The energy costs of sexual dimorphism in mole-rats are morphological not behavioural

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Different reproductive strategies of males and females may lead to the evolution of differences in their energetic costs of reproduction, overall energetic requirements and physiological performances. Sexual dimorphism is often associated with costly behaviours (e.g. large males might have a competitive advantage in fighting, which is energetically expensive). However, few studies of mammals have directly compared the energy costs of reproductive activities between sexes. We compared the daily energy expenditure (DEE) and resting metabolic rate (RMR) of males and females of two species of mole-rat, *Bathyergus janetta* and *Georchus capensis* (the former is sexually dimorphic in body size and the latter is not) during a period of intense digging when males seek females. We hypothesized that large body size might be indicative of greater digging or fighting capabilities, and hence greater mass-independent DEE values in males of the sexually dimorphic species. In contrast to this prediction, although absolute values of DEE were greater in *B. janetta* males, mass-independent values were not. No differences were apparent between sexes in *G. capensis*. By comparison, although RMR values were greater in *B. janetta* than *G. capensis*, no differences were apparent between the sexes for either species. The energy cost of dimorphism is most likely to be the cost of maintenance of a large body size, and not the cost of behaviours performed when an individual is large.

Keywords: mole-rat; daily energy expenditure; resting metabolic rate; doubly labelled water; sexual selection

1. INTRODUCTION

Lifetimes can be regarded as being composed of somatic and reproductive effort, with energy allocated and expended on each (Gadgil & Bossert 1970; Alexander 1979). In sexually reproducing organisms, males and females commonly apportion their life effort in different ways (Alexander 1987; Davies 1991; Low 2001). Specifically, in eutheria, females make substantial energetic investments into the reproductive 'parental' component (e.g. through gestation, lactation and care of neonates) (Millar 1977; Alexander 1987; Loudon & Racey 1987). By comparison, males are often emancipated from parental duties and in many cases invest the bulk of their energies into the 'mating' component of life effort (e.g. being able to dominate other males and females to gain copulations) (Alexander *et al.* 1979). Reproductive output of females is therefore often limited by access to resources (e.g. food and/or territory availability), whereas that of males is limited by their ability to compete successfully for access to females (Bateman 1948; Bradbury & Vehrencamp 1977; Low 2001). Accordingly, while direct investment in the parental component of reproduction by males may be small, they often invest considerable time and energy in activities and traits that are associated with increasing their competitive abilities (e.g. territorial defence, large body size and fighting capabilities) (Bateman 1948; Trivers 1972; Kappeler & van Schaik 2004). In some periods their energy expenditure may substantially exceed that of females

(e.g. in sage-grouse *Centrocercus urophasianus*, display may account for 40–50% of the overall energy budgets for the more active and successful males (Vehrencamp *et al.* 1989)); yet, the energy costs of reproductive activities in (male) mammals have seldom been quantified, presumably because of the difficulty of measuring the energy expenditure of activities such as territorial defence (Bennett & Nagy 1977; Congdon 1989; although see Costa 1991; Slip *et al.* 1992; Boyd *et al.* 1994; Costa & Williams 2000, for studies in marine mammals).

A second issue with respect to the energetics of reproduction in males concerns the phenomenon of sexual dimorphism. In some species, the competition between males has led to the evolution of exaggerated body size relative to females. The 'increased-energy' hypothesis predicts that in species in which males are larger, males incur disproportionately higher rates of metabolism in relation to their body size than females (Shillington & Peterson 2002). This hypothesis predicts that high-energy demands are sustained for protracted periods, which are sufficient to elevate the overall daily energy expenditure (DEE) to a value that is high, even when the effects of body size are taken into account. By comparison, the 'body-maintenance' hypothesis (Key & Ross 1999) advocates that peak energy demands in large (sexually dimorphic) individuals may actually be relatively short-lived, and therefore not contribute substantially to the daily energy demands of the animal. Therefore, the real costs of dimorphism may simply be the costs of being large enough

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to compete (because they are big all the time and therefore incur costs all the time) as opposed to what they do when they are big (because these costs are more transitory).

