The energetics of huddling in two species of mole-rat (Rodentia: Bathyergidae)

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Abstract

Small rodents with a large surface-area-to-volume ratio and a high thermal conductance are likely to experience conditions where they have to expend large amounts of energy in order to maintain a constant body temperature at low ambient temperatures. The survival of small rodents is thus dependent on their ability to reduce heat loss and increase heat production at low ambient temperatures. Two such animals are the social subterranean rodents *Cryptomys damarensis* (the Damaraland mole-rat) and *Cryptomys hottentotus natalensis* (the Natal mole-rat). This study examined the energy savings associated with huddling as a behavioural thermoregulatory mechanism to conserve energy in both these species. Individual oxygen consumption (VO_2) was measured in groups ranging in size from one to 15 huddling animals for both species at ambient temperatures of 14, 18, 22, 26 and 30 °C. Savings in energy (VO_2) were then compared between the two species. Significant differences in VO_2 ($p < 0.05$) were found within each species, indicating that both Damaraland mole-rats and Natal mole-rats saved more energy in larger as opposed to smaller groups. VO_2 was also different between the two species, with Damaraland mole-rats showing a higher decrease in VO_2 with increasing group size compared to Natal mole-rats. These findings suggest that huddling confers significant energy savings in both species and that the amount of energy saved is related to each species' ecology. More generally, these findings suggest that group living desert-adapted species are likely to be more prone to heat loss at low ambient temperatures than temperate-adapted species, especially at low group sizes. This is presumably offset against the advantages obtained by having a low metabolic rate and avoiding hyperthermia when temperatures are hot.

Article Outline

1. Introduction

Endothermic homeothermy is the process whereby an organism regulates the rate of heat production and heat loss in its body in order to maintain a core temperature that is independent of environmental temperature [1]. Endothermic homeothermy provides a steady state for biochemical and physiological functions such as locomotion, digestion, growth, excretion, enzymatic activity, membrane and action potentials; as well as allowing an animal to remain active for longer periods of time and over a wider range of habitats [2], [3], [4], [5] and [6].

The survival of small mammals depends on their ability to reduce heat loss and increase heat production at low ambient temperatures (T_a) [7]. This is facilitated by a number of physiological and behavioural mechanisms. Physiological adaptations used by rodents in the cold include shivering, increased vasoconstriction in the extremities of the appendages, brown fat thermogenesis and daily torpor [8], [9] and [10]. By comparison, huddling, nest building, microclimate selection, postural modifications and changes in locomotory behaviour are among the behavioural changes which facilitate behavioural conservation of heat [11], [12] and [13].

Huddling has been shown to increase thermal insulation and considerably reduce energy expenditure of rodents housed at low T_a [7]. Oxygen consumption in house mice is inversely proportional to the number of animals in a huddling group [14]. This decrease in oxygen consumption with huddling has also been shown in yellow-necked mice (*Apodemus flavicollis*) [15], striped field mice (*Apodemus agrarius*) [16], the Mongolian gerbil (*Meriones unguiculatus*) [17] and in African four-striped grass mice (*Rhabdomys pumilio*) [18]. The metabolic rate of both harvest mice [14] and white footed mice [10] decreased by between 28% and 33% respectively when housed in groups as opposed to being housed alone. Huddling has also been found to result in a reduced food intake [19] and [20]. Prychodko [21] showed that house mice that occurred in groups at low T_a's had a reduced food intake rate when compared to those living alone. The magnitude of the decrease was directly proportional to the number of animals in the group. Huddling animals also showed longer survival time when exposed to low T_a [11] and [21], and a

lower rate of body mass loss and higher T_b [22]. Huddling therefore apparently reduces the energetic costs of thermoregulation, thereby decreasing the reliance on non-shivering thermogenesis [9] and [23]. Additionally, it has been shown that at a lower T_a, huddling animals experience a 'subjective ambient temperature' that can vary between 6 and 9 °C higher than that of solitary animals [9] and [21]. It therefore appears that the benefits of huddling increases as T_a declines [13] and that the energy savings achieved whilst huddling is absent when animals in pairs are prevented from making direct contact with one another [24]. The primary reasons why the energy expenditure of an individual decreases due to huddling is presumed to occur as a result of a reduced surface-area-to-volume ratio of the huddling group [25], [26] and [27], the effect of the grouped animals on the local microclimate [28] as well as chemically mediated effects (psycho-physiological causes of reductions in metabolic rate) between individuals [29].

