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

Dittmann, Marie T ; Hebel, Christiana ; Hammer, Sven ; Hummel, Jürgen ; Ortmann, Sylvia ; Arif, Abdi ; Bouts, Tim ; Kreuzer, Michael ; Clauss, Marcus

**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 (ME<sub>m</sub>) for metabolizable energy (ME). The ME<sub>m</sub> averaged at  $404 \pm 20$  kJ ME kg BM<sup>-0.75</sup> d<sup>-1</sup>. In addition we conducted 24 h-chamber respirometry with seven fed (non-fasted) individuals. Their mean metabolic rate as calculated from oxygen consumption was  $403 \pm 51$  kJ kg BM<sup>-0.75</sup> d<sup>-1</sup>, corroborating the results of the feeding trials. Selecting the 20 lowest values of the respiration measurement period to estimate resting metabolic rate (RMR) resulted in a mean RMR of  $244 \pm 39$  kJ kg BM<sup>-0.75</sup> d<sup>-1</sup>, which was numerically (but not significantly) lower than the expected basal metabolic rate of  $293$  kJ kg BM<sup>-0.75</sup> d<sup>-1</sup>. 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 ME<sub>m</sub> similar to measurements reported for small domestic ruminants, but considerably lower than those reported for other wild ruminant species inhabiting temperate and cold climates.

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

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24 A B S T R A C T

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26 ecological factors. Some mammalian species inhabiting hot, dry environments were found to  
27 have lower metabolic rates compared to temperate species. We studied energy metabolism in  
28 Phillip's dikdik (*Madoqua saltiana phillipsi*), a small antelope inhabiting xeric shrubland  
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35 respiration measurement period to estimate resting metabolic rate (RMR) resulted in a mean  
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37 the expected basal metabolic rate of  $293 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$ . Therefore, *resting* metabolism was  
38 similar to the expected average *basal* metabolism of a mammal of this size, which suggests a  
39 comparatively low metabolic rate in dikdiks. Compared to literature data Phillip's dikdiks  
40 have a MEM similar to measurements reported for small domestic ruminants, but  
41 considerably lower than those reported for other wild ruminant species inhabiting temperate  
42 and cold climates.

44

45 *Keywords:*

46 Metabolism, dikdik, *Madoqua*, energy, respiration, maintenance requirements, resting  
47 metabolic rate, arid

48

49

## 50 **1. Introduction**

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

71 In ruminants, dikdiks (*Madoqua* spp.), amongst the smallest extant species, have been  
72 labeled a miniature model for comparative physiological investigations (Maloiy et al., 1988).  
73 These animals inhabit the dry bush country of eastern and southern Africa, where conditions  
74 are semi-arid to arid, ambient temperatures are typically high, and surface water availability is  
75 low (Hendrichs and Hendrichs, 1971; Maloiy, 1973). During the dry season, dikdiks are

76 additionally forced to cope with food scarcity (Manser and Brotherton, 1995). Several studies  
77 have already used dikdiks to study organismal adaptations, such as thermoregulation and  
78 water metabolism, to these harsh environmental conditions (Maloiy, 1973; Maskrey and  
79 Hoppe, 1979; Kamau and Maloiy, 1985; Kamau, 1988). However, results have been  
80 inconsistent across studies, and therefore generalized conclusions are difficult to make. For  
81 instance, a mammal of dikdik size is expected to have a metabolic rate around  $293 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$   
82  $^{0.75} \text{ d}^{-1}$  (based on the equation of Kleiber, 1961; see Methods), but values above and below this  
83 level have been reported. Maskrey and Hoppe (1979), using flow-through face masks, found a  
84 20% higher-than-expected metabolic rate of  $354 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$  in Kirk's dikdik (*M. kirkii*),  
85 which they ascribed to the fact that subjects were not in a basal, post-absorptive condition  
86 during measurement. Another explanation could be that the high metabolic rates reflected a  
87 response to stress because the respiratory measurements had been carried out using face-  
88 masks. Applying chamber respirometry, Kamau and Maloiy (1981) found relatively low  
89 fasting metabolic rates of 154 to  $218 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$ , and suggested that this was an  
90 adaptation to heat and aridity. High metabolic rates have also been reported by Hoppe (1983)  
91 ( $374 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$  in fasting, and  $406 \pm 17 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$  in fed, animals respectively),  
92 and low rates of 168 (dehydrated, fed individuals) to  $223 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$  (hydrated, fed  
93 individuals) were shown again by Kamau and Maloiy (1983). The most recent finding of  $296$   
94  $\text{kJ kg BM}^{-0.75} \text{ d}^{-1}$  (Kamau, 1988) is close to the expected mammal average. This illustrates a  
95 huge between-study variation, which might at least partly be a consequence of the differences  
96 between the methods applied.

