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The respiratory environment of the Namib Desert Golden Mole

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We measured the partial pressure of oxygen (Po_2) in the interstitial gas surrounding the sand-swimming Namib mole *Eremitalpa granti namibensis*. At a sand temperature of 26 °C, which produced a nearly maximal rate of oxygen consumption, the Po_2 near the noses of the animals averaged only 0·9 kPa (6·7 Torr) below the level in the free atmosphere. High oxygen availability was a result of the notably low metabolic rate in the 20 g mammals and the dry, porous and metabolically inactive nature of dune sand. A mathematical model indicated that normal mammals weighing 200 g or more could comfortably exist completely encased in dune sand. We concluded that the moles' small size and low metabolic rate are not adaptations to hypoxia or hypercapnia underground but are probably related to low food availability and the energetic cost of foraging in their desert environment.

Keywords: mammal; mole; burrow; respiration; gas exchange; diffusion; allometry

Introduction

Respiration of fossorial mammals has been of interest to comparative physiologists because the animals are often separated from the free atmosphere by soil, which impedes the movement of oxygen and carbon dioxide. Measurements of the gaseous environments inside mammal burrows have shown wide-ranging depressions in oxygen and elevations in carbon dioxide (see Withers, 1975; Nevo, 1979; Kuhnen, 1986; and references therein). The potential severity of the underground atmosphere depends on the metabolic intensities of the animals and soil micro-organisms, the gaseous permeability of the soil and the geometry of the burrow. There have been several attempts to analyse gas exchange from the atmosphere to a burrow system with simple mathematical models (McNab, 1966; Wilson & Kilgore, 1978; Withers, 1978). All authors agree that the dimensions of plugged burrows must be sufficiently matched

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to the metabolic demands of the mammal and the characteristics of the soil to prevent stressful hypoxic and hypercapnic conditions.

Sand-swimming moles differ from most fossorial mammals because they burrow through loose sand, which collapses behind them, rather than producing tunnels in cohesive soil. While underground, therefore, they are completely surrounded by sand, so there are no tunnels that facilitate the convective movements of gas. The animals must rebreathe the interstitial gas around them, and respiratory gases must move through the sand largely by diffusion.

This study addresses the question of the respiratory environment of the Namib Desert Golden Mole *Eremitalpa granti namibensis*, a blind, solitary insectivore of the African family Chrysochloridae. This small (about 15–40 g) sand-swimming subspecies lives only in the desert dunes of the western coasts of Namibia and South Africa. The moles emerge at night and run over the surface of the sand, periodically dipping beneath the surface in search of food, mainly termites (Fielden *et al.*, 1990*b*). During the day, however, they remain buried in soft sand, often associated with hummocks of dune vegetation. Fielden (1989) observed that periods underground could be as long as 2 days at a particular refuge, but the details of underground activity in the field remain unknown. Moles in sand-filled terraria in the laboratory typically rest for over 12h after feeding (Holm, 1969; Fielden, 1989), so it is likely that the same occurs naturally.

The Namib mole is remarkable because of its extremely labile body temperature, weak ability to thermoregulate and exceptionally low metabolic rate (Fielden *et al.*, 1990*a*). Its standard rate of oxygen consumption of 0·52 ml g^{-1} h^{-1} at a body temperature of 34·7 °C is only 22% of the value expected of insectivores in general. Fielden *et al.* (1990*a*) concluded that low resting rates of metabolism may be adaptations to an aeolian environment in which food energy is scarce and patchy, underground locomotion is energetically expensive, and hypoxia and hypercapnia may limit metabolic rate. The present study addresses the last point by comparing actual measurements of oxygen pressures (P_{O_2}) around buried moles with predictions of a simple model of diffusion of oxygen through dune sand.

