

LETTER

Stoichiometry of endothermy: shifting the quest from nitrogen to carbon

Marcel Klaassen^{1,2*} and
Bart A. Nolet¹

¹Centre for Limnology,
Netherlands Institute of Ecology
(NIOO-KNAW), PO Box 1299,
NL-3600 BG Maarssen, The
Netherlands

²The Ecology Centre, University
of Queensland, School of
Integrative Biology, St Lucia,
Qld 4072, Australia

*Correspondence: E-mail:
m.klaassen@nioo.knaw.nl

Abstract

For many animals, notably herbivores, plants are often an inadequate food source given the low content of protein and high content of C-rich material. This conception is mainly based on studies on ectotherms. The validity of this conception for endotherms is unclear given their much higher carbon requirements for maintenance energy metabolism than ectotherms. Applying stoichiometric principles, we hypothesized that endotherms can cope with diets with much higher (metabolizable) carbon to nitrogen ratios than ectotherms. Using empirical data on birds, eutherian mammals, marsupials and reptiles, we compiled and compared measurements and allometric equations for energy metabolism as well as nitrogen requirements. Our analysis supports our hypothesis that plants, and especially their leaves, are generally sufficiently rich in nitrogen to fulfil protein demands in endotherms, at least during maintenance conditions, but less so in ectotherms. This has important implications with respect to community functioning and the evolution of endothermy.

Keywords

Biological stoichiometry, C : N ratio, energy requirements, evolution of endothermy, N : C ratio, nitrogen requirements.

Ecology Letters (2008) 11: 785–792

INTRODUCTION

Chemical stoichiometry studies the amounts of elements that are involved in chemical reactions, based on the principles of an elemental balance in reactants and products. Biological stoichiometry uses this mass balance principle to link genetics, organismal physiology, community structure and ecosystem processes involving all organisms (plants, fungi, bacteria, animals; e.g. Sterner & Elser 2002). Biological stoichiometry thus deals with the match that should exist between the composition of food and its consumers. With respect to nutritional composition the focus is mainly on the ratio in which carbon (C), nitrogen (N) and phosphorus (P) occur. Achieving stoichiometric balance is especially challenging for heterotrophs consuming autotrophs due to fundamental structural and metabolic differences between these two groups (Hessen 2004). Because autotrophs tend to be richer in C than heterotrophs, heterotrophs must often excrete or egest excess C and other nutrients relative to the limiting resources they seek, and this may come at a considerable metabolic cost (Anderson *et al.* 2005; Boersma & Elser 2006). At the same time, burning of C-rich compounds like fat or carbohydrates

and respiring C would yield much energy (Hessen 2004). When applying the principles of stoichiometry to animals, one should therefore take the energy, and thus C, requirements, carefully into account. According to stoichiometric theory, high energetic requirements would allow for the ingestion of food low in metabolizable N and P content relative to metabolizable C. This is very pertinent to endotherms, as their metabolic requirements are one to two orders of magnitude higher than that of ectotherms (Bernays 1982; Sterner & Elser 2002: p. 222). This would make the content of P and N in the diet of much less importance for endotherms than for ectotherms.

Although it has long been known that nutritional requirements of endotherms and ectotherms deviate largely, the ecological consequence of this on endotherms or systems in which they play a major role has rarely been considered from a stoichiometric perspective, despite the popularity of biological stoichiometry (cf. Sterner & Elser 2002; Frost *et al.* 2005; Boersma & Elser 2006). This is somewhat surprising, as an understanding of the fundamental differences in energy metabolism, and therefore nutrient requirements, between and among ectotherms and endotherms has tremendous implications for understanding

ecosystem relations of animals and plants. We therefore explore how variations in energy requirements affect dietary requirements with respect to the diet's N : C ratio. In doing so, we will focus on the energy and nitrogen requirements of endotherms, which we will use to calculate threshold elemental ratios (Sterner & Elser 2002), distinguishing between birds, marsupials and eutherian mammals. For comparison, we also examine reptiles, representing a largely terrestrial ectothermic group with an overlapping body size range but with a metabolic rate an order of magnitude lower than that found in similar-sized birds and mammals (Nagy *et al.* 1999). As only few species-specific data on the P-requirements of animals are available, and because N is often thought to be a limiting factor in most terrestrial biomes (e.g. Mattson 1980; Hohman *et al.* 1992; White 1993; Klasing 1998), we will focus on N, which is an important constituent of proteins. We will furthermore focus on herbivory (i.e. folivory, granivory, frugivory and nectarivory) as N or protein limitation is generally not considered to be a problem for vertebrate carnivores and omnivores. We discuss the consequences of dietary requirements on diet choice of herbivores and the evolution of endothermy.