97 The disparity in published data for dikdik metabolic rates has resulted in inconsistent  
98 inclusion of this species in broader-scale comparative studies. Špála et al. (1987) used the  
99 results of Kamau and Maloiy (1981) in a comparative dataset to investigate energy  
100 requirements of domestic and captive wild ruminants. In that instance, the dikdik had an  
101 extraordinarily low value, which the authors had interpreted as a special adaptation to hot arid

102 environments. In the comparative data collection of Lovegrove (2000), (which was later also  
103 used by Savage et al., 2004), an average value from the studies of Maskrey and Hoppe (1979)  
104 and Kamau and Maloiy (1982) was used, with a classification of the dikdik as a species  
105 inhabiting mesic rather than desert environments. Using this average, the dikdik's metabolism  
106 would be very close to the general mammalian average. In contrast, in the data collection of  
107 McNab (2008), only the data of Kamau (1988) were used, with a classification of the dikdik  
108 as inhabiting xeric environments. Although disparate categorization of a single species is  
109 unlikely to influence the overall result of these comparative studies which comprise data for  
110 large numbers of taxa - both Lovegrove (2000) and McNab (2008) – the question whether or  
111 not dikdiks show dry-region adaptations in their metabolic rate remains unsolved.

112 In order to clarify this controversy, we (i) evaluated the relationship between digestible  
113 energy intake and BM change as a means to estimate maintenance energy requirements  
114 (MEM), using data from a completed experiment in captive Phillip's dikdik (Hebel et al.  
115 2011), and (ii) conducted individual gas exchange measurements in transportable respiratory  
116 chambers for the determination of metabolic rates. For comparison, we carried out a literature  
117 review on energy requirements in ruminants.

118

## 119 **2. Materials and Methods**

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

125

### 126 *2.1. Measurement of maintenance energy requirements (Experiment 1)*

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

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

148 All samples were air dried at about 50°C immediately after sampling, and ground to 0.75  
149 mm with a mill (Retsch GmbH, Haan, Germany). Foods, refusals and feces were analyzed for  
150 dry matter content by drying at 103°C to constant weight. Gross energy (GE) was determined  
151 by bomb calorimetry (IKA-Kalorimeter C4000, Ika, Stauffen, Germany). Total ash was  
152 analyzed as outlined in Naumann and Bassler (1976) in a muffle furnace, and the difference

153 from dry matter was considered as organic matter. For determinations of nitrogen (N) by the  
154 Dumas method, an Elementar rapid N III Analyzer (Elementar Analysensysteme, Hanau,  
155 Germany) was used. Crude protein (CP) was calculated as  $6.25 \times N$ . Neutral detergent fiber  
156 (NDF; after treatment with  $\alpha$ -amylase) and acid detergent fiber (ADF) were analyzed as  
157 described previously (Van Soest, 1967; Van Soest et al., 1991) using the Ankom200 Fiber  
158 Analyzer. The fiber data were corrected for ash content.

159 Using intakes and fecal losses of energy as well as BM, the daily intake of digestible  
160 energy (in  $\text{kJ kg BM}^{-0.75} \text{d}^{-1}$ ) was computed for each animal. Metabolizable energy (ME) was  
161 calculated as digestible energy (DE)  $\times 0.82$  (NRC, 1984). The average body mass change  
162 measured during the collection period was calculated as the percentage of BM change per day  
163 in relation to BM measured at the beginning of each treatment period. To estimate MEM from  
164 these data, we applied a linear mixed model with daily BM change as the dependent and daily  
165 ME intake (MEi) as the independent variable, including individual as a random factor. Based  
166 on the resulting regression, MEM was determined as the MEi where there was zero BM  
167 change. Analyses were carried out with R 2.15.0 using the package nlme (Pinheiro et al.,  
168 2007). In addition to the experiment, a literature research on MEM values of other ruminant  
169 species was carried out to allow a comparative interpretation of the values obtained in the  
170 present study.

