A preliminary investigation of the bioenergetics of pregnancy and lactation of *Praomys natalensis* and *Saccostomus campestris*

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The energy requirements of pregnant, lactating and non-reproductive *Praomys natalensis* and *Saccostomus campestris* were studied in metabolism cages and respirometers. Ingestion rate during pregnancy and lactation was not increased significantly in either species. *P. natalensis* and *S. campestris* showed non-significant increases in respiratory rate during pregnancy (18% and 55% respectively) but significant increases in oxygen consumption during lactation (79% and 110% respectively). The results highlight the need for studies quantifying lipid and protein flux during pregnancy and lactation, since quantifying energy turnover alone is inadequate and misleading. The energetic costs of reproduction are discussed in relation to previous studies.

Die energiebehoeftes van swanger, lakterende en nie-voortplantende *Praomys natalensis* en *Saccostomus campestris* is in metabolismehokke en respirometers ondersoek. Die voedingstempo van albei spesies het, gedurende swangerskap en laktering, geen betekenisvolle toename getoon nie. Hoewel *P. natalensis* en *S. campestris* albei 'n verhoging in respirasietempo (onderskeidelik 18% en 55%) gedurende swangerskap getoon het, was die toenames nie statisties betekenisvol nie. Daar was egter betekenisvolle verhogings in suurstofverbruik (onderskeidelik 79% en 110%) gedurende laktering. Die resultate dui op die noodsaaklikheid vir studies wat vet- en proteïnewisseling sal kwantifiseer, aangesien energie-omkeer alleen onvoldoende en misleidend is. Die energiekoste van voortplanting word bespreek met verwysing na voorafgaande studies.

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Theories concerning demographic aspects of resource allocation to reproduction in mammalian populations, such as *r* and *K* selection and bet-hedging, have frequently been investigated and reiterated (Perrin 1980). However, there have been few investigations of the energetic costs of reproduction in individual mammalian species. In order to satisfactorily interpret the energetic and evolutionary significance of reproductive tactics of a species, one must examine both the demographic and physiological aspects of species populations (Hanks 1981; McNab 1986; Millar 1977; Perrin 1980; Stearns 1976). In mammals, physiological aspects focus on females and concern resource allocation during pregnancy and lactation. (Costs of mate acquisition and courtship in males may well be significant but such ethological studies are difficult for wild small mammals).

Energy expenditure of pregnant/lactating individuals can be quantified in the laboratory using calorimetry and/or respirometry (Kaczmarski 1966; Migula 1969; Randolph, Randolph, Mattingly & Foster 1977). Quantification of food ingestion rate and faecal output (the balance method: Drozdz 1968) using metabolism cages (Drozdz, Gorecki, Grodzinski & Pelikan 1971) with chemical analysis of food and faeces permits determination of protein, energy (and other nutrient/mineral requirements) thereby providing a sound, broad-based foundation for quantifying reproductive effort. Determination of oxygen consumption however, yields an immediate numerical value of total energy flux, but does not indicate the energy source (i.e. protein or fat catabolism, or increased ingestion rate).

The pouched mouse *Saccostomus campestris* and the multimammate mouse *Praomys natalensis* were selected for study because of their differences in reproductive tactics, and habituation to laboratory conditions and experimentation (Keogh & Isaacson 1978; Randeria 1978). *S. campestris* was thought to be relatively *K* selected while *P. natalensis* is an extreme *r* strategist (Meester, Lloyd & Rowe-Rowe 1979). [In fact *S. campestris* has a dynamic reproductive strategy and an extremely variable litter size (Perrin 1986): Table 1 presents information on reported litter size for each species.]

The purpose of this preliminary study therefore was to investigate the energy and protein requirements of two species of African rodents with different litter sizes during pregnancy and lactation.

