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

HELEN F. DALLAS[1], BARBARA A. CURTIS[2], and DAVID WARD[3]

Desert Ecological Research Unit of Namibia, Gobabeb, P.O.Box 1592, Swakopmund 9000, Namibia.

[1] Current address: Mitrani Centre for Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben Gurion University of the Negev, Sede Boqer Campus 84993, Israel.

[2] State Museum, P.O.Box 1203, Windhoek 9000, Namibia.

[3] Current address and address for correspondence: Mitrani Centre for Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben Gurion University of the Negev, Sede Boqer Campus 84993, Israel.

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% relative humidity, mean water loss and potential food and water uptake were 5.95 $mg.day^{-1}$ and 628 $mg.day^{-1}$, respectively. Body temperature tracked sand temperature. Snails tolerated sand temperatures as high as 45°C. Mean ±S.D. oxygen consumption rates were 32.0 ±9.7 $\mu lO_2.g$ body $mass^{-1}.h^{-1}$ (at 15 °C, active) and 12.6 ±5.4 $\mu lO_2.g$ body $mass^{-1}.h^{-1}$ (at 25 °C, 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, in addition to the burying behaviour of these snails during high temperatures, suggests that they limit stress by restricting activity to physiologically-favourable periods, even though under experimental conditions 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 (Herreid 1976). Various aspects of land snail physiology have been investigated, including water exchange (Machin 1967, 1972; Yom-Tov 1971a), temperature tolerance (Schmidt-Nielsen *et al.* 1971, 1972; Yom-Tov 1971b) and metabolism/respiration (Riddle 1975; Barnhart 1983, 1986, Barnhart & MacMahon 1987).

Southern Africa has an abundant terrestrial snail fauna, including numerous desert families, most notable of which is the endemic family Dorcasiidae (Van Bruggen 1978). The genus *Trigonephrus* (ten species), is distributed from the south-western Cape to southern Namibia (Connolly 1931, Bequaert & Miller 1973, Van Bruggen 1978) in arid and semi-arid habitats. Two species have been described from the southern Namib desert, *Trigonephrus haughtoni* and *T. connollyi*. While the taxonomic status of these two morphologically-similar species is in dispute (Van Bruggen 1978), both species have been described from the sandy areas of the Namib desert. From the descriptions and the type locations (Connolly 1931) it is likely that the study species is *T. haughtoni*.

Conditions here for a desert snail are particularly harsh - mean monthly ambient temperature is 20.6°C. Mean monthly maximum temperature in the hottest month (March) and mean monthly minimum temperatures in the coldest month (August) are 39.8°C and 2.7°C, respectively (Lancaster et al. 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 1978).

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.

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. Voucher specimens were interred in the State Museum, Windhoek (Namibia). The partially-vegetated dunes are bordered by gravel plains fringed by the Swartkloofberg 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). Average summer windspeed (southerly to south-westerly direction) is about $25 km.h^{-1}$ (for Aus, about 100 km from the study site - Anon. 1944).

Water exchange

Twelve inactive snails (mean ±S.D. mass prior to desiccation experiments = 9.01 ±1.25g) were placed in separate open-topped containers within a desiccating chamber containing silica gel (Relative Humidity ±15%). The activity of snails was classified as follows: dormant snails have the body retracted and epiphragmated; 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 ±1°C) for ten days. Subsequent trials (n=3) were 10 days long and snails were weighed after each trial to determine water loss. The presence of faeces was noted and the relevant corrections made. For parametric statistical analyses, we arcsin transformed 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 up free water and food was assessed gravimetrically. Snails were placed in individual containers with moist sand, and fed *ad libitum* (pieces of lettuce) and maintained at 25±1°C for four days. This was repeated twice and activity, particularly feeding, was noted.

Deep-body and environmental temperatures

The deep-body temperatures (T_b) of five snails in the field were monitored hourly over a 48 h period in January 1989, 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 50cm. Sand temperatures (5 cm intervals from 0-30 cm depth) were monitored simultaneously. Monitoring was started at 21h00 (snails positioned on the sand surface); from 12h00 until 18h00 on Day One (first full day) shading was erected over the snails to eliminate any risk of thermal death, and at 12h00 on Day Two the snails were dug up and reburied at 10-15 cm.