The solitary African mole-rats (family Bathyergidae) include some species that exhibit sexual dimorphism of body size (such as Cape dune mole-rats, *Bathyergus suillus* and Namaqua mole-rats, *Bathyergus janetta*) and others that do not (such as Cape bles mole-rats, *Georchus capensis*) (Bennett & Faulkes 2000). In both *B. janetta* and *G. capensis*, males excavate linear tunnel systems which shift from year to year, whereas females excavate circular burrow systems of a reticulate nature and maintain home ranges that are more or less permanent (R. F. Nanni 1988, unpublished work; Herbst *et al.* 2004). Fresh burrow excavation usually occurs at the onset of the first winter rainfall, when the soil has been sufficiently softened by moisture to make the extrusion of excavated soil onto the surface possible. During this period, males enhance their chances of finding new mates by extending their burrow systems. Extrusion rates of soil are greater in males than females, presumably because of an increased amount of burrowing (Herbst *et al.* 2004). There is a direct relationship between the mass of soil excavated and the energy costs of burrowing (Vleck 1979, 1981; Lovegrove 1989). Energetic constraints are therefore likely to play an important role in limiting the capacity of males to find females.

In this study, we used measurements of DEE and resting metabolic rate (RMR), first to explore whether energy costs (both absolute and mass independent) are generally higher in males than females during the 'mate-seeking' digging period, and second, to determine whether sexual dimorphism in body size is related to an increased DEE and RMR in males of species with high sexual dimorphism. Finally, although measurements of DEE provide a valuable comparison between animals, it is widely recognized that a useful independent index of how hard an animal is working is the sustained metabolic scope (SusMS, DEE/RMR); this reaches a limit variously suggested to be around $4 \times \text{RMR}$ (Drent & Daan 1980; Weiner 1992) to $6\text{--}7 \times \text{RMR}$ (Hammond & Diamond 1997). We therefore also determined whether SusMS values differ between species and between sexes. We explored the following specific predictions:

- (i) Mass-independent DEE will be greater in males than females in both species during a period when males are seeking females.
- (ii) If the body-magnitude hypothesis is correct, the energy demands of the males in the dimorphic species will be at a level anticipated for their body size, relative to the other groups. However, if the increased-energy hypothesis is correct, the energy costs in the males of the dimorphic species will be disproportionately elevated.
- (iii) The rate of energy expenditure of males will be limited by the maximal rate of SusMS, and males of the more dimorphic species might approach this level.

2. MATERIAL AND METHODS

(a) Study sites and animals

Cape mole-rats (*G. capensis*) were captured with live Hickman traps (Hickman 1979) in August 2003 near the town of

Darling (33°22' S 15°25' E) in the southwestern Cape, South Africa. Namaqua dune mole-rats (*B. janetta*) were trapped in September 2003 near Kamieskroon (30°9' S 17°56' E), in the northern Cape, South Africa. These habitats are characterized by indigenous Fynbos and succulent Karoo, respectively (Rutherford & Westfall 1986). Both areas have fairly predictable winter rainfall and moderate temperatures throughout the year (Hoffman & Cowling 1987). Both species were studied just prior to their respective breeding seasons, and (for both species) all individuals were initially caught in a period of about 5 days. Both these species mature within their first year of life. We used data from the growth curves of M. Herbst (2003, unpublished work) and G. Gutjahr (unpublished) to define the weights achieved by each species at 12 months of age. We only used individuals that exceeded this weight and hence we are confident that the animals we used were over 12 months old and therefore adults. Animals were not anaesthetized and we handled them in cotton bags to minimize stress. Although initial trapping took place throughout the day, we injected animals at approximately the same time (09.00) each day. If they were captured before 09.00, they were injected with doubly labelled water (DLW) (see below) and released that day. If they were captured after 09.00, they were maintained overnight before being injected and released the next day (they were kept overnight in a field laboratory in plastic containers 30 cm diameter, 50 cm height with sawdust as bedding and sweet potatoes provided *ad libitum* as food). Traps were set at approximately 06.30 on the intended day of recapture in an attempt to capture them before 09.00, so that we could have measurements of isotope turnover for whole 24 h periods (Speakman & Racey 1988). On completion of experiments, animals were returned to their original capture sites. All experimental procedures and all animal husbandry practices were approved by the Animal Ethics Committee, University of Pretoria.

