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Short Communication

Differences in resting metabolic rates of two southern African tortoises: *Psammobates oculiferus* and *Geochelone pardalis*

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Abstract.—Energy metabolism varies considerably between different groups of endotherms, yet there is little or no reported variation among extant groups of reptiles. We measured lower resting metabolic rates (RMRs) in Kalahari tent tortoises (*Psammobates oculiferus*) than in sympatric Leopard tortoises (*Geochelone pardalis*). *G. pardalis* also had RMR values that were higher than the allometric prediction for reptiles whereas *P. oculiferus* had RMR values that were not significantly different from the prediction. Differences in RMR between the two species may have occurred because of the large differences in body mass, differing body temperatures, differences in growth rates, or because there may have been differences in the heat increment of feeding.

Key words.—Tortoise, reptile, resting metabolic rate, energy expenditure, Kalahari

There is a large variation in metabolic capabilities among groups of endotherms (Kleiber 1961). This can be exemplified by differences in basal metabolic rate (BMR), which varies across zoogeographical zones (Lovegrove 2000). By comparison, there is little diversity in resting metabolic rate (RMR) (Bennett & Dawson 1976, Andrews & Pough 1985) or field metabolic rate (Nagy 2001) within or among extant groups of reptiles from a range of different habitats. The cost of maintenance is considered a conservative parameter in reptilian evolution (Bennett & Dawson 1976). In the current study, we found differences in RMR between two sympatric southern African species of tortoise: the Kalahari tent tortoise (*Psammobates oculiferus*), which is predominantly a dry-country species, and the Leopard tortoise (*Geochelone pardalis*), which has a wide distribution spanning both mesic and arid areas (Boycott & Bourquin 1988).

Fieldwork took place during the summer (January 2004) on farmland near Van Zyl's Rus in the South African Kalahari (25°58'S; 21°49'E). The area consists of sparsely vegetated sand dunes and river terraces on either side of the dry Kuruman riverbed. Data were collected from 10 *G. pardalis* (5 males and 5 females) and 10 *P. oculiferus* (5 males and 5 females). RMR values were determined for each animal immediately after they were collected from the field. Animals were placed in a respirometry chamber for an initial period of at least 30 minutes in which tortoises seemed to calm. After this initial period, we measured oxygen consumption every 30 seconds for at least 30 minutes (longer if the animals required more time to settle). We calculated the mean of the lowest 10 readings of oxygen consumption (ml O_2/h) when animals were at rest. Values of oxygen consumption were then converted to energy expenditure using an energy equivalence per litre of O_2 consumed that is appropriate for carbohydrate metabolism (5.04 kcal per litre O_2) (Arch *et al.* in press). Measurements were completed between 11:00-14:00, when animals would otherwise be sheltering from the midday summer heat. Shaded air temperatures ranged from 29°C to 34°C during this period (mean 32°C SD = 0.90°C: Scantlebury & Minting unpublished data). We used an open circuit respirometry system to measure oxygen consumption (Hill 1972). Three different sizes of metabolic chamber were used (1.6 L, 22.1 L and 43.3L) to accommodate the different sizes of animals (100 g to 5 kg). The temperature of the chambers was maintained at 31±1ºC by immersing them in a temperature-controlled water bath (Labotec, LAUDA, Königshofen, Germany). The temperature of the chamber was measured using a standard mercury thermometer (±0.5ºC). Dried air was pumped into the chamber at rates between 300 and 3000 ml/min so that depressions in oxygen concentration were maintained at 0.25 - 0.40% for each animal. The air passed through approximately 4 m of copper coil that was submerged in the water before it entered the chamber. This ensured the temperature of air that entered the chamber was the same as the water bath. For the larger animals, oxygen concentration stabilised in 2-3 minutes. (i.e., if animals were inactive, active and then inactive again, it took 2-3 minutes for oxygen concentration readings to return to the levels observed before they became active). We are confident that we recorded values of minimal oxygen concentration because most animals were inactive for periods of at least 10 minutes while they were in the chamber. The flow of air into the chamber was controlled by a flow regulator (Omega FMA-A2310, Stamford, CT) that was placed upstream of the chamber. Oxygen consumption was measured using an oxygen analyser (S-2A Applied Electrochemistry, AEI Technologies, Inc. USA), which was calibrated to an upper value (20.95% O_2, atmospheric) prior to the measurement of each animal and to a lower value (0.0% O_2, N_2 gas) prior to all measurements of oxygen consumption. Air was dried using silica gel before entering the chamber and again before entering the analyser. One species was not more active in the chamber than the other species. Results were corrected to standard temperature and pressure (barometric pressure was obtained from a local weather station). Using a paired-t test, RMR values were then compared with allometrically predicted values for all reptiles (at 30°C) (Bennett & Dawson 1976). We used analysis of covariance to examine differences in RMR between the two species, with body mass as the covariate. Data were log-transformed prior to analysis. Means are displayed ± one standard deviation.