Oxygen consumption

Oxygen consumption of 12 Trigonephrus sp. and six H. aspersa was measured at 5 °C increments (10-30 °C) by placing the snails in 60ml syringes and withdrawing air samples (20 ml). Oxygen concentration of these samples was measured with a Beckman through-flow oxygen analyzer, following the method of Bartholomew & Casey (1977). Relative humidity was not controlled, although it was kept >50% for all experiments.

Activity

The relationship between activity and temperature (at 5 °C intervals from 10-30 °C) was determined by placing 12 snails in separate 60ml syringes in water baths. Relative humidity was >50% at all times. Observations were conducted on the temporal activity pattern of snails in open-air enclosures 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 in the original site in the southern Namib desert (Lancaster *et al.* 1984).

In January 1989 a field study was conducted at the area where snails had been collected. Ambient and sand temperatures (0, 5, 10 and 15cm depths), relative humidity and windspeed measurements were taken three times daily (06h30, 14h00 and 20h00). A sling psychrometer was used to measure ambient temperature. 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. Snail activity was monitored simultaneous to temperature measurements.

RESULTS

Water loss

There was no significant difference in water loss among the three trials (ANCOVA, covariate = body mass, $p>0.05$), so the data for each trial were lumped together. Some snails (a total of 16 out of 36 snails over the three trials) were epiphragmated during the ten-day desiccation trials, either in the beginning ($n=6$), at the end ($n=5$) or throughout ($n=5$). 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 ±S.D. percentage water loss (shelled mass of live snail) for each snail (Fig. 1), indicates that there is a large amount of intra- and inter-snail variation. The overall mean ±S.D. water loss of snails in the 10-day desiccation trials, calculated on a daily basis, was 5.95 ±3.11 mg.day^{-1}. The mean ±S.D. percentage water loss per unit total snail body mass was 0.07 ±0.04%.g^{-1}.day^{-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). Extrapolating from our water loss data, we estimate that *Trigonephrus* sp. snails subjected to 25°C and 15% relative humidity would be able to survive for about 400 days. This is longer than the 0.6 years predicted for *H. aspersa*, similar to that predicted for *Otala lactea* (1.1 years), but considerably shorter than the 3.6 years predicted for *Sphincterochila boisseri* (Machin 1967).

Shell thickness was highly variable, but considerably thicker (mean ±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)(Machin 1967). The shell thickness of the desert snail *S. boisseri* is similar (0.84 ±0.04 mm) to that of *Trigonephrus* sp.. There was no significant correlation ($p > 0.05$) between shell thickness and shell size in *Trigonephrus* sp..

Mean maximum ±S.D. aperture length and width were 15.23 ±1.40 mm and 13.50 ±1.04 mm, respectively. An estimate of mean aperture area was calculated, assuming a square opening, to be 2.07 ±0.33 cm^2.

Water uptake

During the water-uptake experiments, three snails only fed in the first trial (mean mass gain = 314 ±62.1 $mg.day^{-1}$), while 11 snails fed in the second trial (mean mass gain = 628 ±281 $mg.day^{-1}$). Mean ±S.D. percentage mass increase per gram body mass was 6.9 ±2.7$\%.g^{-1}.day^{-1}$. There was no significant correlation between percentage mass increase per gram body mass (arcsin transformed) 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 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). For this reason, we compared oxygen consumption values among species at 15°C (when all snails were active) and 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 ±S.D. oxygen consumption of *Trigonephrus* sp. during activity (15°C) was 32.0 ±9.7 $\mu l O_2.g$ total $mass^{-1}.h^{-1}$ and inactivity (25°C) was 12.6 ±5.4 $\mu l O_2 . g$ total mass^{-1}1.h^{-1}. There was no significant difference in the oxygen consumption of active and inactive Helix aspersa (ANOVA, $p>0.05$). Active (15°C, n=6) and inactive (25°C, n=3) oxygen consumption of H. aspersa was 62.7 ±15.5 $\mu l O_2 . g$ total mass^{-1}.h^{-1} and 57.4 ±3.6 $\mu l O_2 . g$ total mass^{-1}.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_b among the five snails throughout the 48h period (ANCOVA; covariate = sand temperature; $p>0.05$). Thus, we combined these data and a mean value was obtained for each hour (Fig. 3). Between 03h00 and 08h00, all five snails buried down into the sand to a depth of 1-5 cm. Throughout the experimental period, T_b closely tracked sand temperature. The following least-squares regression equation was obtained:

T_b = 1.03(sand temperature) + 0.17 (r^2 = 0.93, F=3054.97, $p<0.0001$).