METHODS

Allometric relationships for maintenance nitrogen requirements (MNR, mgN day^{-1}), basal metabolic rate (BMR, kJ day^{-1}) and field metabolic rate of free-ranging animals (FMR, kJ day^{-1}) as a function of body mass (M , kg) for reptiles, birds, marsupials and eutherian mammals were taken or calculated from literature data. Only the results of classical regression procedures on log–log transformed data were used, since (i) not all studies included phylogenetic regression procedures, (ii) when applied, phylogenetic regression procedures varied between studies and (iii), when tested, classical and phylogenetic regression procedures often yielded statistically indistinguishable relationships (e.g. Reynolds & Lee 1996; Nagy 2005; Withers *et al.* 2006). To assess an index of the required nutritive quality of the diets for the four groups of animals, we calculated the ratio between the allometric regressions for MNR and energy metabolism (BMR and FMR) of the animals, thus providing an estimate of the metabolizable nitrogen content of a diet relative to its metabolizable energy content. For the calculation of this ratio, both BMR and FMR were used to yield a natural range of energy needs, where the ratio MNR : BMR would represent the minimum energy intake for maintenance costs and, thus, the more conservative of the two.

The literature was also scanned for species-specific data points where either both MNR and BMR or MNR and FMR were available. Although fewer data points were involved than in the above-mentioned allometric analysis the resulting species-specific ratios of MNR : BMR and

MNR : FMR provide a better impression of the within-group variance in these ratios, also allowing for an explicit statistical analysis for group differences and their relationship with body mass (using generalized linear models on log-transformed ratios and body mass data).

To convert the MNR : BMR and MNR : FMR ratios into gross nitrogen over gross energy food content, protein and energy assimilation efficiencies (i.e. the amount of metabolizable energy, respectively, nitrogen, that an animal extracts from its food through digestion relative to the gross contents of that food) are required. Using a range of literature studies, we compiled a database from which we extracted these values. To allow for a comparison between MNR over energy metabolism ratios with published data on N : C ratios in plants, energy metabolism in animals needs to be converted to their carbon catabolism. The conversion of energy to carbon content depends on the composition of the metabolized diet, with values ranging between 19.0 and 25.6 mgC kJ^{-1} depending on the catabolized plant tissue (carbohydrates, lipids or protein) and the end product of protein catabolism (urea or uric acid; Gessaman & Nagy 1988). Following Buchsbaum *et al.* (1986), we assumed an average of 40, 40 and 20% of the metabolized energy of the food in herbivores to originate from the metabolism of lipids, carbohydrates and proteins, respectively, resulting in a conversion factor of 21.7 and 22.4 mgC kJ^{-1} for uricotelic and ureotelic animals, respectively, of which the average of 22.1 mgC kJ^{-1} was used in all subsequent calculations.

RESULTS

For reptiles, marsupials, eutherian mammals and birds, allometric relationships for MNR, BMR and FMR are presented in Table 1. A comparison of BMR allometric relationships confirms the expected patterns of highest metabolic rates in birds (typical body temperature 40 °C), followed by eutherian mammals (37 °C), marsupials (35.5 °C) and reptiles (ectothermic; Schmidt-Nielsen 1979). For FMR, a very similar pattern appears although the differences between marsupials and eutherian mammals do not extend over the entire body mass range. The relationships for MNR are less consistent across the animal groups as the mass exponents vary greatly. However, the allometric exponents for MNR and for the ratios between MNR : BMR and MNR : FMR in reptiles should be considered with caution, as only limited data are available for this group ($n = 3$). More importantly, over the body mass ranges measured, endotherms exhibit lower ratios than the ectothermic reptiles. For most of the body mass range birds have the lowest MNR : BMR and MNR : FMR ratios of all (Fig. 1).

