brief communications

- Frankenberg-Schwager, M. Radiat. Environ. Biophys. 29, 273–292 (1990).
- Sadamoto, S. et al. Int. J. Radiat. Biol. 65, 549–557 (1994).
- Dubrova, Y. E., Plumb, M., Brown, J. & Jeffreys, A. J. Int. J. Radiat. Biol. 74, 689–696 (1998).
- Crow, J. F. & Kimura, M. An Introduction to Population Genetics Theory (Harper, New York, 1970).

Metabolic scaling

Energy constraints on carnivore diet

he energy expenditure of mammals reflects their habits and environments¹, subject to limitations associated with body size. Carbone et al.² combined scaling relationships to argue that large species of the mammalian order Carnivora (weighing more than 21.5 kg) do not specialize on invertebrate prey. However, many tropical mammals that feed exclusively on ants and termites are much heavier than this, often weighing up to 60-70 kg; they survive by progressively reducing their metabolic rate to below that expected from their body size. I believe that this response indicates that it is not body size that limits the determination of diet, but rather the maximal rate of energy expenditure.

The size limit for a predator exclusively dependent on invertebrate prey is not absolute. For example, the sloth bear (*Ursus ursinus*), a carnivore that can weigh as much as 145 kg and feeds extensively (but not exclusively³) on termites, was considered by Carbone *et al.* to be an outlier — but outliers should not be ignored as they may tell us that our theories are incomplete. Their analysis² fails to recognize that all scaling relationships contain biologically relevant variation, and inherent in this residual scatter are adjustments that permit a large mass in carnivores and other terrestrial mammals that consume invertebrate prey.

Large mammals (over 20 kg) that specialize in eating tropical ants and termites include the aardvark (*Orycteropus afer*) and some pangolins (*Manis temmincki* and *M. gigantea*), tamanduas (*Myrmecophaga tridactyla*) and armadillos (*Priodontes maxima*). These^{4,5} and the sloth bear⁶ generally have lower standard rates of energy expenditure than other mammals. As ant and termite predators increase in size, their basal rate of metabolism decreases (Fig. 1), a trend that is particularly evident when species in a family are compared (to correct for any putative effect of phylogeny or ecological/behavioural uniformity).

A reduction in metabolic rate reduces the effective body size, which can be estimated from the total basal rate of the largest committed ant/termite eaters. If an allmammal standard⁷ for basal metabolic rate



Figure 1 Basal rate of metabolism, expressed as a percentage of the basal rate expected from an all-mammal curve⁷, in various mammals⁴⁻⁶ that specialize on soil invertebrates, as a function of body mass. Species that belong to the same family are connected.

is used, a 15.9-kg *Manis crassicaudata* has the basal rate of a 3.4-kg standard mammal, a 30.6-kg *Myrmecophaga* has that of a 10.9kg standard mammal, a 45.2-kg *Priodontes* has that of a 13.4-kg standard mammal, a 48-kg *Orycteropus* has that of a 36.2-kg standard mammal, and a 67.0-kg *U. ursinus* has that of a 56.5-kg standard mammal.

These calculations indicate that the maximum body mass in a standard mammal compatible with an ant/termite-eating habit is 11–13 kg, with the exception of the aardvark and sloth bear. This calculation may account for the comparatively high basal rate in *Proteles* (Fig. 1), which weighs less than 10 kg — at that mass, an adjustment of basal rate may not be required. What seems to be limited is the total rate of energy expenditure, not body mass: a limiting rate may be encountered in various masses at the expense of conforming to a standard curve and having effective endothermic temperature regulation.

Two of the species shown in Fig. 1 exceed the 11-13-kg limit to the 'adjusted' mass. The large mass and comparatively high basal rate of the sloth bear correlate with a diet that is about 50% fruit³, although it is not clear whether addition of fruit to the diet permits a higher expenditure or size. The most distinctive large terrestrial specialist insectivore is the aardvark, which conforms neither to the original analysis², nor to the evasion described here. How it can have its comparatively high basal rate and a large body mass, and eat only ants and termites, is unknown. Under the assumption that a limiting energy expenditure exists, some other evasion may apply.

A limit to the exclusive use of invertebrates by terrestrial mammals, if one exists, may be associated with the cost of prey col-

🟁 © 2000 Macmillan Magazines Ltd

lection, which is why the largest species are tropical and feed on ants and termites: only these prey occur in sufficiently large colonies to make prey acquisition energetically feasible, and such large colonies occur only in the lowland tropics. In the absence of colonial ants and termites, terrestrial invertebrate-eaters might attain a maximal mass of 10 kg (ref. 5). The absence of an ant/termite specialization in large carnivores may occur because this niche was occupied by other mammals before the evolution or arrival of carnivores, the only opportunity available being at intermediate masses, which was exploited in Africa by the aardwolf and the bat-eared fox (Otocyon megalotis).

Although it might be argued that this analysis fails to take phylogenetic history into consideration, it has been pointed out⁸ that 'corrections' for proposed phylogeny erroneously assume the priority of phylogeny as a factor influencing phenotypic characters, thus ignoring the complex interactions among determinative factors. The model of Carbone *et al.*² is ultimately called into question because it ignores the residual variation and therefore the biological flexibility inherent in all scaling functions.

Brian K. McNab

Department of Zoology, University of Florida, Gainesville, Florida 32611, USA e-mail: mcnab@zoo.ufl.edu

- e-maii: mcnab@zoo.uji.eau
- 1. McNab, B. K. Funct. Ecol. 6, 672–679 (1992).
- Carbone, C., Mace, G. M., Roberts, S. C. & Macdonald, D. W. Nature 402, 286–288 (1999).
- Laurie, A. & Seidensticker, J. J. Zool. Lond. 182, 187–204 (1977).
- McNab, B. K. J. Mammal. 61, 606–627 (1980).
 McNab, B. K. J. Zool, Lond, 203, 485–510 (1984).
- McNab, B. K. J. Zool. Lond. 203, 485–510 (198
 McNab, B. K. J. Mammal, 73, 168–172 (1992).
- McNab, B. K. J. Mammal. 75, 168–172 (1992)
 McNab, B. K. Q. Rev. Biol. 63, 25–54 (1988).
- Westoby, M., Leishman, M. R. & Lord, J. M. J. Ecol. 83, 531–534 (1995).

NATURE | VOL 407 | 5 OCTOBER 2000 | www.nature.com