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Energy requirements and metabolism of the Phillip's dikdik (*Madoqua saltiana phillipsi*)

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ABSTRACT

Basal metabolic rates in mammals are mainly determined by body mass, but also by ecological factors. Some mammalian species inhabiting hot, dry environments were found to have lower metabolic rates compared to temperate species. We studied energy metabolism in Phillip's dikdik (*Madoqua saltiana phillipsi*), a small antelope inhabiting xeric shrubland habitats in the Eastern 'horn' of Africa, and compared results to literature data. We measured body mass (BM) changes and digestibility in 12 adults kept on different food intake levels to determine, by extrapolation to zero BM change, maintenance energy requirements (MEm) for metabolizable energy (ME). The MEm averaged at 404 ± 20 kJ ME kg $BM^{-0.75}$ d^{-1}. In addition we conducted 24 h-chamber respirometry with seven fed (non-fasted) individuals. Their mean metabolic rate as calculated from oxygen consumption was 403 ± 51 kJ kg $BM^{-0.75}$ d^{-1}, corroborating the results of the feeding experiments. Selecting the 20 lowest values of the respiration measurement period to estimate resting metabolic rate (RMR) resulted in a mean RMR of 244 ± 39 kJ kg $BM^{-0.75}$ d^{-1}, which was not significantly lower than the expected basal metabolic rate of 293 kJ kg $BM^{-0.75}$ d^{-1}. Therefore, *resting* metabolism was similar to the expected average *basal* metabolism of a mammal of this size, which suggests a comparatively low metabolic rate in dikdiks. Compared to literature data Phillip's dikdiks have a MEm similar to measurements reported for small domestic ruminants, but considerably lower than those reported for other wild ruminant species inhabiting temperate and cold climates.

1. Introduction

The basal metabolic rate (BMR) of mammals is mainly influenced by body mass (BM) (Kleiber, 1932; Brody, 1945; McNab, 2008), even though the exact scaling exponent of this allometric relationship has been the subject of intensive discussion (Glazier, 2005; Müller et al., 2012). However, it was repeatedly shown that there are other important factors besides BM influencing BMR such as habitat, climate, phylogeny, feeding habits or reproductive strategies, which explain some of the occasional deviation from the regression based on BM alone (e.g. McNab, 2008; Müller et al., 2012). Although Scholander et al. (1950) stated that animals do not adapt metabolic rate to climate, in particular McNab (2008) found that polar and cold-temperate habitats are inhabited by species with comparably high metabolic rates. Other studies demonstrated a lower metabolic rate in some mammals from hot environments when compared to species living in cold regions (as shown for an extensive dataset by Lovegrove, 2000, for canids in Careau et al., 2007, or small mammals in Lovegrove, 2003). Having a low metabolic rate in hot and/or arid environments can have several advantages: (1) it reduces endogenous heat load and thereby (2) reduces water loss for evaporative cooling (panting, sweating), which is the only physiological means for mammals to cool themselves (von Engelhardt and Breves, 2009); (3) it reduces energy requirements for maintenance, which is an important aspect in habitats that are not only characterized by drought but also where food can be limiting (Lovegrove, 2000). Overall, we can expect mammalian species living in hot, arid environments to have lower metabolic rates and energy requirements compared with species inhabiting regions with temperate climates.

In ruminants, dikdiks (*Madoqua* spp.), amongst the smallest extant species, have been labeled a miniature model for comparative physiological investigations (Maloiy et al., 1988). These animals inhabit the

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dry bush country of eastern and southern Africa, where conditions are semi-arid to arid, ambient temperatures are typically high, and surface water availability is low (Hendrichs and Hendrichs, 1971; Maloiy, 1973). During the dry season, dikdiks are additionally forced to cope with food scarcity (Manser and Brotherton, 1995). Several studies have already used dikdiks to study organismal adaptations, such as thermoregulation and water metabolism, to these harsh environmental conditions (Maloiy, 1973; Maskrey and Hoppe, 1979; Kamau and Maloiy, 1985; Kamau, 1988). However, results have been inconsistent across studies, and therefore generalizing conclusions are difficult to make. For instance, a mammal of dikdik size is expected to have a metabolic rate around 293 kJ kg $BM^{-0.75}$ d^{-1} (based on the equation of Kleiber, 1961; see Methods), but values above and below this level have been reported. Maskrey and Hoppe (1979), using flow-through face masks, found a 20% higher-than-expected metabolic rate of 354 kJ kg $BM^{-0.75}$ d^{-1} in Kirk's dikdik (*Madoqua kirki*), which they ascribed to the fact that subjects were not in a basal, post-absorptive condition during measurement. Another explanation could be that the high metabolic rates reflected a response to stress because the respiratory measurements had been carried out using face-masks. Applying chamber respirometry, Kamau and Maloiy (1981) found relatively low fasting metabolic rates of 154 to 218 kJ kg $BM^{-0.75}$ d^{-1}, and suggested that this was an adaptation to heat and aridity. Also high metabolic rates have been reported by Hoppe et al. (1983) (374 kJ kg $BM^{-0.75}$ d^{-1} in fasting, and 406 ± 17 kJ kg $BM^{-0.75}$ d^{-1} in fed, animals respectively), and low rates of 168 (dehydrated, fed individuals) to 223 kJ kg $BM^{-0.75}$ d^{-1} (hydrated, fed individuals) were shown again by Kamau and Maloiy (1983). The most recent finding of 296 kJ kg $BM^{-0.75}$ d^{-1} (Kamau, 1988) is close to the expected mammal average. This illustrates a huge between-study variation, which might at least partly be a consequence of the differences between the methods applied.

