A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores

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Abstract: As gut capacity is assumed to scale linearly to body mass (BM), and dry matter intake (DMI) to metabolic body weight (BM(0.75)), it has been proposed that ingesta mean retention time (MRT) should scale to BM(0.25) in herbivorous mammals. We test these assumptions with the most comprehensive literature data collations (n=74 species for gut capacity, n=93 species for DMI and MRT) to date. For MRT, only data from studies was used during which DMI was also recorded. Gut capacity scaled to BM(1.06). In spite of large differences in feeding regimes, absolute DMI (kg/d) scaled to BM(0.76) across all species tested. Regardless of this allometry inherent in the dataset, there was only a very low allometric scaling of MRT with BM(0.14) across all species. If species were divided according to the morphophysiological design of their digestive tract, there was non-significant scaling of MRT with BM(0.04) in colon fermenters, BM(0.08) in non-ruminant foregut fermenters, BM(0.06) in browsing and BM(0.04) in grazing ruminants. In contrast, MRT significantly scaled to BM(0.24) (CI 0.16-0.33) in the caecum fermenters. The results suggest that below a certain body size, long MRTs cannot be achieved even though coprophagy is performed; this supports the assumption of a potential body size limitation for herbivory on the lower end of the body size range. However, above a 500 g-threshold, there is no indication of a substantial general increase of MRT with BM. We therefore consider ingesta retention in mammalian herbivores an example of a biological, time-dependent variable that can, on an interspecific level, be dissociated from a supposed obligatory allometric scaling by the morphophysiological design of the digestive tract. We propose that very large body size does not automatically imply a digestive advantage, because long MRTs do not seem to be a characteristic of very large species only. A comparison of the relative DMI (g/kg(0.75)) with MRT indicates that, on an interspecific level, higher intakes are correlated to shorter MRTs in caecum, colon and non-ruminant foregut fermenters; in contrast, no significant correlation between relative DMI and MRT is evident in ruminants.

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Data appendix (Table 1 and 2). Literature references for these data collections are included in the reference list of the main article.

Appendix Table 1. Data collection of body mass (BM) and gastrointestinal (GIT) capacity (measured as total contents wet weight) in herbivorous mammals.

Spezies	BM (kg)	GIT contents (kg)	Source
Caecum fermenter			
Peromyscus maniculatus	0.015	0.001	(Demment and Van Soest 1983)
Clethrionomys gapperi	0.017	0.003	(Demment and Van Soest 1983)
Zapus hudsonius	0.018	0.002	(Demment and Van Soest 1983)
Microtus pennsylvanicus	0.020	0.004	(Demment and Van Soest 1983)
Zapus princeps	0.031	0.007	(Demment and Van Soest 1983)
Eutamius minimus	0.034	0.003	(Demment and Van Soest 1983)
Phyllotis darwini	0.040	0.001	(Karasov et al. 1986)
Microtus orchogaster	0.042	0.006	(Gross et al. 1985b; Hammond and Wunder 1991; Castle and Wunder 1995)
Dicrostonyx groenlandicus	0.047	0.007	(Hammond and Wunder 1991)
Meriones unguiculatus	0.050	0.001	(Pei et al. 2001b)
Sciurus carolensis	0.080	0.007	(Demment and Van Soest 1983)
Neotoma lepida	0.100	0.003	(Karasov et al. 1986)
Tamias striatus	0.101	0.008	(Demment and Van Soest 1983)
Thomomys bottae	0.118	0.004	(Loeb et al. 1991)
Thomomys talpoides	0.125	0.017	(Demment and Van Soest 1983)
Spermophilus lateralis	0.199	0.017	(Demment and Van Soest 1983)
Neotoma cinerea	0.203	0.029	(Demment and Van Soest 1983)
Spermophilus richardsoni	0.253	0.035	(Demment and Van Soest 1983)
Cynomys leucurus	0.574	0.110	(Demment and Van Soest 1983)
Cavia porcellus	0.685	0.055	(Parra 1978)
Sylvilagus auduboni	0.860	0.126	(Demment and Van Soest 1983)
Sylvilagus floridanus	1.077	0.126	(Demment and Van Soest 1983)
Omdatra zibethicus	1.315	0.084	(Demment and Van Soest 1983)
Oryctolagus cuniculus	2.023	0.228	(Parra 1978; Dierenfeld 1984)
Marmota monax	2.112	0.439	(Demment and Van Soest 1983)
Lagostomus maximus	2.800	0.221	(Besselmann 2005)
Myocastor coypus	5.750	0.453	(Snipes et al. 1988)
Phascolarctos cinereus	7.250	1.432	(Cork and Warner 1983)
Castor canadensis	11.025	0.847	(Demment and Van Soest 1983)
Hydrochaeris hydrochaeris	45.385	6.164	(Parra 1978; Borges et al. 1996)
Colon fermenter			
Procavia habessinica	2.200	0.251	(Björnhag et al. 1995)
Procavia capensis	2.210	0.277	(Leon 1980)
Papio anubis	7.180	0.630	(Demment and Van Soest 1983)
Lasiorhinus latifrons	20.300	4.439	(Dierenfeld 1984)
Phacochoerus africanus	74.000	9.916	(Parra 1978)
Equus asinus	191.500	31.190	(Demment and Van Soest 1983)
Trichechus manatus	401.288	31.864	(Reynolds and Rommel 1996)
Equus caballus	426.000	69.864	(Parra 1978)
Diceros bicornis	1140.000	158.670	(Clauss pers. obs. 2006)
Loxodonta africana	3140.000	542.000	(Clauss et al. 2005d)
Non-ruminant foregut fermenter			
Bradypus tridactylus	2.400	0.648	(Foley et al. 1995)
Wallabia	4.500	0.252	(Parra 1978)
Macropus eugenii	5.150	0.459	(Dellow and Hume 1982; Munn et al. 2006)
Thylogale thetis	5.850	0.590	(Dellow and Hume 1982)
Macropus rufogriseus spec	16.158	2.466	(Schwarm and Clauss, pers. obs. 2006)
Tayassu tajacu	17.897	1.663	(Schwarm and Clauss, pers. obs. 2006)