The Damaraland mole-rat (*Cryptomys damarensis*) and the Natal mole-rat (*Cryptomys hottentotus natalensis*) are social subterranean rodents (Rodentia: Bathyergidae) [30] and [31]. Animals that have adopted subterranean lifestyles typically exhibit a low resting metabolic rate (RMR) and a high thermal conductance [32], [33] and [34]. A low RMR has been suggested to be an adaptation to the hypoxic (low oxygen levels) and hypercapnic (high carbon dioxide levels) conditions encountered within sealed burrow systems [35] and [36]. Low RMR's may also represent energy saving adaptations to lessen the large energetic costs incurred during burrowing [37], [38], [39] and [34]. The Damaraland mole-rat, is eusocial [40] and [41], diurnal and has a colony size ranging from 2 to 41 individuals (mean 11 adult individuals) [40] and [42]. It is endemic to southern Africa (northern South Africa, central and southern Namibia, Botswana, western Zimbabwe and western Zambia) and occurs in red Kalahari sands in environments that typically exhibit high daily and low nocturnal ambient temperatures and low, unpredictable rainfall [43]. They are homeothermic and maintain a stable T_b (35.1 °C) over an T_a range of 12–33 °C [44]. Burrow temperatures are moderate and the air contained within them is both hypoxic and hypercapnic [45] and [46]. A large network of superficial foraging tunnels lead to a central nest area (25–30 cm in diameter) that occurs some 2.5 m below ground [47]. By comparison, the Natal mole-rat is a semi-social, nocturnal rodent with a colony size of up to 16 individuals (mean = 9 adult individuals) [48] and [49]. They are distributed across the Mpumalanga and KwaZulu-Natal provinces of South Africa [50]. They maintain a stable T_b (33.4 ± 0.83 °C) over an T_a range of 10–30 °C [48]. The burrow systems of these mole-rats are completely sealed from the surface and consist of many foraging tunnels leading to a central nest area (12–18 cm in diameter) and only 30 cm below ground [48].

Huddling may presumably be more important in colder environments and in areas where rainfall is more unpredictable. Additionally, animals that have shallow burrow systems and shallow nests may obtain the greatest benefits by huddling. Eusocial species live in larger groups and occupy hotter and drier habitats than purely social species. Because eusocial species have lower RMR values and poorer thermoregulatory capabilities [51] more individual animals might be required in huddling groups to maintain stable T_b's than in purely social species. Lower oxygen consumption values, which indicate a lower rate of metabolism, would be an advantage for small mammals inhabiting arid areas as well as

subterranean habitats [52]. This study reports the minimum oxygen consumption (VO_2) of Damaraland and Natal mole-rats when huddling in groups of increasing sizes, and compares the savings in energy expenditure achieved by huddling between the two species.

2. Materials and methods

2.1. Experimental animals
Damaraland mole-rats were trapped near the town of Hotazel in the Northern Cape province, South Africa (27°58′S, 17°41′E), and near the town of Dordabis in the Rehoboth district of Namibia (22°58′S, 17°41′E). Natal mole were trapped in the foothills of the Drakensberg Mountains, on a 40 ha golf course, surrounded my montane grassland (25°58′S, 21°49′E) in KwaZulu-Natal province, South Africa. Animals of both species were housed at the University of Pretoria in plastic containers with wood shavings for nesting material at a constant temperature of 26 °C. Colonies were housed individually in separate plastic containers. A 12L:12D light cycle was maintained. All mole-rats were acclimated to laboratory conditions for at least 2 weeks. Animals were fed daily, as they do not drink free water [47]. Animals were fed a variety of fresh fruit and vegetables, including apples, gem squash and sweet potato replacing the natural geophytes upon which they feed [53].