(b) Daily energy expenditure (DEE)

We measured the DEE (kJ d^{-1}) of 17 adult Cape mole-rats (six males and 11 females) and 14 Namaqua dune mole-rats (six males and eight females) using the DLW technique (Lifson & McClintock 1966; Speakman 1997). On day 1, the animals were weighed (± 0.1 g Sartorius balance) and a 0.2 ml blood sample was obtained from the cephalic vein in the foot to estimate the background isotope enrichments of ^2H and ^{18}O . Blood samples were immediately heat sealed into $4 \times 50 \mu\text{L}$ glass capillaries, which were stored at room temperature. Afterwards, a known mass of DLW (100 g 95% APE enriched ^{18}O water (Rotem Industries Ltd, Beer Sheva, Israel) and 50 g 99.9% APE enriched ^2H water (Isotec, Inc. Miamisburg OH, USA) mixed with 342 g $^1\text{H}_2^{16}\text{O}$) was administered (IP, 0.3 g/100 g body weight). Syringes were weighed before and after administration (± 0.0001 g, Sartorius balance) to calculate the mass of DLW injected. Blood samples were taken after 1 h to estimate initial isotope enrichments. Animals were recaptured 2–5 days post dose and final blood samples (0.2 ml) were taken after whole 24 h periods (Speakman & Racey 1988) to estimate isotope elimination rates. We recaptured all 14 Namaqua dune mole-rats but only 17 out of the 20 initially injected Cape mole-rats. Capillaries that contained the blood samples were then vacuum distilled (Nagy 1983) and water from the resulting distillate was used to produce CO_2 and H_2 (methods in Speakman 1997 for CO_2 and Speakman & Król

2005 for H_2). The time between blood sampling and eventual sample analysis was approximately three months. The isotope ratios $^{18}O : ^{16}O$ and $^2H : ^1H$ were then analysed using gas source isotope ratio mass spectrometry (Optima, Micromass IRMS and Isochrom μG , Manchester, UK), prior to calculation of DEE (Lemen & Speakman 1997). We assumed that the DEE estimate was robust to isotope recycling. This is because the largest effects of recycling do not involve animals re-breathing their own isotopes, but taking in label from other individuals, or being unduly diluted by re-breathing unlabelled CO_2 from other individuals (e.g. in lactating domestic dogs, *Canis familiaris*: Scantlebury *et al.* 2000). Moreover, in a validation study of the DLW method in European moles (*Talpa europaea*) living in a fossorial environment, there was no impact on the accuracy of the method on the DEE estimate (Fears *et al.* unpublished, cited in Speakman 1997).

(c) Resting metabolic rate (RMR)

Upon final recapture, animals were taken to a field laboratory, where their RMR was measured. We used an open circuit respirometry system (Depocas & Hart 1957; Hill 1972). A metabolic chamber (1610 cm^3 volume for *G. capensis* and 6912 cm^3 for *B. janetta*) was immersed in a temperature-controlled water bath (Labotec) and maintained at 28–29 °C (LAUDA, Königshofen, Germany), within the thermoneutral zone of each of the species (Lovegrove 1986, 1987). Dried air was pumped into the chamber at a rate of approximately 500 $ml\ min^{-1}$ for *G. capensis* and 900 $ml\ min^{-1}$ for *B. janetta*. Air flow was controlled by a flow regulator (F900, Applied Electrochemistry, AEI Technologies, Inc. USA) placed upstream of the metabolism chamber. Measurements of VO_2 were taken using an oxygen analyser (S-2A Applied Electrochemistry, AEI Technologies, Inc. USA). The analyser was calibrated to an upper value (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) every two weeks. After an initial hour in which animals were observed to settle down in the respirometry chamber (Speakman *et al.* 2003), measurements were taken every minute for half an hour. The mean of the lowest 10 readings of oxygen consumption ($mlO_2\ h^{-1}$) was taken, when animals were seen to be at rest (Bennett *et al.* 1992). Measurements were carried out between 11.00 and 17.00. Results were corrected to standard temperature and pressure. In addition to DEE and RMR, we also calculated sustained metabolic scope ($SusMS = DEE/RMR$) for each animal (Drent & Daan 1980).

