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DESERT SNAILS: PROBLEMS OF HEAT, WATER AND FOOD

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INTRODUCTION

It will be a surprise to many biologists that snails are found in large numbers on the dry, barren surfaces of certain hot deserts. The present study is concerned with one such snail, *Sphincterochila boissieri*, which occurs in the deserts of the Near East. Live specimens of this snail, withdrawn in the shell and dormant, can be found on the desert surface in mid-summer, fully exposed to sun and heat. The surface temperature of these deserts may reach 70 °C and more than a year may pass between rains. Such a severe habitat poses three seemingly insurmountable problems for these snails: (1) thermal death, (2) desiccation, and (3) death from starvation.

This paper will deal with our studies of each of these three problems.

MATERIALS AND METHODS

Animal material. Sphincterochila boissieri (Charpentier, 1847) is a fairly small snail (average weight about 4 g) with a chalky-white shell. Animals used for laboratory studies were collected in the central Negev near Avdat and Sde Bokher and shipped by air to Duke University. Summer field studies were carried out in the same area, where the mean annual rainfall is less than 100 mm. The rains are concentrated in the winter months, from November to March, and during this period the snails are active, feed, and reproduce. During the remainder of the year the snails presumably remain dormant.

Three types of mineral surface material are common in this area: (*a*) a firmly packed powdery soil or loess, (*b*) limestone rocks and pebbles with a granular, disintegrating surface, and (*c*) broken-up black flint. While *Sphincterochila* is common in the loess–limestone areas, it is much less common on the flint substratum. *Sphincterochila* is a mud-eater; that is, after rain it comes out and eats large quantities of the surface material (loess); and, in our experience, also material from the surface of limestone rocks and pebbles. The digestible material contained in this predominantly mineral diet is primarily algae and lichens. *Sphincterochila* shows no obvious interest in those higher plants which are eaten by other snails in the same area, such as *Eremina* and *Helicella*. More detailed information about the ecology of these desert snails has recently become available (Yom-Tov, 1970).

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Temperature measurements were carried out with copper–constantan thermocouples made from insulated wire of 0·125 mm or 0·025 mm diameter calibrated against standard mercury thermometers. The accuracy was ±0·2 °C. For soil surface temperature butt-soldered thermocouples and several centimeters of the leads were placed in direct contact with the surface. Thermocouples made from 0·25 mm diameter or smaller wire give the actual surface temperatures within a few tenths of a degree, provided that the thermocouples as well as the leads are placed within the thin stagnant boundary layer of air at the surface (Molnar & Rosenbaum, 1963), and for our purposes this accuracy suffices. Temperatures inside the snails were measured with thermocouples inserted through minute holes drilled in the shell with a high-speed needle-point steel drill and cemented in place with epoxy cement. Air temperature was measured with thermocouples placed at the centre of reflecting aluminum-foil cylinders of 10 mm diameter and 30 mm length, thus excluding solar radiation and most extraneous radiation from the environment. The readings were independent of changes in air flow through the cylinder and can thus be assumed to represent actual air temperature. (Mercury thermometers placed in the shade, if not shielded from radiation from sky, surrounding objects, and ground, do not show actual air temperature.)

Lethal temperature was determined by observing survival of snails which were placed in individual water-tight containers and immersed in constant-temperature water baths at 50, 55 and 60 °C. To monitor the temperature actually attained by the animals, one snail in each group of 20 was equipped with a thermocouple, and exposure time was recorded, beginning when this snail was within 1 °C of the water bath.

Reflectance measurements were made by Dr W. J. Hamilton III, using a Beckman DK-2 reflectance spectrophotometer. We are grateful for his help.

Water loss was determined by weighing. The validity of using weight loss can be questioned because it includes carbon loss in the form of CO_2. It is reasonably certain, however, that actual water loss could not exceed the recorded weight loss. We have therefore used weight loss as a valid approximation to water loss.

Weighings were made on a Mettler Model H balance with a precision of 0·05 mg. The accuracy is similar, but is irrelevant since all measurements refer to weight changes.

Chemical analyses. Snails were analysed for water, protein, lipid, carbohydrate and ash content. Samples of 100 snails (about 400 g total weight) were collected each month throughout one year. The snails were removed from the shell, pooled and analysed. The shells were weighed, dried at 105 °C until constant weight, the recorded weight loss giving the amount of water remaining on the shells after removal of the animals.

The chemical analyses were carried out by the Israel Bureau of Standards at Tel-Aviv according to standard methods (Horwitz, 1965). Total carbohydrate was obtained as the sum of sugar (as glucose) and polysaccharides (glucose × 0·9).

Oxygen consumption was determined on individual snails in Scholander-type respirometers (Wennesland, 1951) at various constant temperatures. The level of illumination was kept constant day and night. Readings were taken every 4 h as oxygen was added from a 1 ml syringe. To avoid frequent removal of the syringe for refilling with oxygen, a larger syringe (10 ml) was attached to a sidearm of a T-stopcock valve so that the smaller syringe could be recharged with oxygen without being detached from the

respirometer. This arrangement permitted undisturbed readings of oxygen consumption for days, and at times for several weeks.

When the snails were placed in the apparatus their initial oxygen consumption was so high that it was impractical to determine the rate with our instrumentation (which was designed for accurate determinations of very low rates). The initial high values are evidently caused by the mechanical disturbances of placing the animal in the apparatus; we circumvented this period by placing the snails in their glass jars with open access to the atmosphere for 1 week before the manometer and oyxgen syringe were attached. This 1-week waiting period provided ample time for the snails to return to what we consider a quiescent metabolic rate.