2.2. Oxygen consumption (VO_2) measurements
Measurements of oxygen consumption (VO_2) were obtained in an open-flow system with an Applied Electrochemistry oxygen analyzer (S-2A Applied Electrochemistry, AEI Technologies, Inc., USA). The analyzer was calibrated to an upper value in dry air (20.95% O_2) prior to the measurement of each animal, and to a lower value (0% O_2 in N_2 gas, AFROX, South Africa) prior to initial measurements. Dry air was pumped into the metabolic chamber. Carbon dioxide and water were absorbed from the gas stream before measuring flow rate. The flow rate through the analyzer was set at 700 cm^3/min (F900 flow meter, AEI Technologies, Inc., USA). The flow rate through the chamber was set at approximately 700 cm^3/min for one animal and thereafter increased depending on the number of animals contained within the chamber. Flow rates were adjusted for different group sizes of animals within the chamber so that depressions in oxygen concentration were maintained at 0.25–0.4%. The flow of air into the chamber was controlled by a flow regulator (Omega FMA-A2310, Stamford, CT) placed upstream. Ambient temperature was controlled by submerging the metabolic chamber into a thermoregulated water bath. The air passed through approximately 4 m of copper coil that was submerged in the water before it entered the chamber. This ensured the temperature of the air that entered the chamber was the same as the water bath. The water temperature was measured using a mercury thermometer, accurate to ± 0.5 °C. Temperatures of 14, 18, 22, 26 and 30 °C were used for all individual groups of mole-rats. These temperatures were selected to span a range and include temperatures from those which animals could barely maintain stable body temperatures to temperatures where no more benefit can be gained from huddling, i.e. within the thermoneutral zone [44] and [48].

We used group sizes of 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 for *C. damarensis*, and 1, 2, 3, 4, 5, 7, 8, 10 and 15 for *C. h. natalensis*. Six replicates for each group size were used. No replication of individuals took place (i.e. if an individual animal was used in a measurement for a group size of two, it was not used again for a measurement in any other group size). Groups were placed in the respirometry chamber at 14 °C for 30 min prior to measurements taking place to allow the animals to settle (usually within 5–10 min) [54]. After this period of time, measurements were taken every 30 s for 10 min. The temperature of the water bath was then increased by 4 °C to 18 °C, and the animals were again allowed 30 min to settle down before measurements were taken every 30 s for 10 min. This process was repeated for all temperatures. At each temperature, the mean of the lowest 10 readings of % O_2 were taken when the animals were seen to be at rest [44]. Body mass of the animals was measured at the start of each experiment (Adventurer Pro AV812, Ohaus Corporation, USA). Body temperature of each individual animal was measured at each ambient temperature (below). Oxygen consumption was calculated using the equation:

(1)

$$VO_2 = (f_1O_2 - f_2O_2) \cdot (V_2) \cdot (60)/\text{mass}.$$

Where: f_1O_2 is the O_2 fraction of the inlet air and f_2O_2 is the O_2 fraction of the outlet air. VO_2 was measured in cm^3 of dry air per hour. It was thus multiplied by 60 to give cm^3/min. This was divided by total mass of the huddling group to give VO_2 in cm^3 $O_2/g \cdot h$.

2.3. Body temperature (T_b) measurements

The groups of mole-rats were placed in an incubator (LABCON, Low-temperature incubator, L.T.I.E.) for 30 min at temperatures of 14, 18, 22, 26 and 30 °C. Body temperatures were subsequently recorded by inserting a copper-constantan thermocouple attached to an APPA 51 digital thermometer (1 mm diameter) 2 cm into the rectum of each tested individual for at least 30 s. A mean value for all individuals at each temperature was then calculated. These measurements took place subsequently (the next week) to oxygen consumption measurements.

2.4. Statistical analysis

Statistica 7.0 (StatSoft Inc.) was used for the statistical analyses. In the study, there were three independent variables (species, group size and T_a) contributing to the outcome of the dependent variable (VO_2). Species and group size were included in the model as categorical variables and T_a as a continuous variable. General Linear Models (GLM) were used, with a separate slopes model to analyze the data. Separate slopes models were used when categorical and continuous predictors interact in influencing responses on the outcome of an experiment. Confidence limits were set at 0.95 and significance levels at 0.05.

Separate slope model analyses were initially performed on each species separately in order to determine whether group size and T_a had any effect on VO_2 within a species. An analysis was then performed on the combined data for both species, including using species as a factor. This was done to determine differences between VO_2 of the two

species, in terms of group size and ambient temperature. A Newman–Keuls post-hoc test was then performed on all data.