The disparity in published data for dikdik metabolic rates has in an inconsistent inclusion of this species in broader-scale comparative studies. Špála et al. (1987) used the results of Kamau and Maloiy (1981) in a comparative dataset to investigate energy requirements of domestic and captive wild ruminants. In that instance, the dikdik had an extraordinarily low value, which the authors had interpreted as a special adaptation to hot arid environments. In the comparative data collection of Lovegrove (2000), (which was later also used by Savage et al., 2004), an average value from the studies of Maskrey and Hoppe (1979) and Kamau and Maloiy (1982) was used, with a classification of the dikdik as a species inhabiting mesic rather than desert environments. Using this average, the dikdik's metabolism would be very close to the general mammalian average. In contrast, in the data collection of McNab (2008), only the data of Kamau (1988) were used, with a classification of the dikdik as inhabiting xeric environments. Although disparate categorization of a single species is unlikely to influence the overall result of these comparative studies which comprise data for large numbers of taxa – both Lovegrove (2000) and McNab (2008) – the question whether or not dikdiks show dry-region adaptations in their metabolic rate remains unsolved.

In order to clarify this controversy, we (i) evaluated the relationship between digestible energy intake and BM change as a means to estimate maintenance energy requirements (MEm), using data from a completed experiment in captive Phillip's dikdik (Hebel et al., 2011), and (ii) conducted individual gas exchange measurements in transportable respiratory chambers for the determination of metabolic rates. For comparison, we carried out a literature review on energy requirements in ruminants.

2. Materials and methods

The two experiments were conducted at Al Wabra Wildlife Preservation (AWWP), Qatar, with adult Phillip's dikdiks (*Madoqua saltiana phillipsi*) (hereafter referred to as dikdiks). Prior to the experiments, the animals were housed and fed according to AWWP guidelines for dikdik husbandry (Hammer, 2009). The animals were monitored constantly by a veterinarian, and subsequently released into their original pens after the experiments.

2.1. Measurement of maintenance energy requirements (Experiment 1)

In Experiment 1, 12 dikdiks (ten males, two females, mean initial body mass 2.36 ± 0.23 kg) were housed in separate indoor pens (2.4 × 1.5 × 2.5 m) without visual contact to their neighbors. The pens were supplied with cat carriers and cardboard plates as shelters as well as a rubber mat, which the animals accepted as a spot for defecation. Water and food were offered in separate stainless steel bowls and pens were cleaned on a daily basis. Artificial light was provided between 06:00 and 18:00 inside the pens and temperatures were maintained between 19 and 25 °C. All animals underwent an initial adaptation period of one week to become accustomed to the pens and the researcher.

All individuals experienced three treatment phases where they received food on different intake levels: ad libitum, 85% of the individual's previous ad libitum intake, and 70% of the ad libitum intake. Each treatment phase consisted of a two-week adaptation period followed by a one-week collection period. The ad libitum treatment was performed by offering unrestricted access to two types of pellets (Table 1). In addition to the pellets, each animal received between 45 and 60 g of fresh alfalfa (*Medicago sativa*) leaves daily, which were removed from their stalks by hand, and 14 g of a grated mix of carrots and apple mixed with 1 g wheat bran (see Table 1 for nutrient composition). The animals received fresh food every morning. Every day, food samples were taken and the animals were weighed daily. In order to determine the intake of digestible energy, both feces and food refusals were completely collected during the collection periods for later analyses (controlling for exsiccation by a separate food sample exposed to the same environmental conditions as the food provided). More details on the experiment can be obtained from Hebel et al. (2011).

All samples were air dried at about 50 °C immediately after sampling, and ground to 0.75 mm with a mill (Retsch GmbH, Haan, Germany). Foods, refusals and feces were analyzed for dry matter content by drying at 103 °C to constant weight. Gross energy (GE) was determined by bomb calorimetry (IKA-Calorimeter C4000, Ika, Stauffen, Germany). Total ash was analyzed as outlined in Naumann and Bassler (1976) in a muffle furnace, and the difference from dry matter was considered as organic matter. For determination of nitrogen (N) by the Dumas method, an Elementar rapid N III Analyzer (Elementar Analysensysteme, Hanau, Germany) was used. Crude protein (CP) was calculated as 6.25 × N. Neutral detergent fiber (NDF; after treatment with α-amylase) and acid detergent fiber (ADF) were analyzed as described previously (Van Soest, 1967; Van Soest et al., 1991) using the Ankom200 Fiber Analyzer (Ankom, Macedon, NY, USA). The fiber data were corrected for ash content.

Using intakes and fecal losses of energy as well as BM, the daily intake of digestible energy (in kJ kg $BM^{-0.75}$ d^{-1}) was computed for each animal. Metabolizable energy (ME) was calculated as digestible energy (DE) × 0.82 (NRC, 1984). The average body mass change measured during the collection period was calculated as the percentage of BM change per day in relation to BM measured at the beginning of each treatment period. To estimate MEm from these data, we applied a linear mixed model with daily BM change as the dependent and daily ME intake (MEi) as the independent variable, including individual as a random factor. Based on the resulting regression, MEm was determined as the MEi where there was zero BM change. Analyses were carried out with R 2.15.0 using the package nlme (Pinheiro et al., 2007). In addition to the experiment, a literature research on MEm values of other ruminant species was carried out to allow a comparative interpretation of the values obtained in the present study.