171

## 172 *2.2. Measurements of metabolic rate in respiratory chambers (Experiment 2)*

173 Measuring body mass changes to determine energy requirements without simultaneously  
174 monitoring body composition bears the risk that the use of adipose tissue (which is replaced  
175 by water) is not detected, and that the consistency in weight is interpreted as a balanced  
176 energy turnover (Kirchgessner, 2011). Therefore, we additionally performed respiration  
177 measurements.

178 In Experiment 2, seven individual dikdiks (mean body mass  $2.00 \pm 0.15$  kg) were kept  
179 with *ad libitum* access to a diet of fresh alfalfa (see Table 1 for nutrient composition) and  
180 water in  $2.4 \times 1.0$  m pens for 3 weeks prior to the measurements. Dry matter intake was  
181 determined for one week prior to the measurements, averaging  $31 \pm 4$  g kg BM<sup>-0.75</sup> d<sup>-1</sup> per  
182 individual. Temperatures were held at  $\sim 25^\circ\text{C}$  which ensured that the subjects were under  
183 thermoneutral conditions (Kaumau, 1988, reported a thermoneutral zone of  $24 - 35^\circ\text{C}$  for  
184 Kirk's dikdiks). The subjects were then put separately for 24 h into one of three airtight  
185 wooden transport-type boxes ( $1.0 \times 0.7 \times 0.6$  m) used as respiration chambers. There, a carpet  
186 of woodchips and fresh alfalfa (in amounts exceeding the previously recorded *ad libitum*  
187 intake) were provided. Chambers were fitted with air inlets on the bottom and air outlets on  
188 top of the box to ensure a constant airflow ( $10$  to  $15$  l min<sup>-1</sup>) generated by a pump (Flowkit  
189 100, Sable Systems, Las Vegas, USA). Out-flowing air was ducted via flexible hoses to a gas  
190 multiplexer, which allowed the measurement of data on three individuals and baseline values  
191 from ambient air simultaneously, at alternating intervals of 120 to 180 seconds each. Gas  
192 concentrations were measured by O<sub>2</sub> and CO<sub>2</sub> analyzers (Turbofox, Sable Systems). Data  
193 were adjusted for barometric pressure, water vapor pressure and air flow rates, which were  
194 constantly recorded during respirometry. The gas analyzers were calibrated prior to each  
195 measurement by using pure nitrogen and a span gas (PanGas, 20% O<sub>2</sub> and 1% CO<sub>2</sub> dissolved  
196 in nitrogen). Data obtained by the respiratory system were analyzed with the software  
197 ExpeData (Sable Systems) for O<sub>2</sub> consumed and CO<sub>2</sub> emitted after correcting for gas  
198 concentrations in ingoing air. The mean metabolic rate was calculated based on the entire  
199 measurement and therefore accounts for the activity of the animals inside the box (e.g.  
200 walking around and feeding), while the resting metabolic rate (RMR) of the animals was  
201 determined by selecting the 20 lowest O<sub>2</sub> measurements per individual within the 24-h period  
202 (adapted from Derno et al. 2005). In order to calculate MR we multiplied the amount of O<sub>2</sub>  
203 consumed (in l h<sup>-1</sup>) by 20.08 kJ (McNab, 2008).

204 To compare the MR of our animals to their expected BMR, we used the equation of  
205 Kleiber (1961), which yielded an expected BMR of  $293 \text{ kJ} \times \text{kg BM}^{-0.75}$ . This equation uses  
206 a scaling exponent of 0.75, which has been confirmed to be appropriate for artiodactyls by  
207 McNab (2008). The values of our measurements were tested for normal distribution and then  
208 statistically compared with the expected values by applying a Mann-Whitney-U test in R  
209 2.15.0.

210

### 211 3. Results

212 In Experiment 1, out of the 12 individuals used in this study, 3 animals did not gain  
213 weight on any of the treatments used, i.e., not even when feed was offered *ad libitum*. For  
214 animal welfare reasons, the experimental period with an intake level of 70% had to be  
215 replaced by a second *ad libitum* session in two individuals. The regression equation  
216 determined based on the mixed model ( $\text{BM change} = 0.0016 (\pm 0.0004) \times \text{MEi} - 0.64 (\pm$   
217  $0.13)$ ,  $n = 12$ ) resulted in a MEM of  $404 \pm 20 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$  for our subjects (Fig. 1).