(d) Analysis

We used generalized linear modelling to examine differences in DEE, RMR and $SusMS$ between males and females and between the two species (McKenzie & Goldman 1998); body mass was included as a covariate with sex and species as categorical factors. We fitted one model for each energy expenditure measure. We determined all interaction terms. In particular, interactions between sex and species were examined as these indicated possible effects of sexual selection. *Post hoc* tests were used to determine differences between specific groups: least-squares regressions were used to calculate the relationships between DEE and body mass and between RMR and body mass; two-sample *t*-tests were used to determine differences between absolute values of DEE between males and females within species. Mass-corrected DEE and RMR (figures 1b and 2b, respectively)

Figure 1. (a) Daily energy expenditure (DEE, $kJ\ d^{-1}$) against body mass (g) of *B. janetta* males and females (open and solid squares, respectively) and *G. capensis* males and females (open and solid circles, respectively). (b) Mass corrected daily energy expenditure (DEE, $kJ\ d^{-1}$) of *B. janetta* males and females (BJ male and BJ female), *G. capensis* males and females (GC male and GC female). Values were calculated using the mean residual for each of the groups of animals added to the grand mean across all animal groups. Error bars denote the standard deviations of the residual mean estimates.

values were calculated using the mean residual for each of the groups of animals added to the grand mean across all animal groups (Packard & Boardman 1987, 1988).

3. RESULTS

(a) Body mass

Bathyergus janetta males were significantly heavier on initial capture than *B. janetta* females ($F_{1,12}=4.95$, $p=0.046$) (table 1). Initial masses of *G. capensis* were only 36% of *B. janetta*, and in this species there was no difference in body mass between males and females ($F_{1,14}=0.21$, $p=0.654$). The ratio of male to female bodyweight (an index of dimorphism) was 1.45 in *B. janetta* and 1.08 in *G. capensis*.

(b) Daily energy expenditure (DEE)

Bathyergus janetta had greater absolute DEE values than *G. capensis* (312 ± 124 and $132 \pm 25\ kJ\ d^{-1}$, respectively; $F_{1,27}=42.45$, $p<0.001$) (table 1). *Bathyergus janetta* males had greater absolute values than *B. janetta* females ($t=2.20$, $p<0.05$). However, there was no significant difference in DEE between male and female *G. capensis* ($t=1.29$, $p=0.22$). The ratio of male to female DEE was 1.46 in *B. janetta* and 0.98 in *G. capensis*. There was a strong effect of mass on DEE ($F_{1,24}=23.76$, $p<0.001$). The least-squares fitted regression

$$DEE\ (kJ\ d^{-1}) = 31.0 + 0.795 \times \text{body mass (g)}, \quad (3.1)$$

explained 86.2% of the variation ($F_{1,26}=161.9$, $p<0.001$) (data for all animals) (figure 1a). However, there was no

Table 1. Body mass, resting metabolic rate, daily energy expenditure and sustained metabolic scope. (Mean and standard deviations (s.d.) of body mass (mass, g), resting metabolic rate (RMR; $\text{mlO}_2 \text{ h}^{-1}$ and $\text{mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$), daily energy expenditure (DEE; kJ d^{-1} and $\text{kJ g}^{-1} \text{ d}^{-1}$) and sustained metabolic scope (SusMS) of Namaqua dune mole-rats (*Bathyergus janetta*, BJ) and Cape mole-rats (*Georchus capensis*, GC). *, BJ and GC marked on the variable denote a significant difference in that variable between the two species (*B. janetta* and *G. capensis*), a significant difference in that variable between male and female *B. janetta*, and a significant difference in that variable between male and female *G. capensis*, respectively. *n* denotes sample sizes.)

