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WATER EXCHANGE, TEMPERATURE TOLERANCE, OXYGEN CONSUMPTION AND ACTIVITY OF THE NAMIB DESERT SNAIL, *TRIGONEPHRUS* SP.

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ABSTRACT

Water exchange, temperature tolerance and oxygen consumption of the snail, *Trigonephrus* sp., from the southern Namib desert of Namibia were examined and related to activity. At 25°C and 15% R.H., mean water loss and food and water uptake were 5.95 mg·day⁻¹ and 630 mg·day⁻¹, respectively. Body temperature tracked sand temperature. Snails tolerated sand temperatures as high as 45°C. Mean \pm S.D. oxygen consumption rates were 32.0 \pm 2.94 μ lO₂·g total body mass⁻¹·h⁻¹ at 15°C, when the snails were active, and 11.27 μ lO₂·g total body mass⁻¹·h⁻¹ at 25°C, when the snails were inactive. These values are 2-6 times lower than those recorded for the similarly sized mesic snail, *Helix aspersa*. Activity experiments indicated that low ambient temperatures and high humidities were favoured by the snails. This, together with the burying behaviour of these snails during high temperatures, suggests that they limit stress by restricting activity to physiologically-favourable periods, even though more-extreme conditions may be tolerated.

INTRODUCTION

The abundance of pulmonate snails in many arid areas has resulted in a wide range of studies of environmental triggers leading to dormancy, arousal and activity (Herreid & Rokitka, 1976) and of the physiological responses of snails while in these states. Various aspects of land snail physiology have been investigated, including water exchange (Machin, 1967, 1972; Yom-Tov, 1971a), temperature tolerance (Schmidt-Nielsen, Taylor & Shkolnik, 1971, 1972; Yom-Tov, 1971b) and metabolism/respiration (Riddle, 1975; Barnhart, 1983, 1986; Barnhart & MacMahon, 1987).

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Southern Africa has an abundant terrestrial snail fauna, consisting of numerous desert families, including the endemic family Dorcasiidae (Van Bruggen, 1978). This family includes the 10 species of the genus *Trigonephrus*, which is distributed from the south-western Cape to southern Namibia (Connolly, 1939; Bequaert & Miller, 1973; Van Bruggen, 1978) in arid and semi-arid habitats. Several species of *Trigonephrus* have been described from the Namib desert (Connolly, 1939). While the taxonomic status of these species is currently in dispute, it would appear from the description and type location (Connolly, 1931) that the study species is *T. haughtoni* Connolly.

Conditions here for a desert snail are particularly harsh—the mean monthly maximum temperature in the hottest month (March) is 39.8°C and the mean monthly minimum temperature in the coldest month (August) is 2.7°C (Lancaster, Lancaster & Seely, 1984). Rainfall is low, averaging 8.04 mm per month. The mean rainfall in the wettest month (March) is 20.3 mm, while in the driest month (November) an average of 2.5 mm rain falls (Schulze & McGee, 1976).

Our aims in this study were to describe the water exchange temperature preferences, oxygen consumption and activity of *Trigonephrus* sp., and to compare these values with those of other desert snails, and with the mesic snail *Helix aspersa* Müller.

MATERIALS AND METHODS

Study site

Snails were collected from or below (to -15 cm) the sand surface in the southern Namib dunes (27°40'S 16°12'E) in April 1988. The partially-vegetated dunes are bordered by gravel plains fringed by the Swartkloof mountains on the eastern side and extend to the

Atlantic Ocean in the west. These snails occur in habitats that have a surface layer of coarse sand and a degree of protection from the prevailing wind (Dallas & Curtis, in press). The average summer windspeed for Aus, about 100 km from the study site, is about $25 \text{ km} \cdot \text{h}^{-1}$ in a southerly to south-westerly direction (Anon., 1944). Voucher specimens were deposited in the State Museum, Windhoek (Namibia).

Water exchange

Twelve inactive snails with a mean \pm S.D. weight prior to desiccation experiments of $9.01 \pm 1.25 \text{ g}$ were placed in separate open-topped containers within a desiccating chamber containing silica gel (R.H. 15%). The activity state of snails was classified as follows: dormant snails are retracted and possess an epiphragm; inactive snails are retracted but lack an epiphragm; and active snails have their foot extended outside the shell. The desiccation container was sealed and maintained at a constant temperature (25°C) for ten days, and activity scored daily. Two further trials were conducted in an identical way and snails were weighed after each trial to determine water loss. The presence of faeces was noted and corrections to water loss values made for mass loss due to faecal material. Parametric statistical analyses were carried out on the arcsin transforms of the percentage water loss values.