218 In Experiment 2,  $\text{O}_2$  consumption and  $\text{CO}_2$  production fluctuated throughout the 24 h of  
219 measurement, indicating the presence of different phases of activity (and potentially also  
220 endogenous circadian rhythms).  $\text{O}_2$  consumption was highest during daytime, decreasing  
221 through the night (Fig. 2). However, small peaks in  $\text{O}_2$  consumption and  $\text{CO}_2$  production  
222 indicate that regular phases of activity still occurred at night, which were accompanied by an  
223 elevated respiratory quotient (RQ) indicating a relatively higher  $\text{CO}_2$  production. The mean  
224 metabolic rate of the animals was  $403 \pm 51 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$ . Selecting the lowest 20  $\text{O}_2$   
225 measurements led to a mean RMR of  $244 \pm 39 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$ , a value that is lower than the  
226 expected  $293 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$ . However, this difference was not significant when we  
227 compared the measured RMR and the estimated BMR of each individual ( $n = 7$ ,  $U = 19$ ,  $p =$   
228  $0.47$ ) (Fig. 3).

229

#### 230 4. Discussion

231 Comparing the MEm values for dikdiks from the present study, as measured by feeding  
232 trials and respiration measurements, with literature data for other selected species (Table 2)  
233 reveals that the dikdik is located at the lower end of the range in MEm covered by the  
234 ruminant species for which data exist. However, the dataset includes only few species that can  
235 be classified as inhabiting tropical environments (e.g, the mouse deer). This impedes the  
236 comparison among species. Additionally, the literature data comprises a number of  
237 domesticated species, which have often been intensively selected for high productivity rather  
238 than for low MEm. Nevertheless, the low MEm values obtained in the present study are  
239 remarkable, as it has to be considered that the experiments were carried out with non-  
240 domestic animals not used to regular handling. Our subjects seemed to cope well with the  
241 daily disturbance caused by humans, but it still cannot be excluded that the animals exhibited  
242 higher levels of stress, associated with elevated MEm, during the experiments than one would  
243 expect in domestic ruminants or in undisturbed free-ranging specimens.

244 The difference between expected (estimated) and measured RMR was not statistically  
245 significant. The way of estimation was based on the calculation of the basal metabolic rate,  
246 i.e. a post-absorptive, quiescent metabolic state at thermoneutral conditions (Schmidt-Nielsen,  
247 1997). The problem of measuring basal metabolism in herbivores, having a fermentation  
248 chamber that will not be empty most of the time and thereby hardly ever allow a post-  
249 absorptive state to be achieved, was addressed by White and Seymour (2003). Additionally, in  
250 our respiratory chambers, the animals were able to move and eat. Due to these reasons we  
251 were only able to measure resting MR, even though we selected the 20 lowest values of the  
252 set of measurements. As RMR can be assumed to be higher than the BMR, the difference  
253 between expected and actual BMR in dikdiks can be assumed to be even larger. The dikdiks  
254 had a metabolic rate of  $403 \pm 51 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$  when averaged over the entire 24-h  
255 measurement. A similar measurement carried out with goats by Lachica et al. (1997) revealed

256 a heat production of  $405 \text{ kJ kg BM}^{-0.75} \text{ d}^{-1}$ , which is close to the value obtained in this study.  
257 However, the measurements on goats were carried out 16 – 20 h after feeding which impedes  
258 the comparison with our data; actually, if fasted goats have a similar energy turnover as fed  
259 dikdiks, this supports the hypothesis that dikdiks have a comparatively low metabolism.

