

LETTER

Mass invariance of population nitrogen flux by terrestrial mammalian herbivores: an extension of the energetic equivalence rule

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Abstract

According to the energetic equivalence rule, energy use by a population is independent of average adult body mass. Energy use can be equated with carbon flux, and it has been suggested that population fluxes of other materials, such as nitrogen and phosphorus, might also be independent of body mass. We compiled data on individual nitrogen deposition rates (via faeces and urine) and average population densities of 26 species of mammalian herbivores to test the hypothesis of elemental equivalence for nitrogen. We found that the mass scaling of individual nitrogen flux was opposite to that of population density for the species in our dataset. By computing the product of individual nitrogen flux and average population density for each species in our dataset, we found that population-level nitrogen flux was independent of species mass, averaging *c.* 3.22 g N ha⁻¹ day⁻¹. Results from this analysis can be used to understand the influence of mammalian herbivore communities on nitrogen cycling in terrestrial ecosystems.

Keywords

Allometry, body mass, elemental equivalence, energetic equivalence, energy flux, eutheria, herbivore, mammal, metatheria, nitrogen flux.

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INTRODUCTION

The physiological traits of individuals can interact with characteristics of populations to explain, in large part, how groups of organisms contribute to the functioning of ecosystems (Peters 1983; Brown 1995; Bradshaw 2003; Brown *et al.* 2004). An example of this interaction is Damuth's (1981) energetic equivalence rule. The energetic equivalence rule states that, at biome to global scales, per unit area energy use by a population, E_{pop} , is independent of the average body mass of the adults in that population (Damuth 1981; Nee *et al.* 1991). As such, all species populations should flux approximately equal amounts of energy, irrespective of body mass. This empirically derived pattern evolved from the observation that individual energy use, E , and population density, D , of mammalian primary consumers scale reciprocally with body mass, M , such that population energy flux, $E_{\text{pop}} = ED$, was independent of body mass, or $E_{\text{pop}} = ED \propto M^{0.75} M^{-0.75} = M^0$ (Damuth 1981; Nagy 1987).

Soon after the energetic equivalence rule was introduced, Peters (1983) suggested that mass independence of population fluxes should hold for both energetic and material currencies. Peters noted that individual elemental flux rates for domesticated mammals were proportional to metabolic rate (Brody 1945) and conjectured that, if this were true for wild mammals, the product of individual elemental flux and population density should be independent of body mass. The suggestion that mass independence holds for population fluxes of multiple elements is intriguing because it means that the contribution of herbivorous mammals to a variety of biogeochemical cycles is independent of body mass at biome to global scales.

However, strong evidence for mass independence of population-level elemental fluxes has been lacking for wild animals. Previous studies have shown that individual carbon (Nagy 1987, 2005; Anderson & Jetz 2005), phosphorous (Peters & Rigler 1973; Wen & Peters 1994; Schaus *et al.* 1997; Vanni *et al.* 2002) and nitrogen (Wen & Peters 1994; Vanni *et al.* 2002; Hobbs 2006; Meehan & Lindroth 2007)

fluxes scale approximately as mass to the $\frac{3}{4}$ power. Several other studies have demonstrated that population density scales approximately as mass to the negative $\frac{3}{4}$ power (Damuth 1981, 1987; White *et al.* 2007). Hobbs (2006) coupled equations for individual nitrogen flux and population density from several sources and suggested that population-level nitrogen flux is independent of body mass for large ungulates. Inferring mass-invariant fluxes from separate analyses is logical, but deriving flux and density patterns from the same species allows for a more robust test of mass invariance and provides a means to estimate the actual mass-invariant flux for the group. Here we present results from a macroecological study that demonstrates that total daily nitrogen flux per unit area by species populations is independent of average species body mass across a diverse range of wild mammalian herbivores.

METHODS

We collected data on body mass (kg), dietary nitrogen content (N , % dry mass), individual daily nitrogen flux (Q ; g N day⁻¹; deposited as faeces and urine) and population density (ind ha⁻¹) for mammalian primary consumers from peer-reviewed journals (see Appendix S1 in Supporting Information). The search engines Web of Science, Biological Abstracts, JSTOR and Google Scholar were used to locate articles that included several combinations and derivations of the following terms: herbivore, faecal nitrogen, mammal, nitrogen balance, nitrogen digestibility, nitrogen flux, nitrogen requirements, protein requirements and urinary nitrogen. Articles were selected or excluded based on the following criteria: (i) the animal of interest must be a non-domesticated, non-volant terrestrial herbivore and (ii) articles must report or provide the necessary information to calculate body mass, total daily nitrogen excretion and dietary nitrogen content. We used Damuth's (1987) dataset for average population density of species. For species in our dataset that were not also in Damuth (1987), we calculated average species density from all available accounts in the literature and in Nowack (1999).