Shell thickness and aperture size may influence water loss (Machin, 1967). We therefore measured the thickness of 15-30 randomly-selected pieces of broken shell for each of 10 different empty snail shells. Maximum aperture length and width were measured for each snail.

The ability of snails to take free water and food was assessed gravimetrically. Five snails were placed in individual containers with moist sand at $25 \pm 1^\circ\text{C}$ for four days, and fed pieces of lettuce *ad libitum*. This was repeated twice and activity, particularly feeding, was noted daily.

Deep-body and environmental temperatures

The deep-body temperatures (T_b) of five snails in the field were monitored hourly throughout a 48 h period in January 1988, using thermocouples inserted between the snail body and the second whorl of the shell. The thermocouple wire was sufficiently long to enable snails to move about on the surface or to bury down to a depth of 50 cm. Sand temperatures at 5 cm intervals from 0-30 cm depth were monitored simultaneously. Monitoring was started at 21h00 when the snails were positioned on the sand surface; from 12h00 until 18h00 on the next day, shading was erected over the snails to eliminate any risk of thermal death, and at 12h00 on the last day the snails were dug up and reburied at 10-15 cm. Shading was provided because the snails did not move at all under the potentially harmful experimental conditions (high ambient temperature and light intensity), possibly because environmental cues for normal activity (low ambient temperatures and light intensity) were absent.

Oxygen consumption

Oxygen consumption of 12 *Trigonephrus* sp. and six *Helix aspersa* was measured at 5°C increments from 10 to 30°C by placing the snails in 60 ml syringes and withdrawing 20 ml air samples before the temperature was changed. The oxygen concentration of these samples was measured with a Beckman through-flow oxygen analyzer, following the method of Bartholomew & Casey (1977). The relative humidity was not controlled, although remained above 50% for all experiments.

Activity

The relationship between activity and temperature was determined at 5°C intervals from 10 to 30°C by placing 12 snails in separate 60 ml syringes in water baths and scoring their activity every 10 min for the first 30 min, and then hourly for five more hours. Relative humidity (R.H.) was $>50\%$ at all times.

Observations were conducted on the temporal activity pattern of five snails maintained at ambient temperature and humidity at the Desert Ecological Research Unit, Gobabeb in the central Namib during September 1989. Similar ambient temperatures and humidities are experienced there as the original site in the southern Namib desert (Lancaster, Lancaster & Seely, 1984).

In January 1989 a field study was conducted at the area where snails had been collected. Ambient and sand (0, 5, 10 and 15 cm depth) temperatures, relative humidity and windspeed measurements (both at 1 m above ground level) were taken three times daily (06h30, 14h00 and 20h00). A sling psychrometer was used to measure air temperature and R.H. To measure sand temperature, a wooden stick with thermocouples attached at the appropriate depths was hammered into the sand and allowed to equilibrate for 2 h before measurements were made. Simultaneously with temperature measurements, the activity of five snails from the local population was monitored hourly for 48 h.

RESULTS

Water loss

There were no significant differences in water loss between the three trials (ANCOVA, covariate = body mass, $p > 0.05$), so the data for all trials were lumped together. Some snails (16 out of 36 snails) possessed an epiphragm during the ten-day desiccation, six in the beginning, five at the end, and five throughout. No difference, however, was noted in percentage water loss between snails in various states of inactivity/dormancy (ANCOVA, covariate = body mass, $p > 0.05$). Mean and standard deviations for percentage water loss (shelled weight of live snail) for each snail (Fig. 1), indicates that there