The species-level analysis (Fig. 2; data in Appendix S1) yields a similar pattern, with a significant species group effects for both MNR : BMR ($F_{3, 36} = 5.10$, $P < 0.005$) and

Table 1 Allometry of nitrogen and energy use

Reptiles		
MNR = 108 $M^{0.473}$ ($n = 3$, $R^2 = 0.837$)		Data and references in Appendix S1
BMR = 27 $M^{0.77}$ ($n = 44$, $R^2 = 0.828$)		Bennett & Dawson (1976)*†
FMR = 91 $M^{0.889}$ ($n = 55$, $R^2 = 0.945$)		Nagy (2005)
MNR : BMR = 4.00 $M^{-0.297}$		
MNR : FMR = 1.19 $M^{-0.416}$		
Birds		
MNR = 359 $M^{0.825}$ ($n = 31$, $R^2 = 0.835$)		Data and references in Appendix S1
BMR = 343 $M^{0.670}$ ($n = 254$, $R^2 = 0.958$)		Reynolds & Lee (1996)
FMR = 1159 $M^{0.681}$ ($n = 95$, $R^2 = 0.938$)		Nagy (2005)
MNR : BMR = 1.05 $M^{0.155}$		
MNR : FMR = 0.31 $M^{0.144}$		
Marsupial mammals		
MNR = 217 $M^{0.777}$ ($n = 16$, $R^2 = 0.850$)		Data and references in Appendix S1
BMR = 200 $M^{0.74}$ ($n = 61$, $R^2 = 0.98$)		Withers <i>et al.</i> (2006)*
FMR = 525 $M^{0.574}$ ($n = 26$, $R^2 = 0.952$)		Nagy & Bradshaw (2000)
MNR : BMR = 1.09 $M^{0.037}$		
MNR : FMR = 0.41 $M^{0.203}$		
Eutherian mammals		
MNR = 411 $M^{0.863}$ ($n = 11$, $R^2 = 0.980$)		Data and references in Appendix S1
BMR = 241 $M^{0.705}$ ($n = 625$, $R^2 = 0.952$)		Duncan <i>et al.</i> (2007)
FMR = 872 $M^{0.772}$ ($n = 58$, $R^2 = 0.959$)		Nagy <i>et al.</i> (1999)
MNR : BMR = 1.71 $M^{0.158}$		
MNR : FMR = 0.47 $M^{0.091}$		

Relationships for maintenance nitrogen requirements (MNR, mgN day⁻¹), basal and field metabolic rates (respectively, BMR and FMR, kJ day⁻¹) and the ratios between these entities (respectively, MNR : BMR and MNR : FMR, mgN kJ⁻¹) in relation to body mass (M , kg) for reptiles, birds and marsupial and eutherian mammals. All equations were calculated using conventional least-square regression over log₁₀-transformed data.

*Assuming 20 kJ L⁻¹O₂.

†At an ambient temperature of 30 °C.

MNR : FMR ($F_{3, 17} = 8.32$, $P < 0.002$; after correction for body mass, see below), with least-square means being lower in endotherms than in reptiles. Among endotherms the least square means for both MNR : BMR and MNR : FMR ratios were lowest in birds. Only for FMR : BMR ratios a significant body mass effect was found ($F_{1, 17} = 4.89$, $P < 0.05$; interaction between body mass and species group being nonsignificant).

Energy assimilation efficiency (Appendix S2) varied significantly among plant parts (ANOVA $F_{4, 108} = 16.06$, $P < 0.001$). This was mainly due to the significantly lower assimilation efficiency of foliage (Scheffé, $P < 0.05$), with an average energy assimilation efficiency of 39% (SD = 14, $n = 41$), whereas most other plant parts (fruits, tubers, flowers and seeds) had statistically indistinguishable energy assimilation efficiencies, averaging 66% (SD = 19, $n = 72$). As indicated by the relatively high standard deviations for these values, energy assimilation values varied widely, which is probably due to variations in fibre content and retention time (e.g. Demment & van Soest 1985; Prop & Vulink 1992).

Protein assimilation efficiency (Appendix S2) was similar for all plant tissues averaging 44% but also here large variations among efficiencies were apparent within plant tissues (SD = 40, $n = 23$; ANOVA $F_{2, 20} = 2.97$, $P = 0.074$).

Using the average protein assimilation efficiency, average foliage energy assimilation efficiency, data from Table 1 and Appendix S1, and the energy to carbon conversion factor of 22.1 mgC kJ⁻¹, we calculated dietary N : C ratios as required for folivores and compared these with the range of N : C ratios found in terrestrial plants (Elser *et al.* 2000; Figs 1 and 2). Although it should be realized that this comparison is largely based on averages from which specific plant-animal comparisons may deviate considerably, this comparison indicates that N : C ratios among terrestrial plants are generally sufficient to satisfy the N requirements for endotherms. This is notably the case for birds, and at higher than basal levels of energy metabolism. We similarly calculated the consequences of consuming plant parts other than leaves (using data presented in Appendix S2), resulting in a somewhat less positive situation for endotherms with a