Determination of the effect of temperature changes on oxygen consumption was not feasible with the Scholander-type respirometer, one reason being that we could not compensate for the large volume changes caused by temperature change, another being the different thermal expansion of the components of the respirometers which caused the glass vessels to break during temperature increase.

In order to determine the Q_{10} we therefore used groups of 50 snails subjected to a temperature schedule which cycled between 15 and 35 °C. These temperatures were chosen because we already had considerable information about the oxygen consumption of individual snails at these two temperatures, and because day-and-night temperature differences of about 20 °C are common. The 24 h cycle consisted of 14 h at 15 °C, re-setting requiring 1 h to reach 35 °C, 7 h at 35 °C and 2 h to return to 15 °C, giving a total of 24 h for the complete cycle. The snails were placed in a glass container through which air was drawn at a known rate, the change in oxygen concentration of the air being determined with a Beckman paramagnetic oxygen analyser. These experiments were carried out in continuous darkness.

RESULTS

A. *Temperature tolerance*

In order to understand the occurrence of live (but dormant) snails on the open desert surface during summer, it is necessary to know (*a*) the lethal temperature of dormant snails and (*b*) the temperature that the snails attain under natural conditions.

Table 1. *Heat tolerance of* Sphincterochila

(Percentage survival after indicated time. Sample size, 20 individuals for each exposure.)

	Hours				
	0·5	1	2	4	8
50 °C	—	—	100	100	100
55 °C	95	80	30	5	0
60 °C	0	—	—	—	—

Lethal temperature. The temperature tolerance of *Sphincterochila* is evident from Table 1. Snails heated to 60 °C for ½ h invariably died. One hour at 55 °C was lethal to some snails, 2 h at 55 °C killed more than half the snails, and 8 h at 55 °C gave no survivors. We can therefore conclude that 55 °C is lethal, or nearly so, to dormant *Sphincterochila* if the exposure lasts for a few hours. In contrast, 50 °C yielded 100 %

survival, irrespective of exposure time, up to 8 h. Since the peak temperature of a desert day usually occurs during a few hours of the early afternoon, the snails are not likely to be exposed to high temperatures for many hours, and experiments of more than 8 h are therefore of minor interest in the evaluation of heat exposure in nature.

Temperature of snails under field conditions. The temperature of snails located on various natural substrates and fully exposed to the sun was recorded on a total of 40 days in July and early August 1969. The records showed a rather uniform pattern, although there were some characteristic differences. The snails attained a higher temperature on loess than on any other substrate. Since we are interested in the most severe conditions to which the snails are exposed, we have chosen for presentation

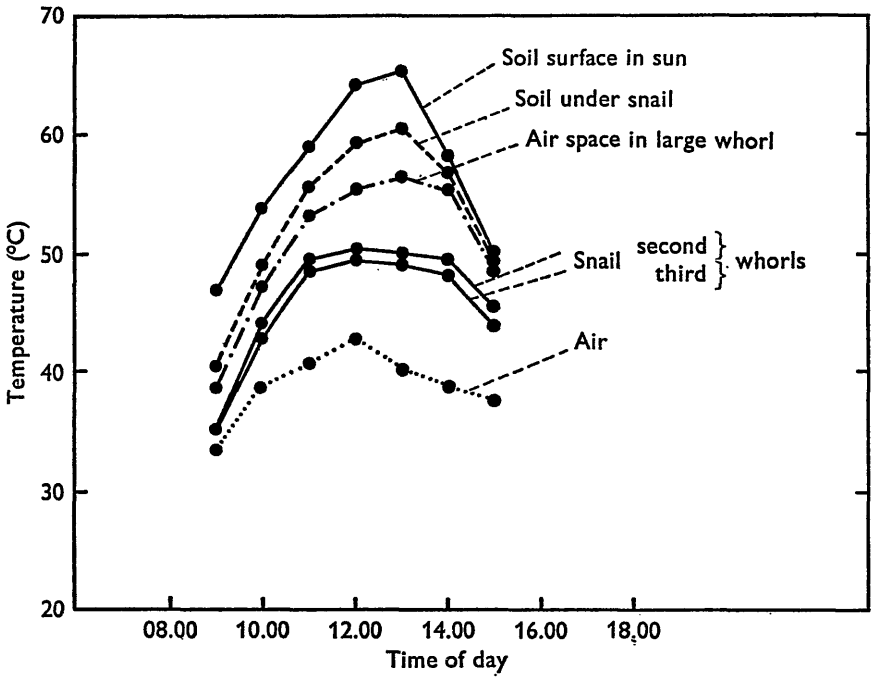

Fig. 1. Temperatures recorded in and around a specimen of the snail, *Sphincterochila boissieri*, on 9 July 1969. Record selected because it includes the highest temperature recorded within any animal (50·3 °C) during 40 days of observation in July and early August 1969.

a record which includes the highest temperature we ever recorded inside a snail with the recording thermocouple located within the living animal itself (see Fig. 1). The maximum air temperature, reached at noon, was 42·6 °C, and the maximum soil surface temperature in the sun, reached at 13.00, was 65·3 °C. Under the snail, in the space between the soil surface and the smooth shell, the maximum temperature was 60·1 °C, or 5·2 °C below the adjacent soil surface in the open sun. The lower temperature under the shell is expected, for the shell provides shade for that particular spot of the soil surface on which it sits. Inside the shell in the largest whorl, located in contact with the ground, the maximum temperature was 56·2 °C. In the second and third whorls the temperature was lower, reaching a maximum of 50·3 °C.