	BJ male		BJ female		GC male		GC female	
	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
<i>n</i>	6		8		6		11	
mass (g)*,BJ	423	161	291	47	137	51	127	36
RMR ($\text{mlO}_2 \text{ h}^{-1}$)*	234	76	193	38	133	11	120	37
RMR ($\text{mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$)	0.557	0.064	0.681	0.154	1.069	0.340	0.842	0.128
DEE (kJ d^{-1})*,BJ	375	132	257	94	137	40	140	28
DEE ($\text{kJ g}^{-1} \text{ d}^{-1}$)	0.903	0.141	0.875	0.243	0.990	0.267	1.103	0.321
^a SusMS ^{GC}	3.24	0.28	2.62	0.78	1.89	0.20	2.75	0.77

^a RMR was converted to kJ d^{-1} in order to calculate SusMS using an oxygen equivalent of $20.51 \text{ kJ L}^{-1} \text{ O}_2$ (Hardy 1972).

effect of sex or species on DEE when body mass was entered as a covariate ($F_{1,24}=0.02$, $p=0.88$ and $F_{1,24}=0.04$, $p=0.85$ for sex and species, respectively; figure 1*b*).

(c) Resting metabolic rate (RMR)

Bathyergus janetta had greater absolute values of RMR than *G. capensis* (211 ± 53 and $124 \pm 31 \text{ mlO}_2 \text{ h}^{-1}$, respectively; $F_{1,31}=34.61$, $p<0.001$) (table 1). However, there was no significant difference in RMR between *B. janetta* males and females ($F_{1,12}=1.95$, $p=0.19$) or between *G. capensis* males and females ($F_{1,17}=0.76$, $p=0.40$). There was a strong effect of mass on RMR; the least-squares fitted regression

$$\text{RMR (mlO}_2 \text{ h}^{-1}) = 67.5 + 0.415 \times \text{body mass (g)}, \quad (3.2)$$

explained 87.2% of the variation ($F_{1,31}=211.26$, $p<0.001$) (data for all animals) (figure 2*a*). RMR was positively correlated with body mass within each species ($F_{1,10}=6.67$, $p=0.027$ for *B. janetta* and $F_{1,15}=50.93$, $p<0.001$ for *G. capensis*). However, there was no effect of sex or species on RMR when body mass was entered as a covariate ($F_{1,29}=0.16$, $p=0.69$ and $F_{1,29}=0.27$, $p=0.61$ for sex and species, respectively; figure 2*b*).

(d) Sustained metabolic scope (SusMS)

There was a significant effect of species on SusMS ($F_{1,24}=6.32$, $p=0.019$); *B. janetta* generally had higher values of SusMS than *G. capensis*. There was also a significant interaction between sex and species ($F_{1,24}=9.19$, $p=0.006$); females had higher values of SusMS than males in *G. capensis*, but not in *B. janetta* (table 1).

4. DISCUSSION

In solitary mole-rats, as in many other species, males are mobile and attempt to locate and mate with as many different females as possible (Bennett & Faulkes 2000). By comparison, females establish stable territories that are resource dependent (Jarvis & Bennett 1993; M. Herbst 2003, unpublished work). Since males encounter females by extending their burrow systems (Herbst *et al.* 2004), and digging is energetically costly (Lovegrove 1989), energetic constraints potentially play an important role in determining male reproductive success. Hence, digging costs and mass-independent DEE values of males were

Figure 2. (a) Resting metabolic rate (RMR, $\text{mlO}_2 \text{ h}^{-1}$) against body mass (g) of *B. janetta* males and females (open and solid squares, respectively) and *G. capensis* males and females (open and solid circles, respectively). (b) Mass corrected resting metabolic rate (RMR, $\text{mlO}_2 \text{ h}^{-1}$) of *B. janetta* males and females (BJ male and BJ female) and *G. capensis* males and females (GC male and GC female). Values were calculated using the mean residual for each of the groups of animals added to the grand mean across all animal groups. Error bars denote the standard deviations of the residual mean estimates.

expected to be higher than for females during the mate-seeking period, before the females invest in reproduction. In contrast to this prediction, we found no significant differences in mass-independent DEE between males and females in either of the two species studied. In addition, SusMS values for all animals were substantially lower than allometric predictions for maximal values (Drent & Daan 1980; Hammond & Diamond 1997)—neither species appeared to be working particularly hard during the

measurement period and values were actually slightly higher in *G. capensis* females than males. Therefore, one can assume that females must have been incurring similar energy costs, relative to their body size, to males. The fact that SusMS values of males were lower than allometric predictions for maximal values may also indicate they were limited by food supply at a time of year before substantial plant growth took place (i.e. just after the first winter rain), and that they could not afford to expend more energy because they were then extrinsically constrained.