The maximum T_b attained by one of the snails was 44.7°C at 12h00 on Day One. The mean ±S.D. maximum T_b was 42.78 ±2.03°C (range = 39.6-44.7°C), and the mean ±S.D. minimum T_b was 11.16 ±0.87°C (range = 10.5-12.8°C). When snails were reburied at 10-15 cm depth, their body temperatures decreased to sand temperatures at those depths.

Activity

(a) Laboratory

At the lower temperatures (10 and 15°C) all snails became active within the 30 min acclimation period (Fig. 3). At 20°C, seven snails were active after 5 h, while at 25°C no snails became active during the 6 h experiment. At 30°C, seven snails were active 20 min into acclimation, but the number of active snails declined until all were inactive by the termination of the experiment.

(b) Outdoor experiments at Gobabeb

Temporal activity observations at Gobabeb in the central Namib in September (Spring) indicated that snails were mainly active during the early hours of the morning (06h00 to 09h00) when mean ±S.E. ambient temperature was 11.2 ±2.2°C and relative humidity was high (79.8 ±9.1%). Mean sand temperature and humidity at -10cm was 10.8 ±1.6°C and 47.4 ±6.0%, respectively.

(c) Field observations

In January (Summer), no active snails or signs of activity were noted. Mean ambient temperature ranged from 10.4°C (surface sand at 06h30) to 52.2°C (air temperature at 14h00). Relative humidity ranged from 21-99% and windspeed from 4.0-26.7 $km.h^{-1}$. Although air temperature dropped to 10.4°C at 06h30 with a humidity of 91%, the sand temperature at the 10 cm and 15 cm depths (where dormant snails were found) ranged from 22.6-33.2°C.

Therefore, we assume that for snail arousal to occur lower ambient temperatures and higher relative humidities need to be experienced.

DISCUSSION

Water loss

The rate of water loss by *Trigonephrus* sp. is low (5.95 mg.day^{-1}) relative to the mesic *Helix aspersa* (29.91 mg.day^{-1}), similar to the mesic snail *Otala lactea* (5.65 mg.day^{-1}), but much higher than that of the desert snail *Sphincterochila boiserri* (1.56 mg.day^{-1})(Machin 1967). The estimated period of survival of *Trigonephrus* sp. without water is also higher than *H. aspersa* and much lower than that of *S. boisseri*. 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 for the desert snails *Eremina (Helix) desertorum* (4 years - Baird 1850) and *Xeranianta veatchii* (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 bury in 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 prolonged periods of deprivation.

The water loss estimate for *Trigonephrus* sp. may however 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. Thus, water loss rates of snails that have been dormant for a long period of time may be considerably lower than those of snails studied here.

Mechanisms affecting water loss may be:

(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 (Machin 1967), e.g. by avoidance of high temperatures by burrowing into moist sand.

Of these potential factors, we were able to examine only shell thickness, aperture size 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. boiserri* have similar water loss rates (Machin 1967). However, *S. boissieri* had a much lower water loss rate than *Trigonephrus* sp.. This large difference in water loss rate between these 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. boissierri*.

Machin (1967) has shown that much of the water loss by *H. aspersa*, *O. lactea* and *S. boisseri* is via the exposed surface in the region of the aperture. The aperture area of *Trigonephrus* sp. (2.07 ±0.33 cm^2) is smaller than that of the similar-sized *H. aspersa* (2.62 ±0.24 cm^2), and larger than that of *O. lactea* (1.25 ±0.08 cm^2)(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 similar-sized *Helix aspersa* and *Otala lactea* (74.13 $\mu lO_2.g^{-1}.h^{-1}$, active; 10.72 $\mu lO_2.g^{-1}.h^{-1}$, dormant - Herreid 1977). Thus, oxygen consumption is the single physiological factor 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 CO_2 release (Barnhart 1986).

