Original Investigation

Metabolic rates of three gazelle species (*Nanger soemmerringii*, *Gazella gazella*, *Gazella spekei*) adapted to arid habitats

Marie T. Dittmann [a,b], Christiana Hebel [c,1], Abdi Arif [c], Michael Kreuzer [b], Marcus Clauss [a,*]

[a] Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty Zurich, University of Zurich, Switzerland
[b] ETH Zurich, Institute for Agricultural Sciences, Zurich, Switzerland
[c] Al Wabra Wildlife Preservation (AWWP), Doha, Qatar

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ABSTRACT

The basal metabolic rate of mammals correlates with body mass, but deviations from this regression have been observed and explanations comprise ecological adaptations, reproductive strategies or phylogeny. Certain mammalian groups, adapted to arid environments, show comparatively lower metabolic rates. To expand existing datasets and to investigate metabolic rates in ruminants adapted to arid environments, we conducted respiration measurements with three gazelle species (*Gazella spekei*, *G. gazella* and *N. soemmerringii*, total $n = 16$). After an adaptation period to a diet of fresh lucerne offered *ad libitum*, subjects were put separately into respiration boxes for 24 h where they had free access to food and water. Oxygen consumption and carbon dioxide production were measured with a modular system of gas analyzers and pumps. Mean and resting metabolic rate (RMR) were calculated by accounting for the entire measurement phase or the lowest 20 oxygen measurements, respectively. *N. soemmerringii* had the lowest relative RMR values and the highest respiratory coefficients compared to the other species. Measured values were compared to expected RMR values calculated based on body mass. *Gazella spekei* and *G. gazella* showed higher RMR values than expected, while the RMR of *N. soemmerringii* was in the range of expected values. Our results indicate that not all mammals adapted to aridity have lower metabolic rates under conditions of unlimited resources and that in these cases other physiological adaptations might be of higher importance. Further extensions of the datasets could allow explaining which deviations of metabolic rate from the body mass regressions result from convergent adaptations.

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Introduction

The basal metabolic rate (BMR) of mammals correlates with a large variety of ecological and biological factors, including phylogeny, habitat, climate, feeding habits or reproductive strategies, which explain some of the occasional deviation from the across-species regression based on body mass (BM) alone (e.g. McNab 2008; Müller et al. 2012). Adaptations to climate and habitat have received particular attention (Lovegrove 2000, 2003; Careau et al. 2007; McNab 2008). In order to detect convergent adaptations to particular niches, such as a lower metabolism in arid environments, large comparative datasets are required. Due to logistical challenges, large species such as ruminants have not been subjected to metabolic rate (MR) measurements as often as smaller species such

as rodents. For example, the comparative data collection of McNab (2008) comprises 579 species of a body mass below, but only 58 species above 10 kg, and only 20 members of the Artiodactyla. In order to contribute to such datasets, we here report results of respiration measurements in three gazelle species that have so far not been included in comparative evaluations – Speke's gazelle (*Gazella spekei*; 11.4–14.1 kg), Idmi or Mountain gazelle (*Gazella gazella*; 14.5–18.0 kg), and Soemmerring's gazelle (*Nanger soemmerringii*; 28.5–38.6 kg).

All three species can be expected to show adaptations to living in arid habitats. *G. spekei* is endemic to the Horn of Africa, and inhabits semi-arid grasslands or barren rangelands (Heckel et al. 2008a). *G. gazella* occurs in southern Lebanon, Syria, Israel, on the Arabian peninsula and isolated regions of Iran, and is reported to be able to withstand severe, hot and dry climatic conditions; some populations allegedly occur in areas without surface water (Mendelssohn 1995). *N. soemmerringii* occurs in semiarid to arid areas from Eritrea to Somalia (Heckel et al. 2008b). One possible adaptation to such climates is a reduced MR as recently reported in another wild

ruminant species from the same geographic region, the Phillip's dikdik (*Madoqua saltiana phillipsi*) (Dittmann et al. 2014a). Therefore, we predicted that the selected gazelle species would, in a similar manner, display lower MR than expected based on their body mass.

Material and methods

An experiment was carried out with five Idmi gazelles (*Gazella gazella*), five Speke's gazelles (*Gazella spekei*) and six Soemmerring's gazelles (*Nanger soemmerringii*) at Al Wabra Wildlife Preservation (AWWP), Qatar. All individuals were adult, male and healthy according to the veterinarian in charge, and all procedures were approved by the internal ethics committee of AWWP. Generally, respiration measurements were identical in setup to those reported previously for Phillip's dikdik (*Madoqua saltiana phillipsi*) (Dittmann et al. 2014a).