Macropus robustus	18.600	2.459	(Freudenberger 1992)
Macropus giganteus	19.050	2.405	(Dellow and Hume 1982)
Macropus fuliginosus	22.300	4.491	(Dierenfeld 1984)
Macropus rufus	29.000	5.648	(Dierenfeld 1984)
Hippopotamus amphibius	1384.000	303.096	(Parra 1978)
Ruminant foregut fermenter			
Gazella thomsoni	20.000	2.560	(Parra 1978)
Capra hircus	32.100	6.551	(Freudenberger 1992)
Litocranius walleri	32.300	3.425	(Parra 1978; Maloiy et al. 1982; Clemens and Maloiy 1983)
Hemitragus jemlahicus	41.600	6.806	(Clauss et al. 2005b)
Gazella granti	53.000	5.535	(Parra 1978; Clemens and Maloiy 1983)
Aepyceros melampus	55.500	5.672	(Parra 1978; Clemens and Maloiy 1983)
Ovis aries	70.000	10.500	(Parra 1978)
Kobus kob	77.000	11.319	(Parra 1978)
Addax nasomaculatus	83.750	21.534	(Clauss pers. obs. 2005)
Tragelaphus imberbis	92.000	8.464	(Parra 1978)
Damaliscus lunatus	123.000	17.602	(Parra 1978; Clemens and Maloiy 1983)
Alcelaphus buselaphus	136.000	17.979	(Parra 1978; Clemens and Maloiy 1983)
Oryx gazella	177.267	29.433	(Parra 1978; Maloiy et al. 1982; Clemens and Maloiy 1983)
Connochaetes taurinus	203.250	35.500	(Parra 1978; Clemens and Maloiy 1983)
Kobus ellipsiprymnus	219.150	34.130	(Parra 1978; Maloiy et al. 1982; Clemens and Maloiy 1983)
Okapia johnstoni	231.000	35.240	(Clauss et al. 2006b)
Camelus dromedarius	294.100	62.200	(Demment and Van Soest 1983)
Bos indicus	391.000	39.213	(Parra 1978)
Bos taurus	447.800	76.486	(Parra 1978)
Taurotragus oryx	497.267	83.127	(Parra 1978; Maloiy et al. 1982; Clemens and Maloiy 1983)
Bos javanicus	600.000	74.800	(Clauss pers. obs. 2006)
Giraffa camelopardalis	663.750	119.200	(Maloiy et al. 1982; Clemens and Maloiy 1983)
Syncerus caffer	671.433	109.752	(Parra 1978; Maloiy et al. 1982; Clemens and Maloiy 1983)

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Appendix Table 2. Data collection of body mass (BM), relative dry matter intake (rDMI) and particle mean retention time (MRT) in herbivorous mammals. In the ruminants, the classification as browser (BR) or grazer (GR) is indicated.