Materials and methods

This research was undertaken at the Desert Ecological Research Unit at Gobabeb, near the Kuiseb River, Namib-Naukluft Park, Namibia. Moles were captured 10 km south of the station, in October 1992. In the early morning, mole tracks were found and followed to their terminus. Short pieces of corrugated roofing steel were pushed into the sand, forming a fenced enclosure. Plastic pit-fall traps (15 cm deep, with 5 cm sand) were buried at two or three breaks in the fence. Moles emerging the following evening encountered the fence and were directed to the traps. The traps were examined the following morning and the moles taken to the research station. All measurements were made in a constant temperature room at an average temperature of 26 °C. Between measurements, the moles were kept in terraria for up to 4 days and were then released in good condition at the site of capture. Captive moles often ate mealworm larvae that were offered on the sand surface during the night.

Gas samples were taken from interstitial spaces in the sand near buried moles. To localize the site of sampling, each mole was placed in a horizontal aluminum mesh cage (75 mm long, 35 mm in diameter and constructed of 7·5 mm opening mesh). One end of the cage was sealed with a rubber stopper, and four PVC tubes (I.D. = 2·0 mm, O.D. = 3·0 mm, length = 500 mm) were attached at 25 mm intervals, opening on the bottom of the cage. Although the cage was large enough to allow the mole to move and turn around, the end of one of the four tubes was always less than 12·5 mm from the animal's nose. Each cage was buried in a plastic bucket (26 cm diameter and 30 cm deep) such that the centre of the cage was 15 cm below the surface and 10 cm above the bottom of the bucket. The moles were left in the cages during the daylight hours when they would normally be underground. Initially, gas samples were taken after 10 min of burial, and then the animal was uncovered to determine its reaction to the cage. Because the confinement was well tolerated, some moles were left buried for up to 12·5 h without ill-effects.

The tubes leading up from the cage were sealed with a three-way stopcock. With a greased, glass 5 ml syringe containing a drop of water, 2 ml of gas was first withdrawn and discarded to flush the dead-space (0·45 ml) in the tubing. Then 3 ml of gas was sampled and analysed immediately. Samples were taken from the four tubes at random.

We also analysed additional samples from five sites where moles had been captured in the field. A 40-cm rod with an attached sampling tube was inserted into the sand at 10 cm intervals, and samples taken and analysed immediately. Field samples were not associated with buried moles at the time.

Oxygen partial pressure (P_{O_2}) was measured by injecting samples into a 0·2 ml, flow-through chamber containing an oxygen electrode (Diamond General Development Corporation model 730 Clark electrode and model 1231 pico-ammeter). Prior to injection, the chamber was filled with water, which was displaced downward by the gas. The electrode was calibrated with a sodium sulphite–sodium tetraborate P_{O_2} zero solution and saturated atmospheric air. Because the temperature of the electrode chamber could not be controlled, air calibration was carried out immediately before and after every measurement and the calibration values were averaged. The P_{O_2} was calculated from differences in electrode current (sample, air and zero solution) and barometric pressure, assuming saturation of the sample with water vapour.

Air-filled porosity of samples of dune sand were measured by filling a 1000 ml graduated cylinder with sand and slowly adding it to 1000 ml of water in a 2000 ml cylinder, avoiding any bubbles. Uncompacted sand and sand that compacted by tapping the cylinder were measured.

Results

We captured six Namib moles of mean mass 19·0 g (range 17·1–23·9 g). All of our animals were smaller than the mean mass (24·6 g) of a larger sample taken by Fielden *et al.* (1990*a*).

Over the course of the experiment, barometric pressure averaged 96·7 kPa (range 96·65–96·99 kPa), and the mean atmospheric P_{O_2} was 19·53 kPa in saturated air. Gas samples from moles buried in the cage under sand were always below atmospheric pressure, even after periods of burial as short as 10 min. The lowest value of the four samples taken at a given time was assumed to represent the environment near the head of the animal. The grand mean of minimum values from six animals was 18·64 (± 0·38 CI) kPa. Linear regression of the P_{O_2} values with duration of burial showed no correlation (Fig. 1).

