



Original Investigation

Allometry of milk intake at peak lactation

Alexander Riek^{a,b,*}^a Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, NSW 2351, Australia^b Department of Animal Sciences, University of Göttingen, Albrecht-Thaer-Weg 3, 37075 Göttingen, Germany

ARTICLE INFO

Article history:

Received 6 October 2009

Accepted 1 March 2010

Keywords:

Allometry

Lactation

Milk intake

Milk nutrients

Phylogeny

ABSTRACT

Much attention has been given to the scaling of milk output and lactational strategies across species. However developed allometric equations for milk output in adult animals cannot be used for suckling young. 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 phylogenetic independent contrasts in order to derive allometric relationships corrected for phylogeny. Milk intake and intake of milk nutrients (solid, fat, protein and sugar) at peak lactation for 40 mammalian species were evaluated for the present analysis to derive allometric relationships for suckling young. K^* -values were calculated in order to detect phylogenetic signals across traits. Phylogenetic signals were high and significant for all traits examined, thus phylogenetically independent contrasts were calculated for \log_{10} transformed milk intake and intake of milk nutrients, body mass and average daily gain to eliminate the potential lack of independence between species, because of their shared evolutionary history. The phylogeny for the species used in the present study was derived from a recently published mammalian Supertree with branch lengths derived from dated estimates of divergence times. Thirty allometric equations were calculated using phylogenetically independent contrasts. A strong ($P < 0.001$) positive relationship exists between neonate body mass and the response variables (milk intake, intake of milk nutrients), whether calculated for all mammals or separately for artiodactyls and carnivores, with the exception of sugar intake in carnivores. However, large deviations for some species and few outliers were found. The present equations could be used to predict values for species similar to those included in the present study that have not been studied, providing that the body mass falls inside the range of masses used to derive the equations. 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 phylogenetically corrected equations.

© 2010 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

Knowledge of milk intake and intake of milk nutrients is essential for a better understanding of the nutrient requirements of suckling mammalian young. While many studies have been conducted dealing with the scaling effects of milk and milk nutrient outputs across species (Linzell 1972; Kleiber 1975; Martin 1984; Oftedal 1984a) to the authors knowledge no such analysis exists for milk intake or intake of milk nutrients in suckling mammalian young. It has been shown that the scaling factor for energy intake in suckling young can deviate substantially from that of adult mammals (Riek 2008). Furthermore, in most allometric summaries on milk and milk nutrients to date (Linzell 1972; Kleiber 1975; Martin 1984; Oftedal 1984a) the

problem of the potential lack of independence between species because of their shared evolutionary history (Felsenstein 1985; Garland et al. 1992) has not been considered. An exception is a recent study by Langer (2008). However, so far no published analysis exists, relating milk intake and intake of milk nutrients in suckling mammalian young to their body mass or average daily gain (ADG) at the time of peak lactation after correcting for phylogeny. Comparative data sets are increasingly analysed by phylogenetic methods because species values cannot be treated as independent data points in statistical analyses as close phylogenetic relatives are more likely to be similar than are distantly related species (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1992, 1993; Garland and Ives 2000). One of the methods to overcome the problem of nonindependence in comparative data sets is Felsenstein's (1985) phylogenetically independent contrasts (PIC). Independent contrasts are calculated as pairwise standardized contrast scores that represent independent character evolution that has occurred since the common ancestor of sister evolution.

* Correspondence address: Centre for Behavioural and Physiological Ecology, Zoology University of New England, Armidale, NSW 2351, Australia.

Tel.: +61 2 6773 3756; fax: +61 2 6773 3814.