Methods

Experiments were conducted on laboratory-bred rodents obtained from the South African Institute for Medical Research, from a stock that had been collected from Tzaneen in the northern Transvaal. Females paired with males were housed in box cages (420 × 240 × 120 mm) provided with sawdust and shredded paper bedding. The cages were kept in an animal room with constant temperature (25°C) and

Table 1 Reported litter sizes of *Praomys natalensis* and *Saccostomus campestris*

Praomys natalensis				*Saccostomus campestris*			
Mean	Range	Sample size	Reference	Mean	Range	Sample size	Reference
–	12 – 20	–	Roberts 1951	7,4	5 – 10	8	Smithers 1971
7,3	–	–	Oliff 1953	4,8	2 – 8	–	Earl 1978
8,5	–	19	Meester 1960	6,7	1 – 10	7	Smithers & Wilson 1979
–	10 – 16	–	Smithers 1975				

photoperiod (12L:12D). Rat pellets (Meadow Feed, Pietermaritzburg) and water were provided *ad libitum*.

Females were examined daily to determine the date of parturition, while the onset of pregnancy was determined by backdating. The gestation period of *S. campestris* is 20 – 21 days (Earl 1978), whereas that of *P. natalensis* is 23 days (Johnston & Oliff 1954).

Females were placed regularly (every 3 – 4 days) in metabolism cages for 24-h periods, enabling separate collection of faeces and urine for bomb calorimetry and/or protein estimation. Food consumption was calculated as follows:

Food consumed = Dry mass of food provided
– dry mass of food not consumed.

(Dry mass = wet mass × 0,8714, since water content of laboratory rat pellets was 12,26%). The relatively minor calorific loss of the urine was not measured directly but calculated indirectly (Kaczmarski 1966).

Animals were weighed alive (wet) at the end of each 24-h period, whereas unconsumed food and faeces were oven dried to constant mass at 80°C before weighing. Dried faecal pellets and urine were stored in sealed containers and refrigerated until analysis.

Energy values of oven-dried samples of food and faeces were determined by (Gallenkamp) ballistic bomb calorimetry (Allen, Grimshaw, Parkinson & Quarmby 1974), using benzoic acid as standard.

Food and faeces were analysed for nitrogen (and hence protein), using the Kjeldahl method of Henry (1964) with the aid of a Buchi 425 digestor and Buchi 325 nitrogen distillation unit. Protein concentration, uncorrected for the presence of non-protein nitrogen, was calculated as follows:

mg protein = 6,25 × mg nitrogen in sample
(Allen *et al.* 1974).

Daily food consumption and digestibility coefficients of pregnant females were compared with those of non-pregnant control animals.

Respiratory rates of subjects were determined individually every 3 – 4 days using an open-circuit system. Each animal was acclimated to the respirometry chamber for 24 h before experimentation. Oxygen consumption was determined over a 4-h period (8h00 to 12h00) at a laboratory temperature of 20°C: the temperature within the respirometer could not be recored (it was probably a few degrees higher, but well within the zone of thermoneutrality).

Effluent air from the respirometer passed through a flowmeter into a Beckman OM-14 oxygen analyser, its output signal being recorded on a Washington 400 MD 1 chart recorder. Desiccant tubes containing silica gel were connected in the system between the inlet and respirometer, respirometer and flowmeter, and flowmeter and oxygen analyser to ensure dry air entered the analyser. A 0,062-kW pump (with a damping chamber connecting the pump to the exhaust tube of the analyser) was used to draw a steady flow of air through the system. The rate of flow of air through the system was constant (at 245 ml/min) for the duration of each experiment. An additional highly stabilized backing-off voltage (Hewlett Packard 6214A power supply) was connected between the oxygen analyser and chart recorder to suppress the background DC voltage in order to allow full scale variation in oxygen consumption traces on the oscillograph. Hence the recorder operated over the range of 16 – 20% oxygen (and not 0 – 20%), which greatly increased the precision of data recording. Oxygen consumption values taken from the oscillograph traces at 5-min intervals were averaged to calculate the resting metabolic rate of the animal; all values were corrected to standard temperature and pressure.

Respiratory rates were expressed graphically on a wet weight basis initially but then converted to dry weight units (tabular presentation) for comparative purposes. It was assumed that the subjects comprised 72% water (Babineau & Page 1955).

All Student's *t* tests for significance were performed using Bessel's correction, being appropriate for small sample sizes (Sokal & Rohlf 1969).

Results

The energy, protein, and water contents of the diet and faeces collected from the feeding experiments are presented in Tables 2 and 3 respectively.

There was a significant decrease ($t = 2,36$; $p < 0,05$) in water consumption when animals were housed in metabolism cages relative to those housed in maintenance cages.