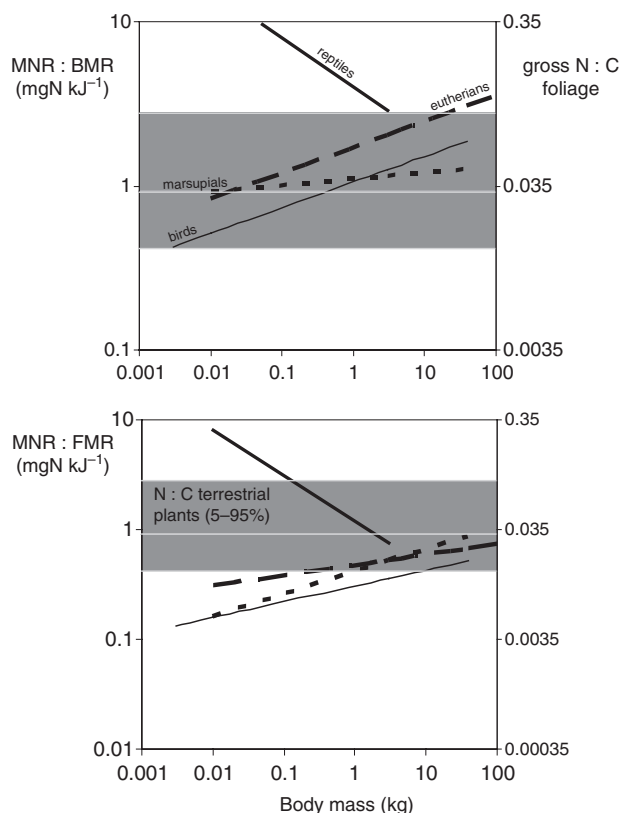


Figure 1 Predicted dietary quality in terms of metabolizable nitrogen vs. energy content and gross N : C ratio in foliage diet for reptiles, marsupials, eutherian mammals and birds of varying body mass (plotted over the body mass range where MNR measurements were conducted). Upper panel: conservative estimate using the ratio between MNR : BMR (mgN kJ^{-1}) calculated from allometric relations (Table 1). Lower panel: the more relaxed estimate using the ratio between MNR : FMR calculated from allometric relations (Table 1). N : C ratios are atomic and corrected for assimilation efficiencies for protein and energy of folivorous diets. For comparison the median (grey line) and 5 and 95 percentiles (shaded area) for N : C ratios in the foliage of 398 terrestrial plants are provided (Elser *et al.* 2000).

14% lower average metabolizable N : C ratio in flowers, fruits, seeds and tubers. Notably mammals and marsupials have higher dietary N : C requirements than those available in flowers, seeds, fruits or tubers, if functioning at basal metabolic levels. However, when functioning at FMR levels, their dietary N : C requirements still largely match those of the plants available.

DISCUSSION

Dietary nitrogen requirements in endotherms

Although maintenance nitrogen requirements and BMR are inherently linked, as protein synthesis comes at an

