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Table 1Mean milk intake and intake of milk nutrients, body mass and average daily gain (ADG) at peak lactation in suckling mammalian young measured either by the isotope transfer technique (IT), the isotope dilution technique (ID) or the weigh-suckle-weigh method (WSW)

Species	Ž.	Peak lactation	z	Litter size	Body mass	Neonate ADG	Milk intake (g d ⁻¹)	Intake of milk nutrients	k nutrients			Method	Reference
		(week)			b <u>0</u>	(, pg)		Solids (g d ⁻¹)	Fat (g d ⁻¹)	Protein (g d ⁻¹)	Sugar (g d ⁻¹)	(Isotope)	
Marsupials Diprotodontia													
Bettongia penicillata	1	14	5	1	183	8.0	23.0	6.9	2.1	2.3	2.5	$ID(^{22}Na)$	1
Macropus eugenii	2	35	11	1	1050	22.7	82.4	31*	19*	9.1*	0.82*	IT(²² H, ²² H)	2, 3
Pseudocheirus peregrinus	3	18-23	2	2	203	6.7	23.0	3.2*	0.34*	1.3*	1.3*	$ID(^{22}Na)$	4, 5
Placentals Chirontera													
Phyllostomus hastatus	4	7	20		63	n.a.	17.7	5.3	2.5	1.6	0.7	ID(²² H)	9
Carnivora			ì		}			}	}			î)
Suricata suricata	5	n.a.	9	4	108	0.9	24.8	n.a.	3.1	2.6	0.79	$ID(^{22}H)$	7
Mustela vison	9	3	9	5	92	4.8	24.5	5.3	1.8	1.4	1.1	$ID(^{22}H)$	∞
Mephitis mephitis	7	2	9	9	161	4.9	26.9	8.2	3.7	2.7	0.81	$ID(^{22}H)$	∞
Felis catus	∞	3	5	4	347	8.1	48.7	11*	3.4*	4.2*	1.7*	$ID(^{22}H)$	9, 10
Canis lupus	6	4	5	9	1200	37	175	39	15	14	7.1	$ID(^{22}H)$	11
Ursus americanus	10	36	3	2	40000	351	881	300	159	141	3.5	IT(²² H, ²² H)	12, 13
Ursus arctos	11	32	3	2	61700	902	1350	473	257	186	5.4	IT(²² H, ²² H)	12, 13
Cystophora cristata	12	-	2	-	42500	2900	10400	6916	6094	645	n.a.	ID(²² H)	14
Erignathus barbatus	13	-	3	-	46700	3300	2600	4385	3420	774	n.a.	ID(²² H)	15
Halichoerus grypus	14	1-2	_∞	1	17600	1920	3150	2223	1800	298	n.a.	$ID(^{22}H)$	16
Phoca groenlandica	15	-	2	-	15600	2300	3840	1866	1375	399	30	ID(²H)	17
Callorhinus ursinus	16	14	23	-	13700	111	719	439*	355*	73*	0.72*	ID(²² H)	18, 19
Arctocephalus australis	17	30	m	1	19800	28	675	381*	284*	70*	n.a.	ID(**H)	20, 21
Perissodactyla	(,	ı	,		,			I C	0	,		C C
Equus caballus	18	9	22	-	91100	1140	17600	1848	227	340	1216	ID(**H)	22
Artiodactyla	((;	,	1	0	0	3	3	1	9	, , , , , , , , ,	
Lama glama	19	י רי	Ξ,	_ ,	18/00	362	2590	394"	113"	10/*	154"	ID(**H)	23, 24
Camelus dromedarius	20	v .	m +	- 0	58500	1280	8600	1023"	310"	2587	378*	ID(*2H)	25, 26
Sus scroja	17	4 (71 -	י ת	0300	507	1035	191	40	0 1	28	ID(=H)	/7
Ovis orientalis	77	m (Ω (7 •	73000	188	1240	226	90	51	29	ID(22H)	, , ,
Bos taurus	57	9	×	_	7,2000	0/11	11711	1390"	415	359	516	ID(==H)	61,87
Capra hircus	24	5-6	11	. ,	7800	134	1510	190*	65*	48*	65*	WSW	29, 30
Capra ıbex	57	6-6	9	_	00/9	104	639	149"	-6/	36"	.87	ID(==H)	29, 30
Oreamnus americanus	26	3-4	7	-	6500	168	800	144	48	48	36	IT(³ H, ⁴ H)	31
Ovibus moschatus	27	2	3	-	26000	474	1887	511*	*500	225*	*0*	IT(²² H, ²² H)	32, 33
Cervus elaphus	28	4	7	-	37800	790	4100	779	275	234	172	ID(²² H)	34
Alces alces	29	4	4	1	33200	785	4760	1000	381	190	176	IT(²² H, ²² H)	35
Odocoileus hemionus	30	4	3	-	12000	265	1230	234	. 62	98	55	IT(²² H, ²² H)	31
Rangifer tarandus	31	3-4	n	-	14700	330	1590	398*	181*	122*	27*	ID(²² H)	36, 37
Cephalophus manticola	32	2-3	13	1	750	17	26	21	9.3	7.4	2.9	WSW	38
Gazella dorcas	33	2-8	4	-1	5400	83	567	137*	*05	_{20*}	32*	ID(³H)	29, 30
Primates Danio amoganhalus	2.7	1	0	-	1740	0.0	700	#U**	*01	***	*10	ID(22H)	20 10
rapio cynocephanas	ţ,	1./	4-0	-	1740	3.2	400	20	10	0.0	10	(ii)di	55, 15

