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Thermoregulation and evaporative water loss in Spiny mice *(Acomys cahirinus* Desmarest, 1819)

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Abstract

Studied basal metabolism, thermoregulatory responses and evaporative water loss in spiny mice *(Acomys cahirinus).* Oxygen consumption was lowest at T_a = 32.5 °C with a mean value of 1.0 ± 0.12 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, which is 24 % below the expected mass-specific level. At ambient temperatures below this narrow thermoneutral zone O_2-uptake did not increase linearly, but showed two clearely distinct segments with different slopes. The dry thermal conductance was found to be not a constant value, but decreased from 0.202 to 0.134 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}$ with falling T_a; only at T_a = 15 °C it was in accordance with the mass-specific theoretical value. At T_a = 32.5 °C mean T_{re} was 36.4 ± 0.4 °C. In the females T_{re} usually was about 0.5 °C higher than in the males. At T_a = 20 °C T_{re} decreased to 35.2 ± 0.2 °C. In the heat T_{re} rose to 39.2 ± 0.3 °C (T_a = 37.5 °C). Total evaporative water loss (TEWL) was rather low with 0.98 ± 0.3 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ (0.96 mg $H_2O \cdot ml\ O_2^{-1}$) at thermoneutral conditions. At T_a = 35 °C only 14.5 % of the metabolic heat production was dissipated through evaporative pathways. When exposed to dry air (r.h. = 15 %) TEWL increased to 1.53 ± 0.2 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ (T_a = 33 °C). Respiration frequency showed no relation to humidity conditions, but was clearly correlated to ambient temperature.

Introduction

Among murid rodents (Family Muridae) spiny mice (genus *Acomys*) are probably the only truely desert adapted forms. They occur from the Indian peninsula westwards through the Middle East and from there southwards through North and East Africa down to the Cape Province. There also exist a few isolated populations in mountainous regions of the western Sahara and on islands in the eastern Mediterranean Sea. The common spiny mouse *(Acomys cahirinus)* is widespread in the Middle East and Northeast Africa, where it preferably inhabits crevices of rock outcrops in dry deserts and savannas, but in some places also lives in human dwellings (Delany and Happold 1979; Osborne and Helmy 1980).

Unlike most other desert adapted small mammals spiny mice do not dig burrows and are such more exposed to the often high air temperatures in their habitat. However, they not only live in dry hot areas with a mean annual rainfall less than 100 mm (Shkolnik 1966), but also occur at altitudes 2000 m above sea level, where temperatures at night can fall below zero (Shkolnik and Borut 1969). Though the microclimatic conditions in the rock crevices are more constant and less severe than in the open desert (Shkolnik 1966), spiny mice certainly suffer more from the stressful desert climate than burrowing species.

Apart from heat water shortage is the greatest threat to desert dwelling mammals. Water is especially needed for thermoregulatory purposes when ambient temperature exceeds body temperature. Under such conditions body heat can only be dissipated through evaporative pathways. The question, therefore, arises, whether spiny mice have developed special adaptations to economize water use for thermoregulatory purposes.

Information about this is contradictory. Shkolnik and Borut (1969) reported an extraordinary high value for total evaporative water loss (TEWL) of spiny mice at

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thermoneutrality: 1.96 mg $H_2O \cdot ml\ O_2^{-1}$ at $T_a = 30\,°C$, which is the highest value ever reported for a desert adapted rodent of this size. In a more recent study DAILY and HAINES (1981) found that TEWL and water turnover rates in hydrated spiny mice fall in the midrange of values for small desert mammals; in water restricted individuals TEWL and water turnover could be reduced significantly. *Acomys* also has been found to possess an excellent capacity to maintain plasma volume during dehydration (HOROWITZ and BORUT 1970). The concentrating ability of the kidney of spiny mice is comparable to that of other desert adapted small rodents (SHKOLNIK and BORUT 1969; BUFFENSTEIN et al. 1985), a finding which is corroborated by the production of large quantities of antidiuretic hormone (CASTEL and HOCHMAN 1976). In spite of these water-saving adaptations, *Acomys* obviously has a limited ability to acclimate to water shortage, as few animals were found to be able to tolerate chronic restriction of water uptake to 1/8 of the voluntary level (DAILY and HAINES 1981).