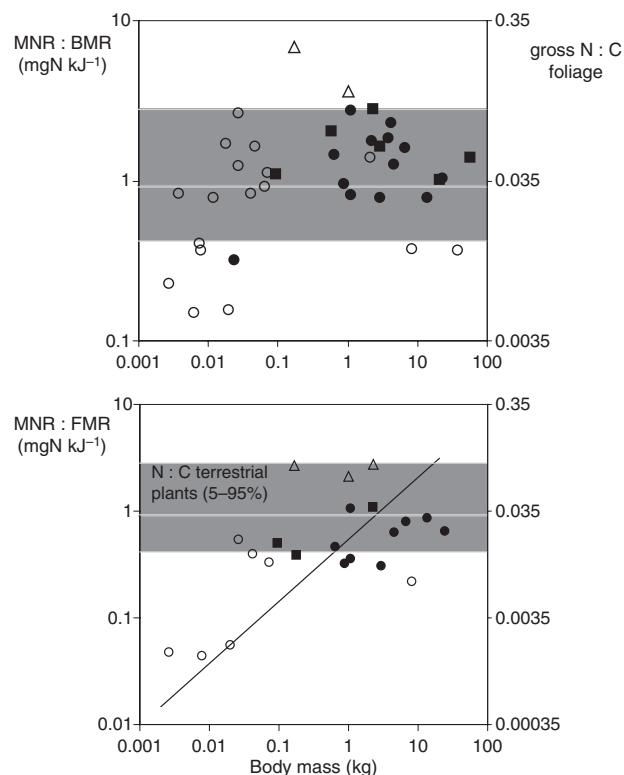


Figure 2 Predicted dietary quality in terms of metabolizable nitrogen vs. energy content and gross N : C ratio in foliage diet for reptiles (open triangles), marsupials (closed dots), eutherian mammals (closed squares) and birds (open dots) of varying body mass. Upper panel: conservative estimate using the ratio between MNR : BMR (mgN kJ^{-1}) as measured within individual species (Appendix S1). Lower panel: the more relaxed estimate using the ratio between MNR : FMR measured within individual species (Appendix S1). For these data a significant overall allometric relationship with body mass was found (see text; least-square regression line drawn). N : C ratios are atomic and corrected for assimilation efficiencies for protein and energy of folivorous diets. For comparison, the median (grey line) and 5 and 95 percentiles (shaded area) for N : C ratios in the foliage of 398 terrestrial plants are provided (Elser *et al.* 2000).

energetic cost (Hume 1999), there are many other factors contributing to the energy requirements of an endotherm of which maintaining homeothermy is a significant part. We argue that the high levels of metabolism typical for endotherms allow for poorer food quality in terms of N (i.e. lower N : C ratios). Our comparison of MNR : BMR and MNR : FMR in vertebrates indeed indicates that (ectothermic) reptiles need food with higher N content than (endothermic) birds or mammals. Considering endotherms only, a trend is also apparent with birds, which have the highest energy requirements, also having the lowest MNR : BMR and MNR : FMR ratios of all.

Admittedly the intergroup comparisons are hampered by the limited data for reptiles, but the argument is also strongly supported by the more robust comparison among endotherms. Because of data constraints for some of the groups, it is premature to speculate on the possible reasons and implications for the variation in MNR over energy requirements with body mass (i.e. the slopes in Fig. 1) for the various groups of animals. Besides increasing research efforts and data on reptiles, one could also extend our analysis by including other groups of ectotherms such as fishes. However, the direct comparison between herbivores from terrestrial and freshwater habitats is hampered by the widely differing N : C ratios of their food species (Elser *et al.* 2000).

For terrestrial plants in natural ecosystems, empirical evidence shows average N : C ratios can be fairly constant, despite variation in temperature, growth rate, nutrient supply or biome type (e.g. Elser *et al.* 2000; McGroddy *et al.* 2004; Kerkhoff *et al.* 2005). Although terrestrial plants generally seem to be of sufficient quality for most endotherms to simultaneously fulfil their protein and energy requirements, not all plants or plant parts contain the appropriate N : C ratio to permit dietary nitrogen balance. For example, tubers, seeds and fruit may be extremely low in protein making it difficult for their consumers to maintain nitrogen balance (e.g. Izhaki & Safriel 1989). However, animals such as small herbivores that are facing foraging time and digestive capacity constraints and very large ruminants that are confronted by digestive time constraint (Demment & van Soest 1985) must have a high and readily available metabolizable energy content in their forage. This is especially true for animals, such as birds, with very high mass-specific energy requirements. Furthermore, apart from secondary plant components, certain essential, highly specific nutrients may be important drivers for plant selection. For birds, for instance, a balanced diet contains *c.* 38 different nutrient compounds including various essential amino acids, fatty acids, minerals and vitamins (Murphy 1996). If nutrient requirements are not directly linked to energy expenditure, high energy requirements may reduce dietary quality requirements for these essential nutrients too.

In summary, we consider that the high energy requirements of endotherms facilitate consumption of plants with a relatively high C content and that most plants allow them to satisfy their general protein relative to energy requirements, at least during non-productive life stages when animals do not grow or reproduce.

Nitrogen as a constraining resource

Our contention that endothermic herbivores can satisfy their protein requirements by eating most plants seems to