260 Together, our results on MEm and RMR qualitatively match the findings for some other  
261 mammal groups that species inhabiting arid and hot regions have a lower metabolism when  
262 compared to species living in cold environments. Regarding their energy requirements,  
263 dikdiks, together with some (but not all) measurements in domestic sheep and goats, range at  
264 the lower end of data in the ruminant spectrum. The available data on ruminants are  
265 somewhat limited as they are based mainly on domestic species typically kept in temperate  
266 regions. Comparing our results to those obtained in other African bovids (Table 3) shows that  
267 the MR of the Phillip's dikdik indeed falls below the reported average values. The  
268 observation that the Phillips dikdik has comparably low energy requirements and a  
269 metabolism that is slightly lower than expected supports the findings of Kamau and Maloyi  
270 (1981, 1983) in Kirk's dikdiks. These findings can be interpreted as adaptation to the harsh  
271 environmental conditions of their natural habitat, i.e. scarcity of food, high temperatures and  
272 low water availability. However, the fact that other ruminant species that are also exposed to  
273 similar climatic challenges, like the Arabian oryx (*Oryx leucoryx*) or the goitered gazelle  
274 (*Gazella subgutturosa*), do not share the characteristic of a comparatively low metabolism  
275 (Table 3) also suggests that ruminants have a variety of physiological and behavioural  
276 adaptations at their disposal (e.g. Ostrowski et al., 2003) that facilitates the use of different  
277 habitats, and that a low metabolism is not a compulsory asset of species inhabiting xeric  
278 niches. Given the low number of ruminant species for which such data are available, a  
279 phylogeny-based analysis of variation in MR with habitat is not feasible.

280 A particular finding was that, during the 24-h measurement, periodical fluctuations in  $\text{O}_2$   
281 consumption and  $\text{CO}_2$  production were observed. The high levels at the beginning of each 24-

282 h measurement were probably not only caused by diurnal activity of the animals but are also a  
283 reflection of stress as a response to the transfer into the respiration chambers. During the  
284 night, O<sub>2</sub> consumption and CO<sub>2</sub> production were generally reduced but interrupted by regular  
285 peaks accompanied with rises in RQ levels, which could reflect phases of rumination or  
286 eating and thereby the effect of the associated specific dynamic action (e.g. McClymont,  
287 1952). Hoppe et al. (1983) reported alternating phases of eating and ruminating in dikdiks,  
288 lasting 1 to 36 min in the former and 1 to 38 min in the latter. However, the time between the  
289 peaks observed in our measurements ranged between 1 and 3 h, which could indicate that  
290 either the Phillip's dikdiks used in this study had a different feeding rhythm, or that these  
291 periods reflect activities independent of rumination and feeding.