In view of the contradictory reports on total evaporative water loss in spiny mice we reinvestigated this point under controlled conditions of various humidities. Additionally, we looked at basal energetics and thermoregulatory capacities.

Material and methods

16 spiny mice (8 females, 8 males) were used for this study. They were taken from a breeding colony at our institute. The animals were 4–12 months old and their mean body mass was 48.5 g. They were kept in a climatic chamber, where ambient temperature and relative humidity were regulated to 25 ± 1 °C and 50 ± 10 % r.h. Lights in the chamber were on for 12 hours; a weak lamp served as illumination during the D-phase.

The spiny mice were housed singly or as unisexual pairs in plastic containers (41 × 26 × 15 cm). Food consisted of a mixture of wheat grains, sun flower seeds, rolled oats and pellets and was supplemented with apples, carrots and lettuce. Drinking water was not offered.

Energetics and thermoregulatory responses were measured in 8 spiny mice (4 females, 4 males) using an experimental set up similar to that described by MÜLLER and ROST (1983) with the following alterations: No telemetric registrations of rectal temperature and heart rate were made in the present study. In addition CO_2-production was measured with an URAS MT (Hartmann and Braun). O_2-uptake was monitored with an Oxytest S (Hartmann and Braun). During the experiments the spiny mice were in a perspex box (volume 980 ml). Air flow was 18.7 l/h at $T_a = 15–35\,°C$ and 22.7 l/h at $T_a = 37.5\,°C$. Relative humidity of the air entering the box was regulated to 40 %, only at $T_a = 37.5\,°C$ it was set to 20 %, humidity inside the box thus never exceeding 60 %. For measuring respiration frequencies a pressure transducer (Bell & Howell 4104, 0–35 mm Hg) was used. Rectal temperatures were determined by use of a thermistor (Ultrakust; accuracy ± 0.1 °C), which was inserted to a depth of 20 mm.

An experimental run lasted 2–4 hours and included an equilibration period of 1 hr. The measurements were always conducted during the L-phase. Each animal was tested twice at the various ambient temperatures. The mean from the two runs was used for further calculations. All gas volumes have been corrected to STPD-conditions.

In a second set of experiments total evaporative water loss and respiration frequency were measured in 8 other spiny mice (4 females, 4 males) at different relative humidities (6, 20 and 40 % r.h.) of the air entering the box. These experiments were done only at $T_a = 25$, 30 and 33 °C. Again each animal was tested twice at any given temperature/humidity combination.

Before testing mean values for the significance of differences (Student t-test or Welch-test) they were checked for homogeneity of variance (F-test). Regression lines were calculated using the method of least squares (LORENZ 1984). Values are given as mean ± S.D.

Results

Rectal temperature (T_{re})

At ambient temperatures from 25–32.5 °C mean T_{re} was 36.0 ± 0.5 °C (Fig. 1). When T_a dropped to 15–20 °C, T_{re} decreased to a mean of 35.2 ± 0.3 °C. At ambient temperatures above 32.5 °C T_{re} rose markedly (to 39.2 ± 0.3 °C at $T_a = 37.5\,°C$).