Average daily food consumption and faecal calorific losses were used to determine digestibility coefficients of the experimental animals (Table 4). The coefficients represent an overestimate of approximately 2 – 4% because the energy losses of urea were not quantified (Kaczsmarski 1966). A between-species comparison of nitrogen balance of non-pregnant animals is given in Table 5.

Table 2 Composition of the laboratory diet, Meadow Feed rat pellets

Parameter	Mean ± *S.E.*	(*n*)
Calorific value (kJ g^{-1} dry weight)	19,25 ± 0,19	(13)
Protein content (% dry weight)	17,88 ± 2,22	(4)
Water content (% wet weight)	12,86 ± 0,27	(9)

Table 4 Digestibility coefficients of the diet consumed by pregnant and non-pregnant *Saccostomus campestris* and *Praomys natalensis*

	Food consumption (kJ g^{-1} dry mass day^{-1})	Faecal losses (kJ g^{-1} dry mass day^{-1})	Digested energy (kJ g^{-1} dry mass day^{-1})	Digestibility coefficient	Sample size (*n*)
Saccostomus campestris					
Non-pregnant	2,39 ± 1,18	1,04 ± 0,14	1,36 ± 1,18	0,29 ± 0,96	33
Pregnant	1,64 ± 1,18	0,75 ± 0,29	0,75 ± 1,04	−0,48 ± 1,89	3
Praomys natalensis					
Non-pregnant	3,00 ± 1,64	0,61 ± 0,46	2,39 ± 1,18	0,78 ± 0,18	24
Pregnant	0,61 ± 0,14	0,46 ± 0,04	1,50 ± 1,04	0,24 ± 0,20	3

Table 3 Composition of faeces (mean ± *S.E.*, with sample size in parenthesis)

	Saccostomus campestris	*Praomys natalensis*
Calorific value (kJ g^{-1})		
Non-pregnant	16,86 ± 0,42 (9)	17,45 ± 0,13 (5)
Pregnant	17,45 ± 0,08 (5)	17,15 ± 0,21 (4)
Protein content (% dry weight)		
Non-pregnant	26,11 ± 1,14 (2)	35,30 ± 10,32 (2)

Respirometry

S. campestris

Only one female fell pregnant during the study, giving birth to a litter of 11 of which only four individuals survived to weaning. The respiratory rates of this individual are presented in Figure 1. During pregnancy body mass increased by 17,7 g (19,5%), while the mean respiratory rate rose to 7,36 ± 0,75 ml O_2 g^{-1} dry mass h^{-1}, representing a non-significant ($p > 0,05$) increase of 32% over the mean vaue of 5,57 ± 0,50 ml O_2 g^{-1} dry mass h^{-1} prior to pregnancy. Total energy intake for the individual increased by 57,8% (because of the increase in mass); this energy demand was required to produce a litter of 11 pups.

Lactation was characterized by a highly significant increase ($t = 7,355$; $p < 0,001$) in respiratory rate over the non-pregnant control (Table 6). Oxygen consumption reached a peak on day 11 of lactation at 11,68 ml O_2 g^{-1} dry mass h^{-1}, being 110% higher than the control. On day 11, there were six surviving young compared with four at weaning. Normally the respiratory rate of the mother would be maximal at the end of lactation if all young survived.

The lactation period of *S. campestris* is given as 19–25 days by Earl (1978), but in the present experiment the period of lactation was prolonged, all young being suckled 30 days after parturition. However, three of the four surviving young were observed feeding on rat pellets 27 days after parturition. This accounts for the slight decrease in respiratory rate of the female after this date, since the energy demands of the young were increasingly satisfied by the ingestion of solid food.

P. natalensis

Three female *P. natalensis* fell pregnant during the study period, but one of them, subject P1 (Figure 2) cannibalized her young at parturition. Subject P2 gave birth to a litter of nine young, of which seven survived to weaning. The male was not separated from the female prior to parturition, resulting in the female falling pregnant while lactating. The second litter of eight young was born 28 days after the first; seven of these survived to weaning. The female fell pregnant on her fouth day of lactation, and the male was separated from the female prior to birth of the second litter. The young were first observed leaving the nest when 13 days old but were suckled by the mother for several days after this time. Subject P3 gave birth to a litter of three, two of which were stillborn, and the remaining individual died four days after parturition.