Body temperatures

Behavioural observations of snail activity at different ambient temperatures (Fig. 1) showed that *Trigonephrus* sp. were more 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 of snails at relatively high temperatures (in *O. lactea*) has been termed an escape response by Herreid & Rokitka (1977), and is probably not a second preferred period of activity. In field observations (Fig. 3), snails were able to tolerate high temperatures (40-45°C). However, 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 and metabolic rates. *Trigonephrus* sp. allowed body temperature 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 subsurface 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 mesic snails, 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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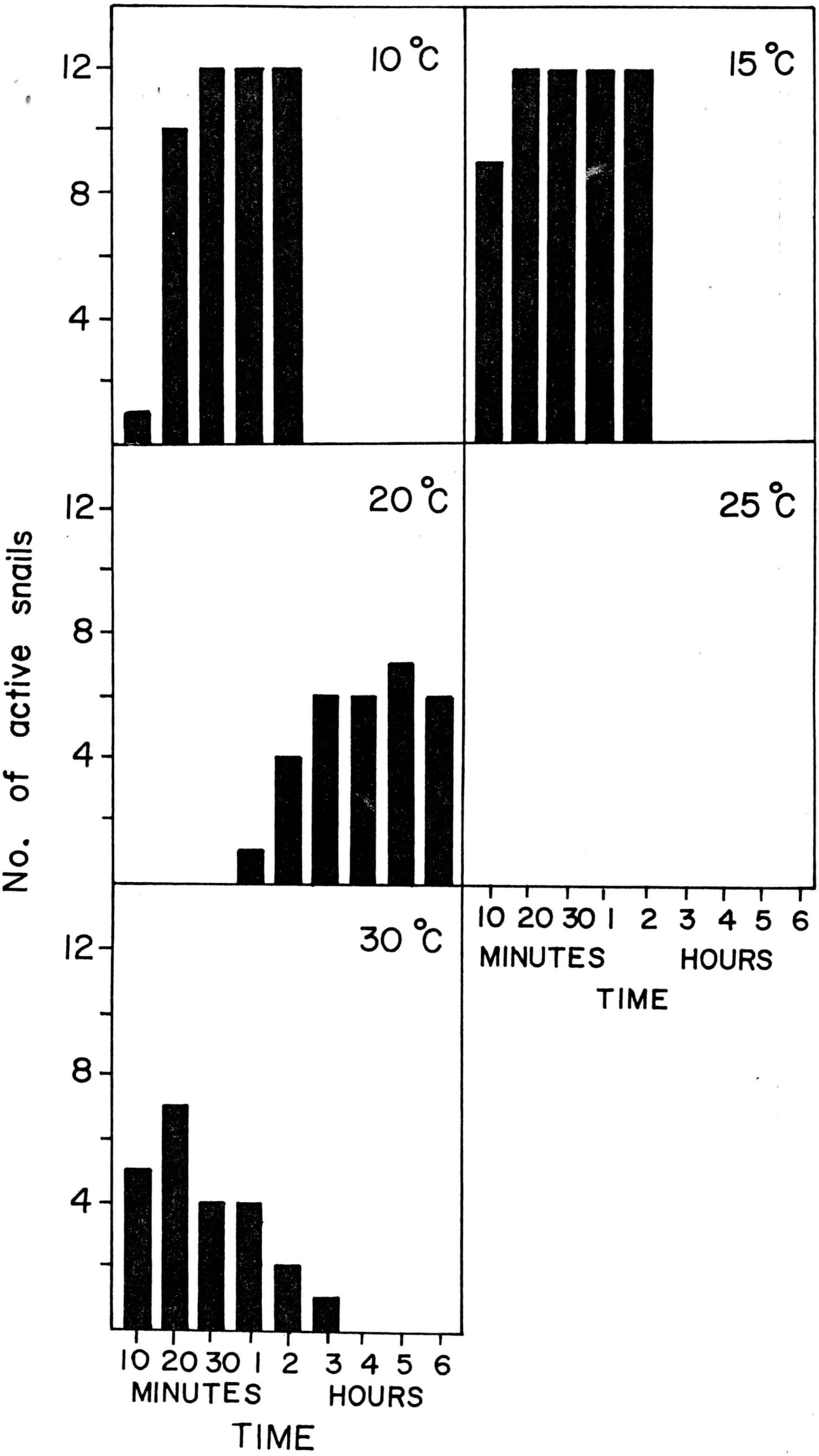
FIGURE CAPTIONS