E-mail address: ariek2@une.edu.au

Table 1
Mean 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	Nr.	Peak lactation	N	Litter size	Body mass (g)	Neonate ADG (g d ⁻¹)	Milk intake (g d ⁻¹)	Intake of milk nutrients				Method	Reference
		(week)						Solids (g d ⁻¹)	Fat (g d ⁻¹)	Protein (g d ⁻¹)	Sugar (g d ⁻¹)	(Isotope)	
Marsupials													
Diprotodontia													
<i>Betongia penicillata</i>	1	14	5	1	183	8.0	23.0	6.9	2.1	2.3	2.5	ID(²² Na)	1
<i>Macropus eugenii</i>	2	35	11	1	1050	22.7	82.4	31*	19*	9.1*	0.82*	IT(²² H, ²² H)	2, 3
<i>Pseudocheirus peregrinus</i>	3	18-23	5	2	203	6.7	23.0	3.2*	0.34*	1.3*	1.3*	ID(²² Na)	4, 5
Placentals													
Chiroptera													
<i>Phyllostomus hastatus</i>	4	7	20	1	63	n.a.	17.7	5.3	2.5	1.6	0.7	ID(²² H)	6
Carnivora													
<i>Suricata suricata</i>	5	n.a.	6	4	108	6.0	24.8	n.a.	3.1	2.6	0.79	ID(²² H)	7
<i>Mustela vison</i>	6	3	6	5	92	4.8	24.5	5.3	1.8	1.4	1.1	ID(²² H)	8
<i>Mephitis mephitis</i>	7	5	6	6	161	4.9	26.9	8.2	3.7	2.7	0.81	ID(²² H)	8
<i>Felis catus</i>	8	3	5	4	347	8.1	48.7	11*	3.4*	4.2*	1.7*	ID(²² H)	9, 10
<i>Canis lupus</i>	9	4	5	6	1200	37	175	39	15	14	7.1	ID(²² H)	11
<i>Ursus americanus</i>	10	36	3	2	40000	351	881	300	159	141	3.5	IT(²² H, ²² H)	12, 13
<i>Ursus arctos</i>	11	32	3	2	61700	605	1350	473	257	186	5.4	IT(²² H, ²² H)	12, 13
<i>Cystophora cristata</i>	12	1	5	1	42500	5900	10400	6916	6094	645	n.a.	ID(²² H)	14
<i>Erignathus barbatus</i>	13	1	3	1	46700	3300	7600	4385	3420	774	n.a.	ID(²² H)	15
<i>Halichoerus grypus</i>	14	1-2	8	1	17600	1920	3150	2223	1800	298	n.a.	ID(²² H)	16
<i>Phoca groenlandica</i>	15	1	5	1	15600	2300	3840	1866	1375	399	30	ID(²² H)	17
<i>Callorhinus ursinus</i>	16	14	23	1	13700	111	719	439*	355*	73*	0.72*	ID(²² H)	18, 19
<i>Arctocephalus australis</i>	17	30	3	1	19800	58	675	381*	284*	70*	n.a.	ID(²² H)	20, 21
Perissodactyla													
<i>Equus caballus</i>	18	6	5	1	91100	1140	17600	1848	227	340	1216	ID(²² H)	22
Artiodactyla													
<i>Lama glama</i>	19	3	11	1	18700	362	2590	394*	113*	107*	154*	ID(²² H)	23, 24
<i>Camelus dromedarius</i>	20	5	3	1	58500	1280	8600	1023*	310*	258*	378*	ID(²² H)	25, 26
<i>Sus scrofa</i>	21	4	12	9	6300	269	1035	191	54	70	58	ID(²² H)	27
<i>Ovis orientalis</i>	22	3	5	2	7700	188	1240	226	90	51	62	ID(²² H)	8
<i>Bos taurus</i>	23	6	8	1	72000	1170	11211	1390*	415*	359*	516*	ID(²² H)	28, 19
<i>Capra hircus</i>	24	5-9	11	1	7800	134	1510	190*	65*	48*	65*	WSW	29, 30
<i>Capra ibex</i>	25	5-9	6	1	6700	104	639	149*	79*	36*	28*	ID(²² H)	29, 30
<i>Oreamnus americanus</i>	26	3-4	7	1	6500	168	800	144	48	48	36	IT(³ H, ²² H)	31
<i>Ovibus moschatus</i>	27	5	3	1	26000	474	1887	511*	206*	225*	40*	IT(²² H, ²² H)	32, 33
<i>Cervus elaphus</i>	28	4	7	1	37800	790	4100	779	275	234	172	ID(²² H)	34
<i>Alces alces</i>	29	4	4	1	33200	785	4760	1000	381	190	176	IT(²² H, ²² H)	35
<i>Odocoileus hemionus</i>	30	4	3	1	12000	265	1230	234	62	86	55	IT(²² H, ²² H)	31
<i>Rangifer tarandus</i>	31	3-4	3	1	14700	330	1590	398*	181*	122*	57*	ID(²² H)	36, 37
<i>Cephalophus manticola</i>	32	2-3	13	1	750	17	76	21	9.3	7.4	2.9	WSW	38
<i>Gazella dorcas</i>	33	5-8	4	1	5400	83	567	137*	50*	50*	32*	ID(³ H)	29, 30
Primates													
<i>Papio cynocephalus</i>	34	17	4-8	1	1740	9.2	400	56*	18*	6.0*	31*	ID(²² H)	39, 19

