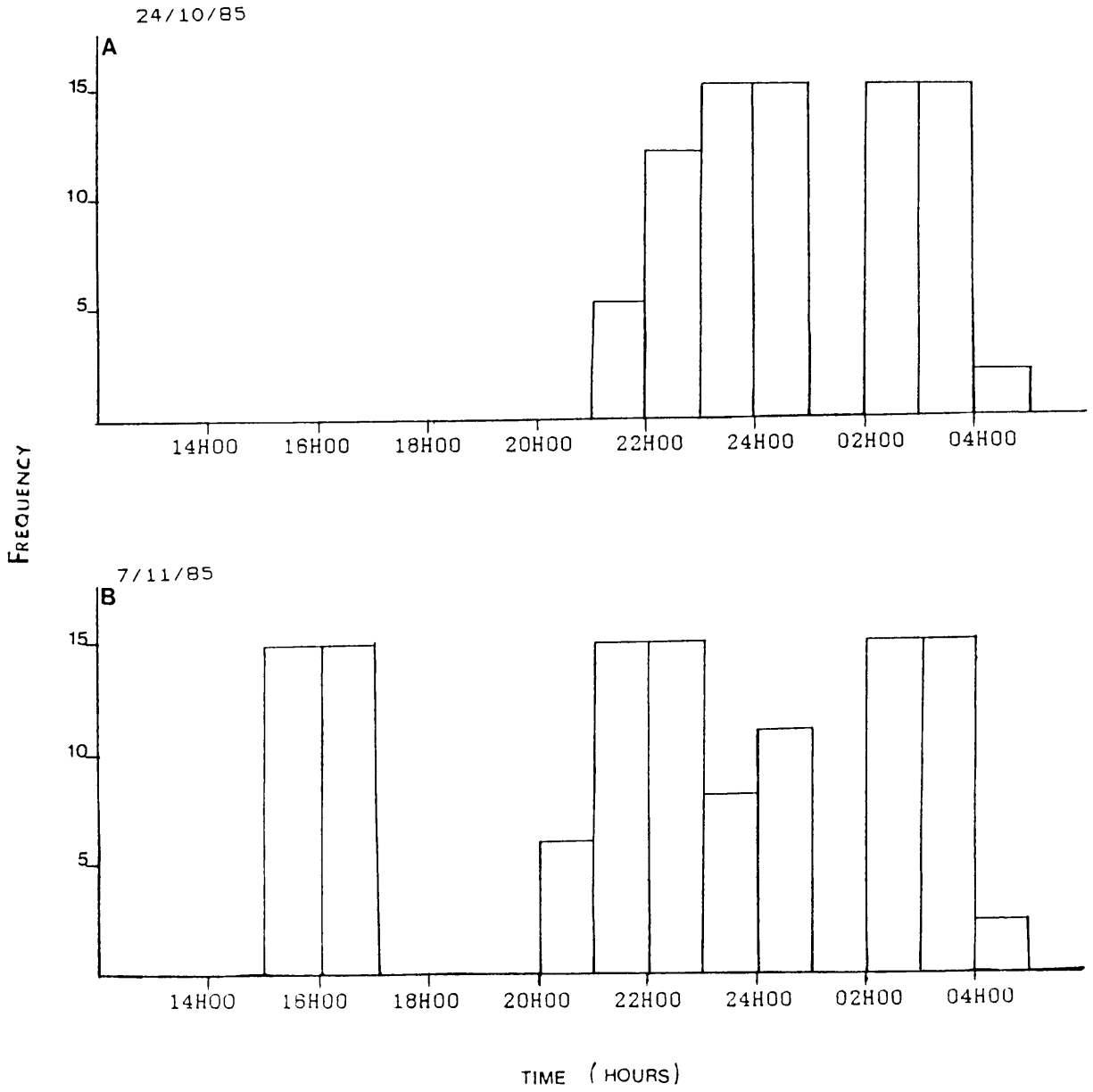

FIG. 13: Changes in the frequency of being alone by young of Female B between 13h00 and 06h00 during:

(a) 24 October 1985 and

(b) 7 November 1985.

The percentage time spent suckling by the young of Female B during the first and second sessions was about 20 %. The percentage of time that the young of Female A suckled during the three sessions was 20 %, 15 % and 10 % respectively.

Huddling was recorded whenever the young lay close to the mother or another female. Huddling, by the young of Female B, occurred at a high frequency from 13h00 to 14h00, 15h00 to 16h00 and 18h00 to 22h00 on 24 October 1985 (Fig. 12a).

During this session, huddling was again recorded from 01h00 to 02h00 and 04h00 to 05h00. During the second session (Fig. 12b) huddling occurred only from 19h00 to 20h00 and 04h00 to 05h00. During the session on 18 November 1985, no huddling was recorded. Huddling occurred at high frequencies during the first session (Fig. 9a) by the young of Female A. It occurred mainly from 17h00 to 23h00 during this session. During the session on 7 November 1985 (Fig. 9b), huddling occurred from 13h00 to 17h00 and again between 22h00 and 02h00. Huddling occurred only from 14h00 to 16h00 and 03h00 to 05h00 on the last session.

The young were recorded as being alone when the mother had left the nestbox or whenever the young ventured out of the nestbox or rested outside the nestbox on their own. During the first session the young of Female B were alone from 21h00 to 01h00 and again between 02h00 and 03h00 (Fig. 13a). On 7 November 1985 the young of Female B were alone from 14h00 to 17h00 and for the largest part of the period from 20h00 to 04h00 (Fig. 13b). These pups were alone during the whole observation session on 18 November 1985. Female A left the pups alone between 16h00 and 17h00 and again between 22h00 and 01h00 on the first session (Fig. 10a). They were also alone from 03h00 to 05h00. On 7 November 1985 the young were alone for most of the time between 18h00 and 05h00 (Fig. 10b). During the last session the pups were alone for almost the whole session except between 14h00 and 17h00 and again from 03h00 to 06h00 (Fig. 10c).

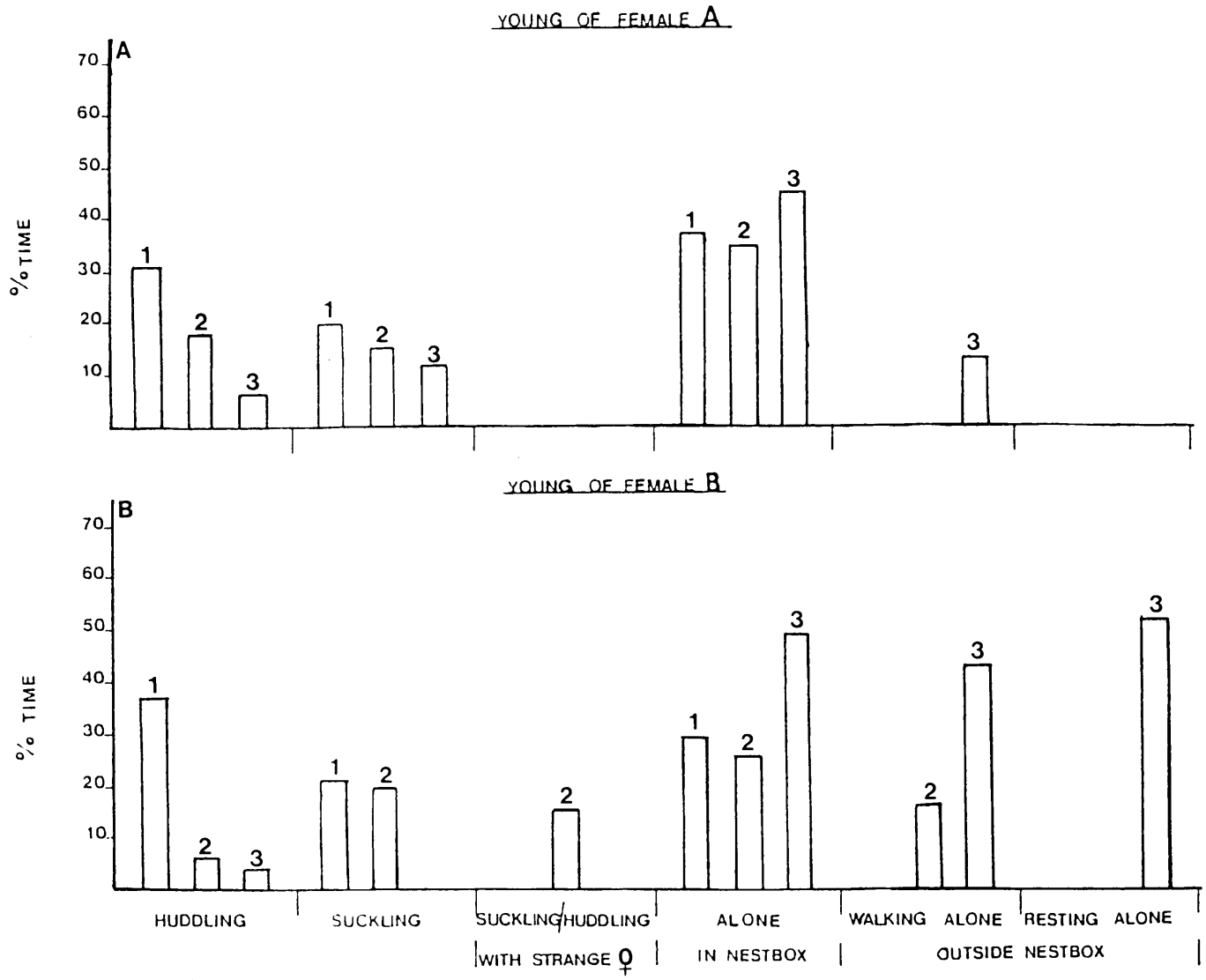

FIG. 14: The percentage time spent by (a) the young of Female A and (b) the young of Female B on different behavioural categories during the three observational sessions. Numbers 1, 2 and 3 represents the observational sessions undertaken on:

(a) 24 October 1985,

(b) 7 November 1985 and

(c) 18 November 1985, respectively.

The percentage time spent by the young of Females A and B on the different behavioural categories, are presented in Figs. 14a and b. The young of both females gradually spent less time in huddling and suckling and more time alone in the nestbox and walking outside the nestbox without the mother. The young of Female B started spending more time resting outside the nestbox during the last session. Only four young of the litter of eleven that was born on 25 November 1985, were reared by the mother. None of her young were found dead. Another female consumed her newborn pups shortly after discovery. In this study all the pups that survived the first day reached weaning age. Female B did not spend any time with her pups when they were 44 days old and they were able to successfully search for food.