It is important that the animal, when withdrawn, does not fill the shell and leaves most of the largest whorl filled with air. Thus, the temperature shown in Fig. 1 for the large whorl is actually the temperature within an air space. The snail, withdrawn

to the upper parts of the shell, is significantly cooler. In Fig. 1 the maximum temperature of the animal itself was 50·3 °C, or about 5 °C below lethal temperature, and this is the highest temperature we recorded in any snail under field conditions.

Why does the snail not heat up to the same temperature as the soil surface? The answer lies in its high reflectivity in combination with the slow conduction of heat from the substrate. Within the visible part of the solar spectrum (which contains about one-half of the total incident solar radiant energy) the reflectance of these snails is about 90 %. In the near infrared, up to 1350 nm, the reflectance is similar to that of magnesium oxide and is estimated to be 95 %. In the total range of the solar spectrum, therefore, we can say that the snails reflect well over 90 % of the incident radiant energy. Their reflectance in the far infrared is not significant in this context because all the longer wavelengths of solar radiation are absorbed in the atmosphere, and the measured range covers about 98 % of the total incident solar radiation.

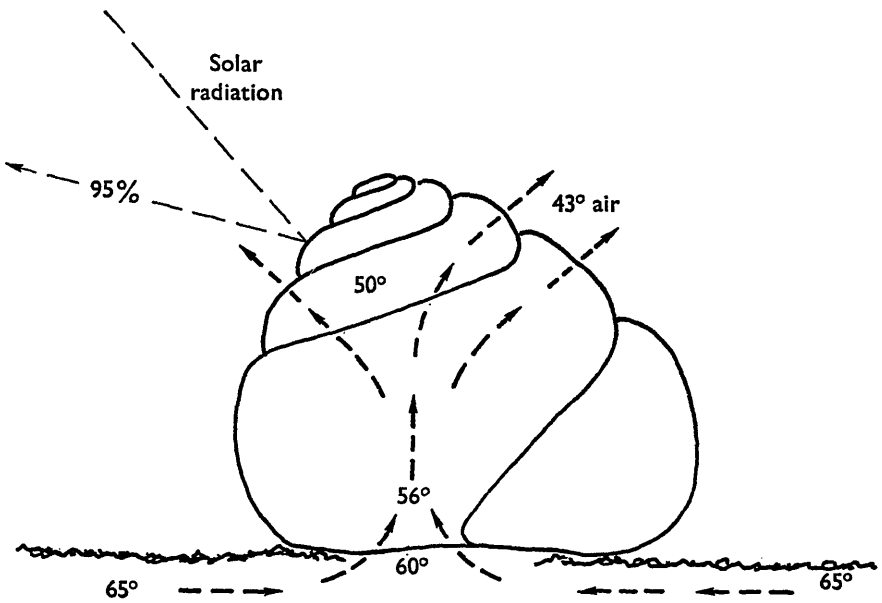

Fig. 2. Diagram of temperature distribution and heat flow in and around a snail exposed to sun on the desert surface. Indicated temperatures represent the maxima from Fig. 1. Direction of heat flow indicated by broken arrows; solar radiation by long dashes.

Since heat flows from a region of higher to one of lower temperature, the heat flow will be as shown in Fig. 2, which depicts the maxima from Fig. 1. The highest temperature, 65 °C, was that of the soil surface in the sun. Heat therefore flows into the shaded area under the snail where the temperature is lower (60 °C). Since the snail is cooler again, heat flows from the substrate into the snail. This heat flow, however, is impeded by two important circumstances. Firstly, the snail shell is in direct contact with the rough soil surface only in a few spots, and a layer of still air separates much of its bottom surface from the ground, forming an insulatng air cushion. Next, and perhaps more important, the snail is withdrawn into the upper parts of the shell and the largest whorl is filled with air; this constitutes a further impediment to heat flow into the snail. Nevertheless, heat does flow in the direction of the snail, which in this

case reached 50 °C. Since this is higher than the air temperature (43 °C), heat now flows into the surrounding air by conduction.

A simple way to demonstrate the importance of the air space in the shell is to fill it with water. To do this we reinforced the epiphragm with a thin layer of epoxy cement, drilled a small hole in the large whorl, filled the air space completely with water, and sealed the hole. When snails prepared in this way were exposed to the sun, the temperatures in the largest and the second whorl were nearly identical. The temperature of the animal itself increased to about 5 °C above that in controls with the air space left intact. Without the insulating air space in the large whorl the animals would thus attain lethal temperatures.

A larger number of snails, equipped with thermocouples in the second whorl (i.e. within the snail itself) were measured in numerous different locations on the various common substrates. Of these snails there was none in which the temperature came near the lethal temperature, 55 °C. To reach 55 °C within the snail would probably require soil surface temperatures of 72 °C and an air temperature near 50 °C. (This extrapolation is based on maintenance of temperature gradients similar to those of Figs. 1 and 2.) Soil temperatures of 72 °C can perhaps be reached, but air temperatures of 50 °C are highly improbable in the deserts where *Sphincterochila* occurs. Maximum air temperatures at the level of the snails may be about 45 °C, and the temperature of the live snail itself would under these circumstances perhaps reach 52 °C, probably well within the tolerance for an 8 h exposure.

It is interesting that in areas where the air temperature during the summer is higher than where our field work was carried out (central Negev near Avdat and Sde Bokher) dormant snails are not found exposed on the soil surface. This is, for example, the case in the vicinity of the Dead Sea, where the snails burrow in summer into the soil up to 10 cm depth or hide beneath stones.