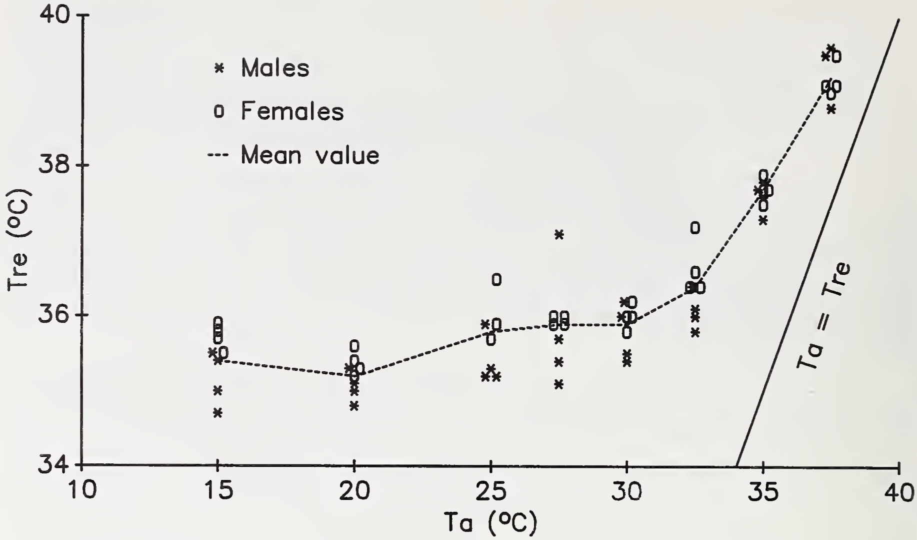

Fig. 1. Rectal temperatures after 2–4 hours exposure to ambient temperatures between 15–37.5 °C

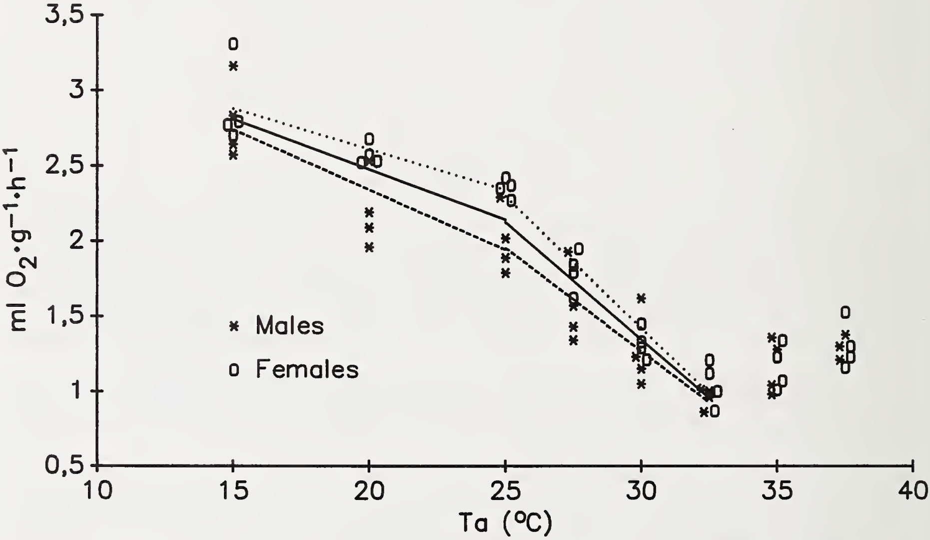

Fig. 2. O_2-consumption at ambient temperatures between 15–37.5 °C. Also given are the regression lines for males (––––), females (····) and both sexes taken together (——); see also Table 1

The maximal T_{re} found was 41.4 °C, which was measured after 60 min exposure to T_a = 37.5 °C. In this case the experiment was disrupted because the animal exhibited signs of severe heat stress (restlessness, urination, defecation, uncoordinated movements). Brought back to the animal room (T_a = 25 °C) T_{re} of this spiny mouse decreased to 31.4 °C within three hours. However, the animal fully recovered and T_{re} rose to 35.2 °C without supplying external heat.

Oxygen consumption (VO_2) and basal metabolic rate (BMR)

Oxygen consumption was lowest at T_a = 32.5 °C (Fig. 2), the values at T_a = 30 °C (α = 0.005) and T_a = 35 °C (α = 0.025) being significantly higher. Within this narrow thermoneutral zone (TNZ) VO_2 was 1.0 ± 0.12 ml $O_2 \cdot g^{-1} \cdot h^{-1}$.

At ambient temperatures below the TNZ the increase of heat production as measured by VO_2 showed two segments with different slopes. Between T_a = 25–32.5 °C VO_2 increased much steeper than between T_a = 15–25 °C. There was also a clear difference in the reaction of males and females: Except at T_a = 15 °C O_2-uptake was always considerably higher in the latter. The data are best described by different regression lines for each sex and temperature segment (Table 1).