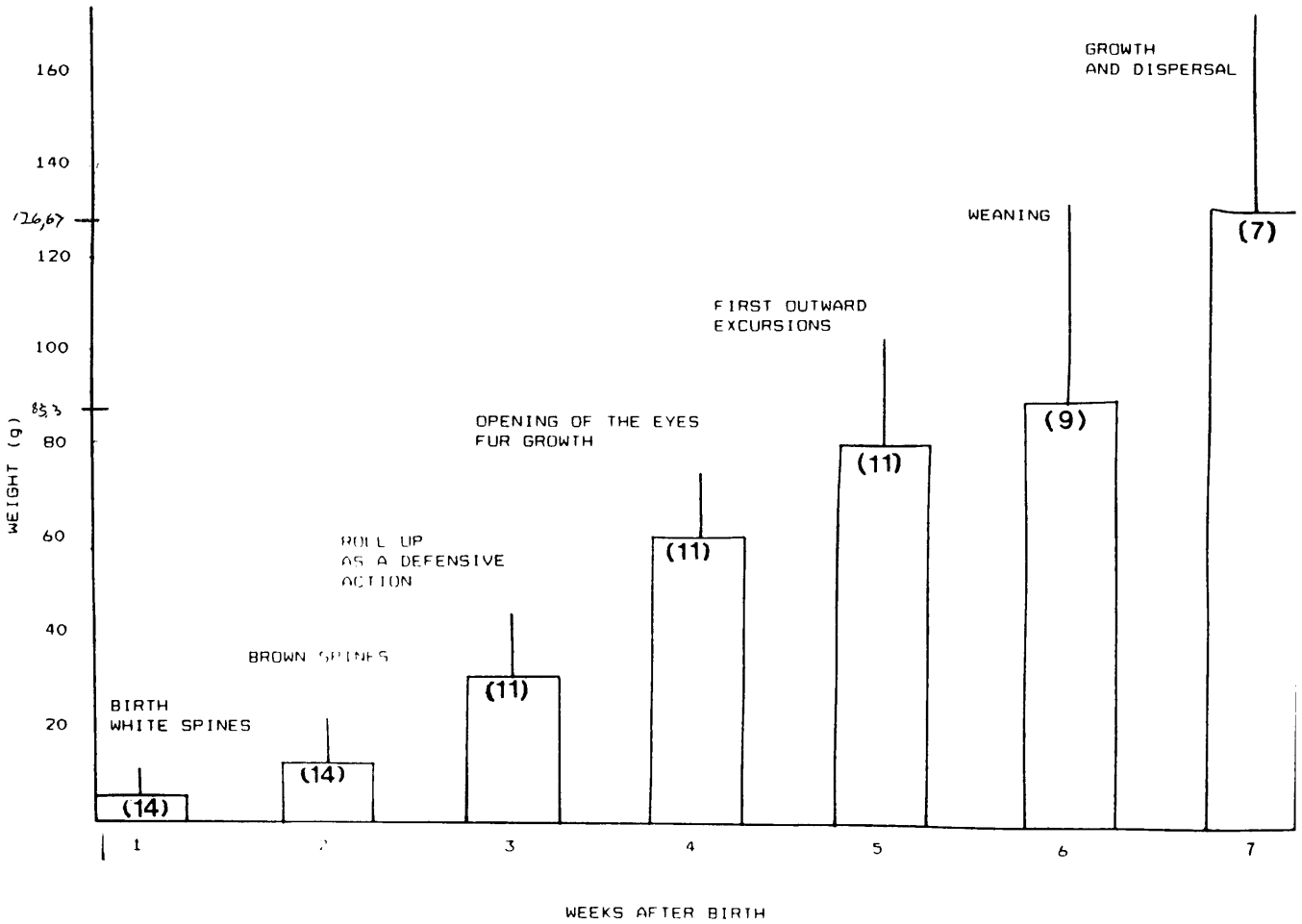

FIG. 15: Growth and development of the South African hedgehog from day of birth to day 57 after birth. The histogram represents age specific mean body mass and the vertical lines the standard deviations of the means. (Figures in brackets denote sample sizes).

Growth and development

A grafic illustration of the development and weight increase of young hedgehogs from birth to week six is presented in Fig. 15. At birth the spines were normally covered by skin and appear as little pimples on the surface. The first few white spines appeared a few hours after birth. New spines grew in distinct tracts with a parting down the middle of the back from the head to the tail. The mean weight at birth was 9 ± 1,4g (N = 16). At the end of the first week the brown spines started to grow up between the white ones. From about 15 days of age the white spines were hardly visible between the brown spines. At the end of the first week the mean weight of the young was 22 ± 4,8g (N = 8). At the end of the second week the young started rolling up as a defensive action and had a mean weight of 40 ± 9,3g (N = 11) and at the end of the third week their eyes opened and their mean weight was 70 ± 16,3g (N = 14). They started to leave the nestbox for short excursions when they were four weeks old although the mother still spent a little time with them. At this stage they weighed 104 ± 12,1g (N = 11). At the end of the fifth week they were weaned and started searching for their own food. From the sixth week, they started finding their own resting sites away from the place that they were born. The young did not mate in the same reproductive season that they were born in. Matings were only recorded in the next mating season after the winter season.

During the first observation session, Female B mated with the male present in the enclosure. She had a second litter on day 48 after her first litter was born and a third pup on 2 January 1986.

DISCUSSION

Young of South African hedgehogs are born from the end of September to the end of January (Smithers 1983). The mother lies down and suckles them soon after birth. Males play no part in the rearing of the young and the female suckles them mainly during the day and early evening. Meritt (1980) noted 6-8 nursings during a 12 hour daylight period in the European hedgehog. Huddling against the females also occured mainly during the day and early evening. The young were left alone from about 22h00 until early morning when the females returned to the nestboxes to suckle the young. The females left the nestboxes to feed, drink and rest outside.

They do not cover the young with nesting material, as observed by Herter (1965) before they leave the nestboxes. According to Rautenbach (1975) litter size ranged from three to six. Jacobsen (1981) recoded the birth of nine young of which four survived. Smithers (1983) recorded litter sizes varying from four to six. According to Walhovd (1984) the average litter size for the European hedgehog **(Erinaceus europaeus)** in Denmark is five. Deanesly (1934) recorded a maximum of seven with an average of five but as many as 10 ruptured follicles in two ovaries were counted. Several authors i.e. Morris (1961), Herter (1965), Parkes (1975), Morris (1977), Lienhardt (1979) and Kristiansson (1981) reported on litter sizes of between two and ten young with average litter sizes of between 4 and 7. As in the present study, Herter (1938) and Kristiansson (1981) recorded litters up to 11 young.It has been indicated by Deanesly (1934) that some hedgehogs can produce two litters per season. According to Kristiansson (1981) and Walhovd (1984) this does not occur in Sweden. Walhovd (1984) attributed this to the fact that no immediate post-partum oestrus exists in the hedgehog and that there is no cycle during the first part of lactation (Deanesly 1934). During the present study a captive female had three litters during the breeding season.

Estimates of the length of the gestation period in the European hedgehog vary between four and seven weeks. Herter (1938) calculated the gestation period of three litters of European hedgehogs at 34 - 49, 34 - 46 and 35 - 42 days while Ranson (1941) describe the gestation period of one female as not more than forty days. Morris (1961) obtained litters which were born 36 - 57 days after the females had been placed in the breeding pens. He concluded that the minimum duration is 34 - 35 days and the maximum 39 days. Based on observations of six litters born to two females, Meritt (1980) reported that the gestation period exceeds 28 but is less than 40 days. According to Racey (1981) it is possible that depressed body temperature (T_b) during gestation, with a consequent reduction in the rate of fetal growth, is responsible for the variability in estimates of gestation length in heterotherms. Fowler (1988) did further investigations on the effect of daily torpor on the gestation length and his results support the suggestion of Racey (1981). According to Smithers (1983) the gestation period of the South African hedgehog is about 35 days.

During the present study a female did not suckle the young at the age of 44 days and she did not spend any time with them. They were not allowed to enter the nestbox at all and were thus weaned at this age. They started eating solid food from about 28 days of age. The young of two litters of the European hedgehog observed by Morris (1961), ate solid food at 25 - 26 days of age. Herter (1965) states that young of about four weeks old can eat solid food although they still suckle until the age of about forty days in these species. Ranson (1941) found that the family group breaks up 38 - 40 days after the young were born and each of them live solitary thereafter. He found that, no matter how fast the young of the European hedgehog grew, they are incapable of breeding in the season in which they were born. This was also found in the present study in the South African hedgehog. The young of the South African hedgehog thus become sexually active a year after they are born.

CHAPTER 5

ASPECTS OF MALE REPRODUCTIVE BIOLOGY

INTRODUCTION

The first studies on the reproductive cycle in the male hedgehog **(Erinaceus europaeus)** (Marchall 1911; Courrier 1927; Allanson 1934; Mombaerts 1943; Girod and Curé 1965; Saure 1969) showed that the exocrine and endocrine functions of the testis are activated in winter, at the end of hibernation, as in many other hibernators (see review in Wimsatt, 1969). Male hedgehogs in Europe exhibit a seasonal cycle in testosterone characterized by low levels in autumn and high levels from the end of winter to the middle of summer. The factors influencing the recrudescence of the testosterone levels have not been studied in the South African hedgehog.

In the European hedgehog factors such as photoperiod, T_a, precipitation and food availability has been shown to influence reproductive cycles by several authors (Reiter 1980, Tucker 1981, Frost & Zucker 1983, Myers, Master & Carrett 1985 and Fowler & Racey 1987).

In the blood, the binding of many steroid hormones by specific plasma proteins is now well established (Westphal 1971). Testosterone is known to bind to a protein of high affinity in man (Mercier, Alfsen & Baulieu 1966; Vermeulen & Verdonck 1968; Murphy 1968; Mercier-Bodard **et al.** 1970). The hedgehog is a hibernating and seasonal breeding mammal and it is therefore an interesting animal to use in a study on the changes in the binding capacity of plasma proteins to the steroid hormones during the different seasons.

This chapter reports on seasonal changes in plasma testosterone levels in male South African hedgehogs and confirms the existence of a substance that binds testosterone.