B. *Water loss*

The ultimate question of water balance is whether the snails have available enough water to sustain the losses during periods when no external water supply is available. In nature rain normally occurs each winter, but at times more than 1 year may pass between rains. To determine the use of water in summer, we measured the rate of water loss from dormant snails exposed to the sun on a number of different substrates. Rates determined in summer should be maximal, for during the cooler parts of the year the vapour pressure deficit is smaller and presumably the rate of water loss lower.

Rate of water loss. Ten snails were weighed and placed on an area of loess, fully exposed to the sun during the day. They were weighed daily before sunrise between 04.30 and 05.00, and again in the evening between 16.00 and 18.00.

During a 5-day period of being weighed twice daily, three snails became active and departed. The remaining seven snails all showed a similar pattern of a weight gain at night and a loss during the day. A representative record is given in Fig. 3. The magnitude of the nightly gain was from a few milligrams up to over 20 mg. Interestingly, dead shells, similarly exposed, gained weight at night at approximately the same rate. During the day, all the snails lost weight again. The dead shells lost almost exactly the amount they had gained during the preceding night; by evening they had returned, within a fraction of a milligram, to their weight of 24 h earlier. The live snails, on the

other hand, lost during the day slightly more than they had gained during the preceding night. A live snail, therefore, showed a day-to-day decline in weight. In Fig. 3 the average decline over 5 days was 1·72 mg/day.

The conclusion that live snails achieve no net advantage from the nightly weight gain is clear from comparison with control animals kept indoors. These snails showed no gain in weight during the night, and their 24 h loss was similar to that of the snails kept outdoors. Since empty shells gain as much weight as live snails outdoors, and snails indoors have no gain, we conclude that water is absorbed on the outside of the shell and evaporates again during the day.

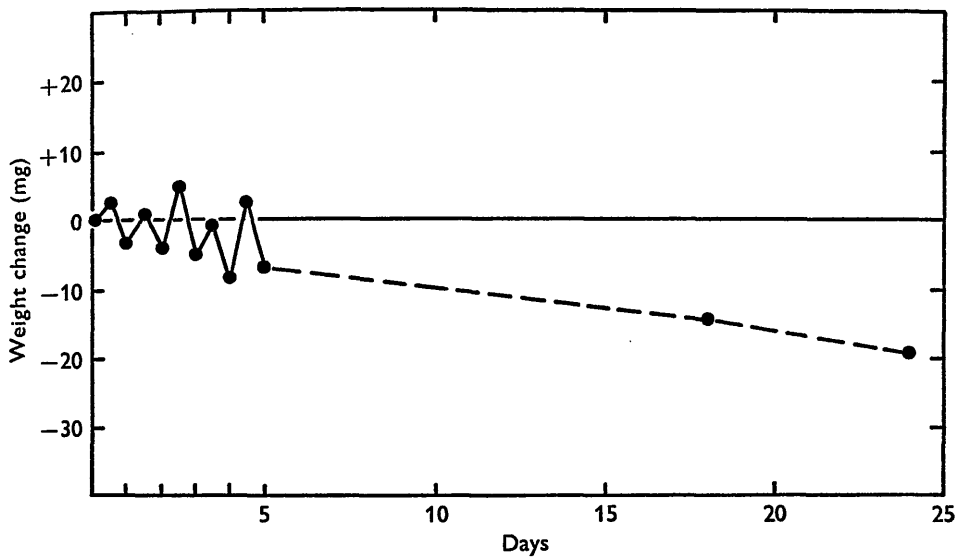

Fig. 3. Weight loss of the snail, *Sphincterochila boissieri*, under natural conditions. Snail placed on desert surface, fully exposed to sun during the day. During days 1–5 weighed twice daily. Between day 5 and day 24 snail weighed only once (day 18).

The question of whether dew can be utilized by the snails remains open. In summer, on nights when visible dew was formed on the shell, no net weight gain was achieved. The excess water evaporated shortly after sunrise and the total daily weight loss was the same as if no dew had occurred (see above). If the snails broke the epiphragm and became active, they lost some 50–150 mg, even on nights with dew. Conditions in winter may be different, and after rain when the soil surface is moist, nights with dew may be of importance to active snails when they are feeding. There is no information available as to whether feeding activity in winter may be supported by dew in the absence of rain.

It has previously been established that even minor disturbances of a dormant snail, such as a slight knock, increase its water loss (Machin, 1956). We therefore discontinued daily weighings and left the snails completely undisturbed for longer periods of time. The average daily weight loss now decreased (see Fig. 3). During 13 days the snail in Fig. 3 lost 5·9 mg, or an average of 0·45 mg/day. Five live snails that remained inactive during the 13-day period had a mean weight loss of 0·66 mg/day snail (range 0·45–0·92).

These results confirm Machin's observation that even moderate disturbance in-

creases the water loss from a dormant and seemingly completely inactive snail (Machin, 1965). The approximate effect of each disturbance on the snail in Fig. 3 can be calculated to be a loss of about 0·5 mg. Weighing twice daily therefore increases the daily weight loss by approximately 1 mg.

The rate of water loss of undisturbed snails during the hot summer, if continued throughout the year, could be tolerated for several years. A 4 g snail contains about 1400 mg water. If it can tolerate losing one-half its water, it would survive for 4 years. However, the water loss during the cooler parts of the year is probably lower. Thus, a snail could survive prolonged periods of drought and even several years without rain.