Table 5 Nitrogen balance of pregnant *Sacostomus campestris* and *Praomys natalensis*

Subject	Nitrogen intake (food) (mgN g^{-1} dry mass)	Nitrogen output (faeces) (mgN g^{-1} dry mass)	Nitrogen output (urine) (mgN g^{-1} dry mass)	Nitrogen balance	*n*
Saccostomus campestris	3,43 ± 1,54	5,36 ± 1,07	0,036 ± 0,014	−1,96 ± 1,14	6
Praomys natalensis	3,89 ± 1,86	3,25 ± 2,82	0,036 ± 0,011	0,61 ± 1,32	5

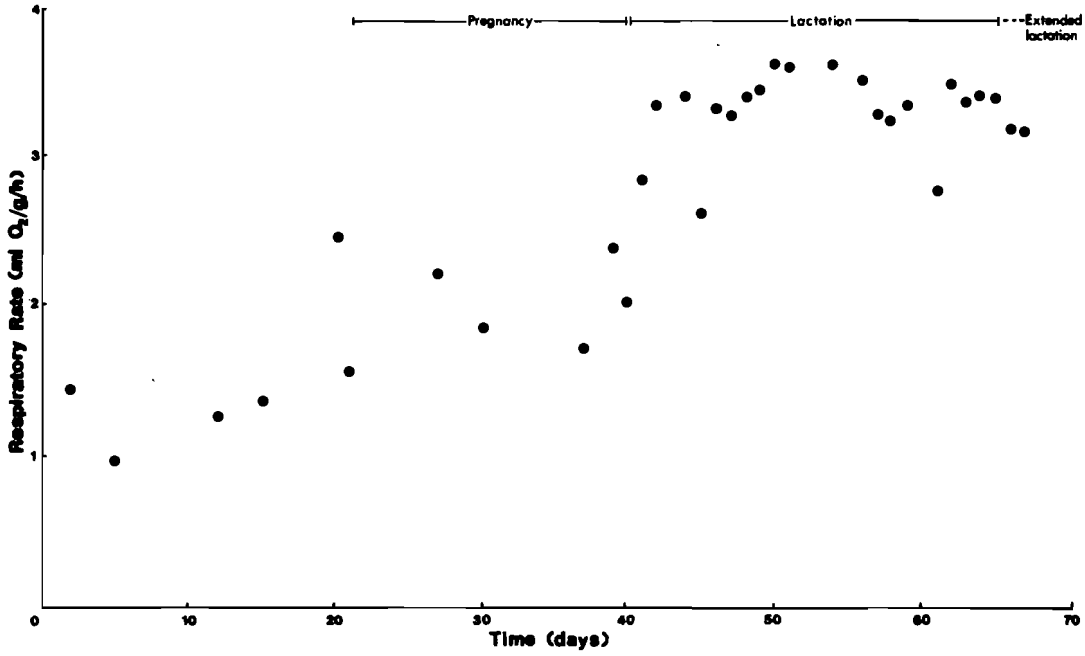

Figure 1 Respiratory rate of a female *Saccostomus campestris* prior to conception, and during pregnancy and lactation (expressed g^{-1} wet weight).