MATERIALS AND METHODS

Animals: Fifteen male hedgehogs obtained from the National Zoological Gardens in Pretoria were kept in concrete enclosures on the experimental farm of the University of Pretoria (25°45'S/28°12'E). They were here exposed to natural conditions of illumination and temperature and were provided daily with food. Heparinized blood samples (2,5 ml) were collected monthly from February 1986 to February 1987 from some of these males by cardiac puncture after anaesthezia with fluothane (ICI South Africa [pharmaceuticals] Ltd). All samples were collected between 12h00-14h00. Plasma were stored, within one hour after collection, at -20 °C until assayed. Rectal temperatures were measured with a fluke 52 K/J thermometer while the animals were still anaesthetized.

Testosterone assay: Plasma testosterone was measured by a radioimmunoassay of duplicate plasma aliquants using a procedure similar to that of Van Aarde and Skinner (1986). To denature sex steroid binding proteins (see Saboureau **et al**. 1982) aliquants were mixed with 0,1 ml NaOH (0,6 M) and incubated at 37 °C for 10 min before extraction (twice) with 4,0 ml diethyl ether (Merck, Darmstadt, FRG). Dried extracts were reconstituted in 0,1 ml phosphate buffer saline (pH 7,0) containing 0,1 % gelatine (w/v) and 0,1 % sodium azide. Standards ranging from 3,9 to 1000 pg testosterone (Δ^4 -androsten-17B-01-3-one; Sigma Chemical Co, Dorset, UK) in 0,1 ml phosphate buffer and buffer blanks were prepared in duplicate and included in each assay. Antiserum in phosphate buffer (0,1 ml) at a dilution of 1:800 was added to standards, reagent blanks and plasma extracts. This was followed by addition of [1,2,6,7- ^{3}H] testosterone (sp. act. 349 mCi/mg; Radiochemical Centre, Amersham, Bucks, UK) in 0,1 ml assay buffer (~ 10 000 cpm). The contents of each tube were mixed thoroughly and incubated at 4 °C for about 24 h.

Separation of antibody bound and free testosterone was carried out at 4 °C by adding 0,8 ml dextran-coated charcoal consisting of a suspension of charcoal (Activole, Merck, Darmstadt, FRG) in assay buffer (0,156 g/100 ml) containing 0,0156 g Dextran T-40 (Pharmacia, Uppsala, Sweden) to the contents of each tube. These solutions were gently mixed for 20 s and incubated at 4 °C for 10 min. The supernatants were decanted into scintillation vials and 4,0 ml scintillation fluid [Ready-solve CP, Beckman Instruments (Pty) Ltd, Johannesburg, South Africa] was added to each vial.

The contents of the vials were mixed properly and radioactivity was measured within 10 h for 2 min, using a Beckman LS 5800 Scintillation Counter.

A standard curve of counts per minute was plotted against the concentrations of testosterone over the range of 3,9-1000 pg/tube. The testosterone content of each tube was determined through interpolation from the standard curve. The recovery of known amounts of [1,2,6,7-^{3}H] testosterone (~ 10 000 cpm) in phosphate buffer to which aliquants (0,1 ml) of pooled plasma 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 concentration of testosterone in plasma samples.

To determine if tritiated testosterone would bind to plasma proteins, pooled plasma from adult males were serially diluted (1:0-1:128) with phosphate buffer. Duplicate aliquants (0,1 ml) of the diluted plasma samples were incubated with 0,1 ml [1,2,6,7-^{3}H] testosterone (~ 10 000 cpm) at 37 °C for 60 min and thereafter for 30 min at 4 °C. Dextran coated charcoal (0,8 ml) were then added following the incubation period of 10 min at 4 °C the solution was centrifuged at the same temperature at 3200 rpm for 10 min. The supernatants were decanted into scintillation vials, scintillation fluid (0,4 ml) added and radioactivity measured as described before.

For the determination of the effect of denaturation of sex steroid binding proteins on extraction efficiency, a duplicate set of plasma dilutions (1:0-1:128) were incubated with 0,1 ml 0,6 M NaOH at 37 °C for 10 min prior to the addition of 0,1 ml ^{3}H testosterone in PBS buffer. Testosterone was extracted as described before after incubating both sets at 37 °C for 10 min. Extracts were decanted into scintillation vials and dried under N at 37 °C. Scintillation fluid (4,0 ml) was added and radioactivity measured.

Validations: The antiserum was raised in a rabbit against testosterone-3-carboxymethyl-oxime conjugated to bovine serum albumin as described by Millar and Kewley (1976). Cross-reaction with all major naturally occurring steroids as determined by the supplier (R P Millar, Departement of Chemical Pathology, University of Cape Town, RSA) was <0,1 % except for dihydrotestosterone for which it was 5,1 %. The sensitivity of the assays, defined as twice the standard deviation of the blank values (Jeffcoate 1981) ranged from 0,05-0,20 ng/ml (mean 0,08 ± 0,06 ng/ml; N = 6). Recovery estimates varied from 82 to 91 % (mean 87 ± 3,3 %; N = 6). Intra-assay coefficient of variation calculated as described by Jeffcoate (1981) was 6,02 %. Inter-assay coefficient of variation for a plasma sample containing 125 pg testosterone/ml was 18 %. Testosterone values in serially diluted plasma followed the expected trend and was closely parallel to the standard curve.

Statistics: A Spearman correlation coefficient was calculated between the mean daylight lengths, minimum temperature and maximum temperature of each period and the mean testosterone levels in each of the three periods. The student's t-test was applied to test significance of differences between mean monthly testosterone levels.

The mean monthly testosterone values were fitted to a fourth grade polynome and the sampling period from February 1986 to February 1987 was devided into three periods according to the turning points of the polynome. There were no significant changes in the testosterone levels during the first period which covered the months February 1986 and March 1986. The second period represents the months April 1986 to November 1986 where the testosterone increased and the third period covered the months December 1986 to February 1987 when the testosterone levels started decreasing.

RESULTS

Extraction efficiency of tritiated-testosterone from plasma increased with a decrease in plasma concentration (Fig. 16). Binding of [^{3}H] testosterone to undiluted plasma was 64 % and at a dilution of 1:128, 12 %. Extraction efficiency increased with a decrease in plasma concentration (Fig. 17) and was also more efficient after denaturation of binding protiens with 0,6M NaOH (Fig. 17).

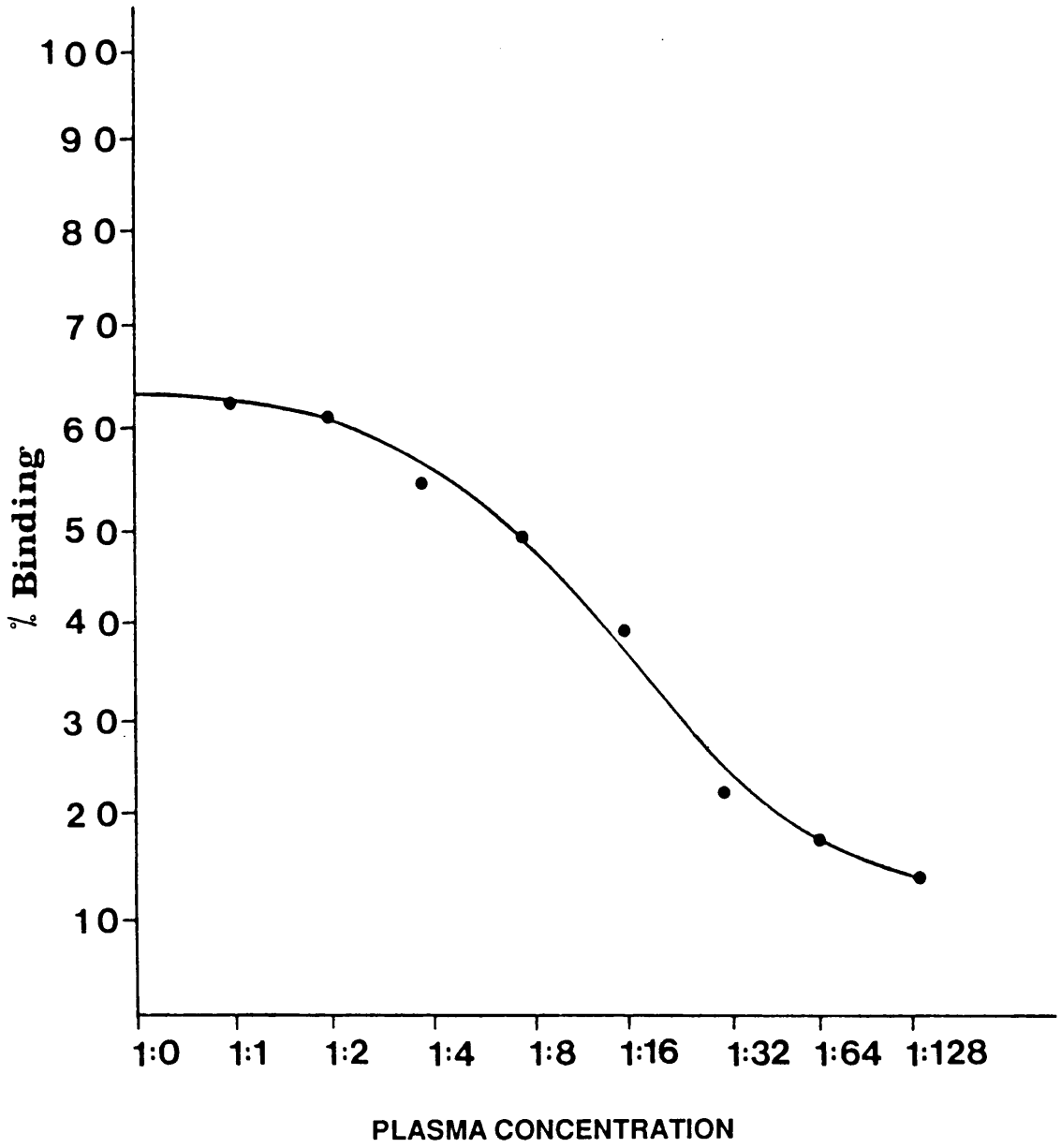

FIG. 16: Binding of 3H testosterone to male plasma diluted with phosphate buffer saline.

