Body size–fecal nutrient patterns of mammalian herbivores

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In the recent article by le Roux et al. (1), the authors elegantly interlink several aspects of savanna ecology, one of which is a theoretically predicted positive relationship between herbivore body size and fecal N:P ratio. Their South African dataset supports this relationship, but our data from four other countries—including two other African savannas—show different patterns (Fig. 1 and Table 1). We therefore question the generality of the predicted positive relationship claimed for mammalian terrestrial herbivores and argue that body size–fecal N:P patterns are controlled by at least three factors operating simultaneously.

The first factor, adopted by both le Roux et al. and Schmitz (2), predicts that fecal N:P increases with herbivore body size, predominantly because large herbivores contain more P-rich bones (i.e., lower body N:P), leading to relatively higher P absorption from food and lower fecal P. This was indeed observed by le Roux et al. However, we only found a significant body size–fecal P pattern in one site, and this pattern was either quadratic or opposite that reported by le Roux et al. (Fig. 1*B*), illustrating that P investment in bones is not the general or only driving force behind body size–fecal N:P patterns. Indeed, Sterner and Elser (3) predicted a quadratic relationship between body size and body N:P, driven by both P investment in bones (factor 1) and metabolic P requirement (factor 2). Our Tanzanian data support this quadratic pattern (Fig. 1*B*), while our other sites and the one reported by le Roux et al. might not be showing this pattern due to more restricted body size ranges.

The predominantly negative body size–fecal N:P relationship in our sites was generally driven by a negative relationship for fecal N (Fig. 1 *A*, *C*, and *D*). This pattern, which is not inconsistent with that reported by le Roux et al., probably reflects that smaller herbivores selectively feed on N-richer food and shows that variation in fecal N:P is at least partly driven by dietary N differences (4) (factor 3). Diet N:P was assumed by le Roux et al. to be constant among herbivore species, but it probably increased with average body size (see their figure 4B), implying that this third factor might have (co) driven the body size–fecal N:P pattern as well.

The relationship between body size and excreted N:P is better studied for aquatic than terrestrial animals. Vanni and McIntyre (5) showed that this relationship is overall positive for aquatic vertebrates but is not strongly driven by variation in body N:P (hence, factor 1). Other factors such as growth rate (directly linked to factor 2) and diet N:P or selectivity of food (factor 3) are more decisive.

That we did find significant body size–fecal N:P patterns in all sites—albeit partly opposite to those found by le Roux et al.—implies that herbivore body size indeed affects ecosystem processes driven by variation in fecal quality. Consistently, the conclusions that le Roux et al. draw about the effects of variation in herbivore fecal N:P on plant community composition or the loss of specifically large herbivores are supported by other studies (5–7). However, it remains poorly understood which of the three (and possibly other) operating factors dominates the body size–fecal N:P relationship. Therefore, we are building a more comprehensive fecal database with le Roux et al. and other researchers, and we are interested in receiving additional data.