Kodentia <i>Rattus norvegicus</i>	36	2	4	∞	17	1.0	4.6	1.0*	0.40*	0.37*	0.17*	ID(K)	
Mus musculus	37	2	7	10	7	0.35	1.5	0.45*	0.20*	0.14*	0.05*	$ID(^{22}H)$	42, 19
Cavia porcellus	38	1	∞	3	123	8.8	25	4.4	1.4	1.6	1.2	IT(²² H, ²² H)	
agomorpha													
Oryctolagus cuniculus	39	e	5	7	270	16	40	12*	6.1*	4.1*	0.72*	WSW	43,
Lepus europaeus	40	4	18	2	902	17	43	18	8.9	6.4	0.48	WSW	45

27. Pluske et al. (1998); 28. Dove and Axelsen (1979); 29. Maltz (1979); 30. Maltz and Shkolnik (1984); 31. Carl and Robbins (1988); 32. Parker et al. (1990); 33. Baker et al. (1970); 34. Robbins et al. (1981); 35. Reese and Robbins Donohue et al. (2002); 19. Oftedal (1984a); 20. Arnould and Hindell (2002); 21. Arnould and Hindell (1999); 22. Oftedal, et al. (1983); 23. Riek et al. (2007); 24. Riek and Gerken (2006); 25. Degen et al. (1987); 26. Sawaya et al. (1984); Reference numbers: 1. Merchant et al. (1994); 2. Dove and Cork (1989); 3. Green (1984); 4. Munks and Green (1997); 5. Munks et al. (1991); 6. Stern et al. (1997); 7. Scantlebury et al. (2002); 8. Oftedal (1981); 9. Hendriks and Wamberg (2000); 10. Dobenecker et al. (1998); 11. Offedal (1984b); 12. Gittleman and Offedal (1987); 13. Farley and Robbins (1995); 14. Lydersen et al. (1997); 15. Lydersen et al. (1996); 16. Iverson et al. (1993); 17. Oftedal et al. (1996); 18. Buss and Voss (1971); 40. 1994); 36. McEwan and Whitehead (1971); 37. Gjostein et al. (2004); 38. Taylor et al. (1990); 39.

Lamothe and Gidenne (2000); 45. Hackländer et al. (2002)

* Indicates values calculated from milk intake and milk composition data reported in different publications.

