

## O<sub>2</sub>-Uptake, Thermoregulation and Heart Rate in the Springhare (*Pedetes capensis*)\*

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**Summary.** 1. O<sub>2</sub>-consumption ( $\dot{V}O_2$ ), rectal temperature ( $T_{re}$ ) and heart rate were measured in two adult springhares (♂,♀; body mass 2.2–2.4 kg) at ambient temperatures ( $T_a$ ) from 6–35 °C. Abdominal temperature in the female and heart rate in both animals were determined by telemetry.

2. At  $T_a$ 's from 23–28 °C rectal temperature in both animals ranged between 35.5–36.3 °C. This range was well maintained at low  $T_a$ 's. Exposure to high  $T_a$ 's, however, led to a considerable rise of the rectal temperature (to above 39 °C at  $T_a = 35$  °C).

3. The lowest oxygen uptake (0.32–0.37 ml O<sub>2</sub>·g<sup>-1</sup>·h<sup>-1</sup>) was found between 23–33 °C. This is only 65–75% of the predicted value in similar sized mammals. Below 23 °C O<sub>2</sub>-consumption increased rapidly up to approximately 2.5 times (6–7 °C) the value in the thermoneutral zone (23–33 °C). At  $T_a$ 's above 33 °C the heat dissipating capacities of the springhares proved to be inadequate and consequently  $T_{re}$  rose steadily.

4. Basal heart rate (75–85 beats·min<sup>-1</sup>) was about 30% below the standard value for similar sized mammals. During exposure to cold the heart rate sometimes exceeded 200 beats·min<sup>-1</sup>.

5. The measured parameters are discussed with special regard to the extent of the springhare's adaptation to arid conditions. It is concluded that these rodents are physiologically adapted to fossorial habits rather than to life in desert environments and are thus restricted to semi-arid areas.

(Walker, 1968). The systematic position of the family is uncertain: taxonomists disagree whether to place the springhares within the hystricomorphs or the sciuricomorphs (Wood, 1955; Fischer and Mossman, 1969; Rowlands and Weir, 1974).

Springhares are distributed throughout the savannahs of East and South Africa. They prefer dry, sandy soils in relatively open flat country, where they can dig their burrows. These kangaroo-like rodents are almost exclusively nocturnal and feed mainly on vegetation but perhaps also take insects. During the dry season they have to cope with conditions of water shortage and considerable daily ambient temperature fluctuation (Walker, 1968; Kingdon, 1974).

The problems of life in arid zones have been repeatedly discussed (e.g. Schmidt-Nielsen, 1964; Maloiy, 1972; Prakash and Ghosh, 1975). To survive in hot deserts, animals must reduce water expenditure and avoid overheating. These requirements are met by behavioural reactions such as being nocturnal and spending the hottest part of the day in burrows. It has been demonstrated that desert mammals also have physiological adaptations, e.g. greater renal concentrating ability, reduction of evaporative water losses and also basal heat production (McNab and Morrison, 1963; Hudson, 1964; McNab, 1966; Ghobrial and Nour, 1975; Reinking et al., 1977). The most successful mammals in adapting to arid conditions are certainly the rodents, but desert species are also found among the marsupials, insectivores, lagomorphs and ungulates. Recently Noll-Banholzer (1978) showed that the fennec, a small carnivore, is well adapted to desert life.

So far no information was available as to how springhares are able to meet the requirements imposed by an arid environment. To find out possible physiological adaptations in these rather large rodents, we measured rectal temperature, oxygen consumption and heart rate at different ambient temperatures.

### Introduction

The family *Pedetidae* includes only one recent genus, *Pedetes*, with probably a single species, *P. capensis*

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## Materials and Methods

The experiments were performed with two adult springhares (male and female). The animals were caught in September, 1977, on a hill about 40 km east of Nairobi, near the Mombasa road. The locality obtains about 250–600 mm rain per year (Russell, 1962) and has well-drained sandy soils with rock outcrops. The vegetation originally was mainly savannah, but is now partly disturbed by agriculture.