Increased sexual dimorphism is often inferred to be correlated with increased energy costs of the larger sex (Harvey & Bradbury 1991; Kappeler & van Schaik 2004). For example, male Red Deer (*Cervus elaphus*) suffer losses in body condition and are thought to incur substantial energy costs during the rut (Clutton-Brock & Albon 1979; Clutton-Brock *et al.* 1979). However, in many cases, it is generally unclear whether larger individuals sustain greater energy costs simply because they are big (Key & Ross 1999), or whether they incur additional energy costs (above what would be expected from increases in body mass alone) because of what they do (Shillington & Peterson 2002). In the current study, absolute DEE was greater in males of the sexually dimorphic *B. janetta* but mass-independent DEE was not. By comparison, there were no significant differences in absolute or mass-independent DEE between male and female *G. capensis*. These data lend support to the body-maintenance hypothesis for sexual dimorphism, and that energy costs are higher simply because animals are bigger. One possible explanation for this dimorphism is that males may become big because they are then better at performing some short-term energetically costly activity, such as fighting potential conspecifics. Although the energy costs of activities such as fighting might well be energetically expensive, they presumably take place for such short periods that in the context of a day's expenditure, the extra costs incurred are minimal (i.e. the true costs of fighting are the costs of being big enough to do so). One line of reasoning leads us to believe that sexual dimorphism for body size might well be promoted by sexual selection for fighting ability in *B. janetta*: male *B. janetta* possess a thick pad of fat around the neck region that is used for protection during tooth-fencing contests (N.C. Bennett unpublished data). Furthermore, in the closely related Cape dune mole-rat *B. suillus*, males are often caught with puncture wounds to the neck region that are sustained during fighting for territory and mates (J.U.M. Jarvis, personal communication). In contrast, this morphological feature is absent in male *G. capensis*, suggesting that there is less competition for mate acquisition in this latter species.

One reason why we did not find a difference between the male and female metabolic rates was perhaps that the males were disturbed by the procedures of the methodology, and, following capture, suspended their digging activities. Several lines of evidence lead us to believe this was not the case. First, when we recaptured the males they had generally moved a substantial distance relative to the initial capture site (males were generally caught further from their capture sites than females, commonly 10–20 m as opposed to 0–10 m for females). Second, males were extremely active upon release and continued to raise new mounds (and also block the traps with sand). Third, many previous attempts have been made to elucidate the

impacts of the DLW method on the behaviour and disturbance of the animals in question. These studies have generally concluded that the impacts are minor—except in penguins injected intramuscularly in the pectoral muscles, which appears to inhibit their swimming behaviours (summarized in Speakman (1997)).

With respect to the energy costs of sexual dimorphism, it is important to recognize that the total sample size was relatively small, although the effort in generating this sample of animals was enormous. Consequently, if fighting is extremely rare, we may have simply missed fighting events in the 14 days for which we have data on male field metabolic rates in *B. janetta* (unfortunately, it was not possible to record the social interactions of the animals that we were measuring). DEE on 'fighting' days may have been much higher than we recorded. However, even if this were the case, while we may have underestimated the level of metabolism on days when fighting did occur, the conclusion that the dominant costs of dimorphism are morphological and not behavioural remains valid because, averaged over many days, the impact of these rare behavioural events would still be relatively small, even if on a given day the impact was large.

In summary, we found large differences in absolute values of DEE between males and females of sexually dimorphic *B. janetta*, but no equivalent differences in non-sexually dimorphic *G. capensis*. Differences in DEE can be explained by differences in body size between the sexes. These results indicate that *B. janetta* support the body maintenance rather than the increased-energy hypothesis, and that the costs of sexual dimorphism are primarily the maintenance of a large body size. This is consistent with ideas that males are dimorphic to potentially perform short-term, but energetically costly activities (such as fighting) and not on long-term activities (such as digging), which would have an overall impact on a day's expenditure. SusMS values were not high compared to allometric predictions of maximal values. Furthermore, the energy costs of males were not high relative to those of females, even during the period when they were actively seeking mates.

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