At high ambient temperatures VO_2 increased less steep and was 30 % higher at T_a = 37.5 °C than at thermoneutral conditions.

Table 1. **Regression lines and regression coefficients for O_2-uptake at ambient temperatures below 32,5 °C**

	Ta = 15–25 °C
Males	Y (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) = 3.937 – 0.080 · Ta (°C); r = –0.82
Females	Y (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) = 3.688 – 0.054 · Ta (°C); r = –0.83
Both sexes	Y (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) = 3.813 – 0.067 · Ta (°C); r = –0.75
	Ta = 25–32,5 °C
Males	Y (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) = 5.375 – 0.137 · Ta (°C); r = –0.90
Females	Y (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) = 6.670 – 0.175 · Ta (°C); r = –0.97
Both sexes	Y (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) = 6.022 – 0.156 · Ta (°C); r = –0.92

Total evaporative water loss (TEWL)

With the air entering the respiration box having a relative humidity (r.h.) of 40 %, r.h. inside the box varied between 45–60 %. TEWL was lowest at T_a = 27.5 °C with 0.82 ± 0.13 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ (Fig. 3). It almost doubled when T_a rose to 35 °C. At T_a = 37.5 °C the spiny mice salivated profusely and spread saliva over the body surface, thereby increasing TEWL drastically to 4.8 ± 1.11 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$. However, it can not be excluded that saliva adhering to the walls of the box and to the wire mesh contributed to elevate the values.

If related to VO_2 TEWL showed a steady increase with increasing ambient temperatures (Table 2). Above the TNZ TEWL rose only slightly at T_a = 35 °C, with 14.5 % of the

Table 2. **Respiratory quotient (RQ), total evaporative water loss (TEWL) and ratio evaporative heat loss vs. metabolic heat production (E/M) at various ambient temperatures** (mean values ± S.D.)

Ta (°C)	RQ	TEWL (ml $H_2O \cdot kg^{-1} \cdot h^{-1}$)	TEWL (mg $H_2O \cdot ml\ O_2^{-1}$)	E/M (%)
15	0.82 ± 0.02	0.98 ± 0.12	0.35 ± 0.05	4.1
20	0.83 ± 0.02	0.91 ± 0.15	0.38 ± 0.06	4.5
25	0.84 ± 0.03	0.92 ± 0.20	0.42 ± 0.09	4.9
27.5	0.82 ± 0.02	0.82 ± 0.13	0.49 ± 0.05	5.8
30	0.89 ± 0.05	0.86 ± 0.15	0.67 ± 0.11	7.8
32.5	0.91 ± 0.02	0.98 ± 0.30	0.96 ± 0.23	11.4
35	0.86 ± 0.02	1.45 ± 0.32	1.25 ± 0.23	14.5
37.5	0.85 ± 0.02	4.80 ± 1.11	3.69 ± 0.81	43.7

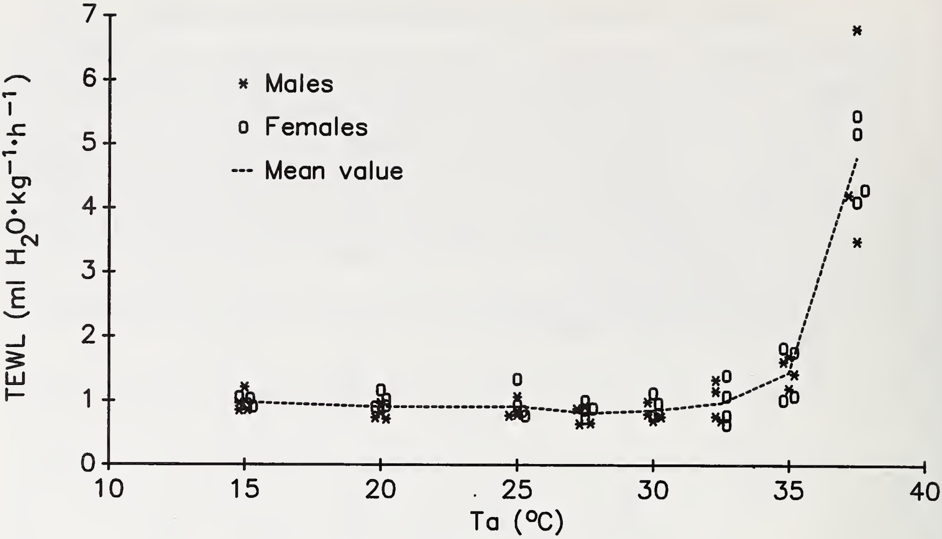

Fig. 3. Total evaporative water loss at ambient temperatures between 15–37.5 °C. During this type of experiments relative humidity inside the respiration box was 45–60 %