In the laboratory the animals were kept together in a cage of 50 × 50 × 90 cm. Ambient temperature and relative humidity of the air were near those prevailing in Nairobi from September to December 1977 and varied between 15–28 °C and 60–90% r.h., respectively. The springhares readily fed on sweet potatoes, carrots, grass and hay. Water was not made available. Under these conditions the animals kept their body mass rather constant between 2.2–2.4 kg.

To reveal variations in the deep body temperature a small temperature transmitter (according to Mackay, 1970; 2 × 1 cm; 3 g with coating material) was surgically implanted in the female's abdominal cavity under halothane B.P. inhalant anaesthesia. The transmitter was coated with a layer of paraplax, soaked into 100% alcohol and covered with sulphanylamide B.P. powder. After the implantation the animal was given combiotic (penicillin/streptomycin) for three days. Experiments with the female started 2 weeks after the operation. The transmitter had previously been calibrated using a water bath. Its signals were caught by a commercial AM-receiver (Sanyo; RP 8700) and counted with a biotachometer (Narco; BT 1200).

For measurement of oxygen consumption the springhares were placed individually in a plexiglass container (volume 52.5 l) which stood in a climatic chamber with temperatures kept constant within ± 1 °C. In most cases the animals were fasted several hours prior to the measurements. The experiments started between 8–9 a.m. and lasted till 2–3 p.m. Air was drawn through the container at a constant rate of 140 l per hour (STP). Air flow was measured with a flowmeter (Brooks Instrument; 1357-01c 1 FEN) which was calibrated by means of a volumeter (Brooks Instrument; Vol-U-Meter). Humidity in the climatic chamber was not controlled; it varied between 40–90% depending on prevailing  $T_a$ . A part of the air leaving the container was dried with drierite before entering a Beckman F3 Oxygen Analyser.  $O_2$ -consumption was continuously monitored and recorded with a pen-recorder (Fisher; Recordal series 5000). Evaluation started two hours after exposure to the various temperatures when the springhares were sleeping (except for high  $T_a$ 's where the animals showed increasing uneasiness). The values represent the mean  $O_2$ -uptake (corrected to STP) during the subsequent period of about 3 h, except for high ambient temperatures where some experiments had to be stopped after only 3–4 h of exposure to spare the animals. Immediately after the end of an experiment rectal temperature was measured with a thermistor at a depth of 8 cm (Testotherm; digital 2500).

For measuring heart rates simultaneously with  $O_2$ -consumption the springhares carried a heart rate transmitter (Mackay, 1970) fastened on the shoulders with an elastic belt. The transmitter and batteries weighed 12 g. Electric connection was provided by two surgical clamps, one fixed in the skin of the left flank and the other in the skin of the right shoulder. This arrangement did not impair the animals at all and gave good signals which were caught by a FM-receiver (Narco Bio-Systems). The signals were either counted directly (five minutes during every quarter of an hour) or stored on a tape recorder (Uher; 4000 report IC). The stored signals were later triggered by means of an oscilloscope (Hameg; HM 512) and counted by the Philips scaler/timer PW 4230/4260.

## Results

### 1. Body Temperature

$T_{re}$  was maintained constant within a very narrow range (35.5–36.3 °C) at  $T_a$ 's from 6–28 °C. Above 28 °C  $T_{re}$  rose gradually with increasing  $T_a$ . At  $T_a = 35$  °C a stable  $T_{re}$  could not be achieved; abdominal temperature in the female followed approximately a similar pattern (Fig. 1).