be at odds with the work of many authors. It is typically stated that the restricted availability of protein in plants compared with other nutrients and energy makes choosing N-rich foods a driving force of their foraging behaviour. Mattson's (1980) and White's (1993) reviews on 'herbivory in relation to plant nitrogen-content' are probably the most influential contributions in this respect. Both mainly built their cases using examples of invertebrate animals, although they also included a number of studies in their works suggesting that herbivorous birds and mammals are protein limited. However, many of the latter studies deal with growing, lactating or otherwise producing animals or take the high standard nitrogen requirements of cattle as a reference (e.g. Sinclair 1975). Still, various authors have observed an apparent selection of the most nitrogen-rich food plants by herbivorous birds and mammals throughout much of the annual cycle. For a proper assessment of the limiting resource it is, however, necessary to measure and compare metabolizable energy content along with metabolizable nitrogen content. One study combining these measurements found that dietary nitrogen was limiting in (ectothermic) green iguanas (*Iguana iguana*) during large parts of the year (Marken-Lichtenbelt 1993). Unfortunately, many studies claiming selection for nitrogen-rich resources in birds failed to simultaneously measure metabolizable energy content of the food sources (e.g. Sedinger 1997; Fox *et al.* 1998; Bucher *et al.* 2003). In addition, it should be noted that protein may not only function as a building block but also as a useful catabolic substrate. Thus protein content may be positively correlated with the metabolizable energy content of a food (e.g. Prop & Deerenberg 1991). Moreover, protein content tends to be negatively correlated with fibre content (e.g. Bucher *et al.* 2003) which in turn importantly determines the metabolizability of food in combination with retention time (e.g. Demment & van Soest 1985; Prop & Vulink 1992).

Thus, when scrutinizing the evidence for endotherms being nitrogen limited there appears to be rather imperfect evidence to make this case, in particular when excluding periods of increased nitrogen demand, such as during growth and reproduction.

Variation in nitrogen requirements

Nitrogen requirements may be increased due to the inclusion of protein-assimilation limiting compounds into the diet such as phenolics and tannins (Izhaki & Safriel 1989; Robbins 1993; Klasing 1998). By contrast, nitrogen requirements may also be reduced by the ingestion of easily digestible and non-abrasive foods (e.g. nectar, fruit), reducing obligatory N losses (e.g. Robbins 1993; Allen & Hume 2001; Tsahar *et al.* 2006). Thus variation in such physical traits of plants may underlie the large coefficient of

variation of 91% we observed in our protein assimilation figures.

Nitrogen requirements may substantially exceed minimum maintenance levels during specific stages of an animal's life or annual cycle. For example, immune responses are known to increase an animal's nitrogen requirement (Lochmiller & Deerenberg 2000) and the ratio between nitrogen and energy requirements will be substantially higher during growth in all animals and during reproduction in females for eggs, embryo and milk formation. However, during these phases energy requirements may also be substantially increased, again mitigating the need to seek N-rich foods (Weathers 1996). Thus, during these demanding phases one should still consider the possibility that food quantity or food metabolizable energy content rather than food nitrogen content may be limiting. In birds, moult will also increase nitrogen requirements and notably the requirement of sulphur-rich amino acids typical of feather protein, which are scarce in green plants (Hohman *et al.* 1992). Still, through behavioural and physiological adaptations during moult, these increased protein requirements might be met without a change in diet (Fox & Kahlert 1999). Clearly, during periods of increased energy demand, such as during cold spells or migration or for many males during the reproductive phase, the nitrogen requirements to the diet may be lower.

Finally, we wish to emphasize that we do not claim that endotherms are never nitrogen limited and notably not during such important and demanding life-history stages as reproduction and growth. We only aim at suggesting that endothermy will assist considerably in relaxing this constraint, even in such demanding phases.

The evolution of endothermy

Above we concluded that endothermy relaxes dietary constraints with respect to N but, put the other way around, could this fact also have played a role in the evolution of endothermy? Endothermy is the ability of animals to maintain body temperature (homeothermy) over a broad range of environmental temperatures through high rates of endogenous heat production. What makes endothermy so intriguing is not just the fact that mammals and birds are endothermic in the strict sense of the term but also because of its extravagant use of energy; a life style that is still fuelling an intensive debate on the mechanisms behind its evolution (Koteja 2004). The debate is centred around the idea that endothermy not only enables homeothermy, but also at the same time allows the maintenance of high levels of locomotor activity (Koteja 2004). The discussion is thus very much centred on the expenditure of resources and not so much its acquisition. It is our conjecture that high dietary C : N ratios may have been an important impetus

for the metabolism of C and thus would contribute to the evolution of endothermy.

Stoichiometry has previously been considered to be an important driver in macro-evolutionary processes (for a review see Kay *et al.* 2005). For instance, the rise of giant herbivorous dinosaurs has been related to the 10 times higher CO₂ concentration during the Cretaceous (e.g. Burness *et al.* 2001; Midgley *et al.* 2002). Of course our hypothesis for the evolution of endothermy need not exclude any of the previously suggested hypotheses as summarized by Koteja (2004). Taking a stoichiometric perspective merely adds a potential additional benefit to the production of heat allowing endothermy: the expulsion of C when dietary C : N ratios are high. As endothermy can also be found among fish, reptiles, insects and plants (see Koteja 2004 for review), studies on other endotherms beyond birds and mammals may be an important avenue to further our insights on the evolution of endothermy from a stoichiometric perspective.