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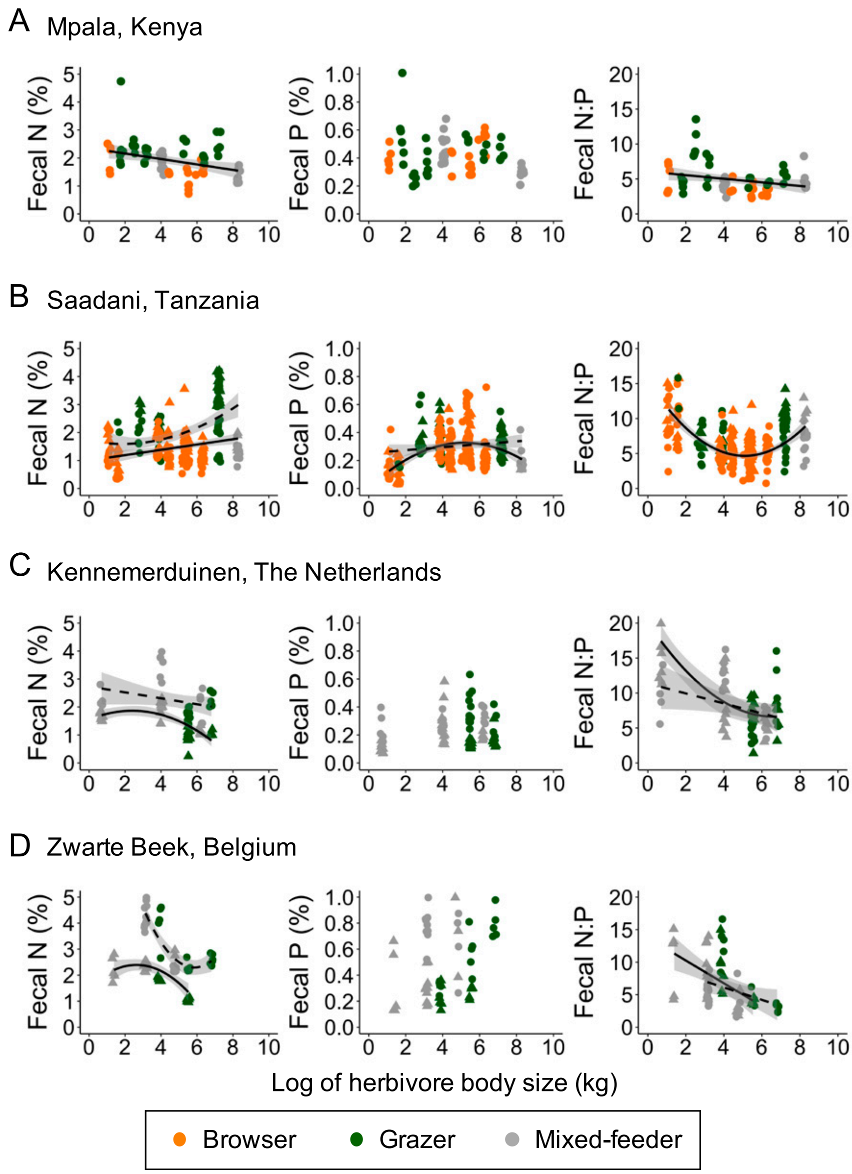

Fig. 1. Fecal N, P, and N:P ratio in relation to herbivore body size (kilograms) from refs. 6 and 8 at (*A*) Mpala, Kenya (9), (*B*) Saadani, Tanzania (10), (*C*) Kennemerduinen, The Netherlands (6), and (*D*) Zwarte Beek, Belgium (6). Different feeding strategies are indicated by color. Points in *B* indicate dung collected during the dry season (February, July, and August–September) and triangles during the wet season (November–January). Points in *C* and *D* indicate dung collected during winter (January) and triangles during spring (April). Trendlines are drawn for significant single-term linear or polynomial model fits to all herbivores regardless of feeding strategy, with separate lines for season in (*B*–*D*).

Table 1. Test statistics and coefficient estimates for generalized least-squares models (either linear or polynomial) of all feeding strategies combined