292

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301

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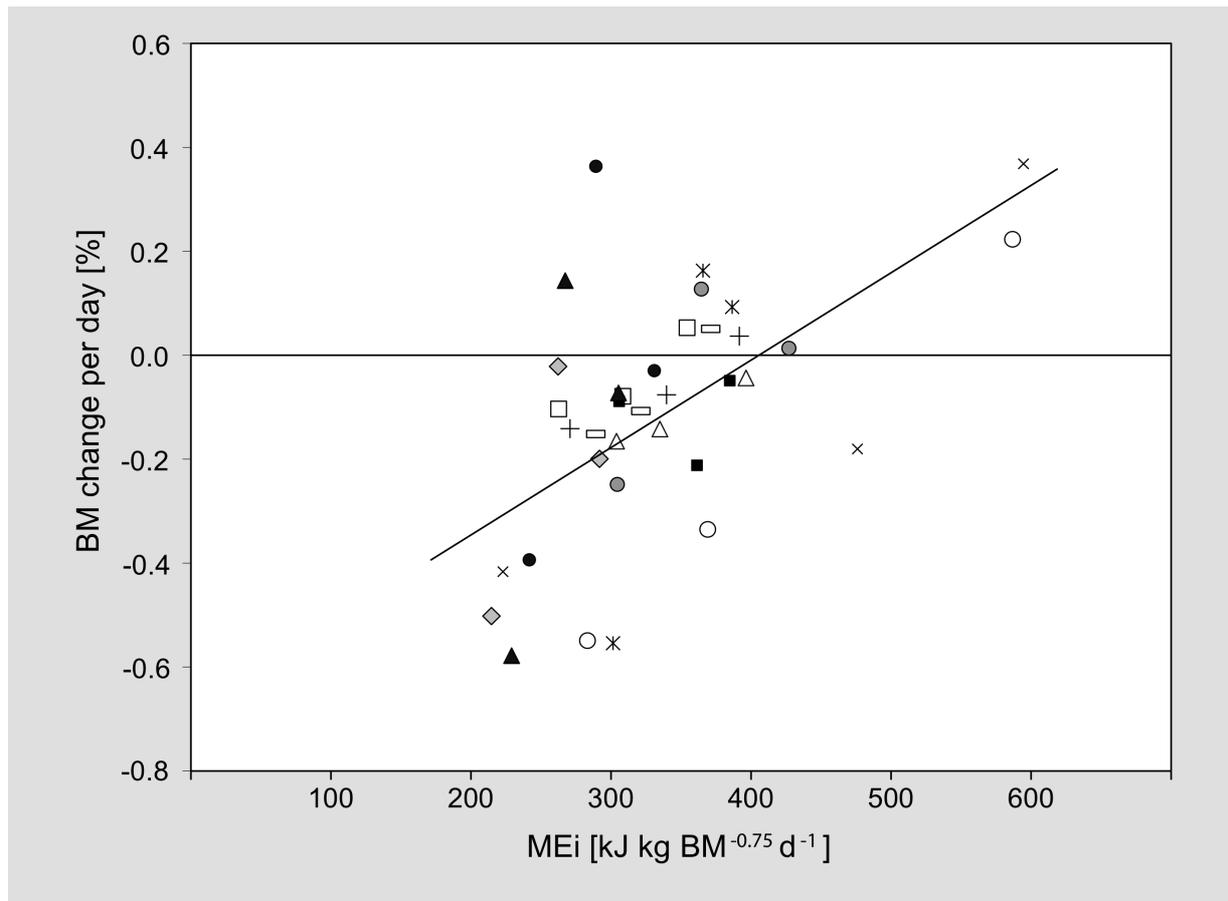
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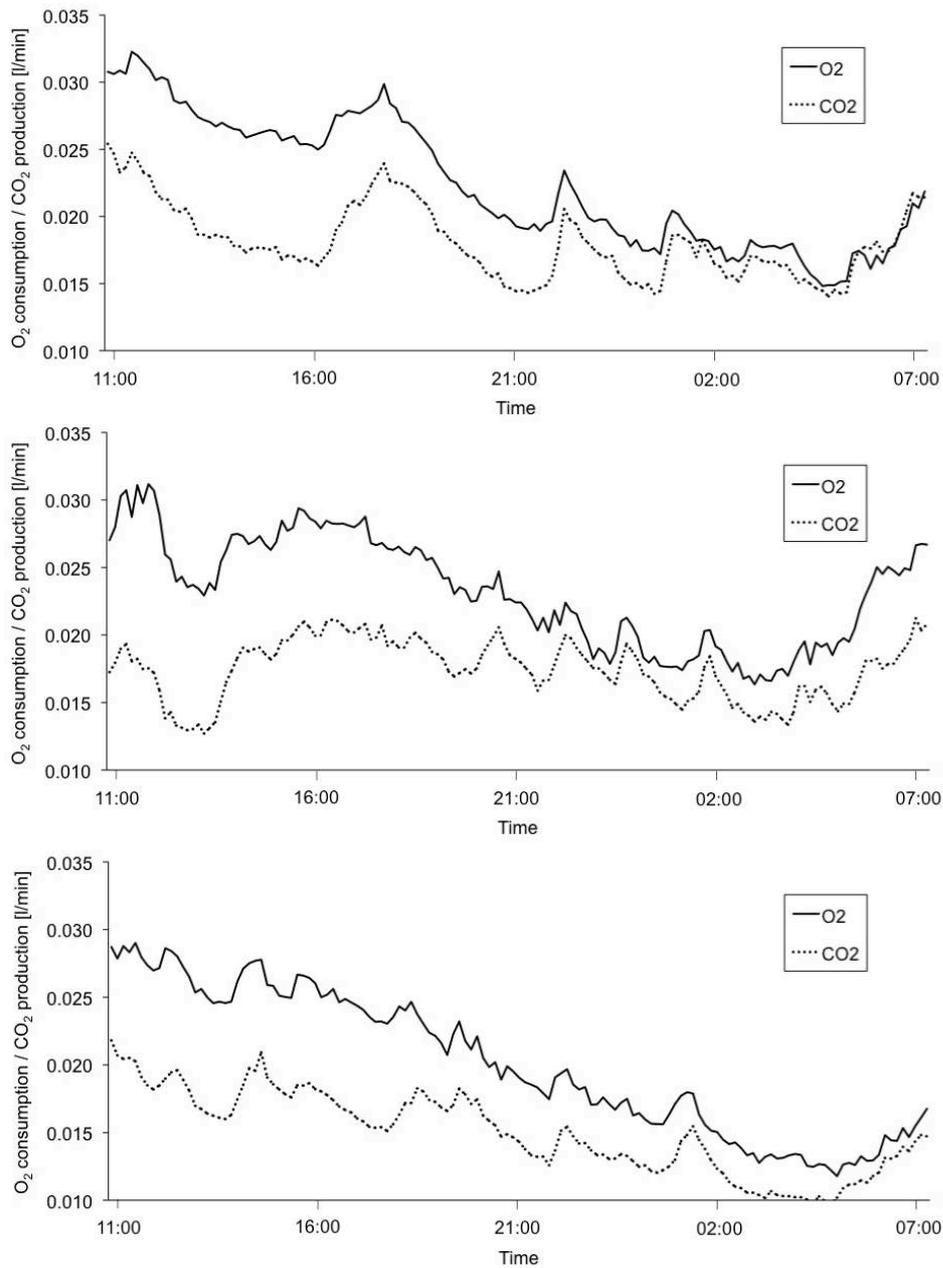
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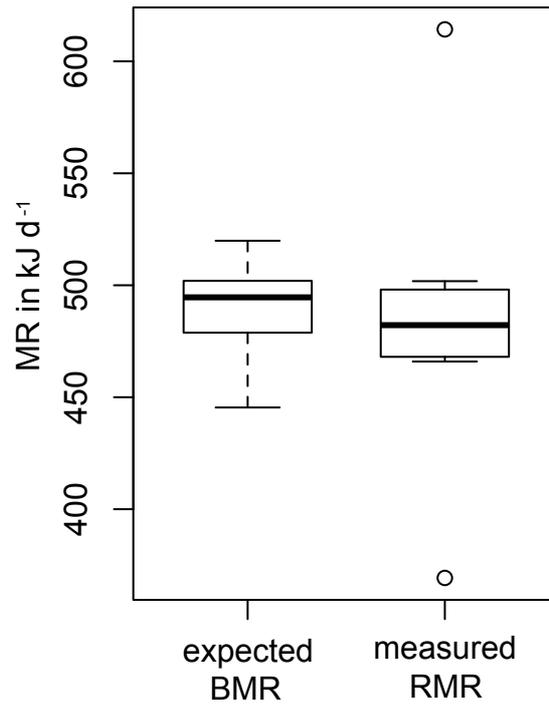
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**Fig. 1.** Individual measurements in Experiment 1 and linear regression of body mass (BM) change in % of the initial weight ( $y$ ) as a function of intake of metabolizable energy (MEi;  $x$ ). The equation is  $y = 0.0016x - 0.64$ . The MEi was calculated as  $0.82 \times$  digestible energy. Each symbol represents one individual at one of the three different intake levels.