There was a significant difference in body mass between the two species (2-sample $t_{18} = 2.64$, $P = 0.027$). However, there were no significant differences in body mass between males and females for either species (one way ANOVA $F_{1,8} = 1.45$, $P = 0.262$ for *G. pardalis* and $F_{1,8} = 0.18$, $P = 0.680$ for *P. oculiferus*). The mean body mass of *G. pardalis* was 1432 ± 1594 g and the mean mass of *P. oculiferus* was 224 ± 85.4 g. There was a positive relationship between RMR and body mass for both species [$F_{1,8} = 138.59$, $P < 0.001$; $\log_{10}$RMR (kJ/day) = 0.208 + 0.506 x $\log_{10}$body mass (g), $r^2 = 0.945$ for *G. pardalis* and $F_{1,8} = 25.21$, $P < 0.001$; $\log_{10}$RMR (kJ/day) = -1.38 + 1.03 x $\log_{10}$body mass (g), $r^2 = 0.759$ for *P. oculiferus*]. RMR values were significantly greater in *G. pardalis* than in *P. oculiferus* when the effects of body mass were taken into account ($F_{1,17} = 33.13$, $P < 0.001$) (Fig. 1). However, the slopes of the relationships between RMR and body mass did not differ between species ($F_{1,16} = 0.68$, $P = 0.421$) and there was no difference in RMR between sexes ($F_{1,8} = 0.73$, $P = 0.419$ for *G. pardalis* and $F_{1,8} = 0.03$, $P = 0.860$ for *P. oculiferus*). When RMR values were compared with values predicted for reptiles of these body masses, the values of *G. pardalis* were significantly greater than predicted (paired $t_9 = 2.72$, $P = 0.026$), whereas those of *P. oculiferus* were not significantly different from predicted