Prior to the measurements, all animals were kept with *ad libitum* access to a diet of fresh lucerne and water at ambient temperatures between 19 and 25 °C. The animals were then put separately for 24 h into dark and airtight wooden transport-type boxes ($1.0 \times 0.7 \times 0.6$ m for *G. spekei* and *G. gazella*; $1.3 \times 1.1 \times 0.5$ m for *N. soemmerringii*), which were used as respiration chambers and in which a carpet of woodchips and fresh lucerne (in amounts exceeding the previously determined *ad libitum* intake) were provided. To ensure a constant airflow ($25–50 \, l \, min^{-1}$) generated by a pump (Flowkit 100, Sable Systems, Las Vegas, USA), chambers were fitted with air inlets on the bottom and air outlets on top. We used flexible hoses to duct out-flowing air to a gas multiplexer, in order to measure three individuals and baseline values from ambient air simultaneously, at alternating intervals of 120–180 s each. The concentrations of O_2 and CO_2 were measured by corresponding analyzers (Turbofox, Sable Systems), which were calibrated prior to each measurement by using pure nitrogen and a span gas (Pan-Gas, 20% O_2 and 1% CO_2 dissolved in nitrogen). After adjustment for barometric pressure, water vapor pressure and air flow rates, which were constantly recorded during respirometry, the data were analyzed with the software ExpeData (Sable Systems) for O_2 and CO_2 concentrations in the chambers after correcting for gas concentrations in the ambient air. The mean MR (MMR) was calculated based on the entire 24-h measurement period, therefore including the activity of the animals inside the box (e.g. standing and feeding), while the resting MR (RMR) of the animals was calculated by selecting the 20 lowest O_2 measurements per individual within the entire measurement (adapted from Derno et al. 2005). Data from the first hour the animals spent inside the respiration chambers were neglected. In order to estimate MR we multiplied the amount of O_2 consumed (in $l \, h^{-1}$) by 20.08 kJ (McNab 2008).

We used the equation of Kleiber (1961) to compare the RMR of the animals to their expected BMR, which yielded an expected daily BMR of 293 kJ kg $BM^{-0.75}$. Additionally, we used the Artiodactyla-specific equation of McNab (2008) for another measure of expected BMR, with an expected hourly BMR of 0.1194 kJ g $BM^{-0.707}$. Data were tested for normal distribution. Expected and measured MR were compared by paired *T*-tests. Between-species comparisons were carried out with ANOVAs followed by Tukeys HSD test in R 2.15.0. The significance level was set to 0.05.

Results

During the respiration measurements, no difference in the subjective degree of nervousness between the species appeared evident. Albeit the transfer into the respiration boxes appeared stressful to the animals, all gazelles calmed down after approximately 1 h and all of them consumed relevant amounts of lucerne during respiration measurements. In all animals, a temporal fluctuation in O_2 consumption and CO_2 production was evident, with a decrease toward the later part of the night (Fig. 1). In general, fluctuations between phases with low and high O_2 consumption were more extreme and less regular in *N. soemmerringii* as compared to the other two species. When expressed per unit metabolic body mass, *G. spekei* had the highest and *N. soemmerringii* the lowest relative MMR and RMR (Table 1). The same pattern was evident for the ratio between RMR and expected BMR. The respiratory quotient (RQ, ratio between CO_2 production and O_2 consumption) was highest in *N. soemmerringii* and lowest in *G. spekei*. Measured RMR were higher than the expected BMR as estimated based on Kleiber (1961) within *G. spekei* ($T = -13.4; P < 0.001$) and *G. gazella* ($T = -5.5; P = 0.005$), while no such difference was found within *N. soemmerringii* ($T = -1.2; P = 0.283$). Estimating BMR from McNab (2008), again the measured RMR was higher than the expected BMR in *G. spekei* ($T = -6.8; P = 0.002$), the difference only tended toward significance in *G. gazella* ($T = -2.5; P = 0.065$), and again no such difference was evident within *N. soemmerringii* ($T = 1.0; P = 0.361$).