We used generalized linear models (GLMs) to test for effects of (i) body mass, taxonomic affiliation (T , eutheria or metatheria) and dietary nitrogen on individual nitrogen flux; (ii) body mass and taxonomic affiliation on average population density and (iii) body mass, taxonomic affiliation and dietary nitrogen on average population nitrogen flux. The data points for individual nitrogen flux used in our analysis represent the average of multiple individuals assigned to a specific diet trial. In a few cases, nitrogen quantities were calculated from crude protein quantities using the conversion factor of 1 unit crude protein = 0.16 units nitrogen (Robbins 1993). Average population nitrogen flux (Q_{pop} , g N ha⁻¹ day⁻¹) was calculated as the product of

species-specific averages for individual nitrogen flux and population density. The analysis of other taxonomic or guild groupings was not possible due to limited data availability. GLM analysis was conducted on log₁₀-transformed variables. Normalization constants were calculated by de-transforming regression intercepts.

RESULTS

We analysed data on individual nitrogen flux from 139 diet trials involving 26 species of mammalian herbivores (Appendix S1). Our dataset included eutherian and metatherian mammals; browsers and grazers; and ruminants, hindgut fermenters and monogastric herbivores. Individual masses ranged from 0.02 to 451.20 kg. The foods used by researchers in the feeding trials varied and included natural forage, commercial or laboratory prepared maintenance feed, or a mixture of the two. Dietary nitrogen concentration used in trials ranged from 0.21 to 5.22%. Individual nitrogen flux ranged from 0.02 to 97.91 g N day⁻¹. We found that daily individual nitrogen flux was related to species body mass ($F_{1,135} = 2756.93$, $P \leq 0.0001$), dietary nitrogen concentration ($F_{1,135} = 145.11$, $P \leq 0.0001$) and taxonomic affiliation ($F_{1,135} = 18.28$, $P \leq 0.0001$) as $Q = 0.43 M^{0.77} N^{0.84} T$, where T was 0.83 for metatherians and 1.20 for eutherians ($R^2 = 0.96$; Fig. 1a,b). The 95% confidence intervals for the body mass and dietary nitrogen exponents were 0.74–0.80 and 0.70–0.98 respectively.

For the same 26 mammal species, we computed an average population density from estimates in the literature. Average species density ranged from 0.01 to 120 individuals ha⁻¹ and was related to average species body mass ($F_{1,23} = 63.80$, $P \leq 0.0001$) as $D = 1.56 M^{-0.81}$ ($R^2 = 0.73$; Fig. 1c). We found no effect of taxonomic affiliation on species density ($F_{1,23} = 0.48$, $P = 0.48$). The 95% confidence interval for the species mass term was -0.60 to -1.02.

We calculated population nitrogen flux per unit area for each of the 26 species as the product of average population density and average individual nitrogen flux. We found that population nitrogen flux was not related to species body mass ($F_{1,22} = 0.49$, $P = 0.49$), dietary nitrogen concentration ($F_{1,22} = 0.32$, $P = 0.58$) or taxonomic affiliation ($F_{1,22} = 1.41$, $P = 0.25$; Fig. 1d). Species averages of dietary nitrogen concentration ranged from 0.77 to 3.07%. The arithmetic mean of population nitrogen flux for mammalian herbivore species was 3.22 g N ha⁻¹ day⁻¹ (geometric mean = 0.93 g N ha⁻¹ day⁻¹), although it ranged from 0.05 to 34.10 g N ha⁻¹ day⁻¹.

DISCUSSION

Our analysis demonstrates that population nitrogen flux by herbivorous mammals is independent of mass – i.e.