The low rate of water loss from the dormant snails raises some interesting problems. It is known that evaporation from the mucous surface of an active snail takes place at approximately the same rate as evaporation from a free water surface (Machin, 1964*a*). It might therefore be assumed that when the shell is closed with an epiphragm (a thin membrane consisting mostly of calcium carbonate), the epiphragm is the major barrier to water loss. If the epiphragm is removed, the water loss increases greatly, but since all disturbances have this effect, it cannot be concluded that the increased water loss is due to the absence of the epiphragm. On the contrary, it seems that the epiphragm is not a major obstacle to water loss, for if a snail dies or is killed within the shell with the epiphragm intact, the rate of evaporation increases tenfold or more.[1] We have no information about the physiological mechanisms which contribute to the exceedingly low evaporation we observed, nor any suggestions as to why minor disturbances, such as placing the snail on a pan balance, increase evaporation measurably. These interesting problems have been discussed in a series of publications by Machin (1964*a*, *b*, *c*, 1966, 1967, 1968), who is continuing their exploration.

C. *Energy requirements*

The energy metabolism of the dormant snail determines the nutrient requirements during the long dry periods when it cannot feed. The effect of temperature on the metabolic rate is important, for the difference between day and night regularly exceeds 20 °C. If the metabolic rate increases to the same extent as is common for other organisms, i.e. with a Q_{10} of 2–3, the metabolic rate in the middle of the day may easily be ten times as high as at night.

Rate of oxygen consumption of individual snails. In order to estimate the expected rate of depletion of energy stores during dormancy, we determined the oxygen consumption of individual snails. It must be emphasized, however, that rates of oxygen consumption determined under laboratory conditions can give only an approximate estimate of the energy requirements under field conditions.

Records for five snails are presented in Fig. 4. One snail (no. 6) died early in the experiment and its oxygen consumption decreased to nil, showing only the random variations of the method. The live snails, typical of a large number studied,[2] showed considerable fluctuations in the oxygen consumption, which varied from values so low that they were not measurable for as much as 2 days, to oxygen consumption as

[1] The permeability of the epiphragm of *Sphincterochila* and several other snails has been reported by Machin (1968).

[2] Thirty individual snails have been followed for periods of 3–4 months each.

high as 30 or 40 μl O_2/hr for more than a day. Periodic increases or 'bursts' in oxygen consumption appeared in many of the snails. Such bursts seemed to occur at somewhat regular intervals, but they were not synchronized from snail to snail. We believe that the 'bursts' we observed were independent of external factors and an inherent characteristic of the snail metabolism. This does not exclude that metabolic cycles may, in nature, be synchronized by external factors such as temperature change, light, and available water.