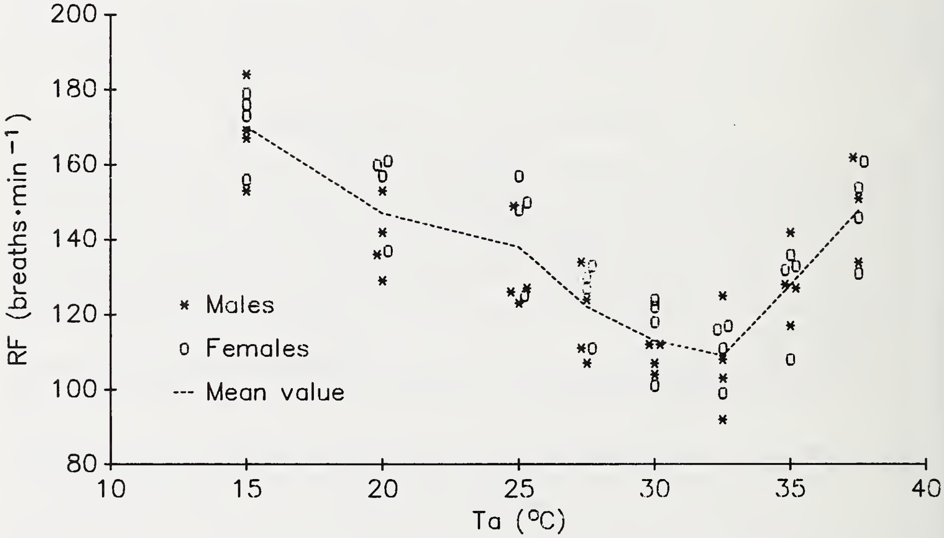

Fig. 4. Respiration frequency at ambient temperatures between 15–37.5 °C

metabolic heat production being dissipated through evaporative pathways, whereas at T_a = 37.5 °C more than 40 % of the endogenous heat was lost by evaporation.

Respiration frequency (RF)

Lowest RF was measured at T_a = 32.5 °C with a mean value of 109 ± 10.7 breaths·min^{-1} (Fig. 4). Like in VO_2 the increase between T_a = 25–32.5 °C was steeper than between 15–25 °C. At ambient temperatures above the TNZ RF increased almost linearly to 148 ±

12.2 breaths·min^{-1} at T_a = 37.5 °C. No panting-like acceleration of breathing could be noticed.

TEWL and RF at different relative humidities (r.h.)

When the air entering the box was regulated to 6, 20 and 40 % r.h., humidity inside the box averaged 15, 27 and 45 % r.h., respectively, the actual value depending on the water added by the evaporation of the tested individuals. TEWL did not differ at T_a = 25 °C and T_a = 30 °C (Fig. 5). At these ambient temperatures it rose from 0.742 at 45 % r.h. to 1.1 ml $H_2O{\cdot}kg^{-1}{\cdot}h^{-1}$ at 15 % r.h. At T_a = 33 °C TEWL was considerably higher, increasing from 0.927 (45 % r.h.) to 1.534 ml $H_2O{\cdot}kg^{-1}{\cdot}h^{-1}$ (15 % r.h.).

RF did not show a correlation to the moisture content of the air, being almost identical at all tested humidities (Fig. 6). Like during the measurements of thermoregulatory responses it exhibited a much closer relation to ambient temperature.