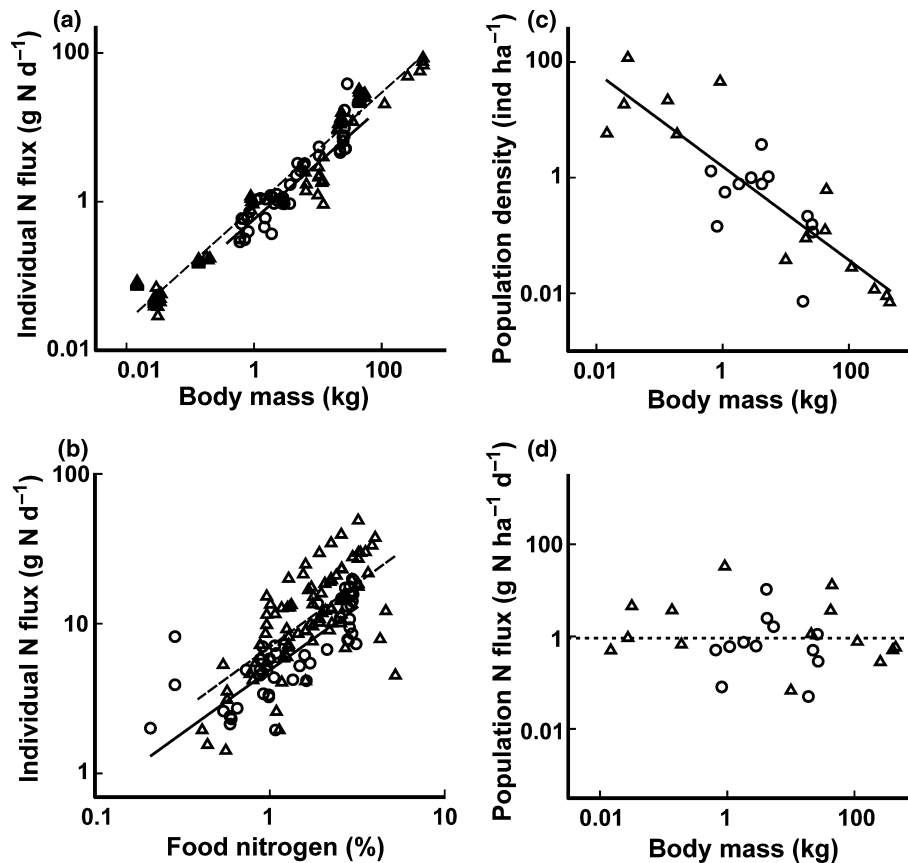


Figure 1 Relationships between (a) body mass, taxonomic affiliation and individual nitrogen flux; (b) dietary nitrogen concentration, taxonomic affiliation and individual nitrogen flux; (c) body mass and population density and (d) body mass and population nitrogen flux. Individual nitrogen flux is standardized for an average dietary nitrogen concentration of 1.8% in (a) and for an average body mass of 30 kg in (b). The data points and least squares lines in (a) and (b) are triangles and dashed lines for eutherians and circles and solid lines for metatherians respectively. The dotted line in (d) depicts the geometric mean of population nitrogen flux for mammalian herbivores.

populations of mice flux, on average, similar quantities of nitrogen per unit area as populations of moose. Damuth (1981) suggested that, at biome to global scales, no mammalian herbivore species fluxes more carbon than another based on size alone. We show that the influence of mammalian herbivore species on nitrogen cycling is also independent of body mass, assuming flux measurements from diet trials are reasonable approximations of flux rates in the wild. The feeding mode (i.e. grazer vs. browser), pattern of deposition and relative availability of excreta-derived nitrogen varies across species, however, which influences spatial patterns and turnover rates of nitrogen at local scales (Pastor *et al.* 1996; Bakker *et al.* 2004).

Individual nitrogen flux differed between taxonomic groups of mammalian herbivores. After controlling for body mass and dietary nitrogen concentration, metatherians fluxed 31% less nitrogen than eutherians (Fig. 1a,b). This flux difference may be related to differences in metabolic rate between the two groups. It is well known

that metatherians have a lower average metabolic rate than eutherians (MacMillen & Nelson 1969; Dawson & Hulbert 1970; McNab 1988, 2005). McNab's (1988) estimate of mass-specific metabolic rates for metatherians was 29% lower than eutherians, which is similar to our estimate of 31% difference for nitrogen flux. This similarity suggests that the difference in average metabolic rate between groups may be a reasonable predictor of differences in the flux rates of multiple elements. The difference in individual nitrogen flux between groups, however, was not manifest at the population level. It is not clear to us whether this was an artefact of sample size or a real phenomenon.

Our analysis demonstrates that, on average, mammalian herbivore populations flux *c.* 3.22 g N ha⁻¹ day⁻¹. This estimate of nitrogen flux is similar to what others have found for individual species using different methods. For instance, Frank *et al.* (1994) estimated nitrogen deposition by elk (*Cervus elaphus*) populations in Yellowstone National

Park using field measurements of faecal deposition rates, lab measurements of faecal nitrogen content and allometric relationships of nitrogen loss via faeces vs. urine. They found that daily nitrogen fluxed by elk populations was $7.4 \text{ g N ha}^{-1} \text{ day}^{-1}$ when averaged across sites. Also, Clark *et al.* (2005) used data from balanced feeding trials and live trapping and found that a community of five rodent species fluxed $10.1 \text{ g N ha}^{-1} \text{ day}^{-1}$, or $2.0 \text{ g N ha}^{-1} \text{ day}^{-1}$ per species.