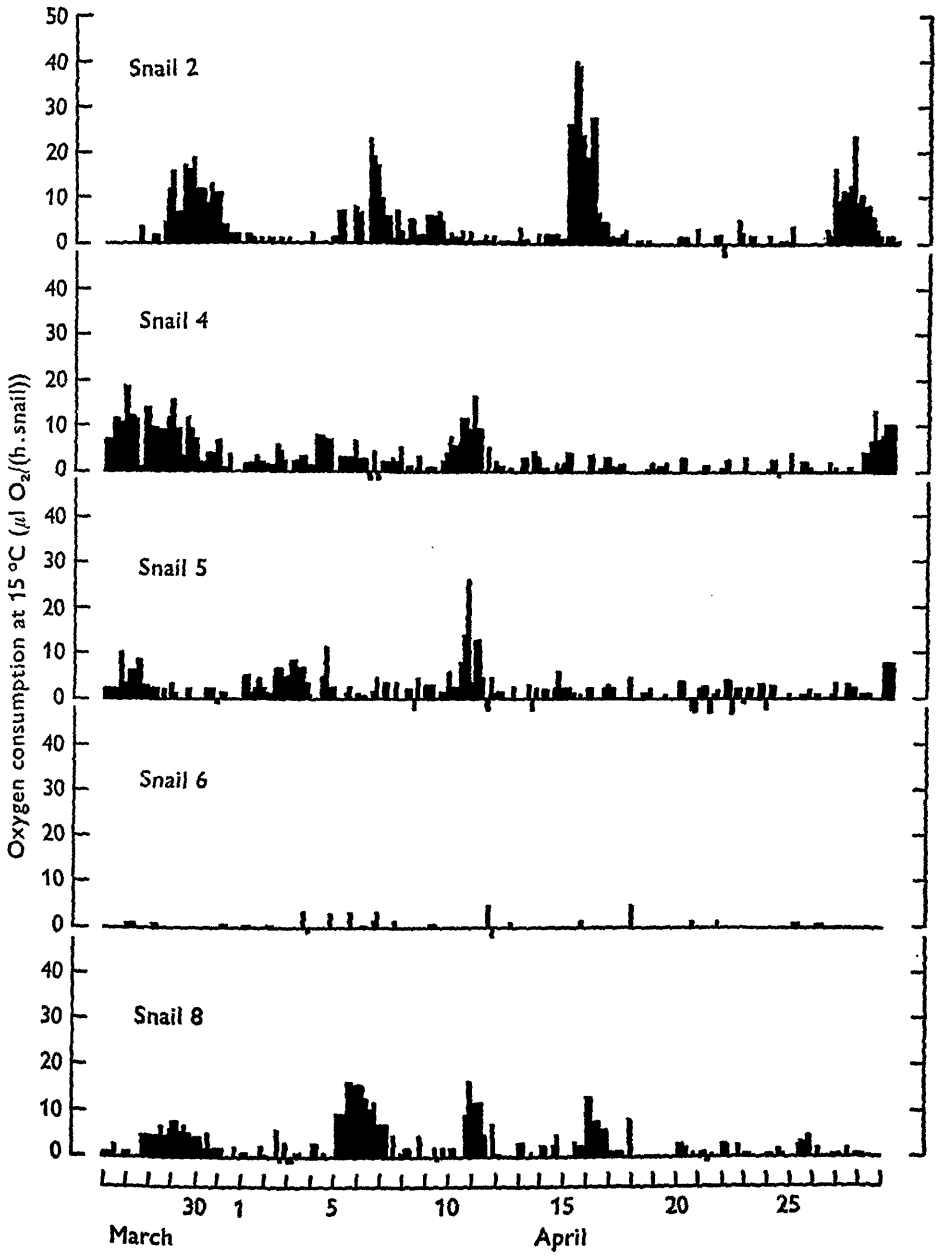

Fig. 4. Oxygen consumption at 15 °C of five individuals of the snail, *Sphincterochila boissieri*. Snail no. 6 was dead and its record indicates the magnitude of random fluctuations inherent in the method. Experiment in continuous light.

Fig. 5 shows records obtained after the temperature was increased from 15 to 25 °C, but without any other disturbance. There was an immediate burst in oxygen consumption, which in all the snails subsided in about 1 or 2 days. The oxygen consumption then continued in a pattern similar to that at 15 °C, with occasional bursts, but at a higher level.

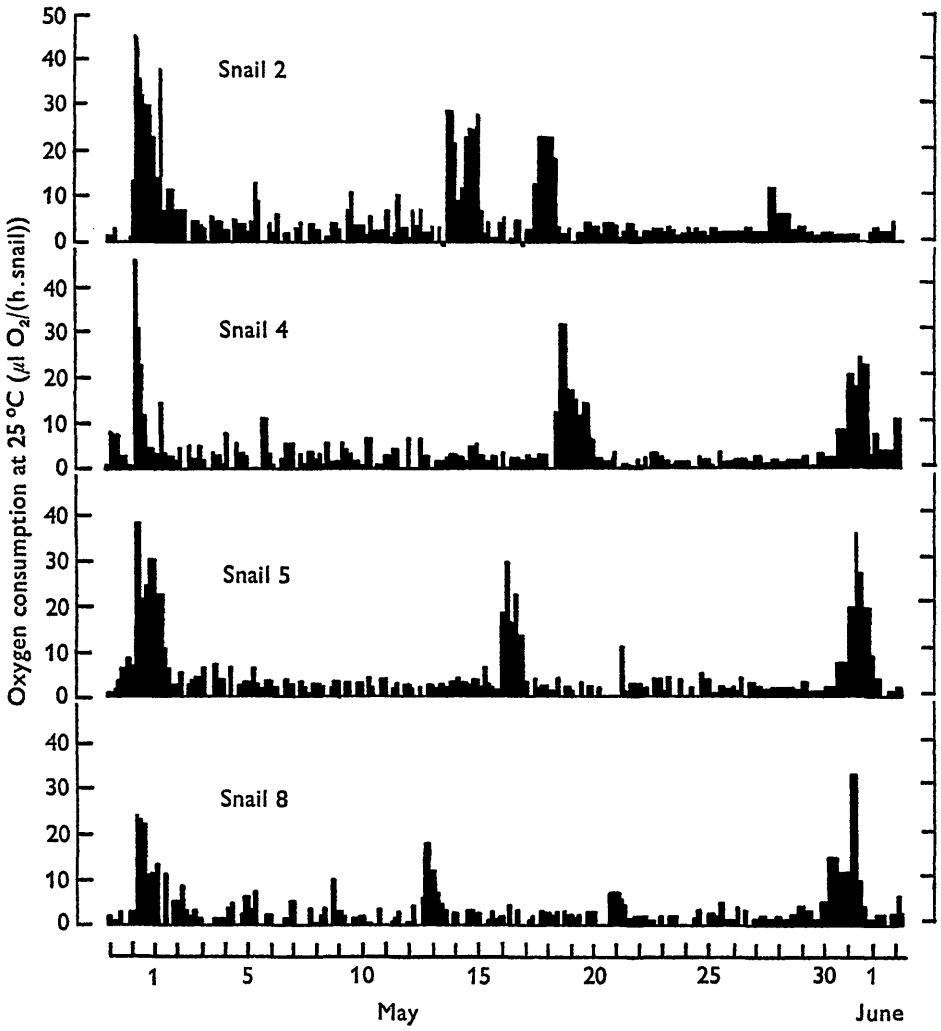

Fig. 5. Oxygen consumption at 25 °C of the snail, *Sphincterochila boissieri*. The animals are the same as the live specimens recorded in Fig. 4. Experiment in continuous light.

At 35 °C, and in particular at 40 °C, the oxygen consumption was high and irregular, and it became impractical to make continuous day-and-night observations on individual snails. The effect of high temperature was therefore studied in larger groups of dormant snails.

Determination of Q_{10}. To determine the acute effect of temperature change on the oxygen consumption, a group of 50 dormant snails was exposed to a temperature cycle on a 24 h schedule. The large number of snails would average out individual differences and the timing cycle was similar to the natural daily change in temperature.

At the end of the experiment all 50 snails were alive and emerged in response to being moved from the respirometer and moistened.