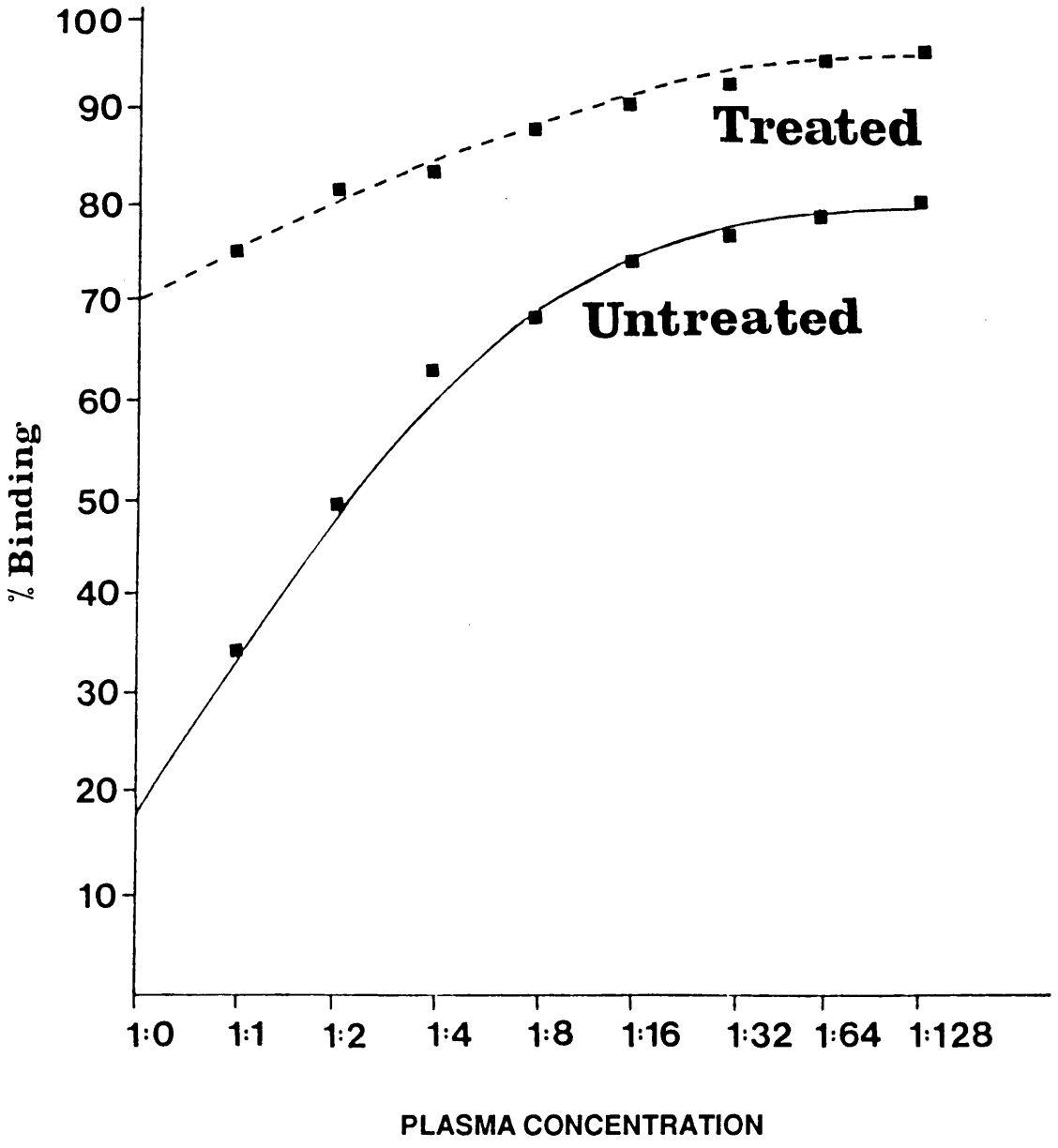

FIG. 17: The effect of denaturation of plasma with 0,6M Na0H on extraction efficiency of an adult male plasma pool.

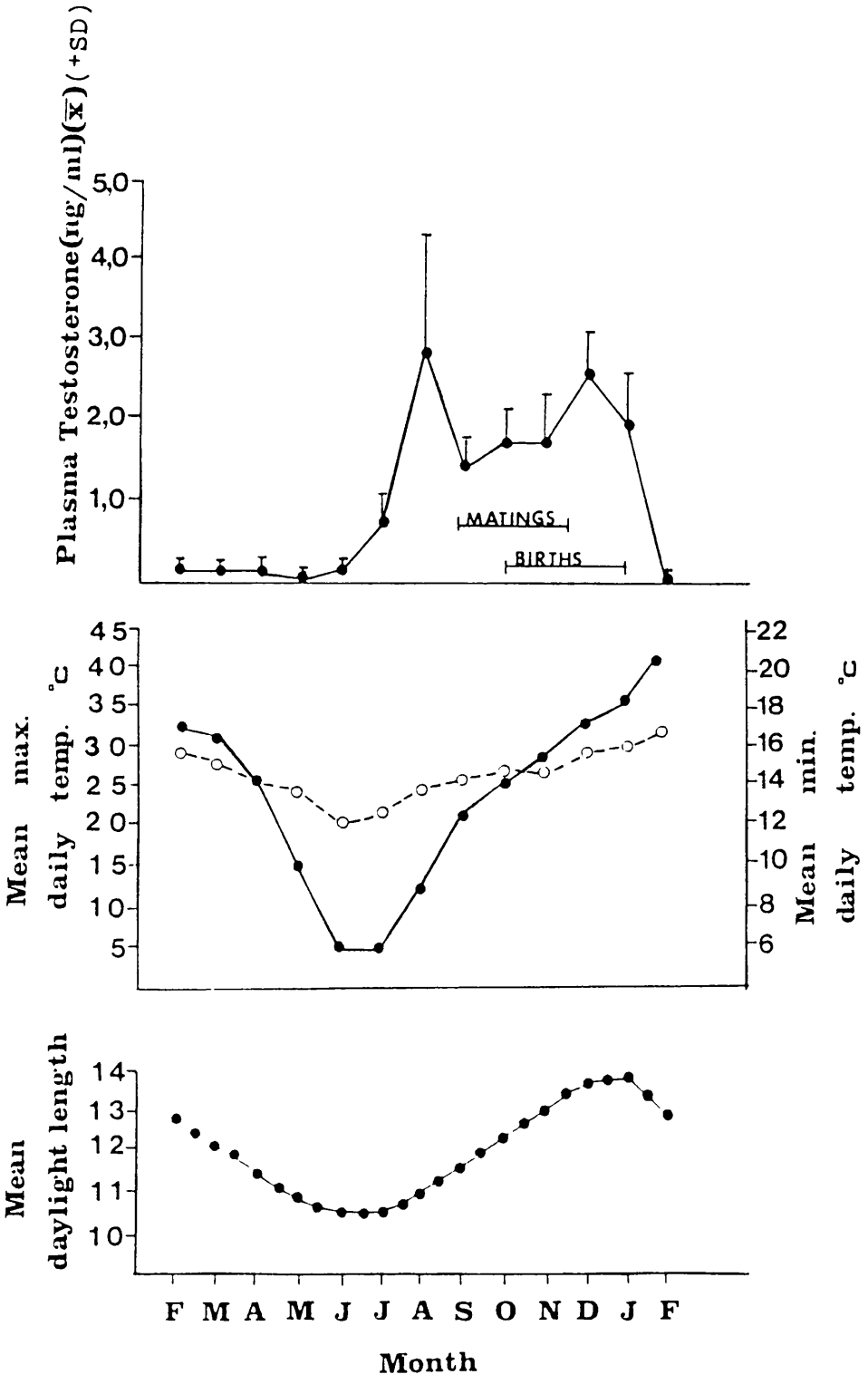

FIG. 18: Mean plasma testosterone levels in adult male hedgehogs, maximum daily temperatures (o----o), minimum daily temperatures (●—●) and daylight lengths as recorded monthly from February 1986 to February 1987. (Vertical lines denote one standard deviation of the mean).

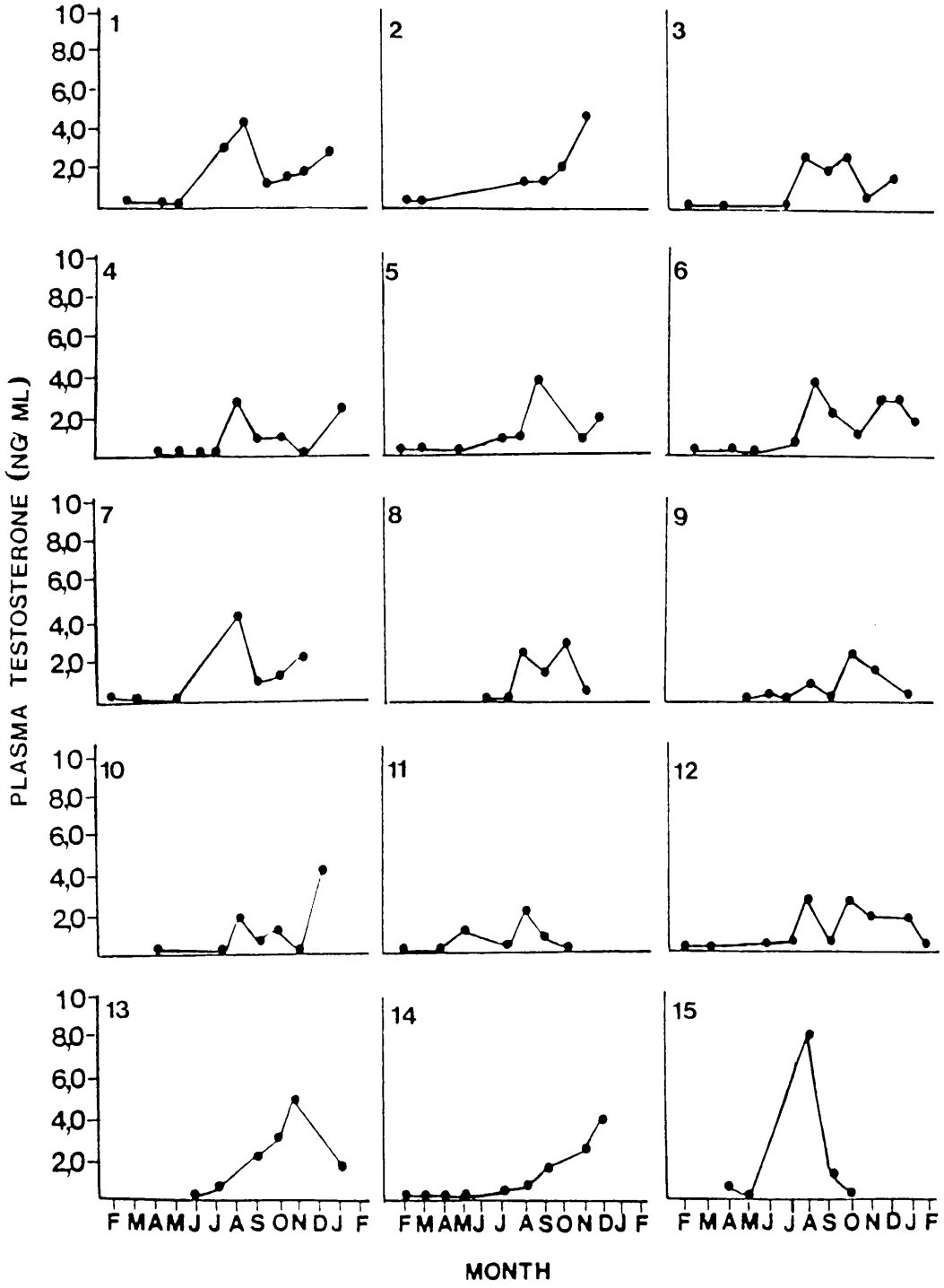

FIG. 19: Plasma testosterone levels of individual male hedgehogs recorded monthly in captivity from February 1986 to February 1987.