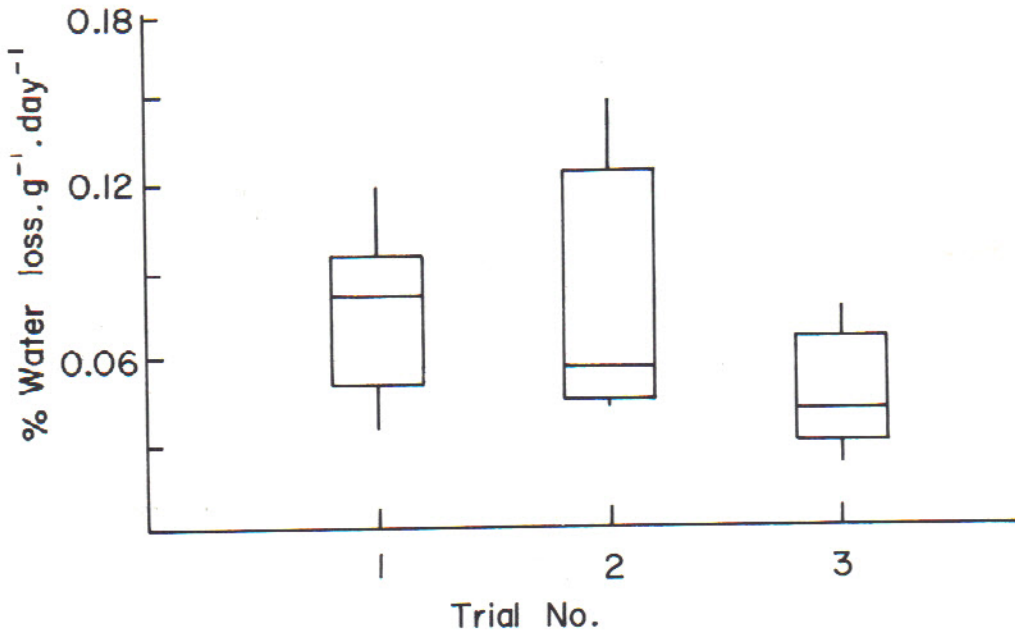


Figure 1. Box-and-whiskers plot (median, quartiles and range) of % water loss $\cdot g^{-1} \cdot day^{-1}$ by *Trigonephrus* sp. during three 10-day desiccation trials ($n = 12$ snails for each trial).

is a large amount of intra- and inter-snail variation. The overall mean \pm S.D. water loss of snails in the 10-day desiccation trials was $5.95 \pm 1.79 mg \cdot day^{-1}$. The mean \pm S.D. percentage water loss per unit of the total snail mass was $0.07 \pm 0.04\% \cdot g^{-1} \cdot d^{-1}$. There was no significant correlation ($p > 0.05$) between the percentage water loss and snail size (length).

It has been calculated that a snail can survive a loss of at least 35% of its body water (about 80% of total body mass) (Kamanda, 1933; Machin, 1967; Schmidt-Nielsen *et al.* 1971). Assuming that *Trigonephrus* sp. has similar ability to withstand water loss, we estimate that *Trigonephrus* sp. snails subjected to 25°C and 15% R.H. would be able to survive for about 400 days. This is longer than the 0.6 years predicted for *H. aspersa*, similar to that for *Otala lactea* (Müller) (1.1 years), but considerably shorter than the 3.6 years predicted for *Sphincterochila boissieri* (Charpentier) (Machin 1967). It is possible, however, that a specific adaptation of *Trigonephrus* sp. to desert conditions is the ability to survive a loss of more than 35% body water. This remains to be tested experimentally.

Shell thickness was highly variable, but considerably thicker (mean \pm S.E. = 0.73 ± 0.11 mm) than that of the mesic snails *H.*

aspersa (0.42 ± 0.05 mm) and *O. lactea* (0.37 ± 0.04 mm) and similar to the desert snail *S. boissieri* (0.84 ± 0.04 mm) (Machin 1967). There was no significant correlation ($p > 0.05$) between shell thickness and shell size in *Trigonephrus* sp.

Mean maximum \pm S.D. aperture length and width were 15.23 ± 1.40 mm and 13.50 ± 1.04 mm, respectively. An estimate of mean aperture was calculated, assuming a square opening, to be 2.07 ± 0.33 cm².

Water uptake

During the water-uptake experiments, only three snails fed in the first trial (mean mass gain of feeding snails = 314 ± 62.1 mg $\cdot d^{-1}$), while 11 snails fed in the second trial (mean mass gain of feeding snails = 628 ± 281 mg $\cdot d^{-1}$). Mean \pm S.D. percentage mass increase per gram body mass was $6.9 \pm 2.7\% \cdot g^{-1} \cdot day^{-1}$. There was no significant correlation between the arcsin transform of the percentage mass increase per gram body mass and initial body mass ($p > 0.05$, $n = 12$ snails, three trials for each snail).