3. Results

3.1. Effects of group size and ambient temperature (T_a) on oxygen consumption (VO_2)

3.1.1. *C. damarensis*

An overall trend of decreasing VO_2 with an increase in group size was observed. Standard error for group sizes between 1 and 6 was below 11%; standard error for group size 8 was 28.2%, and standard error for group sizes 7, 9 and 10 was between 68% and 77%. The data for *C. damarensis* followed a normal distribution ($p < 0.01$). As group size increased, individual VO_2 showed an overall decrease at a mean T_a of 22 °C (Fig. 1). A maximum VO_2 value of 0.74 cm^3 O$_2$/g · h, and a minimum VO_2 value of 0.09 cm^3 O$_2$/g · h was recorded, resulting in a mean overall decrease in individual VO_2 of 0.65 cm^3 O$_2$/g · h.
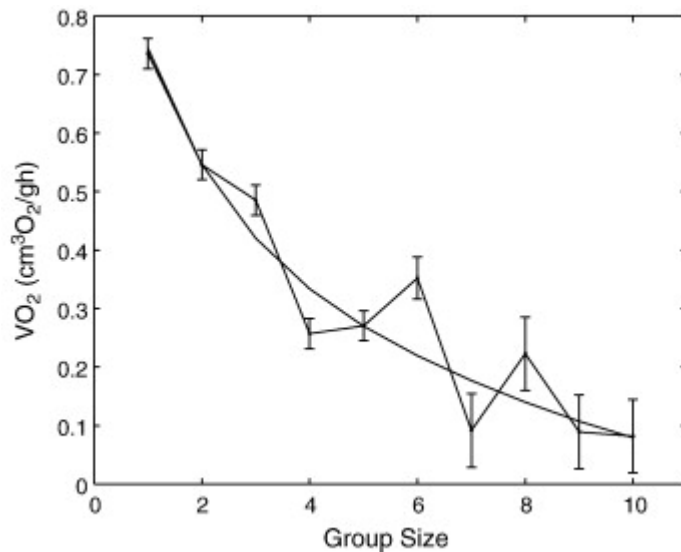

Fig. 1. Individual oxygen consumption values [VO_2 (cm^3 O$_2$/g · h)] of *Cryptomys damarensis* for different group sizes at a mean T_a of 22 °C. Points represent means ± SE for each group size. The trend line represents a logarithmic function indicated by the equation: $y = (- 0.2834)Ln(x) + 0.7413$; $F_{9,165} = 12.596$; $p < 0.05$.

The separate slopes model showed an adjusted r^2 value of 0.730 ($F = 26.90$; $p < 0.05$) indicating that group size and T_a combined accounted for 73% of the variance in VO_2 observed. An analysis calculating the effect of group size alone on VO_2 showed an adjusted R^2 value of 0.498 ($F = 21.31$; $p < 0.05$) indicating that 50% of the variance in VO_2 was explained by group size and that 23% was explained by the effect of T_a. Significant differences existed between and within group size and T_a.

3.1.2. *C. h. natalensis*

An overall trend of decreasing VO_2 with an increase in group size was observed. Standard errors for group sizes 1 to 3 were below 10.5%; standard errors for group sizes 4 and 5 were between 13% and 20.6%, and standard errors for group sizes 7, 8, 10 and 15 were between 34% and 55%. The data for *C. h. natalensis* followed a normal distribution ($p < 0.05$). As group size increased, individual VO_2 showed an overall decrease at a mean T_a of 22 °C (Fig. 2). A maximum VO_2 value of 0.53 cm³ O_2/g · h and a minimum VO_2 value of 0.13 cm³ O_2/g · h were recorded, resulting in a mean overall decrease in individual VO_2 of 0.40 cm³ O_2/g · h.
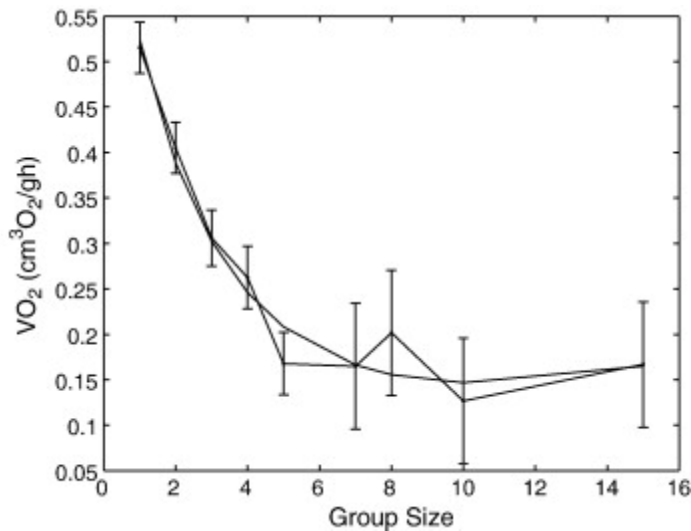
Fig. 2. Individual oxygen consumption values [VO_2 (cm³ O_2/g · h)] of *Cryptomys hottentotus natalensis* for different group sizes at a mean T_a of 22 °C. Points represent means ± SE for each group size. The trend line represents a logarithmic function indicated by the equation: $y = (- 0.1756)Ln(x) + 0.5071$; $F_{8,127} = 1.596$; $p = 0.132$.