ACKNOWLEDGEMENTS

We thank Steffen Hahn for his help in bringing the assimilation efficiency data together and Liesbeth Bakker and Bill Buttemer as well as four referees for their constructive and stimulating comments on an earlier draft of the manuscript. In part, this work was supported by NWO-grant 851.30.012. This is publication 4273 of the Netherlands Institute of Ecology (NIOO-KNAW).

REFERENCES

- Allen, L.R. & Hume, I.D. (2001). The maintenance nitrogen requirement of the zebra finch *Taeniopygia guttata*. *Physiol. Biochem. Zool.*, 74, 366–375.
- Anderson, T.R., Hessen, D.O., Elser, J.J. & Urabe, J. (2005). Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers. *Am. Nat.*, 165, 1–15.
- Bennett, A.F. & Dawson, W.R. (1976). Metabolism. In: *Biology of the Reptilia* (eds Gans, C. & Dawson, W.R.). Academic Press, London, pp. 127–223.
- Bernays, E.A. (1982). The insect on the plant – a closer look. In: *Proceedings of the 5th International Symposium on Insect–Plant Relationships* (eds Visser, J.H. & Minks, A.K.). Pudoc, Wageningen, pp. 3–17.
- Boersma, M. & Elser, J.J. (2006). Too much of a good thing: on stoichiometrically balanced diets and maximal growth. *Ecology*, 87, 1325–1330.
- Bucher, E.H., Tamburini, D., Abril, A. & Torres, P. (2003). Foli-vory in the white-tipped plantcutter *Phytotoma rutila*: seasonal variations in diet composition and quality. *J. Avian Biol.*, 34, 211–216.
- Buchsbaum, R., Wilson, J. & Valiela, I. (1986). Digestibility of plant constituents by Canada Geese and Atlantic Brant. *Ecology*, 67, 386–393.