Oxygen consumption when the temperature was cycled between 15 and 35 °C is shown in Fig. 6. The initial 3 days showed a high and irregular oxygen consumption, after which the snails established a lower and more regular patttern of response to the temperature cycle. The mean oxygen consumption for 12 days of cycling was 8·37 μl O_2 h^{-1} per snail (the initial 3-day period not included in mean). The mean oyxgen consumption for the total time spent at 15 °C (excluding temperature transients) was 2·62 μl O_2 h^{-1} per snail and for the total time at 35 °C (excluding temperature transients) 15·63 μl O_2 h^{-1} per snail. These figures correspond to Q_{10} = 2·44. In

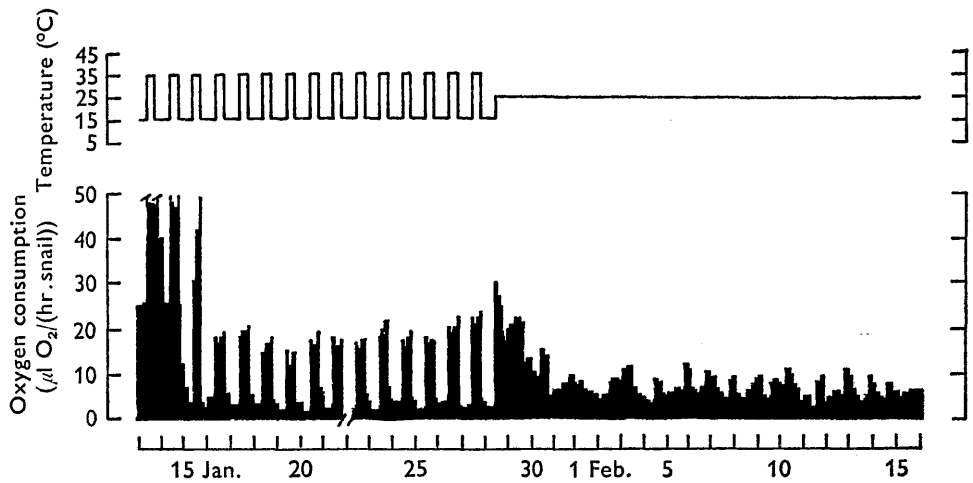

Fig. 6. Oxygen consumption of the snail, *Sphincterochila boissieri*. Determination made on a group of 50 dormant snails. To facilitate comparison with Figs. 4 and 5, the mean oxygen consumption per snail is given. For 15 days the temperature was cycled between 15 and 35 °C; temperature was then maintained constant at 25 °C for 18 days. Experiment in total darkness.

other words, the oxygen consumption of the snails was influenced by temperature to the same extent as is common in non-desert animals; the desert snails thus seem to have no special adaptation involving a reduced metabolic response to increased temperature. To ascertain whether this holds at even higher temperatures, the studies should be extended to temperatures closer to the lethal limit.

After 12 days of temperature cycling the temperature was maintained constant at 25 °C for 11 days. The first 2 days showed a high oxygen consumption, in excess of the mean oxygen consumption at 35 °C. The oxygen consumption then gradually subsided to a more uniform level; the mean was 6·96 μl O_2 h^{-1} per snail (excluding the initial 3 days). This is close to the predicted value of 6·40 μl O_2 h^{-1} per snail for 25 °C using a Q_{10} of 2·44. It should be noted that this is the mean for 50 snails, and if any periodicity occurred (which probably was the case) it was not sufficiently well synchronized to be clearly distinguished in the record at a constant temperature of 25 °C.

Composition and water content of snails. The average composition of *Sphincterochila* is shown in Fig. 7A. Well over one-half (56 %) of the total weight is shell, the remainder being the living snail itself (including blood and body fluids). The average composition

of the animal, less shell, is indicated in Fig. 7B. Thus, the snail itself contains about 81 % water, 11 % protein, minor amounts of other organic components, and finally nearly 4 % ash.

In order to evaluate the use of water and of stored nutrients during the long dry season we followed the variations of the composition during 1 year. Samples of 100 snails were collected each month in the same location (8 km east of Mashabei Sadeh) and analysed (Table 2).

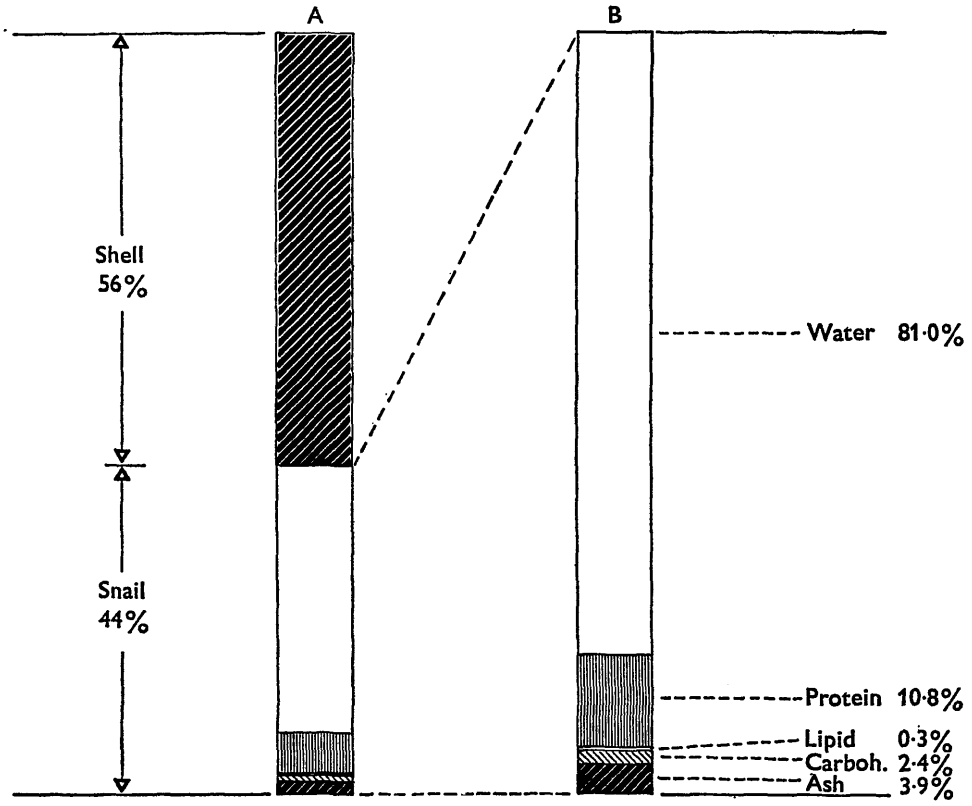

Fig. 7. Composition of the snail, *Sphincterochila boissieri*. A, Mean composition of a sample of 100 snails. B, Mean composition of animals less shell. Sample of 100 snails.