Samples taken adjacent to the site of minimum P_{O_2} confirmed the existence of a diffusion gradient toward the site. In the 10 cases in which the minimum P_{O_2} existed at one end of the buried cage, the mean P_{O_2} increased from 18·40 (± 0·44 CI) kPa at the minimum to 18·77 (± 0·23 CI), 19·02 (± 0·22 CI) and 19·13 (± 0·19 CI) kPa at 25, 50 and 75 mm distance from the end. These data, corrected to standard pressure, are presented with confidence intervals in Fig. 2.

No significant difference in P_{O_2} was found at depths of 10, 20, 30 and 40 cm in seven transects in sand at the diurnal resting sites of Namib moles in the field. The mean depression of P_{O_2} below atmospheric was 0·02 kPa (± 0·05 CI; n = 7), which was not significantly different from zero. Fractional pore space (f_a) of three samples of

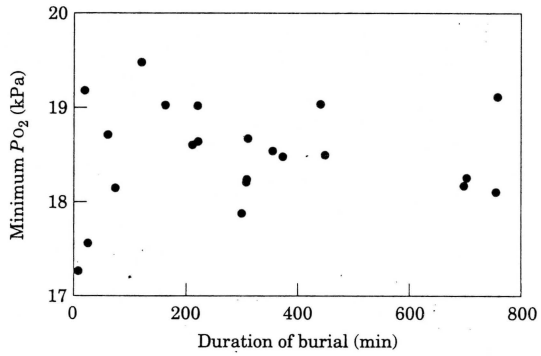

Figure 1. Minimum oxygen partial pressure (kPa) adjacent to Namib moles buried in dune sand in relation to duration of burial. Least squares regression showed no significant correlation (r = 0·06).

compacted and non-compacted dune sand were 0·336 (± 0·023 CI) and 0·410 (± 0·033 CI), respectively.

Discussion

The gaseous environment of buried Namib moles

Our results show that the immediate oxygen environment of buried Namib moles is less than 1 kPa lower than the atmospheric level. This deviation is probably close to the

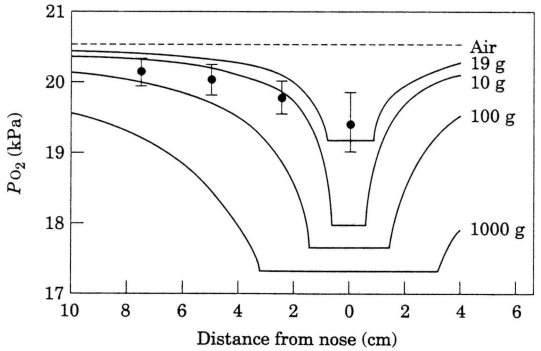

Figure 2. Steady-state distribution of P_{O_2} adjacent to hypothetical mammals breathing interstitial gas at standard pressure and 26°C. Three curves are for small insectivores of 10, 100 and 1000 g body mass, and are calculated with allometric equations of tidal volume (Stahl, 1967) and standard rate of oxygen consumption (McNab, 1986). The upper curve represents an average 19 g Namib mole resting under sand, consuming oxygen at 0·38 ml min^{-1} (Fielden *et al.*, 1990*a*). The points are means (± 95% CI) of measurements from six Namib moles buried in the laboratory, corrected to standard barometric pressure. The lengths of the horizontal lines indicate the diameter of the assumed 'tidal space'. The horizontal dashed line at the top is atmospheric P_{O_2}.

maximum encountered by the moles, because our measurements were taken in a bucket of sand that, if anything, would reduce oxygen availability. In addition, the sand temperature of 26 °C results in a resting rate of oxygen consumption of 1·2 ml g^{-1} h^{-1}, or close to the maximum of 1·4 ml g^{-1} h^{-1} shown at 21 °C; below 21 °C, the rate decreases as the buried moles completely abandon efforts to thermoregulate (Fielden *et al.*, 1990*a*). In the thermal neutral zone of 31–36 °C, standard metabolic rate is only 0·6 ml g^{-1} h^{-1}, so we would expect a depression in oxygen of about 0·5 kPa near the animal. A 1 kPa depression is unlikely to restrict the metabolism of a buried mammal. Arieli *et al.* (1977) showed that the maximum rate of oxygen consumption of white rats was unaffected by oxygen depressions of 4 kPa below the atmosphere.