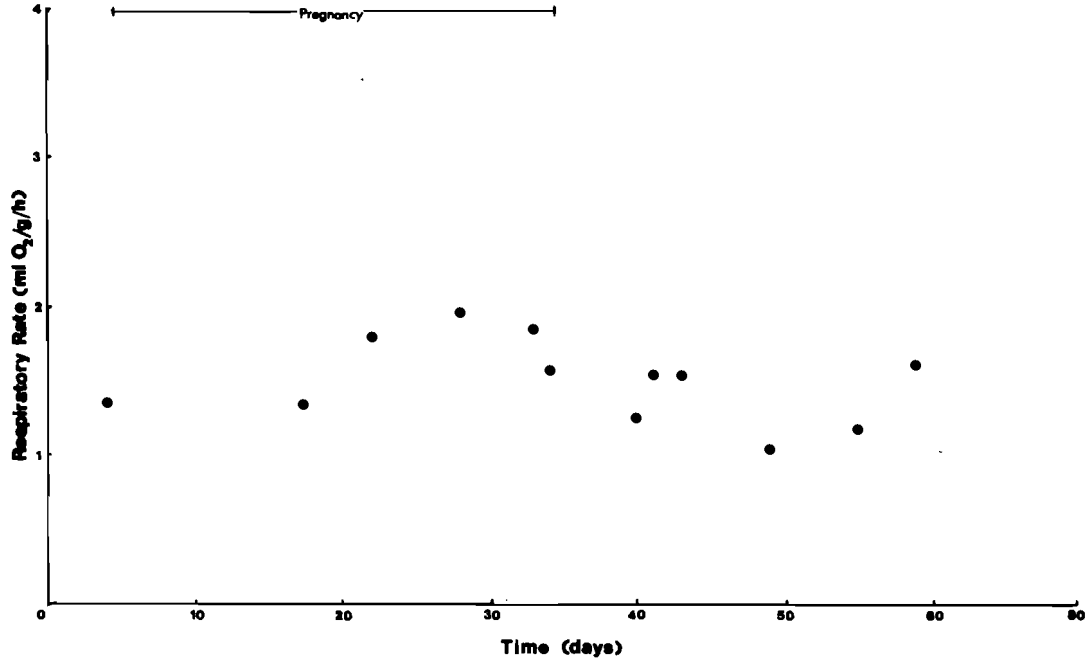

Figure 2 Respiratory rate of a female *Praomys natalensis* (P1) during pregnancy (expressed g^{-1} wet weight).

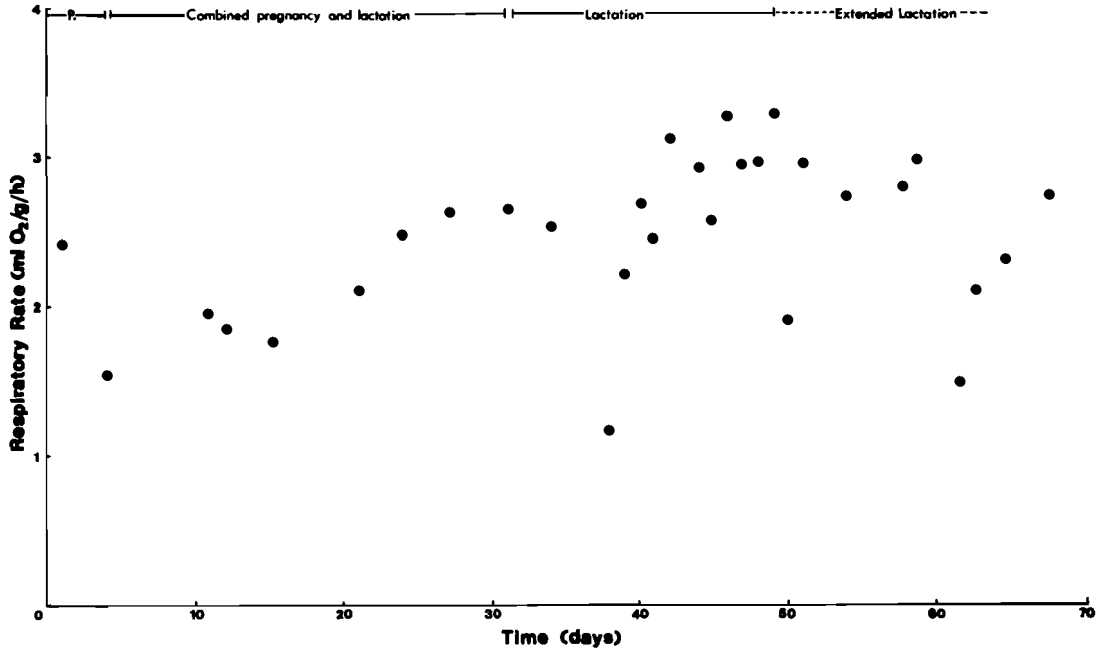

Figure 3 Respiratory rate of a female *Praomys natalensis* (P2) during pregnancy, and combined pregnancy and lactation (expressed g^{-1} wet weight).

Respiratory rates of individual *P. natalensis* are presented in Figures 2–4 and compared in Table 6.

A one-way analysis of variance of the respiratory rates of non-reproductive females showed no significant difference between individuals. For this reason respiratory rates of pregnant individuals were combined and the mean compared with that of non-reproductive females.