**Fig. 2.** Time course of O<sub>2</sub> consumption and CO<sub>2</sub> production of three exemplary individuals during 20 h of measurement in the respiration chambers during Experiment 2. Note the regular peaks interrupting the general decrease in both values during the night.



**Fig. 3.** Comparison of the measured resting metabolic rate (RMR) with the expected basal metabolic rate (BMR) for the individuals in Experiment 2 ( $U = 19, p = 0.47$ ).

**Table 1**

Nutrient composition (g/kg dry matter) of the diet items offered during the experiments.

Food	Crude protein	Neutral detergent fiber	Acid detergent fiber	Ash
Experiment 1				
Carrot	62.0	109.2	80.8	75.8
Apple	19.0	78.0	52.8	14.8
Pellets (Mazuri) <sup>a</sup>	169.0	392.9	186.6	84.4
Pellets (Altromin) <sup>b</sup>	198.3	335.5	187.6	92.7
Wheat bran	163.3	440.0	134.3	51.7
Alfalfa leaves	280.4	210.3	125.6	162.5
Experiment 2				
Alfalfa leaves	296.3	203.4	149.5	187.0

<sup>a</sup> Composed of wheat, wheat feed, soy bean meal, soy bean hulls, soy bean oil, glucose, molasses, grass meal, cellulose powder, vitamin premix, and mineral premix; produced by Mazuri Zoo Foods (Altrip, Germany), Browser Maintenance.