Oxygen consumption

There was no significant correlation between oxygen consumption per gram body mass and

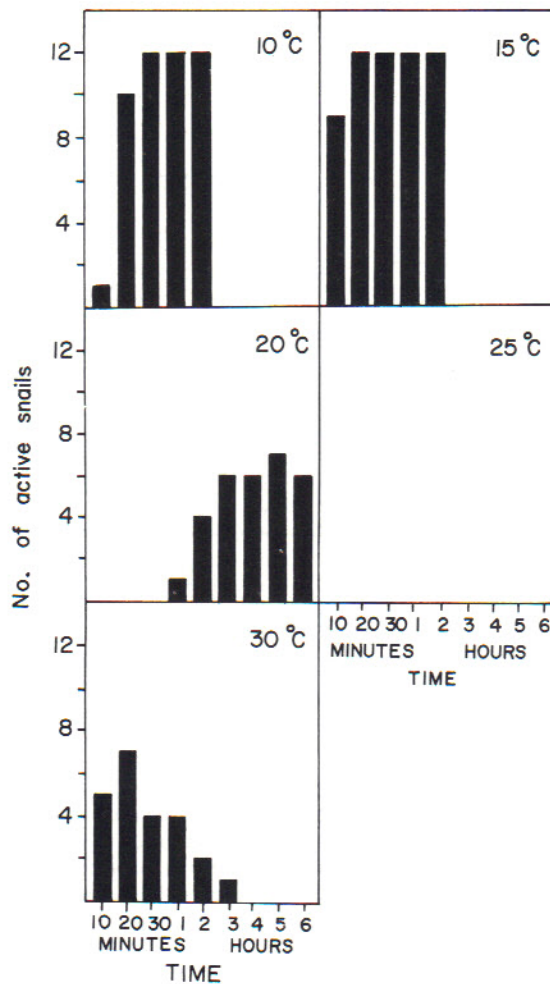


Figure 2. The number of active *Trigonephrus* sp. with time at five different temperatures.

air temperature in either *Trigonephrus* sp. or *H. aspersa* ($p > 0.05$). This may have been related to variation in activity states among snails (Fig. 2) or variation in pneumostome opening by individuals (Barnhart & McMahon, 1987; see Kratochvil, 1978 for discussion of this phenomenon). For this reason, we compared oxygen consumption values among species at 15°C (when all snails were active) and at 25°C (all snails inactive).

There was a significant change in oxygen consumption by *Trigonephrus* sp. between active and inactive states (ANOVA, $p < 0.05$). Mean \pm S.D. oxygen consumption of *Trigonephrus* sp. during activity (15°C) was $32.0 \pm 9.7 \mu\text{O}_2 \cdot \text{g total mass}^{-1} \cdot \text{h}^{-1}$ and during inactivity (25°C) it

was $12.6 \pm 5.4 \mu\text{O}_2 \cdot \text{g total mass}^{-1} \cdot \text{h}^{-1}$. There was no significant difference in the oxygen consumption of active and inactive *Helix aspersa* (ANOVA, $p > 0.05$). Oxygen consumption by active (15°C, $n = 6$) and inactive (25°C, $n = 3$) *H. aspersa* was $62.67 \pm 15.5 \mu\text{O}_2 \cdot \text{g total mass}^{-1} \cdot \text{h}^{-1}$ and $57.4 \pm 3.6 \mu\text{O}_2 \cdot \text{g total mass}^{-1} \cdot \text{h}^{-1}$, respectively. Oxygen consumption by *Helix aspersa* was significantly higher than that of *Trigonephrus* sp. at both temperatures tested (ANCOVA; covariate = body mass, $p < 0.0001$).

Body temperatures

There was no significant difference in T. among the five snails throughout the 48 h period

to withstand 35% body water loss, is also higher than *H. aspersa* and much lower than that of *S. boissieri*. Thus, *Trigonephrus* sp. is not considered to be particularly xeric in its physiological adaptations to control water loss. The estimated period of survival of *Trigonephrus* sp. without water (400 days) is particularly insignificant when compared with the records (which are probably maxima rather than mean values) for the desert snails *Eremina (Helix) desertorum* (Forskål) (4 years—Baird, 1850) and *Xerantonita veitchii* (Newcomb) (6 years—Stearns, 1877). However, extreme water loss conditions are unlikely to be experienced by *Trigonephrus* sp. for long periods in the field because they can burrow into the sand where humidity is relatively high. This species may also become active on mornings when there is fog in order to regain moisture (pers. obs.), as do tenebrionid beetles in the Namib desert (Seely, 1979). Also, water uptake by *Trigonephrus* sp. is efficient; the water uptake in a single day is sufficient to sustain a snail for long periods of deprivation.

The deep water-loss estimate for *Trigonephrus* sp. may be conservative because snails were either inactive or in the initial stages of dormancy. Riddle (1975) showed that water loss decreases as exposure to dry air increases, suggesting that water-loss rates of snails that have been dormant for a long period of time will be considerably lower than those of snails studied here.