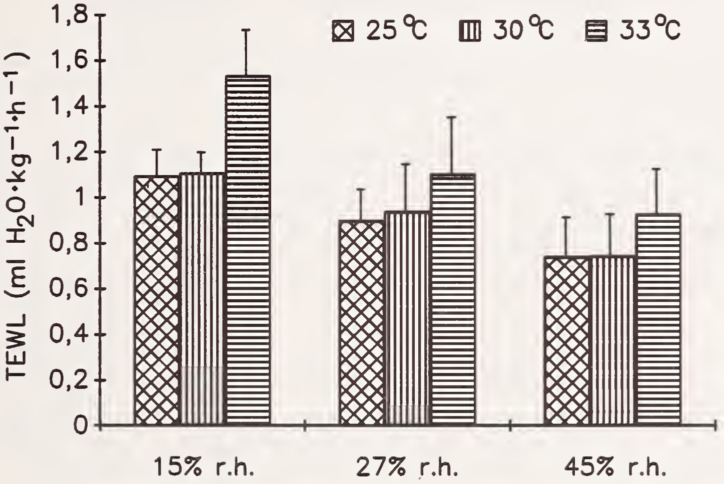

Fig. 5. Total evaporative water loss at various temperature/humidity combinations. Humidity is specified as it appeared inside the respiration box with an animal present. Ingoing air was regulated to 6, 20 and 40 % r.h., respectively

Discussion

If compared to data obtained in previous studies on TEWL in spiny mice, our results closely agree with those of Daily and Haines (1981) (Table 3), whereas they do not confirm the findings of Shkolnik and Borut (1969), who reported values, which were almost double as high. As Daily and Haines (1981) used the same technique for measuring TEWL as we did, it can be supposed that the discrepancies between the results for TEWL must be attributed to technical differences, the reason for the unusual high values in Shkolnik's and Borut's study remaining unclear. From the data now available it must be concluded that part of the adaptive strategies of spiny mice to desert conditions – like in other small desert rodents – mainly rests on an economical use of water for thermoregulatory purposes. This is in contrast to Shkolnik's and Borut's (1969) view, who – on the basis of their results – emphasized the ability of spiny mice to dissipate larger amounts of body heat through evaporative avenues.

The evaporative water loss which we measured at T_a = 30 °C falls in the midrange of

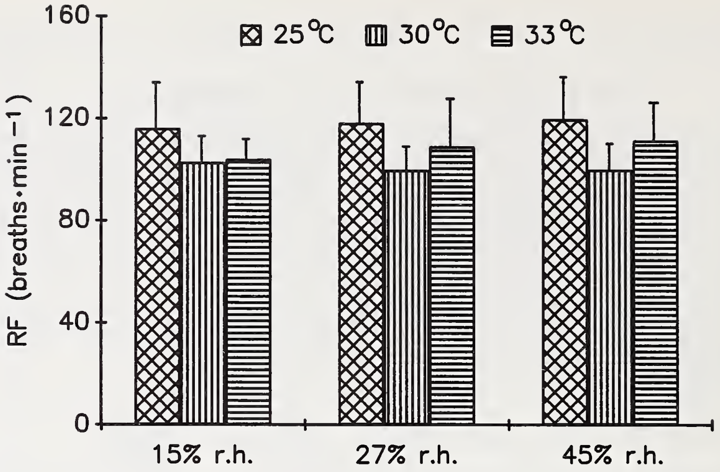

Fig. 6. Respiration frequency at various temperature/humidity combinations. Same experimental conditions as in Fig. 5

Table 3. **Total evaporative water loss (TEWL) in Spiny mice as measured by various authors**

Species	TEWL ml $H_2O \cdot kg^{-1} \cdot h^{-1}$	 mg $H_2O \cdot ml\ O_2^{-1}$	VO_2 ml $O_2 \cdot g^{-1} \cdot h^{-1}$	Ta (°C)	r.h.[a] (%)	Source
A. c.	2.09	1.9	1.1	30	15–30	Shkolnik and Borut (1969)
A. r.	1.84	2.3	0.8	30	15–30	Shkolnik and Borut (1969)
A. sp.	1.3	0.8	(1.63)[b]	?	ca. 50	Fertig and Edmonds (1969)
A. c.	0.86	0.84	1.02	30	ca. 50	Daily and Haines (1981)
A. c.	0.86	0.67	1.29	30	45–60	this study
A. c.	0.75	–	–	30	45	this study
A. c.	0.94	–	–	30	27	this study
A. c.	1.11	–	–	30	15	this study