Therefore, the purpose of the present study was to investigate milk intake and intake of milk nutrients in suckling mammalian young at peak lactation using PIC in order to derive allometric relationships corrected for phylogeny. In the absence of any comparative published data on milk and milk nutrient intakes in suckling mammalian young, the derived phylogenetically corrected allometric relationships could be used to predict intakes for species similar to those included in the present study, which could be of interest for zoo keepers, animal nutritionists, veterinarians and wildlife zoologists. However, predicting values for missing species should be done with caution as they are not included in the phylogenetic tree that was used to derive the present equations.

Material and methods

Database

Data on milk intake, milk composition and ADG for 40 species from 8 orders (Rodentia: n=3, Lagomorpha: n=2, Primates: n=2, Artiodactyla: n=15, Perissodactyla: n=1, Carnivora: n=13, Chiroptera: n=1, Diprotodontia: n=3) were obtained from the literature (Table 1). Intake of milk nutrients (solids, fat, protein, sugar) were used either from the original publication or calculated from milk intake and milk composition data (Table 1). The minimum requirements for an investigation to be included in the analysis were: 1) at least 3 individuals were studied 2) suckling young were reared by their lactating mothers 3) body mass and milk intake at the time of peak lactation were recorded, and 4) the time of peak lactation was known. Only ADG reported for the time of peak lactation in the same study were included in the analysis. The time of peak lactation was chosen to be able to make a valid comparison among species (Oftedal 1981). When a given species was represented by more than one study, the inclusion of the data point into the analysis was based on data quality, method used to measure milk intake (isotope dilution or isotope transfer method preferred over weigh-suckle-weigh method) and the number of observations (larger numbers preferred over smaller numbers), resulting in one data point per

Statistical procedures

Phylogenetic signals

To detect phylogenetic signals across traits (milk and milk nutrients, body mass and ADG), K^* - and P-values were calculated following Blomberg et al. (2003). The calculation of K* essentially involves the observed and expected ratios of the mean squared error of the tip data (measured from the phylogenetically corrected mean) and the mean squared error data calculated using the variance-covariance matrix (derived from the candidate tree). A detailed description of the calculation is given in Blomberg et al. (2003). In brief a K^* less than one for a certain trait implies that relatives resemble each other less than expected under Brownian motion evolution along the candidate tree and a K^* greater than one implies that close relatives are more similar than expected (Blomberg et al. 2003). Additionally, mass- and ADG-corrected values for the original traits (milk and intake of milk nutrients) were computed after Blomberg et al. (2003) as: log[trait/(body mass^b or ADG^b) were b is the slope of the PIC regression line (see below).

Phylogenetically independent contrasts

Phylogenetic signals (K^*) were high and significant for all traits examined (see Results and Discussion), thus PIC analysis were used to derive allometric relationships.

Phylogenetically independent contrasts were calculated for log₁₀ transformed milk intake and intake of milk nutrients, body mass and ADG to eliminate the potential lack of independence between species, because of their shared evolutionary history (Felsenstein 1985; Garland et al. 1992). The method of PIC calculates pairwise standardized contrasts that represent independent character evolution that has occurred since the common ancestor of sister lineages (Felsenstein 1985; Garland et al. 1992). Given a tree topology and branch length, PIC assumes that the phylogeny fully predicts the pattern of variation at the tips under Brownian motion model of evolution.

Equations were calculated including all species and separately for the orders Carnivora and Artiodactyla, as the small sample size allowed conducting regression analysis only in these two orders. Calculations were performed using the computer software Independent Contrasts, version 1.14 (Withers 2008). The program calculates PIC from a phylogenetic distance matrix, using the square root of the product of branch length and variance to standardize PIC. Regression equations for PIC were calculated through the origin following Garland et al. (1992) and had the form:

PIC from $\log y = b$ PIC from $\log x$

After standardization, PICs were not correlated with their standard deviations, indicating that the branch lengths met the assumption of the method (Garland et al. 1992). Figures for the PIC values with their corresponding regression lines and 95 % confidence interval (CI) of prediction are presented as Supplementary Material (Figs. A1–A3).