Our study shows that daily nitrogen flux by mammal populations is independent of species mass. If mass independence of population fluxes held for additional elements, then it would appear that Peters's (1983) contention was correct, that Damuth's (1981, 1987) energetic equivalence concept can be extended to include the flux of both energy and materials. Brody (1945) examined the relationship between total neutral sulphur flux and body mass of domesticated animals and found that sulphur flux scaled approximately as mass to the $3/4$ power. The pattern of sulphur flux in domesticated animals likely holds for wild animals because sulphur excretion is highly correlated with nitrogen excretion, which, in turn, is mainly the product of protein catabolism (Whiting & Draper 1980; Magee *et al.* 2004). We expect that the excretion of other major elements will also scale tightly with metabolic rate because mammals are more or less stoichiometrically homeostatic (Peters 1983; Karasov & Martinez del Rio 2007) and because total dry matter intake rates scale approximately as mass to the $3/4$ power (Peters 1983; Nagy 1987). For elemental equivalence to be clearly demonstrated, however, population density and elemental flux data should be derived from the same group of species. Unfortunately, rigorous testing of general elemental equivalence is currently not possible, as reports of faecal and urinary deposition rates for elements other than nitrogen are scarce for wild mammals.

The invariance of population nitrogen flux demonstrated by this analysis is an empirically derived pattern detected at a global scale for a specific group of species (i.e. mammalian herbivores). The likelihood that elemental equivalence will hold for other taxonomic groups, or at other spatial scales, is currently equivocal. Regarding taxa, it has been shown that the population density of many organisms, including soil arthropods (Meehan *et al.* 2006), raptorial birds (Russo *et al.* 2003), terrestrial mammals (primary and secondary consumers combined, Damuth 1987) and aquatic animals (Damuth 1987) scales approximately as mass raised to the $-3/4$ power. For other taxa, it has been shown that individual fluxes of several elements scale approximately as mass to the $3/4$ power (Peters & Rigler 1973; Nagy 1987, 2005; Wen & Peters 1994; Schaus *et al.* 1997; Vanni *et al.* 2002; Anderson & Jetz 2005; Meehan & Lindroth 2007). Thus, it is quite possible that

general elemental equivalence will hold across several types of organisms. Regarding spatial scales, several studies have shown that mass–density relationships at the global scale break down at a local scale (Currie 1993; Russo *et al.* 2003; White *et al.* 2007). In fact, plots of log-transformed abundance and density for species that coexist in localized areas often show a triangular shape with low r^2 values rather than a negative slope with relatively high r^2 values, which is typical of global datasets (White *et al.* 2007). The possible explanations for the discrepancy between global and local size–density relationships are actively debated (Currie 1993; Blackburn & Gaston 1997; Ackerman *et al.* 2003; White *et al.* 2007). Although there are significant challenges in relating global phenomena to local processes, our equation for predicting individual nitrogen flux from body mass and dietary nitrogen was quite powerful ($r^2 = 0.96$). Thus it can be combined with local density data to estimate population nitrogen flux for different species at the community scale in order to evaluate nitrogen equivalence at the local level.

Our estimate of population nitrogen flux can be used to understand the influence of mammalian herbivores on nitrogen cycling in terrestrial ecosystems. For example, Cleveland *et al.* (1999) estimated that biological nitrogen fixation for grasslands averaged $2.7 \text{ kg N ha}^{-1} \text{ year}^{-1}$. Given a conservative assumption that most grasslands can support a mammalian herbivore community of four relatively abundant species, the nitrogen fluxed through mammalian herbivores would equal $4 \text{ spp} \times 3.22 \text{ g N ha}^{-1} \text{ day}^{-1} \text{ spp}^{-1} \times 365 \text{ days} = 4.70 \text{ kg N ha}^{-1} \text{ year}^{-1}$, or nearly twice the amount of annual biological nitrogen fixation in that biome. This simple math assumes that individual nitrogen flux is relatively static throughout the year, and that the total material fluxed by a functional group is linearly related to the number of species in that group. The former assumption is not strictly accurate but is a reasonable approximation. The latter assumption is probably only reasonable when considering a small number of common species. A more likely scenario might be that total material flux would increase at a decreasing rate with each addition of species due to resource limitation, competition between consumers and compensatory changes in species density.

Patterns of energetic and elemental equivalence are certainly intriguing from an evolutionary standpoint (Damuth 2007). Here, however, we have stressed the practical value of deriving defensible estimates of flux for understanding the role of mammalian herbivores in community- and ecosystem-level processes. We suggest that future research should focus on quantifying the flux of other elements (e.g. phosphorus, potassium and sulphur) through wild herbivores at a variety of spatial and temporal scales, and that the functional relationship between species richness and population fluxes be sorted

out. These measures will allow us to assess the generality of elemental equivalence and to apply it to studies on the relationship between species diversity and ecosystem functioning.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Appendix S1 Data used in this analysis.

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