Location	Fecal N ∼ log(body size)				Fecal P ∼ log(body size)				Fecal N:P ∼ log(body size)			
A: Mpala, Kenya												
AICc (AICc null)	119.86 (126.47)				−75.16 (−76.45)				296.16 (298.72)			
Log-lik ratio	8.80				0.90				4.75			
P value (df)	0.003** (66)				0.343 (66)				0.029* (66)			
	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value
Intercept	2.35	0.16	14.39	<0.001***	0.46	0.04	11.68	<0.001***	6.06	0.60	10.13	<0.001***
Log(body size)	−0.10	0.03	−3.02	0.004**	−0.01	0.01	−0.94	0.352	−0.26	0.12	−2.19	0.032*
B: Saadani, Tanzania (dry period)												
AICc (AICc null)	463.11 (473.75)				−286.79 (−250.03)				1,045.52 (1,129.31)			
Log-lik ratio	12.70				40.89				87.93			
P value (df)	<0.001*** (215)				<0.001*** (214)				<0.001*** (214)			
	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value
Intercept	1.00	0.14	7.16	<0.001***	0.29	0.01	34.2	<0.001***	6.01	0.18	33.27	<0.001***
Log(body size)	0.09	0.03	3.60	<0.001***	0.32	0.12	2.54	0.012*	−8.94	2.66	−3.36	<0.001***
Log(body size)^2					−0.76	0.12	−6.16	<0.001***	26.01	2.66	9.78	<0.001***
B: Saadani, Tanzania (wet period)												
AICc (AICc null)	242.33 (264.72)				−152.34 (−151.54)				557.59 (556.17)			
Log-lik ratio	26.66				2.91				0.69			
P value (df)	<0.001*** (108)				0.088° (109)				0.407 (109)			
	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value
Intercept	2.00	0.07	29.97	<0.001***	0.25	0.03	7.91	<0.001***	6.66	0.78	8.54	<0.001***
Log(body size)	3.52	0.70	5.00	<0.001***	0.01	0.01	1.70	0.092°	0.12	0.15	0.82	0.412
Log(body size)^2	1.46	0.70	2.07	0.041*								
C: Kennemerduinen, The Netherlands (winter)												
AICc (AICc null)	37.97 (67.14)				−78.17 (−78.79)				247.12 (297.01)			
Log-lik ratio	33.85				1.67				57.08			
P value (df)	<0.001*** (44)				0.197 (45)				<0.001*** (44)			
	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value
Intercept	1.39	0.05	26.23	<0.001***	0.14	0.03	4.18	<0.001***	9.56	0.55	17.53	<0.001***
Log(body size)	−2.03	0.31	−6.63	<0.001***	0.01	0.01	1.27	0.209	−27.69	5.19	−5.34	<0.001***
Log(body size)^2	−1.96	0.34	−5.74	<0.001***					7.97	3.29	2.42	0.020*
C: Kennemerduinen, The Netherlands (spring)												
AICc (AICc null)	78.92 (79.44)				−55.30 (−55.32)				197.18 (199.21)			
Log-lik ratio	2.92				2.39				4.43			
P value (df)	0.087° (33)				0.122 (33)				0.035* (33)			
	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value
Intercept	2.73	0.33	8.40	<0.001***	0.25	0.05	5.26	<0.001**	11.37	1.76	6.45	<0.001***
Log(body size)	−0.11	0.06	−1.70	0.099°	0.01	0.01	1.53	0.137	−0.71	0.34	−2.11	0.043*
D: Zwarte Beek, Belgium (winter)												
AICc (AICc null)	41.38 (54.06)				23.54 (22.81)				166.10 (179.41)			
Log-lik ratio	17.79				1.72				18.42			
P value (df)	<0.001*** (28)				0.190 (29)				<0.001*** (29)			
	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value
Intercept	2.05	0.08	26.86	<0.001***	0.18	0.18	1.05	0.301	15.41	2.17	7.10	<0.001***
Log(body size)	−1.51	0.43	−3.54	0.001**	0.06	0.05	1.29	0.208	−2.16	0.47	−4.64	<0.001***
Log(body size)^2	−1.29	0.43	−3.03	0.005**								
D: Zwarte Beek, Belgium (spring)												
AICc (AICc null)	56.30 (97.56)				18.77 (16.34)				180.18 (182.40)			
Log-lik ratio	46.29				0.00				4.65			
P value (df)	<0.001*** (30)				0.995 (31)				0.031* (31)			
	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value	Est	SE	*t* value	*P* value
Intercept	3.32	0.09	36.93	<0.001***	0.73	0.18	4.04	<0.001***	9.93	2.08	4.77	<0.001***
Log(body size)	−4.37	0.52	−8.46	<0.001***	0.00	0.04	0.01	0.995	−0.95	0.44	−2.17	0.038*
Log(body size)^2	2.34	0.52	4.52	<0.001***								

As an indication of overall model fit, the Akaike information criterion (AICc) statistic of each model is presented alongside the AICc of each model's corresponding null model (intercept-only model). The log-likelihood (Log-lik) ratio statistic and associated *P* value for each model compared to the null model are also given with degrees of freedom (df) reported in parentheses. Heteroscedasticity was corrected in the models of fecal N and N:P in the Dutch site for winter. Significance: ***$P <$ 0.001, **$P < 0.01$, *$P < 0.05$, °$P < 0.1$. Est, estimate; SE, standard error.

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