The PIC regression equation was then plotted back onto the original data by using the procedure for computing a Y-intercept from PIC following Garland et al. (1993) and Garland and Ives (2000). In brief, the Y-intercept of the regression line is calculated by using the slope of the PIC regression line and the estimated X and Y values for the root of the tree.

The phylogeny for the species used in the present study was derived from a mammalian supertree, which includes 4510 species with branch lengths derived from dated estimates of divergence times (Bininda-Emonds et al. 2007). The supertree for mammals in Newick format was transformed to a distance matrix using the Analyses in Phylogenetics and Evolution package in R (Paradis et al., 2004) and pruned to include only the species of the present study. The resulting tree had no polytomies. The program PhyloWidget (Jordan and Piel 2008) was used to construct a printable phylogenetic tree from the phylogeny in Newick format (Fig. 1).

Comparisons of slopes between artiodactyls and carnivores were performed using the computer software StatistiXL Release 1.8 (2007). Other statistical analyses were performed using the software package SAS Release 9.01 (2001).

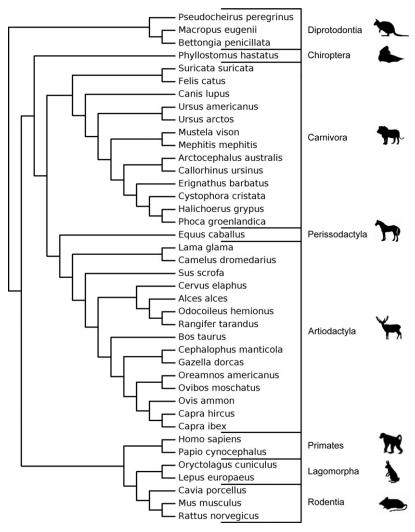


Fig. 1. Phylogenetic tree for mammals included in the present study (constructed from the mammalian Supertree, Bininda-Emonds et al. 2007).

Results and discussion

Mean actual measured daily milk intake ranged from 1.5 g in *Mus musculus* to 17.6 kg in *Equus caballus*. The range of mean daily intake of milk nutrients was 0.5 g (*Mus musculus*) to

Table 2Mass- and average daily gain (ADG) -uncorrected and mass- and ADG-corrected phylogenetic signals (*K**-values) for milk intake and intake of milk nutrients in suckling mammalian young at peak lactation (computed after the method of Blomberg et al. 2003)

Trait	n	K*-values		
		Mass- and ADG-uncorrected	Mass-corrected ¹	ADG- corrected ¹
All				
Milk	40	0.969	0.474	0.819
Solids	39	1.006	0.735	0.682
Fat	40	1.028	0.812	0.654
Protein	40	1.042	0.604	0.411
Sugar	36	1.041	0.678	0.928
Body mass	40	1.050	-	-
ADG	39	1.045	_	_
Artiodactyl	a			
Milk	14	0.556	0.279	0.279
Solids	14	0.540	0.391	0.394
Fat	14	0.491	0.313	0.311
Protein	14	0.519	0.516	0.517
Sugar	14	0.588	0.349	0.346
Body	14	0.591	-	-
mass				
ADG	14	0.586	-	-
Carnivora				
Milk	12	1.534	1.033	1.029
Solids	11	n.s.	n.s.	n.s.
Fat	12	1.605	1.369	1.369
Protein	12	1.569	0.851	0.868
Sugar	9	n.s.	n.s.	n.s.
Body mass	12	1.696	-	-
ADG	12	1.622	-	-

 $^{^1}$ $K^*\!\text{-values}$ calculated from: log[trait/(body mass^b or ADG^b)] following Blomberg et al. (2003).

6.9 kg (*Cystophora cristata*) for solids, 0.2 g (*Mus musculus*) to 6.1 kg (*Cystophora cristata*) for fat, 0.1 g (*Mus musculus*) to 0.8 kg (*Erignathus barbatus*) for protein and 0.05 g (*Mus musculus*) to 1.2 kg (*Equus caballus*) for sugar. Corresponding body masses and ADG at the time of peak lactation in suckling mammalian young ranged from 7.3 g (*Mus musculus*) to 91.1 kg (*Equus caballus*) and from 0.35 g (*Mus musculus*) to 5.9 kg (*Cystophora cristata*), respectively.