Mean plasma testosterone concentration remained low from February to June (0,05-0,24 ng/ml) (Fig. 18) but increased significantly ($t = 3,77$; $P< 0,01$) from July to August.

Testosterone levels peaked in August (2,85 ± 1,37 ng/ml; N = 15) and December (2,73 ± 0,36 ng/ml; N = 6). Levels remained high from August to January and the peak in August was followed by a non-significant ($t = 2,75$; $P< 0,01$) decrease in September (1,49 ± 0,24 ng/ml; N = 15) and a gradual increase during October and November. The peak in December (2,73 ± 63 ng/ml; N = 6) was not significantly higher than the mean value recorded for November ($t = 1,58$; $P< 0,01$). The testosterone levels of individual male hedgehogs peaked during August (Fig. 19).

Matings (n = 3) were recorded from the beginning of September to December and litters (n = 4) were born between October and January.

During the period February to March there was no significant correlation between the change in testosterone levels and the change in maximum temperature ($r_s = -0,12$; $p < 0,05$), the change in minimum temperature ($r_s = -0,12$; $p < 0,05$) and the change in daylight length ($r_s = 0,124$; $p < 0,05$). During the second period, April to November, there was a significant correlation between the change in testosterone levels and the change in maximum temperature ($r_s = 0,27$; $p <0,05$) and daylight length ($r_s = 0,42$; $p < 0,05$).

During the period December to February there was a significant negative correlation between the change in testosterone levels and the change in maximum temperature ($r_s = -0,73$; $p < 0,05$) and the minimum temperature change ($r_s = -0,72$; $p < 0,05$). There was also a positive correlation between the changes in testosterone levels and changes in daylight length ($r_s = 0,73$; $p < 0,05$).

DISCUSSION

The seasonal changes in testosterone levels described in the present study is similar to that described in the related European hedgehog **(Erinaceus europaeus L).** Absolute circulating levels of testosterone (0,05 to 2,73ng/ml) in the South African hedgehog were lower than those of the European hedgehog (0,56 to 20ng/ml) but this might be ascribed to differences in the radioimmunoassay procedures and specificity of the antisera used to determine testosterone levels. The breeding season in the South African hedgehog, extending from September to January, is characterized by high circulating testosterone levels and a decrease at the end of summer. Very low levels of testosterone were recorded from February to June. Testicular activity resumed at the end of winter (July to August) when the hedgehogs were still hibernating.

In many mammals plasma testosterone is strongly bound to a specific protein known as sex binding protein or testosterone binding globulin (Saboureau **et al.** 1982). Little information on the existence of such a protein in hibernating species was available before Laurent, Maurel, Saboureau & Boissin (1981) proved the presence of a testosterone-binding plasma protein in the European hedgehog. In the South African species the extraction efficiency of testosterone from plasma increased with prior denaturation of proteins, indicating that a substance that binds testosterone is also present in this species.

In both the European and the South African hedgehog the phenomenon of testicular recrudescence occurs at the end of winter during the hibernating period. The reproductive period can thus start as soon as the cold season ends, as the onset of the reproductive period depends on the time of spring arousal (Saboureau **et al**. 1983a). The results on the annual breeding cycle of the hedgehog is compatable with the hypothesis of Pengelly Asmundson (1974), who stated that spring arousal may be an endogenous event caused by external conditions, and so become synchronized with those conditions. Saboureau, Castaing & Boissin (1984) agrees with this and showed that this endogenous factor is not influenced by the external factors such as environmental temperature and food availability.

By inplanting silastic capsules filled with testosterone and releasing a hormonal level nearly equivalent to those measured during the reproductive season, they showed that hibernation is only possible after a dramatic decrease in plasma testosterone levels. Castration, however, modified neither the beginning of hibernation nor the resumption of locomotor activity (Saboureau **et al.** 1984).

In the present study correlations existed between the changes in testosterone levels and the changes in daylight length and the changes in maximum temperatures. It seems as if these latter mentioned factors only influences the levels to a certain extend during certain periods of the year. It might be that an initial change in both these external factors serves as a trigger for an increased production of testosterone before the reproductive period and likewise a decrease of testosterone production after the reproductive period when these factors change again. Fowler & Racey (1987) found that the most important influence on male testosterone and body mass cycles is the rate of change of the photoperiod. Observations by Saboureau **et al.** (1983a) showed that climatic factors can influence the sexual function and duration of reproduction in relation to lattitude. Saboureau & Boissin (1983b) showed that the peripheral metabolism of testosterone and its metabolic clearance rate change seasonally thereby contributing to our understanding of the control of recrudescence of testicular functions. Fowler & Racey (1987) and Saboureau (1981) stated that melatonin can be involved in the timing of both testicular recrudescence in the following spring and the duration of the autumn refractory period.

CHAPTER 6

ASPECTS OF FEMALE REPRODUCTIVE BIOLOGY

INTRODUCTION

The end of anoestrus marks the beginning of the sexual season and this is characterized by changes in metabolism, gonads and endocrinological secretions (Ecstein & Zuckerman 1956). Little information is available however on the above mentioned aspects in the female hedgehog. Published data include histological changes of reproductive organs during the reproductive cycle of the European female hedgehog (Deanesly 1934; Asdell 1964; Marchal-Dacheux & Peyre 1970). More recently Sharma & Mathur (1974) published data on histomorphological changes in the reproductive tract of female **Hemiechinus auritus collaris** in relation to the estrous cycle. Munshi & Pandey (1987) published information on the oestrous cycle of the large eared hedgehog (**Hemiechinus auritus** Gmelin) by daily examination of vaginal smears. Fowler (1985) did an extensive study yielding information on the effect that environmental cues have an endogenous endocrine cycle.

Most studies indicate that the hedgehog is a long-day breeder and that recrudescence of reproductive organs occur prior to the end of the hibernation period. This is also the case in other hibernators (Wimsatt 1969). It is also well known that females become sexually active later than the males and that in breeding females the onset of hibernation is delayed until after the young are weaned (Fowler 1985). According to him this delay is brought about by continuing high levels of ovarian and hypothalamic activity, added to elevated metabolism.

Saboureau & Castaing (1986) worked on reproductive hormones in the European hedgehog but no information is available on steroid hormone changes during the annual cycle of the female South African hedgehog. This chapter deals with aspects of reproduction in the South African hedgehog with emphasis on seasonal changes in plasma progesterone and urinary progesterone levels during the breeding season.

MATERIALS AND METHODS

Animals: Female hedgehogs (N = 9) obtained from the Zoological Gardens in Pretoria were kept with males as described in Chapter 1. Heparinized blood samples (2,5 ml) were collected monthly from April 1986 to March 1987 by cardiac puncture after anaesthezia with Fluothane (ICI South Africa [pharmaceuticals] Ltd). All samples were collected between 12h00 and 14h00 and plasma was stored within an hour after collection at -20 °C until assayed.

Urine samples were collected from August 1985 to August 1986. During certain months daily urine samples were collected and during the other months three samples per week were collected. The samples were collected by putting the females in small cages between 16h00 and 23h00. The specially designed cages made provision for a gause flooring which covered a funnel shaped receptical below. Daily samples were taken during August and September 1985 whilst for the other 11 months, samples were taken twice weekly. During certain sampling periods, however, it was not possible to collect urine. All the urine was stored at -20 °C and centrifuged before assayed.

Radioimmunoassay: Urinary and plasma progesterone were measured by radioimmunoassay in duplicate and triplicatè aliquants respectively. The procedure used was similar to that of Van Aarde (1985) who used a modified method of Haresign, Foster, Haynes, Crighton & Lamming (1975).

Progesterone was extracted from the urine and plasma samples (100-200 ml) with 4,0 ml petroleum ether (Merck, Darmstadt, FRG). The extraction procedure included mixing of the ether and samples on a vortex mixer for five cycles of one minute each, followed by freezing at -20 °C for 60 min. Dried extracts were reconstituted in 0,1 ml phosphate buffer (PBS) (pH 7,6) containing 0,1 % gelatin (w/v) and sodium azide. Standards ranging from 3,9 to 500 pg progesterone (Δ^4-pregnene-3,20 dione; Sigma Chemical Co, Dorset, UK) in 0,1 ml phosphate buffer and buffer blanks were prepared in triplicate for plasma progesterone assays and in duplicate for urinary progesterone assays and included in each assay. Antiserum in 0,1 ml PBS was added to standards, reagent blanks and plasma and urine extracts.

This was followed by addition of [1,2,6,7 -^{3}H] progesterone (code TRK 413, 308 mCi/mg; Radiochemical Centre, Amersham,Bucks, UK) in PBS (~ 10 000 cpm). The contents of each tube was mixed thoroughly and incubated at 4 °C for ~ 24 h.

Progesterone bound to the antibody was seperated from the free steroid by the addition of 0,8 ml dextran coated charcoal consisting of a suspension of charcoal (Aktivole, Merck, Darmstadt, FRG) in assay buffer (0,156/100 ml) containing 0,0156 Dextran T-40 (Pharmacia, Uppsala, Sweden) to the con- tents of each tube. The solutions were mixed for 20 s and incubated at 4 °C for 10 min. The supernatants were decanted into scintillation vials and scintillation fluid (4,0 ml) [Ready Solve CP; Beckman Instruments (Pty) Ltd, Johannesburg, South Africa] was added to each vial. The contents of the vials were mixed properly and radio-activity were measured within 10 h by using a Scintillation Counter.