A. c. = *A. cahirinus; A. r.* = *A. russatus*; [a]inside the respiration box; [b]estimated value

desert adapted small rodents (data summarized in Daily and Haines 1981; Müller 1985). The economic use of water for thermoregulatory purposes is corroborated by the finding that at an ambient temperature of 35 °C the spiny mice dissipated only 14.5 % of their metabolic heat through evaporative pathways. Instead of keeping T_{re} on the normal resting level, they rather relied on a water saving storage of heat as indicated by the elevation of the rectal temperature by about two degrees. The ability for the temporary storage of excess heat is favoured by the rather low level of T_{re} (<36 °C) at ambient temperatures ≤30 °C.

Only at T_a = 37.5 °C the spiny mice increased TEWL drastically to over 5-times the value at T_a = 30 °C. About 40 % of the endogenous heat load was then evaporated. This rapid increase of TEWL was only possible because the animals salivated profusely. Salivation, however, is regarded as an uneconomic emergency measure. Additionally, at this high ambient temperature the spiny mice frequently changed their position in the respiration box, thus bringing their ventral surface into contact with cooler parts of the wire mesh material. This behaviour has already been noted by Shkolnik and Borut (1969) and certainly serves to increase conductive heat loss.

As long as ambient temperature did not exceed 30 °C, TEWL of the spiny mice remained fairly low. When exposed to the same relative humidity of the air, 15–28 % less water was evaporated at T_a = 30 °C than at T_a = 33 °C. The effect of different humidities on TEWL was more pronounced: At ambient temperatures from 25–33 °C TEWL decreased by 48–65 % when the relative humidity of the air increased from 15 to 45 %. This clearly demonstrates that searching for more favourable microclimatic conditions during the hottest parts of the day pays for the spiny mice with regard to their water budget.

As in most other rodents a panting-like acceleration of the breathing rate did not occur in the spiny mice. Respiration frequency seemed to be correlated to oxygen consumption rather than to the moisture content of the air. With falling ambient temperatures the increase of RF almost paralleled that of VO_2.

The low basal metabolic rate of spiny mice, which has also been found by other investigators (SHKOLNIK and BORUT 1969; WISE 1977; DAILY and HAINES 1981; HAIM and BORUT 1981), is certainly advantageous in a habitat with regular periods of food and water shortage. A reduced basal heat production is common among small desert dwelling rodents (MÜLLER 1985), as it contributes to minimize food and water requirements.

Thermoregulatory responses at temperatures below the TNZ differed from the usual picture in that VO_2 did not increase linearly, but showed two segments with different slopes. The flattening of the heat production curve below T_a = 25 °C was accompanied by a drop of T_{re} from 36.0 ± 0.5 °C at T_a = 25–32.5 °C to 35.2 ± 0.3 °C at lower ambient temperatures. Also dry thermal conductance proved to be not a constant value, but decreased from 0.191 at T_a = 25 °C to 0.134 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}$ at T_a = 15 °C (Fig. 7). A similar reduction of C_{dry} in the cold has been reported for *Gerbillus perpallidus* (MÜLLER 1985). Between T_a = 32.5 °C and T_a = 35 °C C_{dry} rose rapidly, indicating a marked increase of the heat loss by conduction and/or radiation, i.e. through water-saving avenues.