Phylogenetic signals

Phylogenetic signals (K^*) were significant (P < 0.01) for all traits (body mass, ADG, milk, solid, fat, protein, and sugar intake) except for solid and sugar intakes in carnivores (Table 2). When analysing all mammals only the K^* -value for milk intake was less than expected ($K^* < 1$) but higher than expected ($K^* > 1$) for all other traits. Even after accounting for the high phylogenetic signal of body mass and ADG (computed as $\log_{10}[\text{trait}/(\text{body mass}^b)]$ or ADG^b)) phylogenetic signals remained (P < 0.01) for all traits. Analysing phylogenetic signals separately for artiodactyls and carnivores revealed that K^* -values for all traits in artiodactyls were less than expected and more than expected in carnivores (except solid and sugar intake), even after accounting for the high phylogenetic signal of body mass and ADG (Table 2).

As expected mass and ADG exerted a strong phylogenetic signal ($K^* > 1$). The phylogenetic signals were strong and significant for most variables, even after accounting for the high phylogenetic signal of body mass and ADG (Table 2), indicating that the traits follow a mass- and ADG-independent phylogenetic trend. A similar trend was observed for mass-related and physiological traits (Blomberg et al. 2003; Withers et al. 2006).

Effect of body mass and average daily gain on milk intake and intake of milk nutrients

A strong (P < 0.001) positive relationship exists between body mass (and ADG) and milk intake and intake of milk nutrients, whether calculated for all mammals or separately for artiodactyls and carnivores using PIC analysis (Figs. 2 and 3), except for sugar intake in carnivores. Body mass explained 71 to 95%, 86 to 98%

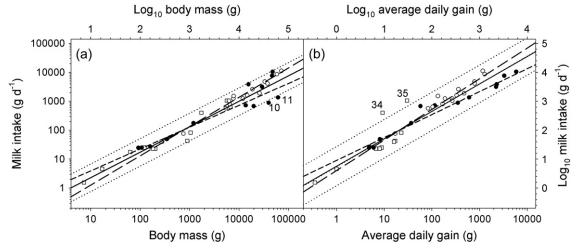


Fig. 2. Relationship between daily milk intake and body mass a) and daily milk intake and average daily gain b) in suckling carnivores (closed circles, short dashed line), artiodactyls (open circles, long dashed line) and other mammals (open squares). The solid line describes the relationship for all data points with the corresponding 95% confidence interval of the prediction (dotted lines). Numbers correspond to species numbers in Table 1 (for detailed statistics of the regression lines see Table 2). Regression lines were calculated using phylogenetic independent contrasts (PIC) on a phylogeny with branch length derived from data estimates of divergence times. Regression equations from PIC were then plotted back onto the original data by using the procedure for computing a Y-intercept from PIC, following Garland et al. (1993) (see text for details).

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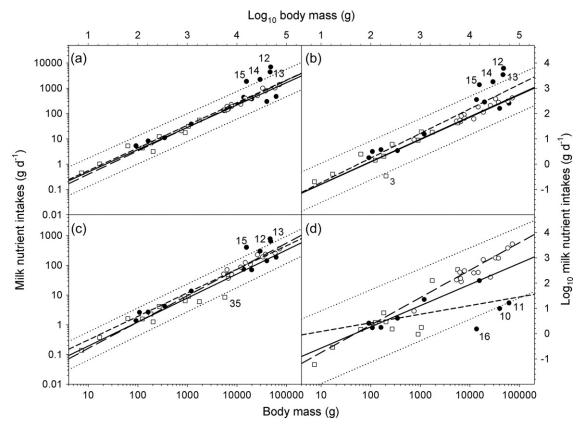