### 2. Oxygen Consumption

The lowest oxygen consumption occurred at  $T_a$ 's between 23–33 °C (Fig. 2). Mean  $O_2$ -uptake within this thermoneutral zone was 0.32 ml  $O_2 \cdot g^{-1} \cdot h^{-1}$  in the female and 0.37 ml  $O_2 \cdot g^{-1} \cdot h^{-1}$  in the male; this is only 65% and 75%, respectively, of the mammalian standard for similar sized mammals. Single values, especially in the female, were considerably lower. Below  $T_a = 23$  °C  $O_2$ -uptake in both animals rose linearly with falling ambient temperatures following the regression lines (method of least squares):

$$\begin{aligned} \text{female: } Y(\text{ml } O_2 \cdot g^{-1} \cdot h^{-1}) &= 0.84 - 0.022 T_a (r=0.97), \\ \text{male: } Y(\text{ml } O_2 \cdot g^{-1} \cdot h^{-1}) &= 1.115 - 0.03 T_a (r=0.99). \end{aligned}$$

At  $T_a$ 's above 33 °C there was a slight increase in  $O_2$ -consumption. The springhares then lay on the side or on the back with the limbs stretched out. Blood circulation to the periphery, especially to the ears, was greatly increased (visual observation). Respiratory frequency rose from normal values of 20–30 breaths  $\cdot \text{min}^{-1}$  to reach 60 breaths  $\cdot \text{min}^{-1}$  at  $T_a = 35$  °C. In some cases face and parts of the fur were wet due to saliva spreading.

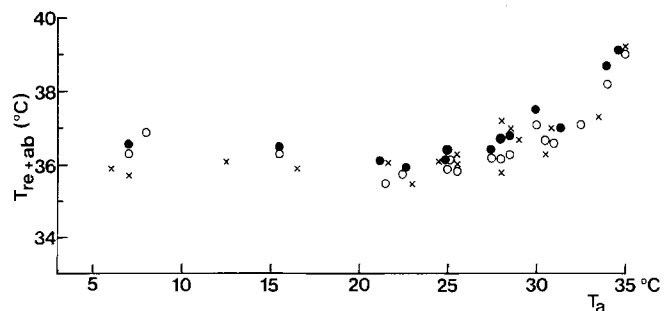
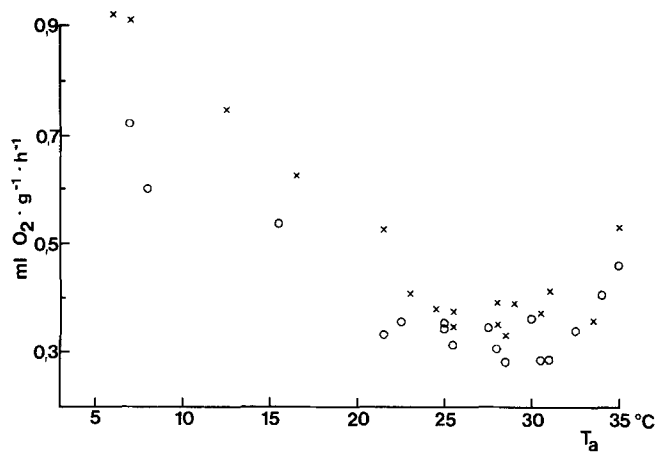


Fig. 1. Rectal and abdominal temperatures of two springhares after a 3–5 h exposure to ambient temperatures from 6–35 °C. ○ = female, rectal; ● = female, abdominal (recorded by telemetry); × = male, rectal



**Fig. 2.**  $O_2$  consumption of two springhares at ambient temperatures from 6–35 °C. Given are mean values (corrected to STP) during 1.5–3 h after an acclimatization time of two hours. Except for  $T_a$ 's above 33 °C the animals were sleeping at all given ambient temperatures. Body mass 2.2–2.4 kg.  $\circ$  = female;  $\times$  = male

**Table 1.** Thermal conductance ( $C = \frac{\dot{V}_{O_2}}{T_{re} - T_a} \text{ ml } O_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot \text{°C}^{-1}$ ) below the thermoneutral zone