A standard curve of counts per minute was plotted against con= centrations of progesterone over the range of 3,9-2000 pg/tube. Progesterone contents of each tube were determined by interpolation from the standard curve. The recovery of known amounts of [1,2,6,7 -^{3}H] proges- terone (~ 10 000 cpm) in phosphate buffer to which aliquants (0,1 ml) of pooled plasma were added, served to determine procedural losses incurred during extraction. To allow for variations in the concentrations of the urine samples, creatinine levels in urine was determined by using a creatinine kit (Sigma Chemical Co, Diagnostic kit no. 555, Labretoria, P O Box 95777, Waterkloof, 0181). Urinary progesterone levels were thus expressed as ng/mg creatinine.

Validations: The sensitivity of the assays, defined as twice the standard deviation of the blank values (Jeffcoate 1981) ranged from 0,05-0,10 ng/ml (mean 0,06 ± 0,02 ng/ml; N = 5) for plasma progesterone assays and 0,05-0,07 ng/mg creatinine (mean 0,054 ± 0,008 ng/mg creatinine; N = 5) for urinary progesterone assays. Recovery estimates for the plasma assays varied between 63 and 84 % (mean 70,6 ± 8,97 %; N = 5) and for urine assays from 91 % to 96,9 % (mean 94,6 ± 2,27 %; N = 5). Intra-assay coefficient of variation calculated as described by Jeffcoate (1981) was 13,5 % and 17 % for urinary and plasma progesterone assays respectively.

Inter-assay coefficient of variation for a urine sample containing 125 pg progesterone/ml was 8,43 %. The inter-assay coefficient of variation for a plasma sample containing 250 pg progesterone/ml was 5,51 %. Progesterone values in serially diluted plasma followed the expected trend and was closely parallel to the standard curve.

RESULTS

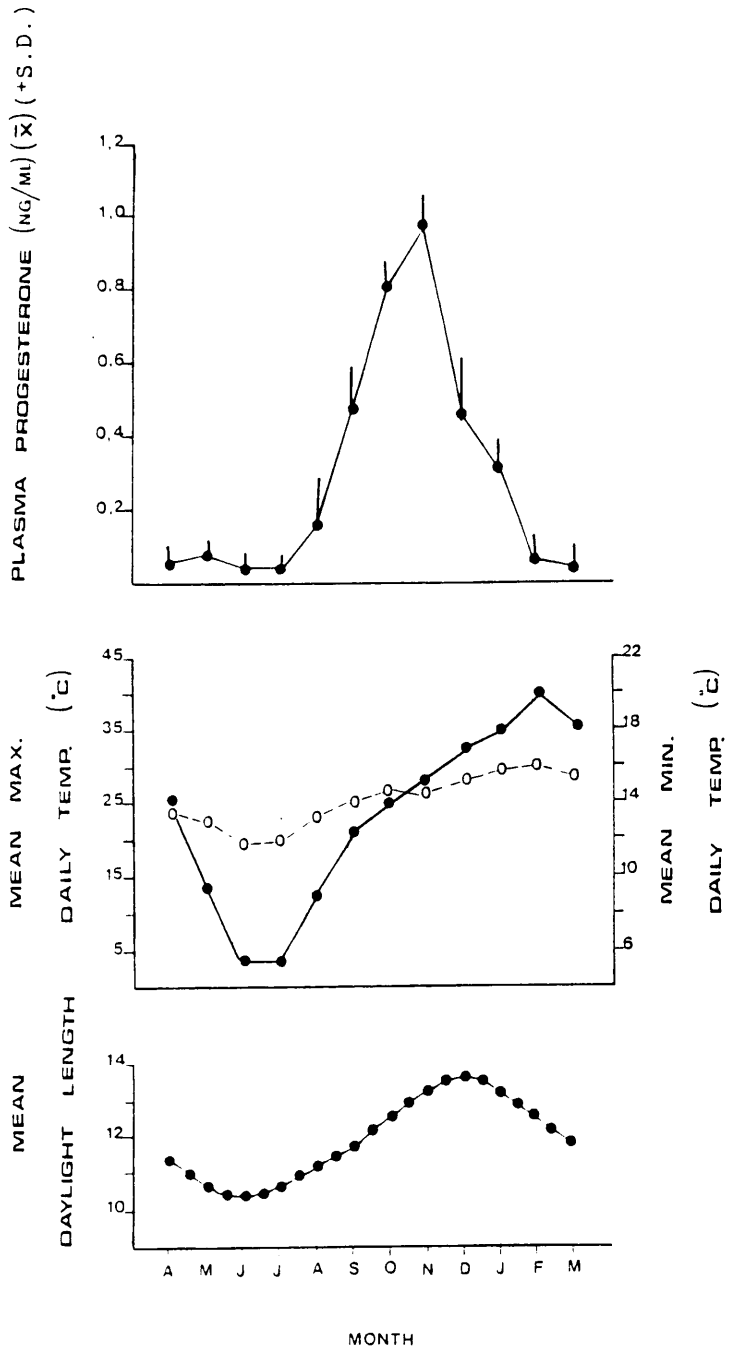

FIG. 20: Mean plasma progesterone levels in adult female hedgehogs, maximum daily temperatures (o----o), minimum daylight temperatures (●—●) and daylight lengths as recorded monthly from April 1986 to March 1987. (Vertical lines denote one standard deviation of the mean).

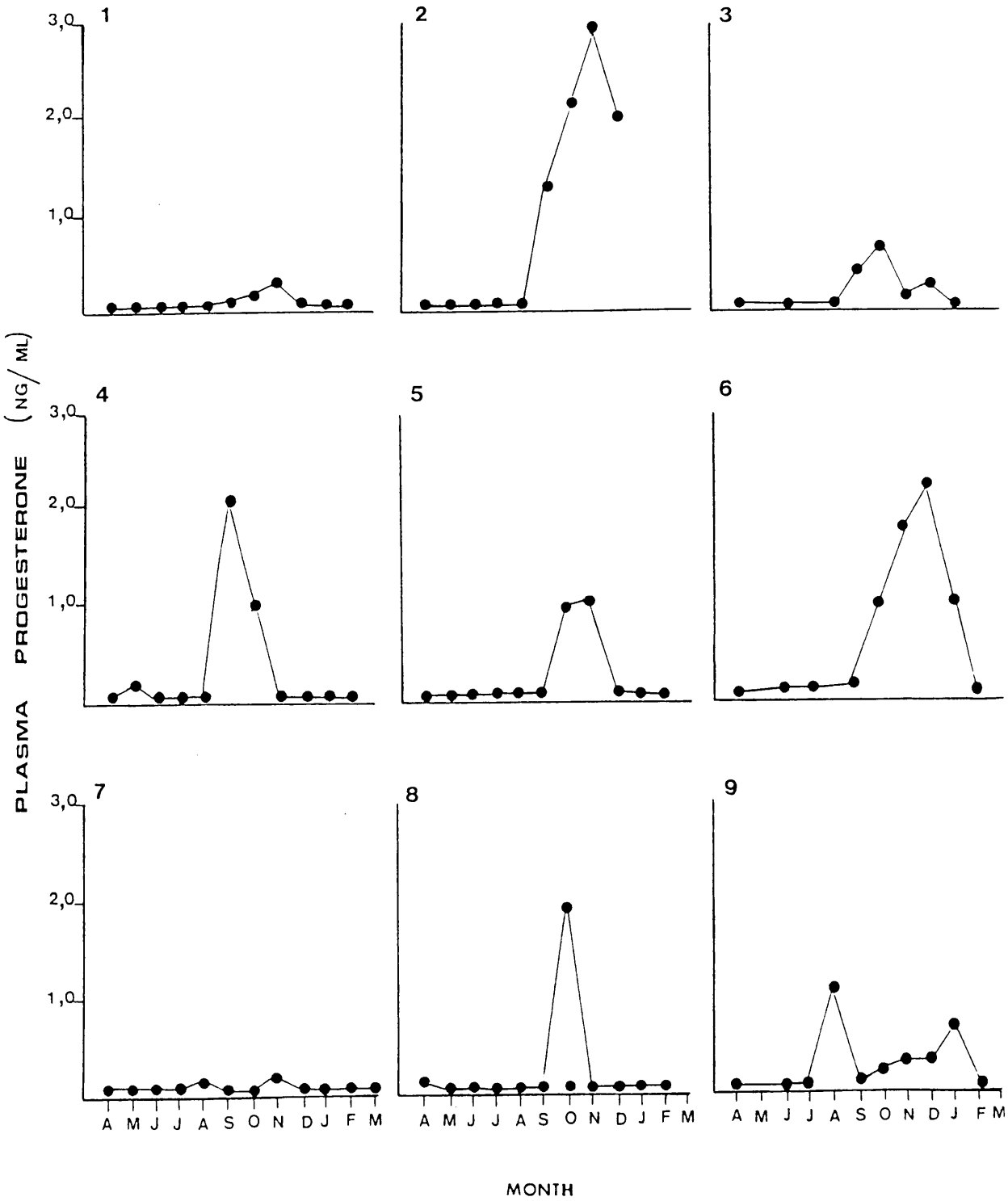

FIG. 21: Plasma progesterone levels of individual female hedgehogs as recorded monthly from April 1986 to March 1987.

Plasma progesterone

Mean plasma progesterone levels remained low from April to July 1986 (0,06 - 0,09 ng/ml) (Fig. 20). The increase in August was not significant ($t = 0,608$; $p < 0,01$). The mean levels peaked in November (0,88 ± 0,07 ng/ml; N = 11) and this was not significantly higher than the values recorded during the previous or the following months. Lower levels were recorded in February (0,07 ± 0,04; N = 7) and March (0,06 ± 0,02; N = 4).

The individual values for the nine females are given in Fig. 21. Except for females one and seven (both born during November 1985) all the other females showed cyclical ovarian activity between September 1986 and January 1987.

Female 2 had a litter of two pups in December. They were only discovered a few days after birth. To avoid the possibility of the young being killed after handling, they were left alone. Unfortunately the mother did kill and devour the young that same evening.