Discussion

Interpretation of the results

In contrast to our hypothesis, there was no indication for a reduced metabolism in the three gazelle species investigated. This is in contrast to findings in another wild ruminant species of similar geographic distribution, the Phillip's dikdik, which was assessed at the same location, and with the same equipment and setup as used in the present study (Dittmann et al. 2014a). Given the closely overlapping and ecologically similar habitats, it cannot be argued that dikdik are exposed to differences in climate that could explain this physiological difference from these gazelle species. Rather, the results show that the detection of convergent rules, such as a lower metabolism in arid-adapted species (e.g. Lovegrove 2000, 2003; McNab 2008), does not necessarily mean that all investigated species share this adaptation. Accordingly, our results suggest that not all bovids that live in arid, hot environments have comparatively low MR. Another bovid from arid environments, apart from the dikdik, that apparently has a comparatively lower MR is the Arabian sand gazelle (*G. subgutturosa marica*) (Ostrowski and Williams 2006), whereas bovids from arid environments without reduced MR include the steenbok (*Raphicerus campestris*) (Haim and Skinner 1991) and the Arabian oryx (*Oryx leucoryx*) (Williams et al. 2001). With respect to *G. gazella*, our result of a RMR that is higher than the mammalian average was also indicated in two hand-raised animals during mask respirometry (Taylor et al. 1974). However, the high values of 529 kJ kg $BM^{-0.75}$ d^{-1} reported in that study are clearly higher than ours (371 kJ kg $BM^{-0.75}$ d^{-1}) which could have been due to the use of a mask and a shorter measurement period that did not allow animals to settle for several hours or simply be a random result when investigating only two animals.

The fluctuations between high and low O_2 consumption were more pronounced and less regular in *N. soemmerringii* than in the other species. While peaks in O_2 consumption *G. spekei* and *G. gazella* could mirror regular cycles of feeding and rumination, the patterns observed in *N. soemmerringii* appears to be less uniform and could be explained by physical activity of these animals. However, despite these putative higher levels in activity or stress, *N. soemmerringii* still had the lowest RMRs when compared to the other species, indicating that the method used for calculating the RMR by considering only the lowest values might be suitable to rule out such phases of agitation.

The RQ, normally ranging from 0.7 to 1.0, mirrors the nutritional state of an animal by the ratio of molecular oxygen and carbon in
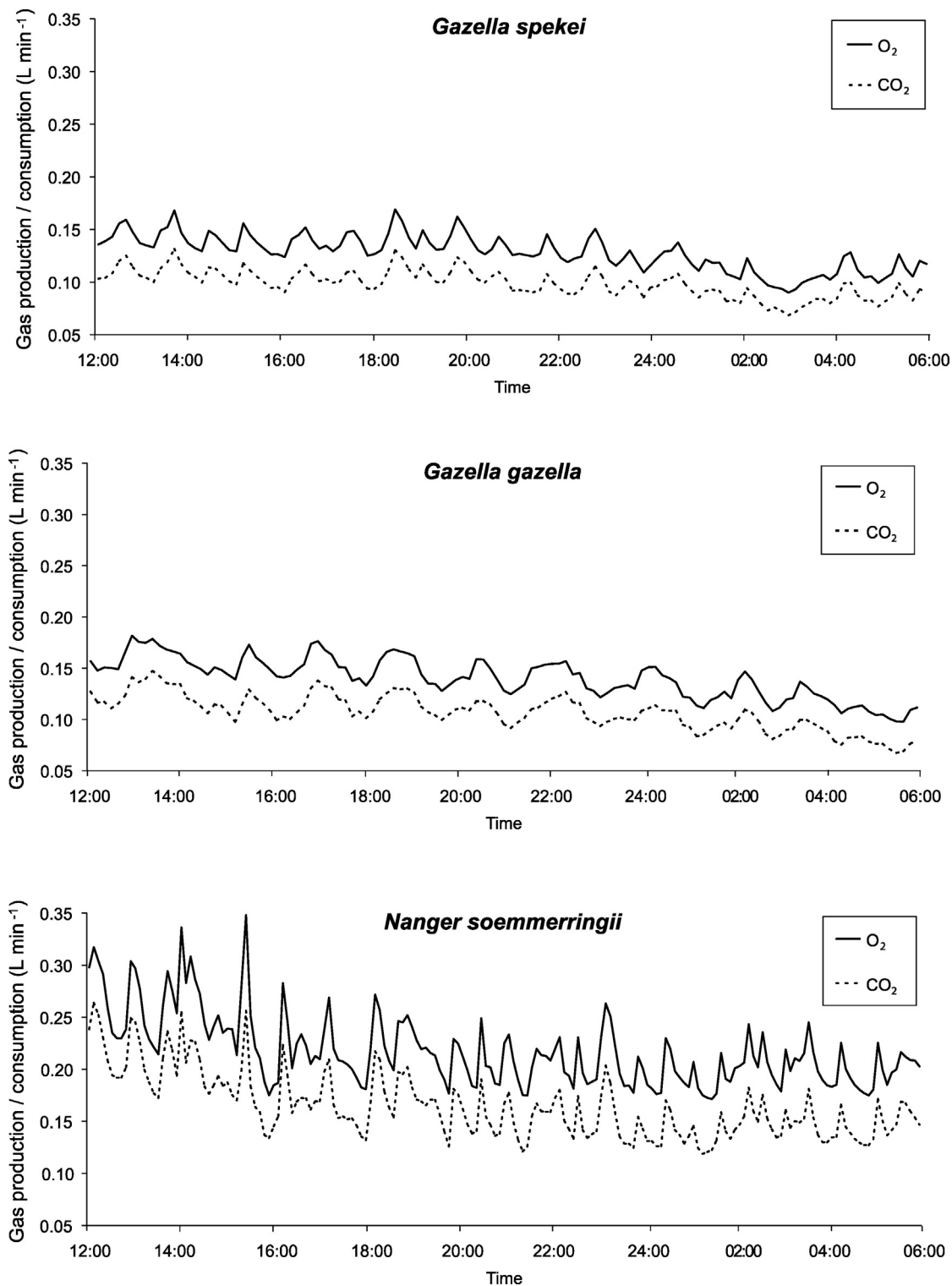
Fig. 1. Time courses of oxygen consumption and carbon dioxide production by exemplary representatives of *Gazella spekei*, *G. gazella* and *Nanger soemmerringii* during 18 h of measurement in the respiration chambers.