- Burness, G.P., Diamond, J. & Flannery, T. (2001). Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. *Proc. Natl Acad. Sci. USA*, 98, 14518–14523.
- Demment, M.W. & van Soest, P.J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.*, 125, 641–672.
- Duncan, R.P., Forsyth, D.M. & Hone, J. (2007). Testing the metabolic theory of ecology: allometric scaling exponents in mammals. *Ecology*, 88, 324–333.
- Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A. *et al.* (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408, 578–580.
- Fox, A.D. & Kahlert, J. (1999). Adjustments to nitrogen metabolism during wing moult in Greylag Geese, *Anser anser*. *Funct. Ecol.*, 13, 661–669.
- Fox, A.D., Kahlert, J. & Ettrup, H. (1998). Diet and habitat use of moulting Greylag Geese *Anser anser* on the Danish island of Saltholm. *Ibis*, 140, 676–683.
- Frost, P.C., Evans-White, M.A., Finkel, Z.V., Jensen, T.C. & Matzek, V. (2005). Are you what you eat? Physiological constraints on organismal stoichiometry in an elementally imbalanced world. *Oikos*, 109, 18–28.
- Gessaman, J.A. & Nagy, K.A. (1988). Energy metabolism: errors in gas-exchange conversion factors. *Physiol. Zool.*, 61, 507–513.
- Hessen, D.O. (2004). Too much energy? *Ecology*, 85, 1177–1178.
- Hohman, W.L., Jefferies, R.L. & Gordon, D.H. (1992). Ecology and management of post-breeding waterfowl. In: *Ecology and Management of Breeding Waterfowl* (eds Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, H., Kadlec, J.A. & Krapu, G.L.). University of Minnesota Press, Minneapolis, pp. 128–189.
- Hume, I.D. (1999). *Marsupial Nutrition*. Cambridge University Press, Cambridge, NY.
- Izhaki, I. & Safriel, U.N. (1989). Why are there so few exclusively frugivorous birds – experiments on fruit digestibility. *Oikos*, 54, 23–32.
- Kay, A.D., Ashton, I.W., Gorokhova, E., Kerkhoff, A.J., Liess, A. & Litchman, E. (2005). Toward a stoichiometric framework for evolutionary biology. *Oikos*, 109, 6–17.
- Kerkhoff, A.J., Enquist, B.J., Elser, J.J. & Fagan, W.F. (2005). Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Glob. Ecol. Biogeogr.*, 14, 585–598.
- Klasing, K.C. (1998). *Comparative Avian Nutrition*. CAB International, London.
- Koteja, P. (2004). The evolution of concepts on the evolution of endothermy in birds and mammals. *Physiol. Biochem. Zool.*, 77, 1043–1050.
- Lochmiller, R.L. & Deerenberg, C. (2000). Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos*, 88, 87–98.
- Marken-Lichtenbelt, W.D.V. (1993). Optimal foraging of a herbivorous lizard, the green iguana in a seasonal environment. *Oecologia*, 95, 246–256.
- Mattson, W.J. (1980). Herbivory in relation to plant nitrogen-content. *Annu. Rev. Ecol. Syst.*, 11, 119–161.
- McGroddy, M.E., Daufresne, T. & Hedin, L.O. (2004). Scaling of C : N : P stoichiometry in forests worldwide: implications of terrestrial redfield-type ratios. *Ecology*, 85, 2390–2401.
- Midgley, J.J., Midgley, G. & Bond, W.J. (2002). Why were dinosaurs so large? A food quality hypothesis. *Evol. Ecol. Res.*, 4, 1093–1095.
- Murphy, M.E. (1996). Nutrition and metabolism. In: *Avian Energetics and Nutritional Ecology* (ed. Carey, C.). Chapman and Hall, New York, pp. 31–60.
- Nagy, K.A. (2005). Field metabolic rate and body size. *J. Exp. Biol.*, 208, 1621–1625.
- Nagy, K.A. & Bradshaw, S.D. (2000). Scaling of energy and water fluxes in free-living arid-zone Australian marsupials. *J. Mammal.*, 81, 962–970.
- Nagy, K.A., Girard, I.A. & Brown, T.K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.*, 19, 247–277.
- Prop, J. & Deerenberg, C. (1991). Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia*, 87, 19–28.
- Prop, J. & Vulink, T. (1992). Digestion by barnacle geese in the annual cycle – the interplay between retention time and food quality. *Funct. Ecol.*, 6, 180–189.
- Reynolds, P.S. & Lee, R.M. (1996). Phylogenetic analysis of avian energetics: passerines and nonpasserines do not differ. *Am. Nat.*, 147, 735–759.
- Robbins, C.T. (1993). *Wildlife Feeding and Nutrition*. Academic Press, San Diego, CA.
- Schmidt-Nielsen, K. (1979). *Animal Physiology: Adaptation and Environment*, 2nd edn. Cambridge University Press, Cambridge.
- Sedinger, J.S. (1997). Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. *Condor*, 99, 314–326.
- Sinclair, A.R.E. (1975). Resource limitation of trophic levels in tropical grassland ecosystems. *J. Anim. Ecol.*, 44, 497–520.
- Sterner, R.W. & Elser, J.J. (2002). *Ecological Stoichiometry: The Biology of Elements From Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.
- Tsahar, E., Ara, Z., Izhaki, I. & Del Rio, C.M. (2006). Do nectar- and fruit-eating birds have lower nitrogen requirements than omnivores? An allometric test. *Auk*, 123, 1004–1012.
- Weathers, W.W. (1996). Energetics of postnatal growth. In: *Avian Energetics and Nutrition* (ed. Carey, C.). Chapman and Hall, New York, pp. 461–496.
- White, T.C.R. (1993). *The Inadequate Environment*. Springer Verlag, Berlin.
- Withers, P.C., Cooper, C.E. & Larcombe, A.N. (2006). Environmental correlates of physiological variables in marsupials. *Physiol. Biochem. Zool.*, 79, 437–453.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Data from the literature on body mass (M , kg), maintenance nitrogen requirements (MNR, mgN day^{-1}), basal metabolic rate (BMR, kJ day^{-1}) and field metabolic rate of free-ranging animals (FMR, kJ day^{-1}) for reptiles, birds, marsupials and eutherian mammals.

Appendix S2 Data from the literature on gross nitrogen and energy food content, and protein and energy assimilation efficiencies for different plant parts (foliage, flowers, fruit, seeds and tubers).

This material is available as part of the online article from:
[http://www.blackwell-synergy.com/doi/full/10.1111/
j.1461-0248.2008.01180.x](http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01180.x).

Please note: Blackwell publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Editor, James Elser

Manuscript received 19 October 2007

First decision made 15 November 2007

Second decision made 18 February 2008

Manuscript accepted 4 March 2008