Urinary progesterone

Urinary progesterone levels as indicators of circulating progesterone levels are presented in Fig. 22a, b, and c. These figures show that female hedgehogs are polyoestrus during the breeding season and anoestrus during the winter season. Cyclical changes in progesterone levels were recorded from August to the end of May.

Female A had at least five oestrous cycles during the breeding season. The mean lengths of the three cycles between 7 October 1985 and 14 February 1986 was 35 days. Baseline values of progesterone varied from the limits of detection (0,05 ng/mg creatinine) to 1,5 ng/mg creatinine. Peak values varied between 7 and 10,4 ng/mg creatinine.

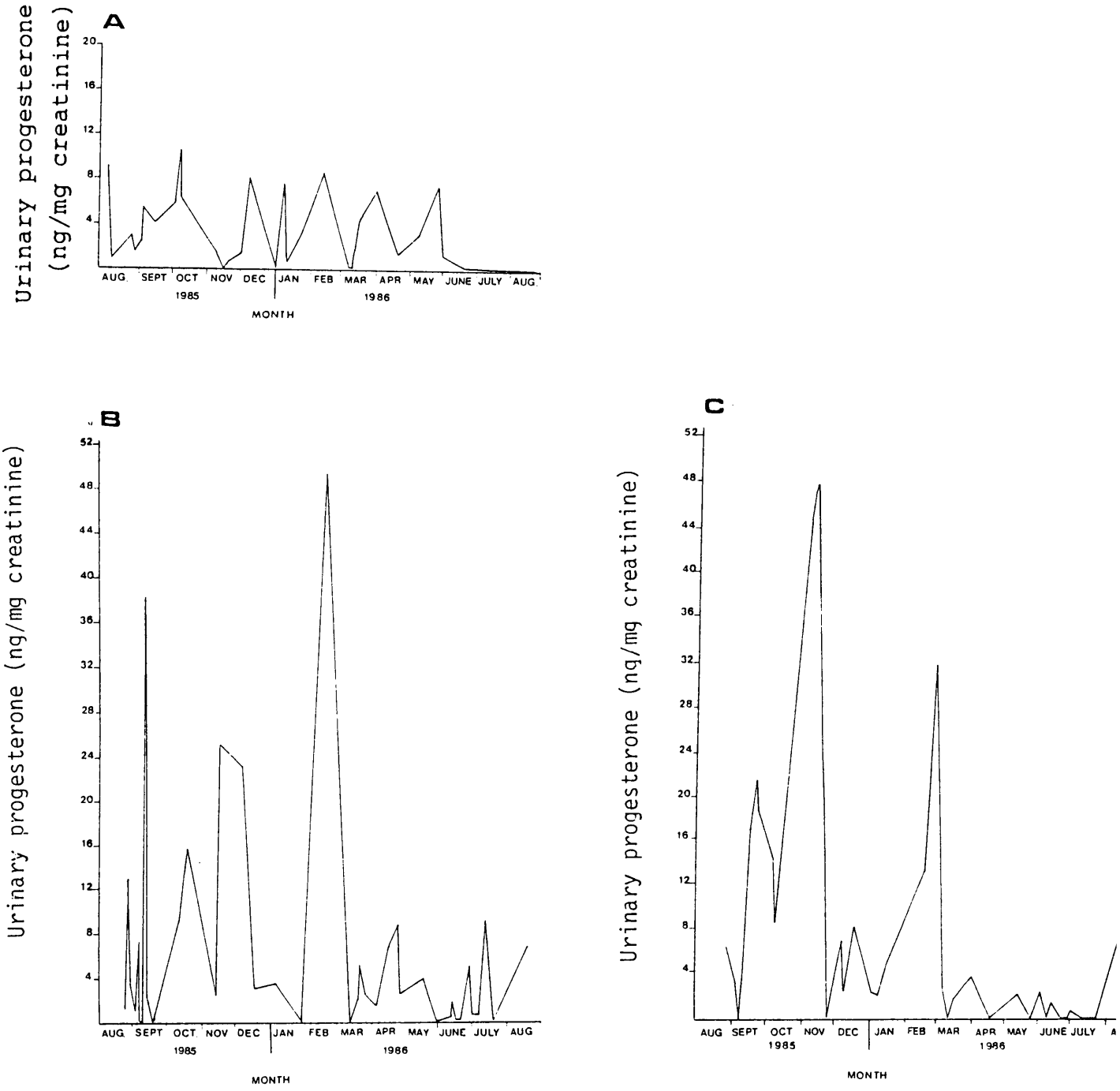

FIG. 22: Urinary progesterone levels (ng/mg creatinine) in three adult female hedgehogs during the period August 1985 to August 1986.

It appears as if there is a correlation between changes in the photoperiod and T_a, and change in plasma progesterone levels.

Female B had four cycles between 12 August and 18 November. The lengths of these cycles ranged from 28 to 38 days with a mean of 32 days. Baseline values of progesterone varied between 0,05 and 2,8 ng/mg creatinine while peak values varied between 12,8 and 49 ng/mg creatinine.

Female C had two cycles between 22 September and 20 December 1985. The length of these cycles were 50 and 39 days. The baseline values were similar to that of Female B. The peak values varied between 18,9 and 47 ng/mg creatinine. It appears as if there was a long cycle or a period of inactivity (extended activity) between September and November 1985. This might be due to the few samples collected in October.

In these females the oestrous cycle length varied between 28 and 38 days (mean 34 ± 8 days; N = 9). None of these females gave birth during this period although Females B and C did have high progesterone levels during February 1986 and November 1985 respectively. The sample sizes during the months January to March were too small to calculate estrous cycle lengths for Females B and C.

DISCUSSION

European hedgehogs generally hibernate from late autumn until spring (Morris 1977). In England the end of the inactive period is at the end of March, breeding occurs between the end of April and June (Ecstein & Zuckerman 1956). According to Deanesly (1934) the females are in anoestrus from October to April. The plasma progesterone and urinary progesterone levels measured in the present study suggest that the female do not cycle from February to the end of August. During the winter anoestrum, immature ova only are in the follicle, and follicular degeneration is especially marked (Asdell 1964). The vagina, uterus and ovaries are regressed during this period (Deanesly 1934).

During prolonged winters hibernating females experience endometrial proliferation, vaginal hypertrophy and follicle growth (Walin, Soivio & Kristoffersson 1968), suggesting that sexual recrudescence begins before permanent arousal. In the South African hedgehog the first signs of cyclic ovarian activity can be seen at the end of August. According to Asdell (1964) there is a remarkable growth of the granulosa during this period of follicular expansion and the preovulatory size of the follicle is 1,25 mm in the European species. According to Deanesly (1934) spontaneous ovulation in spring is followed by one or more dioestrus cycles before mating occur. Saboureau & Castaing (1986) however found that the seasonally polyoestrus European hedgehog is an induced ovulator since there are post copulatory oestradiol and LH peaks in females.

The females in the present study had three or more oestrous cycles during the breeding season. The lengths of the cycles differed from the length determined by Munshi and Panday (1987). Although they also showed that **H. auritus** is a polyestrous species, they determined the mean length of the cycle as 9,9 ± 0,49 days. Based on cyclical changes in vaginal smears they determined the length of pro-estrous, estrous, metestrous and diestrous at 2,5 ± 0,20 days, 3,9 ± 0,32 days, 2,2 ± 0,20 days and 1,8 ± 0,24 days respectively (Fig. 20).

Although the females used for monitoring urinary progesterone levels were seen mating (n = 2) during the breeding season, they failed to become pregnant. The high progesterone levels found during certain months in Females B and C might indicate pseudopregnancies occuring in these animals. According to Asdell (1964) pseudopregnancy is frequent after copulation and the corpus luteum formed then is histologically and endocrinologically similar to that of pregnancy. Repeated pseudopregnant cycles are common in hedgehogs (Deanesly 1934) and ova are often fertilized but they fail to become implanted because of insufficient progestational transformation of the uterus (Deanesly 1934). The extended length of the oestrous cycle reported in the present study maybe ascribed to pseudopregnancies.

The present study showed that there is a correlation between changes in photoperiod and T_a, and the change in plasma progesterone levels, the effect is especially marked in the period after hibernation at the beginning of the breeding season. Fowler (1985) suggested that T_a probably modulates photoperiodic entrainment of endogenous cycles more in the female than in the male. According to Donovan (1986) diestrous cycling begins soon after the females emerge from hibernation, and T_a could act on this, indirectly, via some critical body mass or body condition below which full estrus would not occur. The present study also suggests that changes in T_a and photoperiod plays a role at the end of the breeding season when progesterone levels start decreasing.

CHAPTER 7

CONCLUSIONS

In the most climatic regions, optimal environmental conditions for reproduction occur only during a portion of the year, consequently selective forces have favoured the evolution of distinct breeding seasons (Zucker, Johnston & Frost 1980). Hibernators present an additional complication to seasonal reproduction because of their adaptations to maximise inclusive benefit from favourable climatic conditions pertaining to late spring, summer and early autumn would be a premium (Fowler 1985). The interface between reproductive and thermoregulatory physiology has been of intense interest to comparative physiologists observing the conflict between homeothermic demands of reproduction and the heterothermic demands of hibernation and torpor (Wimsatt 1969). Fowler (1985) came to the conclusion that reproductive and overwintering systems would have to be closely integrated to ensure that reproductive effort did not imbalance the animal's ability to survive through the winter. Reproduction commence as soon as cond tions allowed it, and cease in time for the animal to prepare to survive the following winter.

The hedgehog is a seasonal breeding mammal as well as a hibernating mammal. Before discussing factors responsible for breeding, an overview of the annual cycle of the South African Hedgehog will be presented.

Maximum body weights were attained in April at the beginning of autumn. The lowest body temperature of 11 °C was measured in July. Low frequency of activity was recorded during the July activity study. Plasma testosterone levels were low during the period February to June and plasma and urinary progesterone showed that females were in anestrous during the period April to the end of May.

The lowest body weights were measured in September at the beginning of spring. From the middle of August the frequency of activity became increasingly higher. During the September activity study the hedgehogs were active throughout the study period.

Changes in testosterone and progesterone levels at the beginning of the reproductive season suggests that the male hedgehog emerge from hibernation earlier than the female. It seems as if the change in photoperiod has an influence on the change in plasma testosterone levels. Plasma progesterone and urinary progesterone levels started to increase from August. The change in T_a as well as photoperiod changes coincided with changes in plasma progesterone.