Although we measured only oxygen, the deviation in carbon dioxide is doubtless similar, because the ratio of diffusion coefficients of the two gases in air (D_{CO_2}/D_{O_2} = 0·77; Nobel, 1983) is approximately equivalent to the respiratory quotient of an animal eating a diet of mixed fat and protein (RQ = 0·8; Schmidt-Nielsen, 1990).

Because 1 kPa is equivalent to about 1% of the normal atmosphere, it is easy to compare our data with those of other studies of burrowing mammals that give their results in percent. Kuhnen (1986) summarizes published data on the burrow oxygen and carbon dioxide levels for 13 species of burrowing mammals that generally show much more severe deviations. Most natural deviations have been in the region of 1–3%, but deviations exceeding 10% have occasionally been recorded. Thus the environment of the Namib mole is one of the least extreme among fossorial mammals.

Three factors account for this result. First, at 15–40 g body mass, the Namib mole is small by comparison with many other burrowing mammals and would therefore have a lower absolute metabolic rate. Second, the standard metabolic rate of this species is about one-fifth of the rate expected for small insectivores of its body size (McNab, 1966; Fielden *et al.*, 1990*a*). Third, the dryness and uniformity of distribution of particle size of Namib dune sand ensure a large air-filled porosity, continuity of the pore spaces and low extraneous respiration by soil micro-organisms.

Low standard metabolic rate is a characteristic of burrowing mammals in general (McNab, 1966, 1979). There have been several attempts to explain the adaptive value of this observation (see Fielden *et al.*, 1990*a*), but we believe that, at least in the case of the Namib mole, it is not an adaptation to hypoxia or hypercapnia. Although Fielden *et al.* (1990*a*) showed that oxygen consumption at temperatures below 25 °C was significantly lower in moles buried in sand than in moles on the surface, the difference could result from the moles' preference to become torpid underneath the sand where they are protected, rather than on the surface. It appears more reasonable that low standard metabolic rate is an adaptation to the high cost of foraging in an energy-poor, arid environment (Vleck, 1979; Lovegrove, 1986).

Our measurements were taken from moles presumably at rest under the sand. In these conditions, the rate of oxygen demand would be minimal, but if the animal were to become active, oxygen demand could increase to levels that could cause significant hypoxia and hypercapnia. Unfortunately, nothing is known about the underground activities of Namib moles, nor about the oxygen requirements during activity. We do know, however, that sand-swimming during foraging occurs in the shallow surface layers of the sand (Fielden *et al.*, 1990*b*) and that progress through the sand would continually renew the oxygen supply. Namib dunes are occasionally wetted by fog, which would restrict gas diffusion through the surface layer. This barrier is unlikely to have a significant effect on the moles' environment, however, because it is thin and incomplete, it persists for only a few hours and there is a large volume of interstitial air below it.

A model of sub-sand diffusion

Theoretical modeling is useful to increase our understanding of the oxygen environment around a Namib mole buried in sand, to independently confirm the validity of actual measurements, and to make predictions about the limitations this environment places on the metabolic intensity of sand-swimming animals in general. Modeling of diffusive exchange of respiratory gases through soil is not new, but all previous attempts have considered mammals in subterranean chambers and burrow systems rather than animals entirely encased in sand, and in some cases the assumptions of the models are inappropriate (McNab, 1966; Wilson & Kilgore, 1978; Withers, 1978).

Our approach is to consider the buried animal as completely surrounded by a volume of sand that permits oxygen to diffuse radially toward it from all directions. This assumption is supported by our measurements of uniform atmospheric levels of P_{O_2} under the sand in the field, and by the models of Withers (1978) and Wilson & Kilgore (1978), which show the depth of a nesting chamber has practically no influence on the gas tensions in it as long as the depth is several-fold larger than the radius of the chamber. Therefore it is important to realize that, despite its atmospheric origin, oxygen can diffuse toward a buried animal from below, as well as from above and from the side.