Females showed a mean increase in oxygen consumption of 0,86 ml O_2 g^{-1} dry mass h^{-1} during pregnancy, reflecting the increased energy demands required to produce a litter (mean size = 5,4 ± 2,9; n = 5).

Pregnant females showed no significant increase in respiratory rate when compared with non-pregnant females. However the lactating female showed a highly significant increase (t = 5,867; $p < 0{,}001$) in oxygen consumption when compared with non-reproductive females.

Discussion

The mean nitrogen balance of pregnant *S. campestris* was negative during the metabolism experiments, which indicates the subjects were catabolizing protein and likely explains the observed decrease in body mass. However, whether this result is a natural event or merely the consequence of a poorly designed metabolism cage (preventing access to the nutritive, artificial diet) is open to conjecture. (Reduced water intake by subjects under experimental conditions indicated water stress, but since there was no significant difference in mass loss between animals housed in maintenance and metabolism cages, dehydration may only have been a contributing factor to changes in body mass).

None of the previous parallel studies have examined protein turnover through the breeding period, and only Millar (1975) has examined fat reserves. In *Peromyscus leucopus* fat

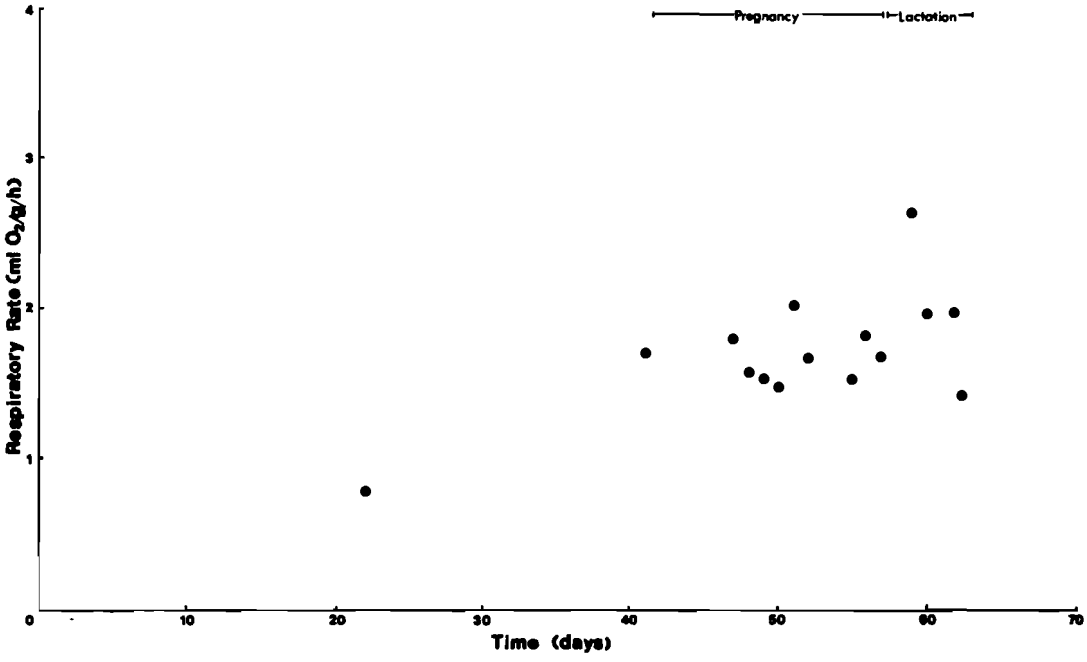

Figure 4 Respiratory rate of a female *Praomys natalensis* (P3) during pregnancy (expressed g^{-1} wet weight).

Table 6 The effect of pregnancy and lactation on the respiratory rate of *Saccostomus campestris* and *Praomys natalensis* (Sample sizes are given in parenthesis)

	Respiratory rate (mlO_2 g^{-1} dry mass h^{-1})
Saccostomus campestris	
Non-pregnant	5,57 ± 0,50 (5)
Pregnant	7,36 ± 0,75 (7)
Lactating	11,68 ± 0,29 (22)
Praomys natalensis	
Non-pregnant	5,39 ± 0,36 (14)
Pregnant	6,25 ± 0,25 (19)
Lactating	9,68 ± 0,64 (12)
Pregnant & lactating	2,21 (1)

deposited before the period of peak energy demand (late lactation) was unimportant in supporting captive offspring, although fat reserves of wild females were lowest during lactation. Further, shortage of food was reflected primarily in the survival and rate of growth of nestlings. It is likely that the high level of juvenile mortality reported here is a consequence of poor feeding and nutrition of suckling mothers forced to catabolize protein following utilization of normal body reserves (fat and glycogen). This speculation highlights the need for studies of lipid and protein flux during pregnancy and lactation; to quantify energy turnover alone is inadequate and misleading.