Fig. 1. Box-and-whiskers plot of % water loss.g^{-1}.day^{-1} during three 10-day desiccation trials (n = 12 snails for each trial) for *Trigonephrus* sp.

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

Fig. 3. Deep-body *Trigonephrus* sp. (solid line) and sand temperatures (surface......, 5cm -..-..-, 10cm - - - - -- depth) each hour for 48 h, when snails were exposed on the surface, buried at 0 to 5 cm depth, and buried at 10cm depth.

10 °C
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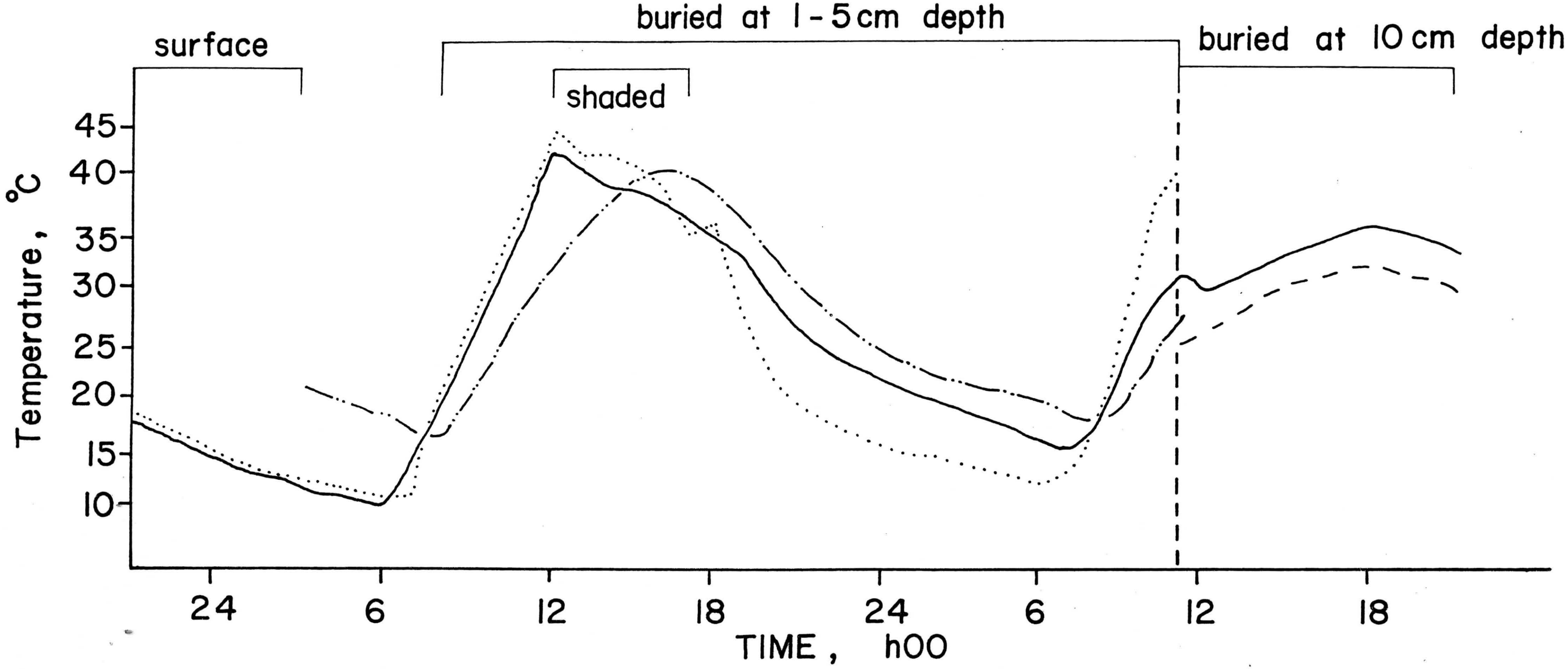
buried at 1-5cm depth
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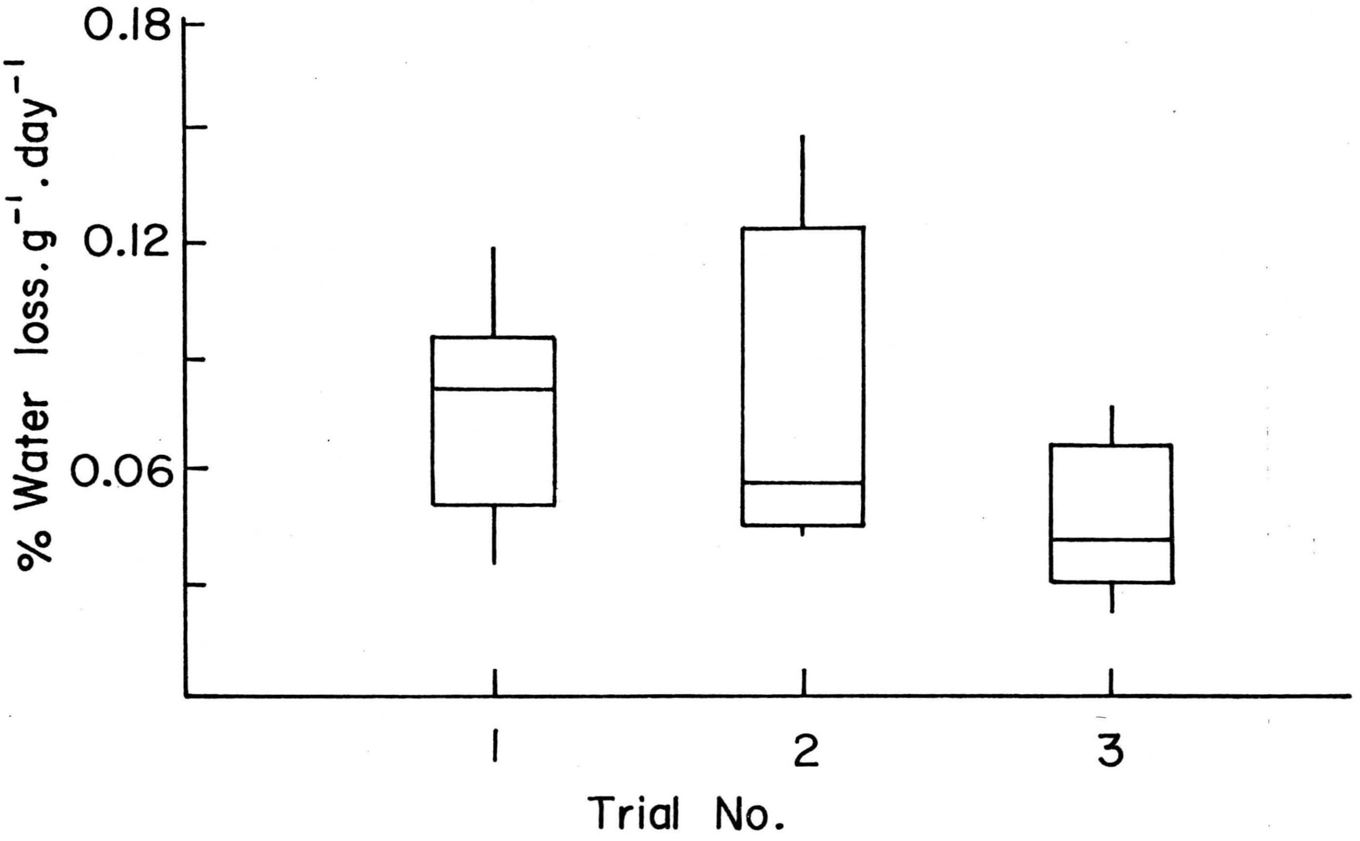
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