In the steady state, the amount of oxygen diffusing radially through a given spherical shell is equal to the rate it is consumed. As oxygen diffuses radially toward the animal, the volume through which it passes decreases, and therefore the P_{O_2} gradient increases, according to the equation:

$$\dot{V}_{O_2} = \frac{K_{O_2}\,(P_o - P_i)\,4\pi r_o r_i}{r_o - r_i}$$

where $\dot{V}_{O_2}$ is the rate of oxygen consumption ($cm^3\ min^{-1}$), K_{O_2} is the diffusion coefficient of oxygen in sand ($cm^2\ min^{-1}\ kPa^{-1}$), P_o and P_i are the oxygen partial pressures at the outer and inner radii of a given spherical shell (kPa), and r_o and r_i are the radii of the shell (cm). This equation has been validated (Seymour & Bradford, 1987) and has been used to model gas exchange by eggs in the incubation mounds of megapode birds (Seymour *et al.*, 1986).

We make the following additional assumptions for the model. (1) K_{O_2} is the product of the binary diffusion coefficient of oxygen in air (D_{O_2} = 12·1 $cm^2\ min^{-1}$ at 25 °C; Nobel, 1983), the oxygen capacitance of air (β_{O_2} = 0·0098 $cm^3\ cm^3\ kPa^{-1}$) and the air-filled porosity coefficient (f_a = 1·5; Marshall, 1959). K_{O_2} is therefore taken as 0·027 $cm^2\ min^{-1}\ kPa^{-1}$ in sand of f_a = 0·375. (2) P_o is assumed to be atmospheric at r_o = 100 cm. Increasing r_o to 1000 cm has a negligible effect on the results. (3) The internal radius is the radius of a sphere of sand containing the tidal volume of the animal. This 'tidal space' is calculated as:

$$r_i = \left(\frac{3V_t}{4\pi f_a}\right)^{\frac{1}{3}}$$

in which V_t is the tidal volume. V_t (cm^3) is calculated from animal mass (kg) according to the allometric relationship of Stahl (1967), $V_t = 7{\cdot}69\ M^{1{\cdot}04}$. The last assumption is based on the idea that a volume of interstitial air in the sand, equal to the tidal volume, is constantly being rebreathed and mixed by the animal. Stahl's (1967) equation predicts a tidal volume of 0·125 ml in a 19 g mole, which yields a radius of 0·43 cm. P_{O_2} in this 'tidal space' may be underestimated because (1) the space is probably not spherical but oscillates in the region between the nose and the middle of the ventral thorax, a distance of about 2·5 cm in the Namib mole, and (2) the tidal air movements

would effectively facilitate diffusion in a volume larger than the assumed sphere. On the other hand, breathing movements in Namib moles may be restricted by the pressure of the sand, and, if tidal volume is reduced in proportion to their low resting metabolic rates (Fielden *et al.*, 1990*a*), tidal volume would be overestimated. Consequently, P_{O_2} in the tidal sphere would be overestimated. Without information on actual tidal volumes or the distribution of the respired gas, we assume that these opposing tendencies cancel each other out.

Figure 2 above shows the distribution of P_{O_2} around a model Namib mole, together with the mean minimum P_{O_2} measured in moles buried in the laboratory. Although the actual and theoretical values are close, there are significant differences that must be explained. The actual mean minimum P_{O_2}, presumably measured near the head of the animal, is greater than predicted by the model (although not significantly), and the adjacent P_{O_2} values are significantly less. This may result from the fact that the mole was able to turn around in its sand-filled cage. Any movement of the animal within the cage would have an averaging effect on the measured P_{O_2} gradient.