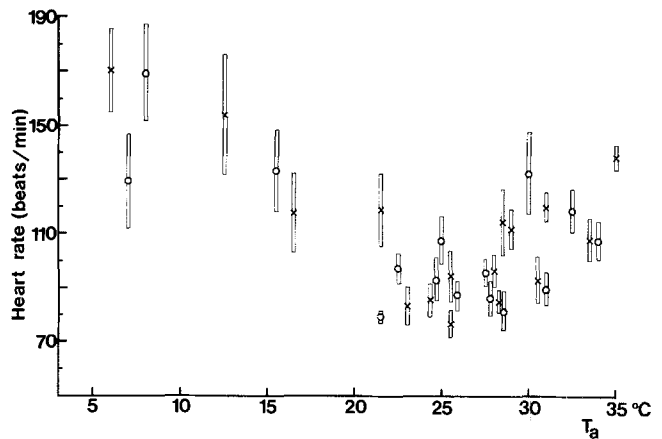
$T_a$ (°C)	6	7	8	12,5	15,5	16,5	21,5	22,5	23
$\delta$	0.031	0.032	—	0.032	—	0.032	0.036	—	0.033
$\text{C}$									
$\text{♀}$	—	0.025	0.021	—	0.026	—	0.024	0.027	—

### 3. Thermal Conductance

In both animals the calculated thermal conductance showed little variation between  $T_a$ 's from 6–23 °C (Table 1). If compared to standard values (Herreid and Kessel, 1967) the conductance was 155% in the male and 120% in the female, respectively. These values differ little from the minimal thermal conductance (147% and 108%, respectively) as indicated by the slope of the regression lines (see chapter above).

### 4. Heart Activity

Within the thermoneutral zone the mean heart rate was 99.1 beats  $\cdot$  min $^{-1}$  in the female and 94.9 beats  $\cdot$  min $^{-1}$  in the male. Lowest values were between 75–85 beats  $\cdot$  min $^{-1}$  in both springhares. Below  $T_a = 23$  °C the mean heart rate almost paralleled  $O_2$ -consumption (Fig. 3). The highest values were found at  $T_a = 6$ –8 °C, sometimes exceeding 200 beats  $\cdot$  min $^{-1}$ . The increase in heart rate above  $T_a = 33$  °C was less marked with rates seldom exceeding 150 beats  $\cdot$  min $^{-1}$ . The oxygen pulse rose with decreasing ambient temperatures (Table 2). The contribution of heart rate to the increased oxygen transport was unclear from



**Fig. 3.** Heart rate (mean  $\pm$  S.D.) of two springhares at ambient temperatures from 6–35 °C. In most experiments more than 30 min were used for calculation. Evaluation started 2 h after exposure to the various ambient temperatures.  $\circ$  = female;  $\times$  = male

calculations. Both springhares showed marked arrhythmia (probably respiratory) over the whole range of tested ambient temperatures.

### Discussion

Adaptation of the energetics to the environment in homeotherms is mainly achieved through modification of behaviour, basal heat production and thermal insulation (McNab, 1966, 1970, 1978; Hildwein, 1972; Müller and Kulzer, 1977; Müller, 1979). The consequences of a lowered basal metabolic rate are various: 1) reduction of energy requirements (important for mammals with specialised food requirements like termite-eaters or folivores, and for mammals living in areas with periodic food shortage); 2) a lowering of metabolic heat production which serves to avoid overheating in warm, humid environments (e.g. tropical rain-forest, burrows of fossorial mammals); 3) reduction of evaporative water loss in desert environments.

The consequences of changes in thermal conductance are more clear-cut: Apart from the effects on the water budget (Dawson and Schmidt-Nielsen, 1966) a low conductance results in heat conservation, whereas a high conductance facilitates heat loss. The biological significance of the ratio basal metabolism/thermal conductance has been discussed by McNab (1970). He concluded that fossorial mammals should have low rates of basal metabolism and high thermal conductances. Desert mammals, however, are expected to have a low heat production in combination with a low conductance. In the springhare a low basal metabolism is combined with a high thermal