In both *P. natalensis* and *S. campestris* there was an appreciable (but non-significant) increase in respiratory rate during lactation when compared with non-reproductive females. Although the observed pattern of increased oxygen consumption during reproduction was similar in each species the magnitude of increase was different. The respiratory rate of *S. campestris* increased by 55% during pregnancy and 110% during lactation whereas the equivalent values for *P. natalensis* were 18% and 79% respectively. Maximum respiratory rates were recorded on days 11 and 15 of lactation for *S. campestris* and *P. natalensis* respectively, but were remarkably similar in magnitude (i.e. increases of 135% and 134%). These increases were lower than the mean reproductive effort of 1,65 (165%) recorded at the end of lactation for eutherian mammals (Millar 1977). The lowered oxygen consumption rate of these breeding females may be innate, but more likely it is an effect of nutritional stress invoked by captivity. However, the values do indicate that *S. campestris* invested more energy in production of a litter than did *P. natalensis*, especially during pregnancy.

Millar's (1977) treatise on adaptive features of mammalian reproduction indicates that litter size (and time-to-weaning) are the major adaptive variable(s) of mammalian reproduction, and that litter size is the dominant factor determining the energy requirements of breeding females. Pianka (1970) identified altricial development and high fecundity as characteristics of *r* selection, while precocial development and low fecundity with high parental investment are characteristics of *K* selection. It was thus expected that *P. natalensis* would show a high level of investment to produce large litters of altricial young, whereas *S. campestris* was predicted to wean small litters with high investment per individual offspring.

The limited results suggest that *S. campestris* may invest more energy in litter production than *P. natalensis*. However, the litter size of captive *P. natalensis* was small and variable ($\bar{x}$ = 5,4 ± 2,9) while the *S. campestris* female had an extremely large litter of 11: [Smithers (1971) gives the average litter size of this species as 4,8 with a range of 2–8 for laboratory-reared animals]. Because the present study was confined to the analysis of respiratory rates of a single female *S. campestris* with an exceptionally large litter, one would have expected the mean respiratory rate during reproduction to have been elevated considerably above average values. However, tremendous plasticity in litter sizes combined with small sample sizes and an artificial laboratory environment make definite conclusions impossible.

The gestation periods of the two species are similar, 20–21 days in *S. campestris* (Earl 1978) and 23 days in *P. natalensis* (Johnston & Oliff 1954), but the duration of lactation appears to be considerably longer in *S. campestris*. Earl (1978) reported the duration of lactation of *S. campestris* as 19–25 days,

which was confirmed by the present study. Results from this study indicate time to weaning to be 15 days in *P. natalensis*. Observations showed both species can extend lactation periods since *S. campestris* and *P. natalensis* young may still be suckled at 30 and 28 days after parturition respectively. Time to weaning is difficult to determine because of partial/intermittent use of solid foods, nevertheless *P. natalensis* young are independent at an earlier age (Johnston & Oliff 1954).

Greater energy expenditure occurs during a reproductive cycle of *S. campestris* because the most energy expensive period, lactation, is longer than in *P. natalensis*. The higher energy costs of lactation than of pregnancy are well established (Kaczmarski 1966; Migula 1969; Randolph, *et al.* 1977).

The ability of *P. natalensis* to produce more than one litter per season is evidenced by combined pregnancy and lactation. Consequently the annual/life-time reproductive effort of *P. natalensis* is likely to be far greater than that of *S. campestris*, because of the increased number of litters produced per season (Meester, *et al.* 1979). This is in spite of the fact that the energy expenditure per litter is greater in *S. campestris*. Further laboratory studies of energetics, and field studies of demography, are required for the quantification and interpretation of *r-K* and temporally-dynamic life-history strategies of African rodents.

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