We may now extend the model by considering how diffusive gas exchange in dune sand might limit the size and metabolic intensity of sand-swimming mammals. Are Namib moles small because of respiratory restrictions? To answer the question, we introduced allometric equations for standard metabolic rates of mammals into the model and solved for interstitial P_{O_2} within the 'tidal space'. The metabolic equations were derived from 'small, invertebrate-eating mammals' (McNab, 1986), insectivores (Hayssen & Lacy, 1985) and mammals in general (Stahl, 1967), and the tidal volume equation was in each case derived from general mammals (Stahl, 1967). Surprisingly, the predicted respiratory environments of small insectivores are almost independent of body size throughout the range of the available data, which extends to just above 200 g (Fig. 3). This result stems from notably low scaling exponents of insectivores (small species such as shrews have unusually high mass-specific metabolic rates) and from the fact that increases in metabolism with larger body mass are largely offset by increases in the 'tidal space'. Extrapolation of the insectivore curves leads to the conclusion that animals exceeding the size of a human could exist breathing interstitial air in dune sand. Such an erroneous conclusion underscores the danger of extrapolating beyond the limits of the data. A better description of the size limits set by diffusive gas exchange comes from general mammals of a wide range in body size (Stahl, 1967). This curve shows interstitial P_{O_2} declining rapidly in animals weighing more than 200 g.

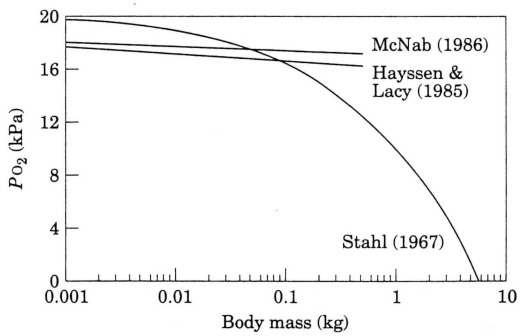

Figure 3. Calculated P_{O_2} adjacent to hypothetical mammals buried in Namib dune sand. The curves are derived from allometric equations for resting oxygen consumption small, invertebrate eaters (McNab, 1986), insectivores (Hayssen & Lacy, 1985) and general mammals (Stahl, 1967).

Wilson & Kilgore (1978) concluded that the maximum size of a mammal in a 'typical' burrow chamber would be about 500 g to avoid 'lethal' levels of carbon dioxide. For mammals completely encased in soil, the upper size limit is logically smaller. We know of no sand-swimming animal that exceeds our predicted 200 g mass limit, but the hatchling chicks of the Mallee Fowl (*Leipoa ocellata*) reach 100 g and survive completely encased in the loose sand of their incubation mound. Embryos in the eggs consume oxygen at about 60 ml h^{-1}, and the hatchlings average a rate of 127 ml h^{-1} while digging out of the mound (Vleck *et al.*, 1984). Even at rest in thermal neutrality, the chicks consume 90 ml h^{-1} (Booth, 1984). By comparison, the basal metabolic rate of a 20 g Namib mole is only 12 ml h^{-1} (Fielden *et al.*, 1990*a*).

We conclude that mammals weighing less than about 200 g could well survive complete burial in dune sand. The small size of Namib moles appears to be unrelated to problems of diffusive gas exchange through the sand. It is more reasonable to believe that their size is related to their phylogeny, their feeding habits, or energetic and mechanical limitations of burrowing and breathing in loose sand.

The mechanical problem of breathing under loose sand by Namib moles remains unanswered. Thoracic movements during breathing must be accomplished without the collapse of sand. Holm (1969) watched under-sand activity of Namib moles through the side of a glass terrarium and observed that movements of the forelimbs downward and the head upward created an air-space below the anterior third of the body. Analysis of sand-swimming by X-ray cinematography also demonstrated upward thrusting of the head and chest, termed 'buttressing' by Gasc *et al.* (1986). How much of the space created beneath the animal is retained at rest, however, is not clear. Holm suggested that the animal became entirely embedded in sand at rest, and we have never been able to observe such a space through the bottom of a glass terrarium. It is probable that all of the ventilation movements occur within the space created by the animal's pelage. The tidal volume of a 20 g mammal is less than 0·2 ml, which we estimate to be only 10% of the amount of air held in the ventral fur.

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