Species	BM (kg)	rDMI ($g/kg^{0.75}$)	MRT (h)	Diet	Marker	Sources
Caecum fermenter						
Mus musculus	0.035	73	13.0	pelleted	sudan III	(Karasov et al. 1986)
Microtus brandti	0.043	86	5.5	pelleted	Cr-f	(Pei et al. 2001a)
Microtus orchogaster	0.050	93	13.5	pelleted	calc.	(Hammond and Wunder 1991)
Meriones unguiculatus	0.052	58	13.1	pelleted	Cr-f	(Pei et al. 2001b)
Microtus townsendii	0.055	71	13.1	pelleted	Cr-f	(Hume et al. 1993)
Eutamias amoenus	0.062	62	14.1	pelleted	Cr-f	(Hume et al. 1993)
Phyllotis darwini	0.064	76	12.9	pelleted	Cr-f, flag tape	(Sakaguchi and Ohmura 1992; Bozinovic and Nespolo 1997)
Cricetus cricetus	0.105	55	9.1	pelleted	Cr-f	(Sakaguchi et al. 1987)
Neotoma lepida	0.125	46	13.0	pelleted	sudan III	(Karasov et al. 1986)
Octodon degus	0.177	38	15.5	pelleted	Cr-f	(Sakaguchi and Ohmura 1992)
Arvicola terrestris	0.230	73	5.4	pelleted	feathers	(Woodall 1989)
Rattus norwegicus	0.295	60	13.1	pelleted	Cr-f	(Sakaguchi et al. 1987)
Cavia porcellus	0.571	56	21.1	pelleted	Cr-f	(Sakaguchi et al. 1987; Sakaguchi and Nabata 1992; Sakaguchi et al. 1992; Sakaguchi and Ohmura 1992)
Pseudocheirus peregrinus	0.621	49	35.0	foliage	^{103}Ru-P	(Chilcott and Hume 1985) (assuming a DMI for the passage experiment as for the uncollared digestibility experiment)
Spermophilus columbianus	0.663	35	22.1	pelleted	Cr-f	(Hume et al. 1993)
Petauroides volans	1.050	44	46.0	foliage	^{103}Ru-P	(Foley and Hume 1987b; Foley and Hume 1987a)
Hapalemur griseus	1.050	26	47.5	artificial diets	Cr-f	(Campbell et al. 2004)
Marmota caligata	2.308	60	28.9	pelleted	Cr-f	(Hume et al. 1993)
Trichosurus vulpecula	2.425	28	44.3	pelleted, foliage	$YbCl_3$, ^{103}Ru-P	(Foley and Hume 1987b; Foley and Hume 1987a; Sakaguchi and Hume 1990)
Propithecus tattersalli	3.087	24	36.3	zoo diet	Cr-f	(Campbell et al. 1999)
Oryctolagus cuniculus	3.192	46	22.6	pelleted	Cr-f	(Sakaguchi et al. 1987; Sakaguchi and Hume 1990; Gidenne et al. 1991; Gidenne 1994)
Lagostomus maximus	3.459	46	27.1	hay only	Cr-f	(Besselmann 2005)
Propithecus verreauxi	3.502	28	33.5	zoo diet, lab diet	Cr-f	(Campbell et al. 1999; Campbell et al. 2004)
Myocaster coypus	4.400	45	45.0	pelleted	Cr-f	(Sakaguchi and Nabata 1992)
Phascolarctos cinereus	7.000	41	100.0	foliage	^{103}Ru-P	(Cork et al. 1983; Cork and Warner 1983)
Dolichotis patagonum	7.400	41	27.3	pelleted	Cr-f	(Sakaguchi et al. 1992)
Erethizon dorsatum	10.300	18	38.4	forage	$YbNO_3$	(Felicetti et al. 2000) (assuming the same BW and DMI as in the digestibility trial)
Castor canadensis	13.133	79	26.1	forage	plastic beads	(Fryxell et al. 1994) (read from Fig. 1 and 2, matching pairs only)
Hydrochoeris hydrochoeris	45.000	44	31.0	grass	Cr-f	(Schwarm, Ortmann, Clauss pers. obs. 2007)