<sup>b</sup> Composed of wheat bran, grass meal, wheat feed, soy bean meal, soy bean hulls, calcium carbonate, sodium chloride, vitamin premix, and mineral premix; produced by Altromin Spezialfutter GmbH & Co. KG (Lippe, Germany), Breeding Maintenance Diet for small ruminants.

**Table 2**

Maintenance requirements for metabolizable energy (ME<sub>m</sub>) of ruminant species as reported in the literature and ordered by ME<sub>m</sub>.

Species	Common name	ME <sub>m</sub> (kJ kg BM <sup>-0.75</sup> d <sup>-1</sup> )	Reference
<i>Odocoileus hemionus</i>	Mule deer	661	Baker et al. (1979)
<i>Odocoileus virginianus</i>	White tailed deer	661	Ullrey et al. (1970)
<i>Capra hircus</i>	Goat (cold environment)	641	Silanikove (1986)
<i>Alces alces</i>	Moose	584	Renecker and Hudson (1985)
<i>Rangifer tarandus</i>	Caribou	572-766	NRC (2007)
<i>Odocoileus virginianus</i>	White tailed deer	565-724	NRC (2007)
<i>Alces alces</i>	Moose	548	Schwartz et al. (1988)
<i>Cervus elaphus</i>	Red deer	544-850	NRC (2007)
<i>Rangifer tarandus</i>	Reindeer	494-607	NRC (2007)
<i>Capra hircus</i>	Goat	462 - 489	NRC (2007)
<i>Capra hircus</i>	Goat	450	GfE (2003)
<i>Capra hircus</i>	Goat	443	Prieto et al. (1990)
<i>Tragulus javanicus</i>	Mouse deer	436	Darlis et al. (2011)
<i>Capra hircus</i>	Goat	431	Luo et al. (2004)
<i>Capra hircus</i>	Sheep	430	GfE (1996)
<i>Bos taurus</i>	Cattle	427 - 674	Ferrell and Jenkins (1985)
<i>Bos taurus</i>	Cattle	426	Solis et al. (1988)
<i>Capra hircus</i>	Goat	422	Lachica and Aguilera (2003)
<i>Capra hircus</i>	Goat (hot environment)	408	Silanikove (1986)
<i>Madoqua saltiana phillipsi</i>	Phillip's dikdik	404 (MR: 403 ± 51)	present study

<i>Ovis aries</i>	Sheep	390-447	NRC (2007)
<i>Ovis aries</i>	Sheep	374	Aguilera et al. (1986)
<i>Ovis aries</i>	Sheep	315	Vermorel et al. (1987)

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**Table 3**

Body mass (BM) and basal metabolic rates (BMR) of selected African bovid species ordered by BM (adapted from McNab, 2008).

Species	Common name	BM (kg)	BMR (kJ kg BM <sup>-0.75</sup> d <sup>-1</sup> )	BMR (kJ h <sup>-1</sup> )	BMR expected from Kleibers equation (kJ h <sup>-1</sup> )	BMR ratio measured / expected	Climate
<i>Madoqua saltiana phillipsi</i>	Phillip's dikdik	2.0 ± 0.2	244 ± 39 <sup>a</sup>	20.2	20.4	1.00	xeric
<i>Philantomba monticola</i>	Blue duiker	4.4	300.1	38.0	37.1	1.02	xeric
<i>Raphicerus campestris</i>	Steenbok	8.5	316.8	65.7	60.8	1.08	xeric
<i>Gazella subgutturosa</i>	Goitered gazelle	17.1	263.6	92.4	102.7	0.90	desert
<i>Oryx leucoryx</i>	Arabian oryx	84.1	323.4	374.2	339.1	1.10	desert
<i>Kobus ellipsiprymnus</i>	Waterbuck	100	406.9	536.1	386.1	1.39	mesic
<i>Connochaetus taurinus</i>	Blue wildebeest	140	331.5	562.2	496.9	1.12	xeric
<i>Taurotragus oryx</i>	Eland	150	404.8	722.9	523.3	1.38	xeric

<sup>a</sup>data from present study, representing resting metabolic rate