the metabolized substrate where fat, as metabolized in fasting animals results in low RQs, whereas carbohydrates metabolized by fed animals result in high RQ values (Robbins 1993). The values of the gazelles ranged between 0.76 and 0.82, which indicates continuous fermentation of a fibrous digesta. Although we did not intend to fast the animals, the lower RQ values indicate that the measured RMR closely represent BMR. BMR is measured in a post-absorptive state (Schmidt-Nielsen 1997) that is hardly ever reached in ruminants,

because they constantly ferment plant material in their reticulo-rumen (White and Seymour 2003; Clauss et al. 2008).

Considerations on metabolic measurements with ruminants

One aspect that can influence metabolic measurements is the nutritional state and history of the experimental animals. Ostrowski et al. (2006a) demonstrated that a reduced food and

Table 1
Body mass, measured and expected metabolic rates and respiratory quotients of the three gazelle species measured in this study.

	G. spekei	G. gazella	N. soemmerringii
n	5	5	6
Body mass (kg)	12.4 ± 1.3^a	16.3 ± 1.4^a	35.1 ± 4.7^b
MMR (kJ kg $BM^{-0.75}$ d^{-1})	524 ± 36^a	495 ± 28^a	426 ± 23^b
RMR (kJ kg $BM^{-0.75}$ d^{-1})	432 ± 32^a	371 ± 31^b	310 ± 32^c
RMR (kJ h^{-1})	119 ± 6^a	126 ± 14^a	185 ± 21^b
BMR (kJ h^{-1})			
(Kleiber)	81 ± 7^a	99 ± 6^a	176 ± 18^b
(McNab)	97 ± 7^a	114 ± 6^a	193 ± 17^b
RMR/BMR ratio			
(Kleiber)	1.47 ± 0.11^a	1.27 ± 0.11^b	1.06 ± 0.11^c
(McNab)	1.23 ± 0.09^a	1.10 ± 0.09^{ab}	0.96 ± 0.09^b
RQ	0.76 ± 0.02^a	0.77 ± 0.05^{ab}	0.82 ± 0.03^b

BM, body mass; MMR, maintenance metabolic rate; RMR, resting metabolic rate; BMR, basal metabolic rate estimated either based on the equation for mammals of Kleiber (1961) or the equation for Artiodactyls of McNab (2008); RQ, respiratory quotient (=CO_2 production/O_2 consumption).
Different superscripts within a row indicate significant differences between the species.

water intake leads to a reduction in fasting metabolism in *G. subgutturosa*. Metabolic adaptations to extreme environments may therefore consist of two components. On the one hand, there may be a generally reduced metabolism even under conditions of unlimited resources, as one can assume for most animals in which metabolic measurements are performed, including the animals of the present study. Such a generally reduced metabolism was, for example, demonstrated in dikdik or (Dittmann et al. 2014a) in camelids (Dittmann et al. 2014b). On the other hand, another possible component of such an adaptation could be the flexibility to reduce the MR under conditions of resource limitation, as was demonstrated in many ruminants from seasonally variable habitats (e.g. reviewed in Mauget et al. 1997).