<i>Homo sapiens</i>	35	9–17	5	1	5700	30	1050	130*	43*	8.4*	71*	ID(²² H)	40, 19
Rodentia													
<i>Rattus norvegicus</i>	36	2	4	8	17	1.0	4.6	1.0*	0.40*	0.37*	0.17*	ID(K)	41, 19
<i>Mus musculus</i>	37	2	7	10	7	0.35	1.5	0.45*	0.20*	0.14*	0.05*	ID(²² H)	42, 19
<i>Cavia porcellus</i>	38	1	8	3	123	8.8	25	4.4	1.4	1.6	1.2	Π(²² H, ²² H)	8
Lagomorpha													
<i>Oryctolagus cuniculus</i>	39	3	5	7	270	16	40	12*	6.1*	4.1*	0.72*	WSW	43, 44
<i>Lepus europaeus</i>	40	4	18	2	902	17	43	18	8.9	6.4	0.48	WSW	45

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. Oftedal (1984b); 12. Gittleman and Oftedal (1987); 13. Farley and Robbins (1995); 14. Lydersen et al. (1997); 15. Iversen et al. (1996); 16. Iversen et al. (1993); 17. Oftedal et al. (1996); 18. Donohue et al. (2002); 19. Oftedal (1984a); 20. Arnould and Hindell (1999); 21. Arnould and Hindell (2002); 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); 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 (1994); 36. McEwan and Whitehead (1971); 37. Gjostein et al. (2004); 38. Taylor et al. (1990); 39. Buss and Voss (1971); 40. Coward et al. (1979); 41. Kametaka et al. (1974); 42. Knight et al. (1986); 43. Cowie (1969); 44. Fortun-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 species.

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 of the 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: $\log[\text{trait}/(\text{body mass}^b \text{ or } \text{ADG}^b)]$ where 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 \log_{10} 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).