Fig. 3. Relationship between daily intake of milk nutrients (a: solids, b: fat, c: protein and d: sugar) and body mass at peak lactation in suckling carnivores (closed circles, short dashed line), artiodactyls (open circles, long dashed line) and other mammals (open squares). The solid line describes the relationship for all data points with the corresponding 95% confidence interval of the prediction (dotted lines). Numbers correspond to species numbers in Table 1 (for detailed statistics of the regression lines see Table 2). Regression lines were calculated using phylogenetic independent contrasts (PIC) on a phylogeny with branch length derived from data estimates of divergence times. Regression equations from PIC were then plotted back onto the original data by using the procedure for computing a Y-intercept from PIC, following Garland et al. (1993) (see text for details).

Table 3 Summary of allometric relationships between body mass (g) (M) and milk intake and intake of milk nutrients (g d^{-1}) calculated by using phylogenetic independent contrasts. Allometric relationships were determined with branch lengths based on divergence dates.

Taxon	Y	Allometric relationship	N	R^2	P	95% CI of	prediction			Eq.
						а		b		
						Lower	Upper	Lower	Upper	
All	Milk	$0.299~M^{0.881}\pm 0.052$	39	0.943	< 0.001	0.100	0.895	0.885	0.877	1
	Solids	$0.064~M^{0.884} \pm 0.045$	38	0.930	< 0.001	0.017	0.229	0.888	0.879	2
	Fat	$0.021~\text{M}^{0.884~\pm~0.062}$	39	0.872	< 0.001	0.004	0.145	0.889	0.879	3
	Protein	$0.030~M^{0.808~\pm~0.042}$	39	0.945	< 0.001	0.010	0.090	0.812	0.805	4
	Sugar	$0.032 \mathrm{M}^{0.713 \pm 0.106}$	35	0.710	< 0.001	0.002	0.582	0.720	0.705	5
Artiodactyla	Milk	$0.123~M^{1.012~\pm~0.088}$	14	0.956	< 0.001	0.062	0.245	1.014	1.010	6
•	Solids	$0.047~M^{0.928~\pm~0.044}$	14	0.978	< 0.001	0.031	0.071	0.929	0.927	7
	Fat	$0.021~M^{0.890\pm0.083}$	14	0.934	< 0.001	0.010	0.040	0.891	0.888	8
	Protein	$0.021~M^{0.885}\pm 0.050$	14	0.961	< 0.001	0.012	0.036	0.886	0.884	9
	Sugar	$0.014~M^{0.923~\pm~0.136}$	14	0.862	< 0.001	0.004	0.049	0.926	0.921	10
Carnivora	Milk	$0.684~M^{0.756\pm0.112}$	12	0.883	< 0.001	0.092	5.070	0.793	0.719	11
	Solids	$0.071~{\rm M}^{0.895~\pm~0.129}$	11	0.848	< 0.001	0.002	0.301	0.951	0.839	12
	Fat	$0.020~M^{0.971~\pm~0.136}$	12	0.863	< 0.001	0.001	0.348	1.016	0.926	13
	Protein	$0.050 \text{ M}^{0.792 \pm 0.101}$	12	0.927	< 0.001	0.029	0.089	0.825	0.758	14
	Sugar	$0.305~M^{0.290\pm0.222}$	8	0.320	n.s.	0.018	5.297	0.374	0.205	15

Note. Regressions from PIC were calculated following Garland et al. (1992) and Garland et al. (1993), see text for details; n.s.=not significant.

and 32 to 93% of the variation in milk intake or intake of milk nutrients in all mammals (Table 3, eqs. 1-5), artiodactyls (eqs. 6-10) and carnivores (eqs. 11-15), respectively. Regressing ADG on milk intake or intake of milk nutrients yielded similar coefficients of determination (Table 4, eqs. 16-30).

No significant differences were detected between artiodactyls and carnivores for the same intake of milk nutrients (P > 0.05). Thus it seems intake of milk nutrients at peak lactation does not differ between these two orders, confirming similar results on energy intakes via milk from a previous study (Riek 2008).