Colon fermenter						
Cercopithecus talapoin	1.600	118	16.8	zoo diet	plastic particles	(Lambert 2002)
Cercopithecus ascanius	5.200	106	27.2	zoo diet	plastic particles	(Lambert 2002)
Alouatta villosa	6.150	35	37.3	extruded	Cr-f	(Edwards and Ullrey 1999)
Cercopithecus neglectus	6.500	81	34.1	zoo diet	plastic particles	(Lambert 2002)
Alouatta seniculus	8.180	30	40.4	extruded	Cr-f	(Edwards and Ullrey 1999)
Cercopithecus mitis	8.600	68	25.0	zoo diet	plastic particles	(Lambert 2002)
Lasiorhinus latifrons	26.200	34	60.5	pelleted	^{103}Ru-P	(Barboza 1993)
Vombatus ursinus	29.450	34	68.5	pelleted	^{103}Ru-P	(Barboza 1993)
Pan troglotydes	52.700	41	37.2	zoo diet	Cr-f, plastic particles	(Milton and Demment 1988; Lambert 2002)
Gorilla gorilla	118.000	30	50.0	zoo diet	plastic particles	(Remis 2000)
Dugong dugong	130.500	37	155.3	sea grass	plastic particles	(Lanyon and Marsh 1995)(assuming a water content of seagrass of 93 %)
Equus asinus	164.167	69	38.2	whole forages	$LaCl_3$, Cr-f	(Izraely et al. 1989; Pearson et al. 2001)
Tapirus terrestris	194.667	43	54.7	zoo diet	Cr-f	(Lang, Clauss and Hummel, pers. obs. 2007)
Equus caballus	274.647	83	28.5	whole forages/mixed diets	undefined coloured particles, ^{103}Ru-P, $YbCl_3$, Cr-f	(Wolter et al. 1976; Orton et al. 1985a; Orton et al. 1985b; Pagan et al. 1998; Pearson et al. 2001; Moore-Colyer et al. 2003)
Tapirus indicus	275.556	53	56.1	zoo diet	Cr-f	(Lang, Clauss and Hummel, pers. obs. 2007)
Diceros bicornis	1196.923	66	45.4	zoo diet	Cr-f	(Clauss et al. 2005a; Steuer et al. 2007)
Rhinoceros unicornis	2125.000	70	60.1	zoo diet	Cr-f	(Clauss et al. 2005c)
Ceratotherium simum	2200.000	71	43.0	grass hay	Cr-f	(Steuer et al. 2007)
Elephas maximus	2551.825	92	24.8	grass hay	rubber rings	(Hackenberger 1987) (calculated using the original data)
Loxodonta africana	2575.152	132	20.3	grass hay	rubber rings	(Hackenberger 1987) (calculated using the original data)
Non-ruminant foregut fermenter						
Potorus tridactylus	0.931	45	27.0	pelleted	^{103}Ru-P	(Wallis 1994)
Bettongia pencillata	1.062	44	33.5	pelleted	^{103}Ru-P	(Wallis 1994)
Lagorchestes hirsutus	1.234	32	38.0	pelleted	Cr-f	(Bridie et al. 1994)
Bradypus tridactylus	2.400	22	146.8	foliage	$YbCl_3$, $LaCl_3$, $SmCl_3$	(Foley et al. 1995)
Aeprymnus rufescens	2.979	34	35.6	pelleted	^{103}Ru-P	(Wallis 1994)
Thylogale thetis	4.050	49	22.4	whole forages	^{103}Ru-P	(Dellow 1982)
Macropus eugenii	4.800	36	24.8	whole forages	^{103}Ru-P	(Dellow 1982)
Trachypithecus auratus	6.000	36	45.0	zoo diet	Cr-f	(Nijboer et al. 2006)
Semnopithecus cristatus	7.000	23	46.8	pelleted	Cr-f	(Sakaguchi et al. 1991)
Rhinopithecus bieti	8.500	11	37.5	browse lichens grass	plastic particles	(Kirkpatrick et al. 2001)
Colobus guereza	10.800	26	53.1	extruded	Cr-f	(Edwards and Ullrey 1999)
Nasalis larvatus	12.000	32	49.0	zoo diet	plastic particles	(Dierenfeld et al. 1992)
Pygathrix nemaeus	12.100	66	33.8	extruded	Cr-f	(Edwards and Ullrey 1999)