The separate slopes model showed an adjusted R^2 value of 0.417 ($F = 7.06$; $p < 0.05$) indicating that group size and T_a combined account for 42% of the variance in VO_2 observed. An analysis calculating the effect of group size alone on VO_2 showed an adjusted R^2 value of 0.371 ($F = 11.61$; $p < 0.05$) indicating that 37% of the variance in VO_2 was explained by group size and that 5% can be explained by T_a. Significant differences existed between group size and T_a.

3.1.3. *C. damarensis* versus *C. h. natalensis*

A group size increased, an overall decrease in individual VO_2 at all ambient temperatures for both species was observed (Fig. 3). Both species followed the same general trend with respect to increases and decreases of VO_2 at certain group sizes and ambient temperature (Fig. 4). *C. damarensis* exhibited higher VO_2 values than *C. h. natalensis* for group sizes of less than 7 individuals, whereas *C. h. natalensis* exhibited higher VO_2 values in comparison to *C. damarensis* in group sizes of 7 animals or more.
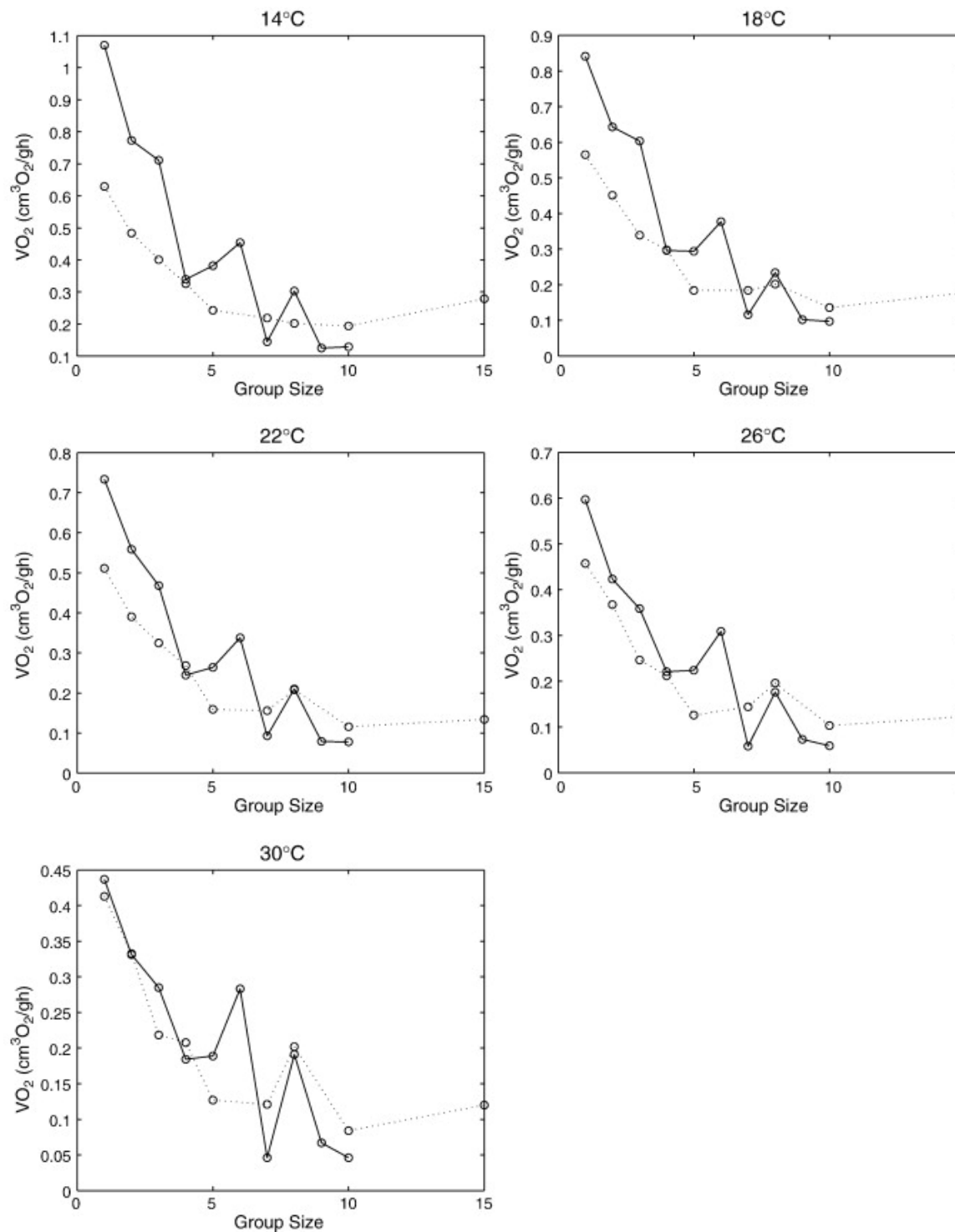
Fig. 3. Individual oxygen consumption values [VO₂ (cm³ O₂/g · h)] of *Cryptomys damarensis* (solid line) and *Cryptomys hottentotus natalensis* (broken line) for different group sizes at ambient temperatures of 14, 18, 22, 26 and 30 °C. Circles represent means at each group size.
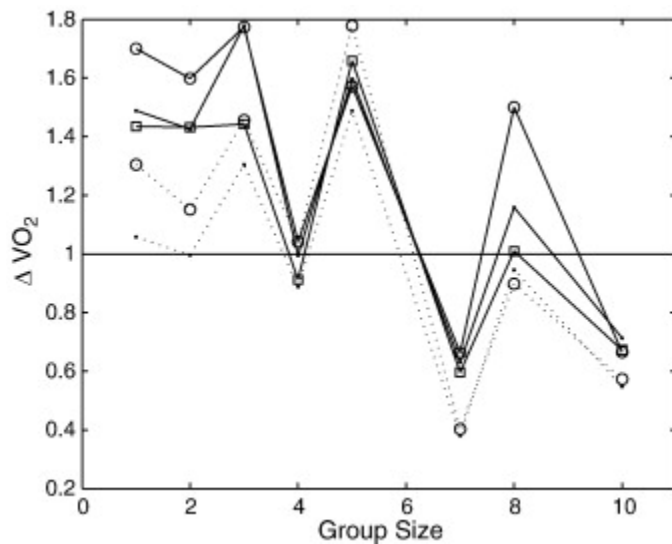