**Table 2.** Cardiovascular responses of two springhares to increased oxygen demands below the thermoneutral zone (TNZ)

$T_a$ (°C)	Male			Female		
	Heart rate (min <sup>-1</sup> )	Oxygen pulse ( $\mu\text{l}\cdot\text{beat}^{-1}$ )	Contribution <sup>a</sup> of heart rate (%)	Heart rate (min <sup>-1</sup> )	Oxygen pulse ( $\mu\text{l}\cdot\text{beat}^{-1}$ )	Contribution <sup>a</sup> of heart rate (%)
6	170.1	210	67	—	—	—
7	—	—	—	129.2	214.5	31.5
8	—	—	—	169.3	138.1	91
12.5	154	177.7	77.9	—	—	—
15.5	—	—	—	133.3	156.8	61.7
16.5	117.7	193.1	46.3	—	—	—
21.5	118.9	163.3	75.6	79.2	161.2	-4.2
22.5	—	—	—	97.1	143	-0.2
TNZ	94.9	151	0	99.1	129.1	0

<sup>a</sup> Calculated according to Bartholomew and Tucker (1963)

conductance. Following McNab's classification it appears, therefore, that these rodents are adapted to fossorial habits rather than to arid conditions. This view is supported by the finding that the maximal urine concentrating ability does not exceed 2,200 mOsmol per kg H<sub>2</sub>O and that the springhares rapidly lose body mass when offered only dry food (unpublished results). By these physiological characteristics springhares closely resemble the black tailed prairie dog, *Cynomys ludovicianus* (Reinking et al., 1977). These rodents periodically encounter xeric conditions in their habitats, but have low rates of metabolism (67% of the expected value according to Kleiber, 1961) and a high thermal conductance (125–150% of the expected value according to Herreid and Kessel, 1967). Likewise, the renal concentrating ability in this species does not exceed 2,000 mOsmol per kg H<sub>2</sub>O. Prairie dogs and springhares both allow their body temperatures to rise considerably when exposed to high ambient temperatures. Such a rise is also known for other mammals and is generally regarded as a water saving mechanism (Schmidt-Nielsen et al., 1957; Taylor, 1970; Maloiy, 1971). However, unlike the prairie dogs and other desert mammals the springhares leave their burrows only at night, thus avoiding the hottest part of the day. The mean burrow temperatures probably never exceed 30 °C (McNab, 1966). Heat storage in the springhare, therefore, seems to be an adaptation to fossorial habits and restricted possibilities for evaporative cooling during their subterranean exercise (digging).

This is supported by the observation that the avenues for evaporative heat dissipation are not well developed: Like most rodents, springhares do not sweat effectively and the respiratory frequency can only be moderately increased. Salivation and urinating must be regarded as emergency measures when

the body temperature is already near lethal levels (Schmidt-Nielsen, 1964).

The basal heart rate of springhares is only about 70% of the theoretical value as predicted by the equation of Jones and Wang (1976). This is certainly related to the reduced basal metabolism. It must not be overlooked, however, that a low heart rate also provides for a wider range to meet the demands for increased oxygen transport during activity or stressful situations (Jones and Wang, 1976; Noll-Banholzer, 1978). As it is difficult to measure heart rate, stroke volume and arterio-venous O<sub>2</sub>-difference simultaneously, information on the contribution of either of these parameters to increased oxygen transport is limited. There is much evidence, however, that changes of the stroke volume play only a minor role (Sanders et al., 1977). Our findings in the springhare suggest that this species may raise the oxygen transport both by cardioacceleration and/or an increase in the arterio-venous O<sub>2</sub>-difference.

From these results it seems that springhares have not developed special physiological adaptations to life in desert environments. The low basal metabolic rate and the rise of body temperature at high ambient temperatures surely reduce water expenditure; but both parameters are more likely to represent an adaptation to the fossorial habits as does the high thermal conductance. Springhares lack completely the ability to highly concentrate the urine, perhaps the most important factor in adaptation to arid conditions. With regard to this it is interesting that during severe droughts these rodents are reported to travel up to 40 km in a night to obtain food and water (Kingdon, 1974). Apparently the behavioural adaptations of springhares (living in burrows; nocturnal activity) do not suffice to survive prolonged periods of water shortage. Thus the animals are probably

restricted to semi-arid areas; invasion of arid environments would be possible only from the periphery when favourable climatic conditions prevail for some time, as was reported for certain Australian rodents (Newsome and Corbett, 1975).

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