By September the breeding season commenced with full oestrous cycling and behavioural receptivity on the part of the female. Courtship and mating behaviour were recorded until December. Litters were born from the end of September to the end of January. Since the gestation period was about 35 days long and since the young were weaned within 40 days, females could produce more than one litter per season. Weight gain by the young were rapid probably to ensure that they survive the hibernation period. Asymptotic body mass was attained within the first eight weeks after birth. The gonadal activity in breeding females continued for a longer period than in males and hibernation was delayed until the young were weaned.

Animals bearing young during the breeding season minimize risks from the environment and increase their fitness while those that may produce young at other times are reduced or eliminated by natural selection (Reiter 1980). Certain conditions prevailing during the breeding season have been termed, the ultimate factors responsible for seasonality (Baker 1938; Thompson 1950). The existance of breeding seasons demands the parallel development of a timing mechanism that causes the necessary preparations for reproduction to occur in advance of optimal environmental conditions (Immelmann 1973). The stimuli animals use to predict the forthcoming optimal season are the proximate causes of factors controlling the breeding season (Baker 1938). The major environmental factors affecting reproduction and hibernation is photoperiod (Goss & Rosen 1973; Tucker 1981; Frost & Rucker 1983), T_a (Millar & Glover 1973; Myers **et al**. 1985) and precipitation (Gunn & Doney 1973; Withers 1983).

Reproduction and hibernation both depend on environmental cues for seasonality (Clarke 1981). Photoperiod is often regarded as a most important factor (Reiter 1980). Other factors, such as T_a and rainfall (Karsch & Foster 1981) can also be included. Hedgehogs have thus evolved ways whereby the changing environment is used to their advantage. Changes in the environmental conditions signal the endocrine system which in turn dictates the reproductive habits of animals (Reiter 1980).

The hedgehog as a hibernator and seasonal breeder, has thus evolved mechanisms to advantageously use environmental cues to a) predict the arrival of optimal conditions for producing their young and successfully raise them to survive the winter period and b) to start physiological preparation for hibernation.

SUMMARY

The seasonal changes in oxygen consumption, activity and levels of certain reproductive hormones of the South African hedgehog were recorded during this study. The South African hedgehog has a definite reproductive season followed by a period of low activity. It seems that photoperiod plays an important role in the maintenance of the endogenous cycle in the hedgehog.

In spring (September to October) the lowest mean metabolic rate was measured when T_a = 30 °C. Hedgehogs were not able to maintain their body temperature when they were placed at an ambient temperature of 10 °C. Maximum body temperatures were recorded during September (mean 33,2 ± 5,35 °C; n = 14) when hedgehogs had a thermal neutral point rather than a thermoneutral zone. During spring the frequency of activity was high and the onset of behaviour such as courtship and mating were recorded during this period. Plasma testosterone and progesterone reached peak levels during September and October.

During summer (November to February) the body temperatures of hedgehogs ranged between 32 - 35 °C at ambient temperatures between 20 - 33 °C. The thermal neutral zone appears to be between 25 °C and 30 °C during this period. Studies done during this period showed that the South African hedgehog does have the ability to increase its body-heat by using non-shivering thermogenesis. It is during this period that most litters were born. The litters were born about 35 days after matings were recorded. During the day the female suckles the young and stays in the nest with the young for the biggest part of the day. At night she leaves the young to forage, maybe mate with another male she encounters, or sleeps a while before returning to the nest in the early morning. Protection and nourishment is rendered to the young only by the female. The mean weight at birth was 9 ± 1,4 g (n = 16). When the young were four weeks old they started to leave the nest for short excursions and the mother still spent time with them. The young weighed 104 ± 12,1 g (n = 11) at this stage, and were weaned when five weeks old.

Thereafter the mother did not spent time with the young and she avoided their intentions of associating with her. Litters of up to eleven young were recorded during this study, and a female can produce more than one litter during the reproductive season.The young became sexually active a year after they were born.

During autumn (March and April) the lowest metabolic rate was recorded when T_a = 28 °C. The thermal neutral zone were between 28 °C and 33 °C. The mean body temperature was 27,8 ± 5,8 °C (n = 14) and body mass peaked in autumn. The highest mean body mass of 542,4 ± 46,1 g (n = 23) was measured in April. This was ascribed to accumulation of fat in preparation for winter and possibly hibernation. Plasma testosterone levels were low during this period and the females were in anestrous.

During winter (May to August) the lowest metabolic rate was recorded at T_a = 30 °C. The thermal neutral zone for winter was between 28 °C and 30 °C. Body temperatures varied between 11,6 and 32 °C in July (mean 20,9 ± 7,9 °C, n = 11) and frequency of activity during this period was low. Plasma testosterone levels were low during May, June.and July but started to increase significantly from July to August with levels reaching a peak in August. The first signs of ovarian activity occurred at the end of August when plasma progesterone levels of some females increased.

The present study confirms the presence of a substance in the plasma of males that binds testosterone. Peculiar behaviour such as self-anointing and hedgehogs running in circles for long periods was also observed during the present study.

The South African hedgehog is a seasonal breeder. It has the ability to advantageously use environmental cues to ensure their survival by producing litters under favourable environmental conditions.

OPSOMMING

Gedurende die huidige studie is die seisonale veranderinge in suurstofverbruik, aktiwiteit en die konsentrasie van sekere voortplantingshormone bepaal. Resultate het gewys dat die Suid-Afrikaanse krimpvarkie 'n definitiewe voortplantingseisoen het wat gevolg word deur 'n periode van lae aktiwiteit. Dit lyk of dagliglengte 'n belangrike rol speel as aandrywer vir die interne siklus van die krimpvarkie.

In die lente (September tot Oktober) is die laagste gemiddelde metaboliese tempo bepaal by 30 °C. Die krimpvarkies kon nie hulle liggaamstemperatuur onderhou toe hulle in 'n omgewingstemperatuur van 10 °C geplaas is nie. Maksimum liggaamstemperature is gemeet in September (gemiddeld 33,2 ± 5,35 °C, n = 14). Dit lyk asof die krimpvarkies tydens die tydstip 'n termoneutrale punt eerder as 'n termoneutrale sone het. Gedurende die lente seisoen is hoë aktiwiteitsperiodes en die begin van seksuele gedrag, soos hofmakery en paring, waargeneem. Plasma testosteroon- en progesteroonvlakke het piekwaardes bereik gedurende September en Oktober.

Gedurende die somerseisoen (November tot Februarie) het liggaamstemperature gewissel tussen 32 en 35 °C by omgewingstemperature van tussen 20 en 33 °C. Die termoneutrale sone skyn tussen 25 en 30 °C te val in hierdie periode. Studies wat gedurende die tydperk gedoen is het getoon dat die Suid-Afrikaanse krimpvarkie die vermoë het om sy liggaamstemperatuur te verhoog deur 'n meganisme van nie-bewende termogenese. Gedurende dié periode is die meeste van die krimpvarkie werpsels gebore. Die draagtydperk was 35 dae lank. Die wyfies het die kleintjies gedurende die dag gesoog en het die grootste gedeelte van die dag by hulle in die nes gebly. Gedurende die nag verlaat die wyfies die nes om kos te soek, moontlik te paar met 'n mannetjie wat sy teekom, of 'n rukkie te slaap voor sy vroegoggend na die nes terugkeer. Beskerming en voeding word alleenlik deur die wyfie aan die kleintjies verskaf. Die gemiddelde gewig by geboorte was 9 ± 1,4 g (n = 16). As die kleintjies 4 weke oud is begin hulle om die nes te verlaat vir kort ekskursies terwyl die ma steeds tyd by hulle spandeer. Op hierdie tydstip weeg hulle 104 ± 12,1 g (n = 11).

Die krimpvarkies word gespeen op 'n ouderdom van vyf weke en die wyfie spandeer dan geen tyd meer aan hulle nie en vermy enige kontak met die kleintjies. Werpsels van tot elf kleintjies is waar= geneem gedurende die huidige studie. Daar is verder gevind dat een wyfie meer as een werpsel per voortplantingsseisoen kan hê en dat die kleintjies eers seksueel aktief raak 'n jaar nadat hulle gebore is. Die sirkulerende testosteroonvlakke is steeds hoog in Desember maar begin afneem aan die einde van die somer. Lae vlakke van plasma progesteroon is in Februarie bepaal.

Gedurende die herfs (Maart tot April) is die laagste metaboliese tempo gemeet by 'n omgewing-stemperatuur van 28 °C. Die termoneutrale sone het tussen 28 en 33 °C geval. Die gemiddelde liggaamstemperatuur is gemeet as 27,8 ± 5,8 °C (n = 14). Die liggaamsgewigte het hulle piekwaardes gedurende herfsmaande bereik. Die hoogste gemiddelde liggaamsgewig van 542,4 ± 46,1 g (n = 23) is in April gemeet. Dit is toegeskryf aan die akkumulasie van vet as voorbereiding op die winter en moontlik hibernasie. Plasma testosteroonvlakke was laag gedurende dié periode en die wyfies was in anestrus.

Gedurende die winter (Mei tot Augustus) is die laagste metaboliese tempo by 'n omgewingstem-peratuur van 30 °C gemeet. Die termoneutrale zone vir die winter was tussen 28 en 30 °C. Die liggaamstemperature het gewissel tussen 11,6 en 32 °C in Julie (gemiddeld 20,9 ± 17,9 °C, n = 11). Die frekwensie van aktiwiteit gedurende die periode was laag. Plasma testosteroonvlakke was laag gedurende Mei, Junie en Julie maar het betekenisvol verhoog vanaf Julie tot Augustus met piekvlakke in Augustus. Die eerste tekens van estrussiklusaktiwiteit in die wyfies is aan die einde van Augustus waargeneem wanneer daar 'n toename is in die plasma progesteroonvlakke van sekere wyfies was.

Die huidige studie het bevestig dat daar 'n bestandeel in die plasma van mannetjies is wat aan testosteroon bind. Buitengewone gedrag soos krimpvarkies wat hulle pennetjies bedek met speeksel of wat vir lank in sirkels hardloop sonder enige klaarblyklike rede, is ook waargeneem.

Die Suid-Afrikaanse krimpvarkie plant seisonaal voort en daar kan onderskeid gemaak word tussen die definitiewe voortplantingsperiode en die periodes van lae aktiwiteit. Die krimpvarkie het dus die vermoë ontwikkel om tot sy voordeel die omgewingsfaktore te gebruik om die oorlewing van die spesie te verseker.

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