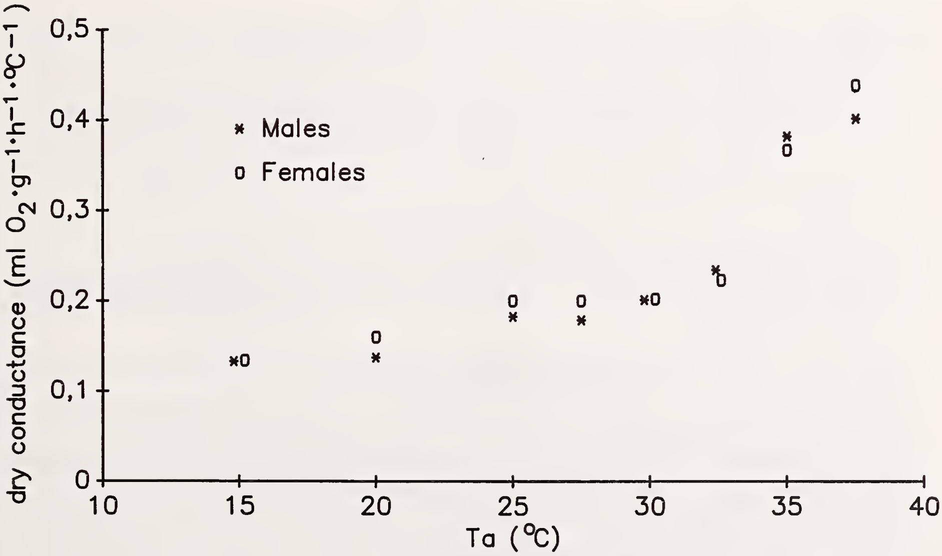

Fig. 7. Dry thermal conductance (C_{dry}) at ambient temperatures between 15–37.5 °C. Calculated after the formula:

$$C_{dry} = \frac{M - E}{T_{re} - T_a}$$

(M = metabolic heat production, E = evaporative heat loss, T_{re} = rectal temperature, T_a = ambient temperature)

These findings, however, do not indicate inappropriate thermoregulatory capacities of the common spiny mice in the cold, but rather represent a well controlled saving of energy by allowing a moderate decrease of the body temperature in a cold environment. Evidence for this comes from the fact that the flattening of the heat production was most pronounced when T_a fell from 25 to 20 °C. To a further drop of T_{re} the spiny mice reacted with an intensified heat production. Their recently found ability to enter torpor during prolonged periods of food reduction (Müller et al. 1988) also supports this view.

Zusammenfassung

Temperaturregulation und evaporative Wasserabgabe bei Stachelmäusen (Acomys cahirinus Desmarest, 1819)

An Stachelmäusen *(Acomys cahirinus)* wurden Basalstoffwechsel, Temperaturregulation und evaporative Wasserabgabe untersucht. Der O_2-Verbrauch war bei einer Umgebungstemperatur von 32.5 °C am niedrigsten und lag mit 1.0 ± 0.12 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ um 24 % unter dem gewichtsspezifischen Erwartungswert. Bei Umgebungstemperaturen unterhalb dieser engen thermischen Neutralzone stieg der O_2-Verbrauch nicht linear an, sondern zeigte zwei deutlich verschiedene Bereiche mit unterschiedlichen Steigungen. Die „trockene" Wärmedurchgangszahl war keine konstante Größe, sondern nahm mit sinkender Umgebungstemperatur von 0.202 auf 0.134 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}$ ab; nur bei T_a = 15 °C stimmte sie mit dem gewichtsspezifischen Erwartungswert überein. Bei T_a = 32.5 °C lag die mittlere Rektaltemperatur bei 36.4 ± 0.4 °C. Bei den Weibchen war T_{re} im allgemeinen um 0.5 °C höher als bei den Männchen. Bei T_a = 20 °C sank T_{re} auf 35.2 ± 0.2 °C. Unter Hitzebedingungen (T_a = 37.5 °C) stieg T_{re} auf 39.2 ± 0.3 °C. Die evaporative Wasserabgabe war unter thermisch neutralen Bedingungen mit 0.98 ± 0.3 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ relativ niedrig. Bei T_a = 35 °C wurden nur 14.5 % der im Stoffwechsel gebildeten Wärme durch Verdunstungskühlung abgegeben. In trockener Luft (r.h. = 15 %) stieg die evaporative Wasserabgabe bei T_a = 33 °C auf 1.53 ± 0.2 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$. Die Atemfrequenz zeigte keine Beziehung zu den Feuchtebedingungen, war aber deutlich korreliert mit der Umgebungstemperatur.

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