The most surprising finding was that the water content of the snails was not depleted during the summer. The water content remained well over 80 %, except for the samples collected in November and February. (The November sample was collected shortly after the first rain of the season. The February sample had an exceptionally high ash content because the snails had been feeding and the digestive tract contained large amounts of mineral matter.)

In regard to nutrient storage it is notable that the lipid content of the snails is extremely low, only a fraction of 1 %. These lipids probably are structural components of the cells, rather than energy reserves. Although many other molluscs store glycogen, the carbohydrate content in *Sphincterochila* is too low to be the major energy store; furthermore, there is neither a build-up of carbohydrate during the wet season nor a depletion during the dry season. The major organic component is protein; but again, the seasonal variations do not indicate any major depletion during the dry season.

Since there are no obvious energy reserves available at any season and no great systematic shifts in composition; the low metabolic rate of the dormant snails is apparently sustained by consumption of all tissue components. If this is so, the starving snail simply gradually reduces its total mass.

Table 2. *Composition of the snail* Sphincterochila boissieri

(Monthly samples of 100 snails collected during one year (1969–1970).)

Sample and date	Total sample weight (g)	Animal tissue (total wt minus dry shell wt)		Composition of animal, minus shell (%)					
		g	% of sample	Water	Protein	Lipid	Carboh.	Ash	Undet'd.
7 July, no. 1	389·1	168·8	43·3	80·6	10·7	0·8	—	3·6	—
6 Aug., no. 2	397·0	177·5	44·7	82·0	10·6	0·7	—	3·6	—
8 Sept., no. 3	371·2	158·7	42·7	83·1	10·9	0·2	2·2	2·7	0·9
7 Oct., no. 4	370·8	155·1	41·8	81·9	11·5	0·2	2·0	3·9	0·5
6 Nov., no. 5	400·7	169·6	42·3	77·8	14·5	0·2	1·7	4·6	1·2
8 Dec., no. 6	410·7	171·8	41·8	82·7	10·2	0·3	—	3·7	—
6 Jan., no. 7	403·9	169·0	41·8	83·4	10·4	0·2	1·5	3·4	1·1
7 Feb., no. 8	462·0	231·8	50·2	74·2	9·9	0·1	2·8	9·7	3·3
5 Mar., no. 9	462·7	217·6	47·0	80·0	10·7	0·2	2·8	3·7	2·6
8 Apr., no. 10	388·1	187·4	48·3	82·8	9·4	0·1	2·2	3·1	2·4
5 May, no. 11	407·4	181·5	44·6	82·6	9·9	0·1	2·9	2·4	2·1
6 Jun., no. 12	413·0	177·1	42·9	81·6	10·7	0·2	3·1	2·6	1·8
Mean	406·4	180·5	44·3	81·0	10·8	0·3	2·4	3·9	1·8

To estimate a possible survival time for a snail which gradually consumes its body substance, we will calculate a theoretical half-life. If a snail metabolizes at a rate of 5 μl O_2 h^{-1}, and this rate decreases with decreasing body size, the estimated half-life of the snail should be 34380 h, or 48 months. Whether the oxygen consumption in reality would be as high as 5 μl O_2 h^{-1} per snail is uncertain. Dormant snails at times display periods of several days during which oxygen consumption is below a measurable magnitude, i.e. less than 1 μl O_2 per day (0·05 μl O_2 h^{-1}) per snail.

Prolonged survival of dormant snails has often been reported in the malacological literature. A number of such reports, including survival in museum collections up to 6 years without food and water, have been compiled by Machin (1967) and by Comfort (1967).

SUMMARY

1. The major physiological problems of survival for desert snails were studied in *Sphincterochila boisseri*, a pulmonate snail common in desert areas in the Near East.

In summer these snails can be found in a dormant state on the barren soil surface, fully exposed to the sun; in winter they become active during rainy periods, when they feed and reproduce.

2. The lethal temperature of *Sphincterochila* is between 50 and 55 °C, depending on time of exposure. The temperature of the dormant animal within the shell, exposed to the sun on the soil surface in summer, does not reach a lethal level, although the temperature of the surrounding soil surface far exceeds this temperature.

3. The rate of water loss from dormant snails, exposed in their natural habitat in summer, is about 0·5 mg per day per snail. This rate, if continued unchanged, would give a yearly loss of less than 200 mg. A 4 g specimen contains about 1400 mg water, and since the water loss during the cooler part of the year probably is reduced, several years should elapse before critical levels of water loss would be reached. In snails collected in summer the water content was not reduced, indicating no measurable depletion of water reserves during the hot season.

4. The oxygen consumption of dormant snails varies with temperature ($Q_{10} = 2{\cdot}4$). It is so low that the tissues could support the metabolic rate for several years, thus permitting continued dormancy even during periods of drought extending over more than 1 year.

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