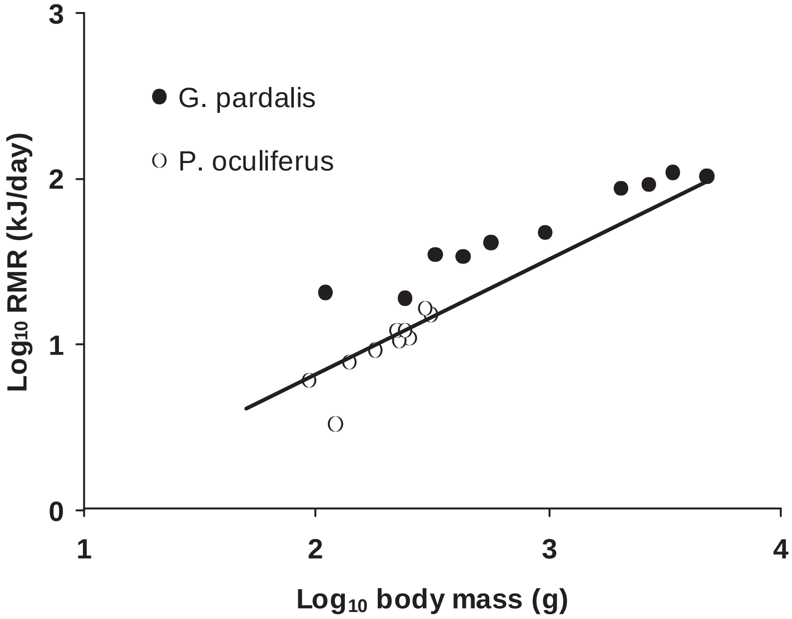

Figure 1. Resting metabolic rate (kJ/d) of *Geochelone pardalis* and *Psammobates oculiferus*. Line shows the allometric prediction of Bennett & Dawson (1976) for all reptiles at 30°C; [Log_{10} (RMR, kJ/d) = Log_{10} (0.278) - 0.23 x $\log_{10}$ (body mass, g)].

values (t_{10}= 0.95, P = 0.37; Fig. 1).

Within ectotherms, RMR and field metabolic rate vary with body mass and ambient temperature (Nagy *et al.* 1999). However, there is less variation due to other characteristics such as age (Nagy 2000), sex (Maxwell *et al.* 2003) and breeding condition (Karasov & Anderson 1998, Ladyman *et al.* 2003). It has been postulated that there may be differences in the energy requirements of ectotherms adapted to different environmental conditions, such as those adapted to arid regions compared with those adapted to more mesic environments (Barboza 1995). Angilletta *et al.* (2004) studied growth rates of eastern fence lizards (*Sceloporus undulatus*) captured from cold and warm environments under identical laboratory conditions. They showed that embryos from colder environments developed faster and grew more efficiently than those from warmer environments, and suggested that geographic variation can produce thermal adaptation in embryonic phenotypes.

Tortoises are remarkable in their ability to withstand shortages of both food and water and are able to thrive at relatively high densities in extreme environments (Barboza 1995; Lagarde *et al.* 2003). Studies on the desert tortoise *Gopherus agassizii* have shown that their adaptability to extreme environments may be due to their extremely low rates of water loss and energy use, their ability to withstand very high levels of plasma osmolality, and their ability to use their urinary bladder as a store for water (Peterson 1996; Henen *et al.* 1998). Several factors may affect the reproductive effort (the ratio of reproductive energy expenditure to the amount of energy available for all expenditures during the year) of female desert tortoises; although body mass is particularly important to reproductive allocations, other effects such as habitat type (e.g., xeric versus mesic) and life-history strategy (e.g., 'r-' versus 'K-' selected) may also be significant (Henen 1997).

In the current study we found differences in RMR between two sympatric species of tortoise. Several factors may have produced these observed differences. One possibility is species-specific differences in RMR. Also, RMR's were measured on animals that were not necessarily post-absorptive, so species differences in RMR could have been influenced in part by differences in the heat increment of feeding. However, more work is needed on this topic.

The large difference in body size between the two species might affect the species' thermoregulatory strategies, particularly the use of thermal inertia. We also cannot discount the fact that core body temperatures may have differed between the two species. Chelonians thermoregulate both behaviourally and physiologically, shunting blood to facilitate heat gain in the morning and reduce heat loss at night (Heisler and Glass 1985, Meek & Avery 1988). Hence, it is possible that the species' core body temperatures differed systematically from the chamber temperatures. However, body temperature was not measured and therefore interpretations need to be made with caution.

Another possibility is that differences in observed RMR might be due to differences in growth rates between the two species. Many of the leopard tortoises measured in this study were of juvenile body size, but only about three of the Kalahari tent tortoises were juveniles. Since Leopard tortoises grow rapidly, especially during the first few years of life (Branch 1998), the RMR of juvenile leopard tortoises may have reflected high production costs at this stage of life.

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LITERATURE CITED

ANDREWS, R.M., & F.H. POUGH. 1985. Metabolism of squamate reptiles: Allometric and ecological relationships. Physiol. Zool. 58: 214-231.

ANGILLETTA, M.J. JR., OUFIERO, C.E. & M.W. SEARS. 2004. Thermal adaptation of maternal and embryonic phenotypes in a geographically widespread ectotherm. International Congress Series 1275: 258-266.