Mechanisms affecting water loss may be (Machin, 1967):

- (1) morphological, i.e. related to shell thickness, aperture size, epiphragm thickness and permeability;
- (2) physiological, i.e. regulated by the mantle collar and frequency of pneumostome opening; or
- (3) behavioural, e.g. by avoidance of high temperatures by burrowing into moist sand.

Of these potential factors we were only able to examine shell thickness and behaviour.

Shell thickness has been shown to retard water loss in terrestrial snails by providing a barrier to evaporation (Gebhardt-Dunkel, 1953). The shells of *Trigonephrus* sp. are thicker than those of the similarly sized mesic snails, *Helix aspersa* and *Otala lactea*, but approximately equal to those of the much smaller desert snail *S. boissieri*. It might, thus, be expected that *Trigonephrus* sp. and *S. boissieri* have similar water loss rates. However, *S. boissieri* had a much lower water loss rate than *Trigonephrus*. This large difference between the two species could be due

partly to *S. boissieri* being in a state of total dormancy during Machin's (1967) experiments. During activity, water loss rates by terrestrial snails are high, e.g. Schmidt-Nielsen *et al.* (1971) measured a daily water loss of 50–150 mg·day⁻¹ for active *S. boissieri*.

Machin (1967) has shown that much of the water loss by *H. aspersa*, *O. lactea* and *S. boissieri* is via the exposed surface in the region of the aperture. The aperture area of *Trigonephrus* sp. (2.07 ± 0.33 cm²) is smaller than that of the similar-sized *H. aspersa* (2.62 ± 0.24 cm²), and larger than that of *O. lactea* (1.25 ± 0.08 cm²) (Machin 1967). Rate of water loss by *Trigonephrus* sp. is lower than in *H. aspersa* and similar to that of *O. lactea*. Thus, aperture area is not the major source of water loss in *Trigonephrus* sp. because it would be expected to have a higher water-loss rate than *O. lactea*.

Oxygen consumption

Trigonephrus sp. has a considerably lower oxygen consumption than the similarly-sized *Helix aspersa* and *Otala lactea* ($74.13 \mu\text{LO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, active; $10.72 \mu\text{LO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, dormant—Herreid, 1977). Thus, oxygen consumption is the single physiological factor of those examined that shows that *Trigonephrus* sp. is more suited to life in xeric conditions than the mesic snail *O. lactea*.

The large amount of variation in oxygen consumption in both *Trigonephrus* sp. and *H. aspersa* is indicative of variation in snail activity, frequency of pneumostome opening and, possibly intermittency of CO₂ release (Barnhart, 1986).

Body temperatures

Behavioural observations of snail activity at different ambient temperatures (Fig. 2) showed that *Trigonephrus* sp. were active at lower ambient temperatures. However, at 30°C, snails became active during the initial stages of the experiment. The rapid emergence and subsequent retraction at relatively high temperatures has been termed an escape response by Herreid & Rokitka (1976), and is probably not a second preferred period of activity. In field observations (Fig. 3), snails were able to tolerate high ambient temperatures (40–45°C). It seems unlikely that under natural circumstances they would allow themselves to be exposed to such high temperatures for any length of time, because of the problems of high water loss by

evaporative cooling. *Trigonephrus* sp. allowed T_b to track sand temperature, thereby minimizing the use of energetically expensive mechanisms to heat or cool themselves.

The ambient temperatures at which *Trigonephrus* sp. were most active were similar to those of other desert snails, which are commonly active at temperatures (20°C and humidities >50% (Yom-Tov, 1971b; Schmidt-Nielsen *et al.*, 1971). Despite the low air temperatures and high humidities at night in January (Fig. 3), no *Trigonephrus* sp. were active on the surface. At 10-15 cm below the surface, where snails were presumably buried for their summer dormancy, temperatures were still relatively high (22.9-33.2°C). Thus, arousal of these snails may require rainfall or lower surface temperatures, which will facilitate moisture penetration and cooling to the depth at which the snails occur.

CONCLUSIONS

The behavioural characteristics (temporal activity patterns and activity states) of *Trigonephrus* sp. appear to limit their exposure to conditions of high ambient temperature and relative humidity which lead to increased water loss and greater oxygen consumption. *Trigonephrus* sp. have lower water loss and oxygen consumption rates than the mesic *H. aspersa*, but are not as xerically adapted as other desert snails studied to date. They are, however, capable of tolerating more-extreme conditions when artificially exposed to them.

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