Fig. 4. Differences in individual oxygen consumption values [VO$_2$ (cm^3 O$_2$/g · h)] between huddling *Cryptomys damarensis* and *Cryptomys hottentotus natalensis* for different group sizes at ambient temperatures of 14, 18, 22, 26 and 30 °C. ΔVO$_2$ represents mean individual difference in oxygen consumption of the huddling group of *C. h. natalensis* minus that of *C. damarensis*. ΔVO$_2$ > 1 represents points where *C. h. natalensis* VO$_2$ > *C. damarensis* VO$_2$, ΔVO$_2$ < 1 represents points where *C. h. natalensis* VO$_2$ < *C. damarensis* VO$_2$ and ΔVO$_2$ = 1 represents points where *C. h. natalensis* VO$_2$ = *C. damarensis* VO$_2$.

3.2. Effect of group size and ambient temperature (T_a) on body temperature (T_b)

As T_a increased, the average individual T_b also increased in both species. Individual T_b also increased with an increase in group size. Body temperature stayed within normal limits throughout the ambient temperature range for all group sizes in both species. Body temperature of *C. damarensis* exceeded that of *C. h. natalensis* for all group sizes. No significant differences existed between T_b measured for different group sizes and T_a's for either *C. damarensis* ($F = 2.55$; $p > 0.05$) or *C. h. natalensis* ($F = 2.82$; $p > 0.05$). Differences in body temperatures between *C. damarensis* and *C. h. natalensis* were found to be significant for all group sizes and ambient temperatures ($F = 15.18$; $p < 0.05$).