Macropus robustus	19.300	62	28.0	whole forages	^{103}Ru-P	(Dellow 1982; Freudenberger and Hume 1992)
Tayassu tajacu	19.500	36	42.3	hay/rice bran	Cr-O	(Comizzoli et al. 1997)
Macropus giganteus	25.483	42	40.2	whole forages	fuchsin, ^{103}Ru-P	(Forbes and Tribe 1970; Dellow 1982)
Macropus rufus	36.961	35	43.1	whole forages	brilliant green, fuchsin, Cr-f	(Foot and Romberg 1965; McIntosh 1966; Forbes and Tribe 1970; Munn and Dawson 2006)
Hexaprotodon liberiensis	238.000	34	66.6	whole forages/zoo diet	Cr-f	(Clauss et al. 2004)
Hippopotamus amphibius	2175.000	37	71.3	whole forages/zoo diet	Cr-f	(Clauss et al. 2004)
Ruminant foregut fermenter						
Tragulus javanicus (BR)	1.400	26	26.5	zoo diet	Cr-O	(Morat and Nordin 1978)(using only the Cr-O data)
Tragulus napu (BR)	2.800	60	49.0	zoo diet	Cr-f	(Conklin and Dierenfeld 1994)
Cephalophus monticola (BR)	3.850	53	24.4	whole forage/pelleted	Cr-f	(Luginbuhl et al. 1990)
Pudu pudu (BR)	9.100	57	30.0	zoo diet	Cr-f	(Conklin-Brittain and Dierenfeld 1996)
Cephalophus maxwelli (BR)	9.400	57	42.0	zoo diet	Cr-f	(Conklin-Brittain and Dierenfeld 1996)
Capreolus capreolus (BR)	24.725	37	27.0	whole forage/pelleted	$YbCl_3$	(Holand 1994)
Capra ibex	35.935	67	39.5	whole forages	Cr-f	(Gross et al. 1996)
Capra hircus	43.255	84	32.7	whole forges/mixed diets	^{103}Ru-P, Cr-f	(Lindberg 1988; Freudenberger and Hume 1992; Kennedy et al. 1992)
Ovis aries (GR)	46.038	55	55.9	whole forges/mixed diets	fuchsin, Cr-f	(Foot and Romberg 1965; Forbes and Tribe 1970; Udén et al. 1982; Udén and Van Soest 1982; Ramanzin et al. 1991; Kennedy et al. 1992; Bartocci et al. 1997)
Odocoileus virginianus (BR)	64.765	60	22.8	whole forages/pelleted	$^{51}CrCl_3$, ^{51}Cr-O	(Mautz and Petrides 1971)
Cervus elaphus	74.500	57	31.9	whole forages/pelleted	^{103}Ru-P	(Milne et al. 1978)
Bubalus depressicornis	90.000	61	39.0	zoo diet	Cr-f	(Flores-Miyamoto et al. 2005)
Addax nasomaculatus (GR)	91.000	59	55.0	hay	Cr-f	(Hummel, Hammer, Clauss, pers. obs. 2007)
Cervus elaphus canadensis	141.286	95	30.1	whole forages/pelleted	Cr-O	(Jiang and Hudson 1996)
Bos grunniens (GR)	176.000	70	78.2	pelleted	Sudan III	(Schaefer et al. 1978)
Bos indicus (GR)	205.000	70	55.0	hay	stained particles	(Maloiy 1972)
Okapia johnstoni (BR)	226.875	61	46.8	zoo diet	Cr-f	(Hummel et al. 2005)
Ovibos moschatus (GR)	249.500	60	40.5	hay	Yb-f	(Barboza et al. 2006)
Bison bison (GR)	279.000	70	78.8	pelleted	Sudan III	(Schaefer et al. 1978)
Bos javanicus (GR)	323.000	55	55.4	grass	Cr-f	(Schwarm, Ortmann, Clauss pers. obs. 2007)
Camelus dromedarius	325.000	42	46.0	hay	stained particles	(Maloiy 1972)
Bos taurus (GR)	341.382	62	70.3	whole forges/mixed diets	$YbCl_3$, Cr-f, Sudan III, Dy	(Schaefer et al. 1978; Udén et al. 1982; Udén and Van Soest 1982; McCollum and Galyean 1985; Luginbuhl et al. 1994; Bartocci et al. 1997; Burns et al. 1997)
Bubalus bubalus (GR)	417.000	50	58.0	mixed diet	Cr-f	(Bartocci et al. 1997)
Giraffa camelopardalis (BR)	665.385	63	49.8	whole forages/zoo diets	Cr-f	(Schaub 2005)
Camelus bactrianus	687.000	19	85.2	hay	Cr-f	(Cahill and McBride 1995)

Cr-f = chromium-mordanted fibre

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