Another aspect that is rarely discussed when measuring MR in individuals of nondomestic species is how handling and confinement stress might influence the results. Our study is no exception in not testing for this effect; instead, we simply followed the common practice of using measurements for 'RMR' that were taken after the animals had stayed in the respiration chamber for several hours (e.g. Haim and Skinner 1991; Ostrowski et al. 2006a). It could be hypothesized that results higher than expected values, as in *G. spekei* and *G. gazella* in our study, might be caused by the excitement due to the unusual handling and confinement. As probably other researchers before, we had decided not to expose the animals to this procedure repeatedly as a habituation program, because we considered the potentially resulting repeated stress to be significant, and did not expect a stress-reducing training effect within a reasonable time period. The possibility to use hand-raised animals accustomed to such procedures was not available to us. To our own experience, gazelles usually become calm when confined in dark, narrow spaces in a quiet environment, and this was our subjective impression in the animals of this experiment. Also, in a former study with Phillip's dikdiks, we followed the same procedures in animal handling and respiration measurements, which resulted in relatively lower values (also corroborated by measures on body mass changes in relation to digstible energy intake) (Dittmann et al. 2014a), suggesting that the higher MR in the gazelles in the present study do not mirror handling stress. However, stress that was not represented by movement but nevertheless influenced the O_2 consumption, and species-specific responses to stressful situations, could not be excluded. In domestic animals, controversial effects of training to respiration chamber stays on O_2 consumption were described. In pigs (Gray and McCracken 1980) and turkeys (MacLeod et al. 1985), training had no effect, and in chicken training even led to an increase in O_2 consumption because individuals accustomed to the respiration chamber increased their food intake (Lundy et al. 1978). The question to which extent habituation of nondomestic species to the respiration chamber will influence

results, even when using only low readings after an adaptation period of several hours, remains to be specifically investigated.

Adaptations to arid environments in ruminants

Various adaptations to hot, arid environments have been described for gazelles and other ruminants (Silanikove 1994; Cain et al. 2006; Fuller et al. 2014). These include a long distal colon for increased water re-absorption (Woodall and Skinner 1993), leading to particularly dry feces (Clauss et al. 2004). Additionally, species adapted to hot, dry environments probably have a comparatively high thermal conductance that facilitates heat loss (Haim and Skinner 1991). Particularly thin keratin sheaths of the horns could contribute to this, as suggested in a comparative study that also included one gazelle species (*G. thompsoni*) (Picard et al. 1999).

G. dorcas and *G. gazella* were reported to be able to survive periods of water deprivation for up to 8–10 days (Ghobrial and Cloudsley-Thompson 1966; Mohamed et al. 1988; Al-Toum and Al-Johany 2000). It was shown that, when water it is freely available, *G. dorcas*, *G. gazella* and *G. subgutturosa* ingest water in amounts comparable to other ruminants under such conditions, and adjust water intake to environmental temperatures (Ghobrial 1970; Williamson and Delima 1991). This suggests that their adaptation to aridity must be due to behavioral and/or physiological mechanisms. Aridity-adapted ruminants may have special structures in the kidney, i.e. longer loops of Henlé or a thicker renal medulla (e.g. Horst and Langworthy 1971; Dunson 1974), which enables them to produce less and more concentrated urine (Maloiy et al. 1979; Beuchat 1990). With a reduced MR, water loss is also reduced by a lower total evaporative water loss, but this can additionally be influenced by other species-specific factors (Ostrowski et al. 2006a, 2006b), such as anatomical adaptation of the nasal passages (Kamau et al. 1984).

Like other ruminants and other mammals (Mitchell and Lust 2008), including dikdiks (Kamau et al. 1984), gazelles probably use a carotid rete as a counter-current heat exchange mechanism to control brain temperatures when overall body temperature increases. This was demonstrated in *G. thompsoni* by Taylor and Lyman (1972). Evidence for the capacity to allow body temperature to increase because of exercise or increased environmental temperatures was reported for *N. granti* and *G. thompsoni* (Taylor 1970; Taylor and Lyman 1972), *G. subgutturosa marica* (Ostrowski and Williams 2006; Hetem et al. 2012), and *G. gazella* and *G. leptoceros* (Al-Johany et al. 1998; Babor et al. 2014).

Conclusions

The various forms of adaptation to hot, dry habitats (Silanikove 1994; Cain et al. 2006) evidently would allow many different

combinations of adaptations that render life in such habitats feasible; and this does not necessarily include a lowered MR. The question which combinations of adaptations a particular species might have evolved is probably related to its phylogenetic and ecological history. While a first step in the comparative evaluation of physiological characteristics usually is to check for a general association with body mass, the second step is to explain deviations from this pattern by convergent adaptations to particular niches (e.g. McNab 2008). As a subsequent step, we propose here to expand datasets to an extent that allows testing and explaining why some species inhabiting the same ecological niches show specific convergent adaptations while others do not.

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