4. Discussion

Rodents depend on both physiological and behavioural mechanisms in order to thermoregulate [7]. Social aggregation is one of several behavioural options available to small-bodied endotherms for reducing metabolic rate and energy expenditure [55]. Several laboratory studies have shown that small mammals in large groups have more energetic savings than single individuals [7], [18], [27], [28], [56] and [57]. This would suggest that social mole-rats should also derive an appreciable energetic saving by

huddling together. Results obtained in the current study demonstrate that VO_2 decreased in individual animals in both species of mole-rats with an increase in huddling group size. Our results also show that *C. damarensis* experienced a greater reduction in VO_2 per individual animal with increasing group size compared to *C. h. natalensis*. This may perhaps be explained by the fact that *C. damarensis* has a very low RMR for its body mass [44]. These results, which agree with a study on gerbils, may also explain the distribution of *C. damarensis* which only occurs in areas which are extremely arid and where food is scarce [58].

In the current study, Damaraland mole-rats exhibited higher individual VO_2 values in groups of between 1 and 7 animals, regardless of ambient temperature, compared with groups of Natal mole-rats of similar size. The opposite was true for the relationship of the two species with groups of more than 8 individuals. Thus, *C. damarensis* showed greater energy savings in groups of more than 7 individuals. This may be a result of the deeper tunnel systems in which Damaraland mole-rats inhabit and because they occupy a nest chamber which is some 2 m below the surface, in which they have to cope with conditions of hypoxia (low O_2) and hypercapnia (high CO_2). *C. damarensis* also occur in larger groups than *C. h. natalensis* and thus may need more individuals in a huddling group to effectively conserve energy.

The metabolic savings associated with increased group size in *C. damarensis* and *C. h. natalensis* are comparable to that determined in other small rodents. Trojan and Wojciechowska [59] reported a strong relationship between group size and energy savings in huddling common voles (*Microtus arvalis*). Bazin and MacArthur [55] showed that metabolic rate of muskrats (*Odatra zibethicus*) in an aggregate of four animals averaged 11–14% below that of single animals and Scantlebury et al. [18] showed that huddling African four-striped grass mice (*R. pumilio*) expended less energy in larger groups than smaller groups at temperatures below the thermoneutral zone.

As ambient temperature increased, individual body temperature also increased in both species, indicating that heat generation and energy conservation took place — more individuals in a huddling group led to greater heat conservation. This effect might be expected to be particularly important in cold climates [55]. On the whole, but particularly in group sizes of one to seven individuals, *C. h. natalensis* displayed higher average individual body temperatures than *C. damarensis*. This might be explained by *C. h. natalensis* having a thicker pelage than *C. damarensis*. It is possible that a less dense pelage is useful in *C. damarensis* in which the burrow temperature is warm (close to thermoneutral: [51]) and deep. That is, the difficulties faced are avoiding hyperthermia. By comparison, in *C. h. natalensis*, the tunnel systems are comparatively shallow and temperatures vary greatly between seasons as well as between night and day. Hence, in contrast the difficulties *C. h. natalensis* face for much of the year are in keeping sufficiently warm.

5. Conclusions

Our findings suggest that aggregation behaviour, in particular the huddling of conspecifics, provides significant energy savings to both Damaraland mole-rat and Natal. The larger reduction in VO_2 observed in the Damaraland mole-rat as well as the greater energetic savings in larger groups compared to smaller groups may be an adaptive response of living in a sealed burrow system with deep tunnel systems and a central nest that can occur 2 m below the surface of the ground. Lower VO_2 values in the Damaraland mole-rat compared to the Natal mole-rat may also indicate adaptation to inhabiting hot arid areas where food is scarce. More generally, these findings suggest that group living desert-adapted species are likely to be more prone to heat loss at low ambient temperatures, especially at low group sizes. This is presumably traded off against the advantages obtained by having a low metabolic rate and not overheating when temperatures are hot. Group conservation of heat as well as increased energy savings through reduced individual VO_2 probably represents the major ecological advantages of aggregation behaviour in these species of African mole-rats.

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