ARCH, J.R.S., HISLOP, D., WANG, S.J.Y. & J.R. SPEAKMAN. Some mathematical and technical issues in the measurement and interpretation of open-circuit indirect calorimetry in small animals. Int. J. Obesity. In press.

BARBOZA, P.S. 1995. Nutrient balances and maintenance requirements for nitrogen and energy in desert tortoises (*Xerobates agassizii*) consuming forages. Comp. Biochem. Physiol. A. 112: 537-545.

BENNETT, A. F. & W.R. DAWSON. 1976. Metabolism. Pp. 127-224. *In* C. Gans (Ed.), Biology of the Reptilia. Volume 5. Academic Press, New York.

BOYCOTT, R.C. & O. BOURQUIN. 1988. The South African Tortoise Book. A Guide to South African Tortoises, Terrapins and Turtles. 1st edn. Southern Book Publishers (Pty) Limited, Johannesburg, South Africa.

BRANCH, W.R. 1998. Field guide to Snakes and other Reptiles of Southern Africa. 3rd Edn. Struik, Cape Town.

HEISLER, N. & M.L. GLASS. 1985. Mechanisms and regulation of central vascular shunts in reptiles. Pp. 334-353. *In* K. Johansen & W. Burggren (Eds.) Cardiovascular shunts: phylogenetic, ontogenetic and clinical aspects. Munksgaard, Copenhagen.

HENEN, B.T. 1997. Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). Ecology. 78: 283-296.

HENEN, B.T., PETERSON, C.C., WALLIS, I.R., BERRY, H. & K.A. NAGY. 1998. Desert tortoise field metabolic rates and water fluxes track local and global climatic conditions. Oecologia. 117: 365-373.

HILL, R.W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J. Appl. Physiol. 33: 261-263.

KARASOV, W.H. & R.A. ANDERSON. 1998. Correlates of average daily metabolism of field-active zebra-tailed lizards (*Callisaurus draconoides*). Physiol. Zool. 71: 93-105.

KLEIBER, M. 1961. The Fire of Life. Wiley, New York, pp. 177-216.

LADYMAN, M., BONNET, X., LOURDAIS, O., BRADSHAW, D. & G. NAULLEAU. 2003. Gestation, thermoregulation, and metabolism in a viviparous snake, *Vipera aspis*: evidence for fecundity-independent costs. Physiol. Biochem. Zool. 76: 497-510.

LAGARDE, F., BONNET, X., CORBIN, J., HENEN, B., NAGY, K., MARDONOV, B. & G. NAULLEAU. 2003. Foraging behaviour and diet of an ectothermic herbivore: *Testudo horsfieldi*. Ecography. 26: 236-242.

LOVEGROVE, B.G., 2000. The zoogeography of mammalian basal metabolic rate. Am. Nat. 156: 201-219.

MAXWELL, L.K., JACOBSON, E.R. & B.K. MCNAB. 2003. Intraspecific allometry of standard metabolic rate in green iguanas, *Iguana iguana*. Comp. Biochem. Physiol. A. 136: 301-310.

MEEK, R., & R.A. AVERY. 1988. Thermoregulation in Chelonians. Herpetol. J. 7: 253-259.

NAGY, K.A. 2000. Energy costs of growth in neonate reptiles. Herpetological Monographs. 14: 378-387.

NAGY, K.A. 2001. Food requirements of wild animals: predictive equations for free-living mammals, reptiles and birds. Nutrition Abstracts and Reviews, Series B. 71: 21R-31R.

NAGY, K.A., GIRARD, I.A. & T.K. BROWN. 1999. Energetics of free-ranging mammals, reptiles and birds. Ann. Rev. Nut. 19: 247-277.

PETERSON, C.C. 1996. Anhomeostasis: Seasonal water and solute relations in two populations of the desert tortoise (*Gopherus agassizii*) during chronic drought. Physiol. Zool. 69: 1324-1358.

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