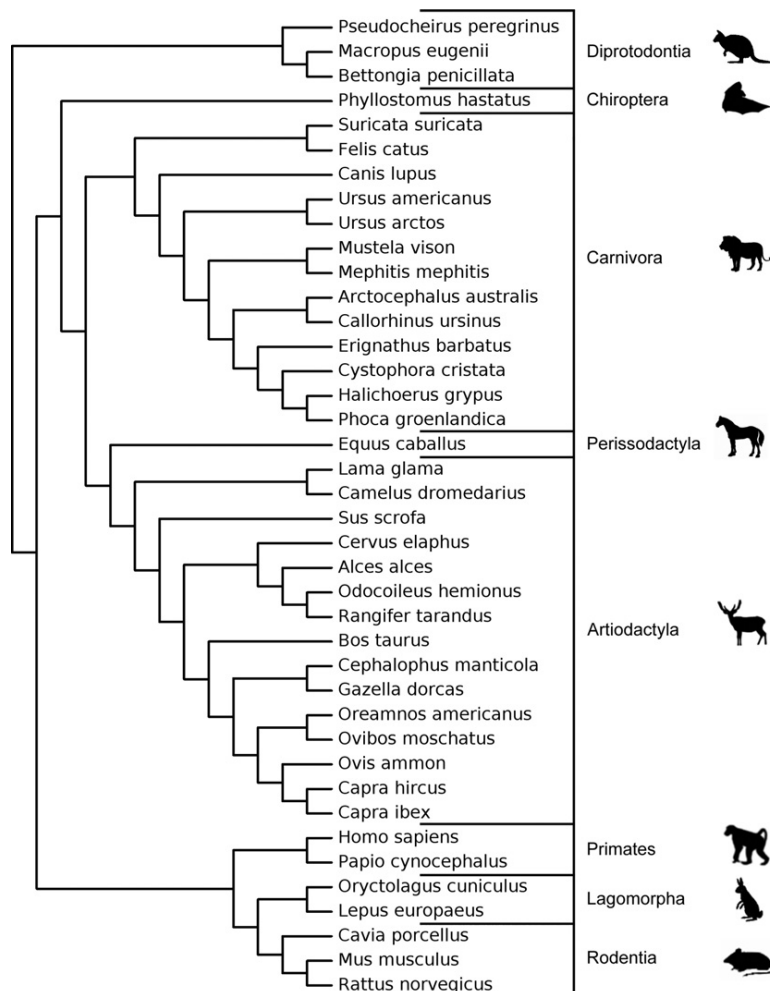


Fig. 1. Phylogenetic tree for mammals included in the present study (constructed from the mammalian Supertree, Bininda-Emonds et al. 2007).

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

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.

Table 2

Mass- 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	-	-
Artiodactyla				
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 mass	14	0.591	-	-
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^* -values calculated from: $\log[\text{trait}/(\text{body mass}^b \text{ or ADG}^b)]$ following Blomberg et al. (2003).

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 $\log_{10}[\text{trait}/(\text{body mass}^b \text{ or ADG}^b)]$) 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%

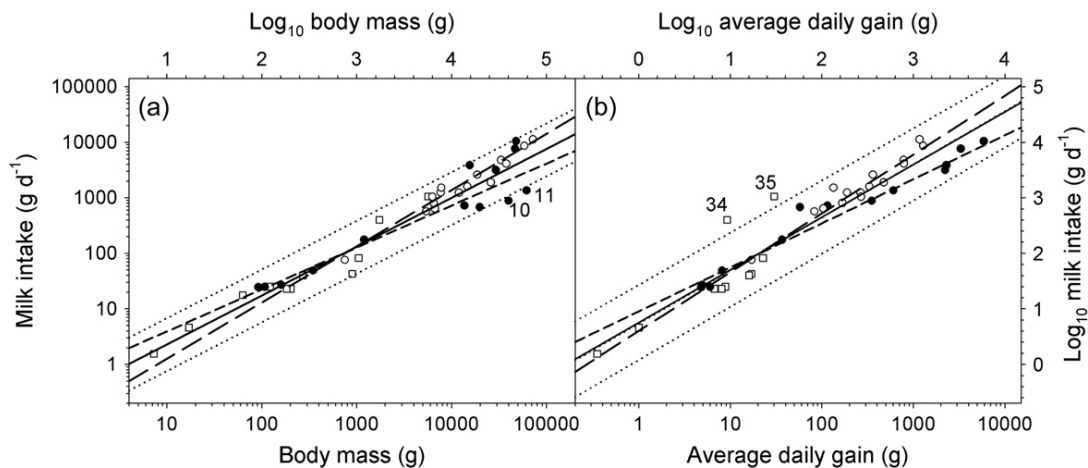


Fig. 2. Relationship between daily milk intake and body mass a) and daily milk intake and average daily gain b) in suckling carnivores (closed circles, short dashed line), artiodactyls (open circles, long dashed line) and other mammals (open squares). The solid line describes the relationship for all 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).

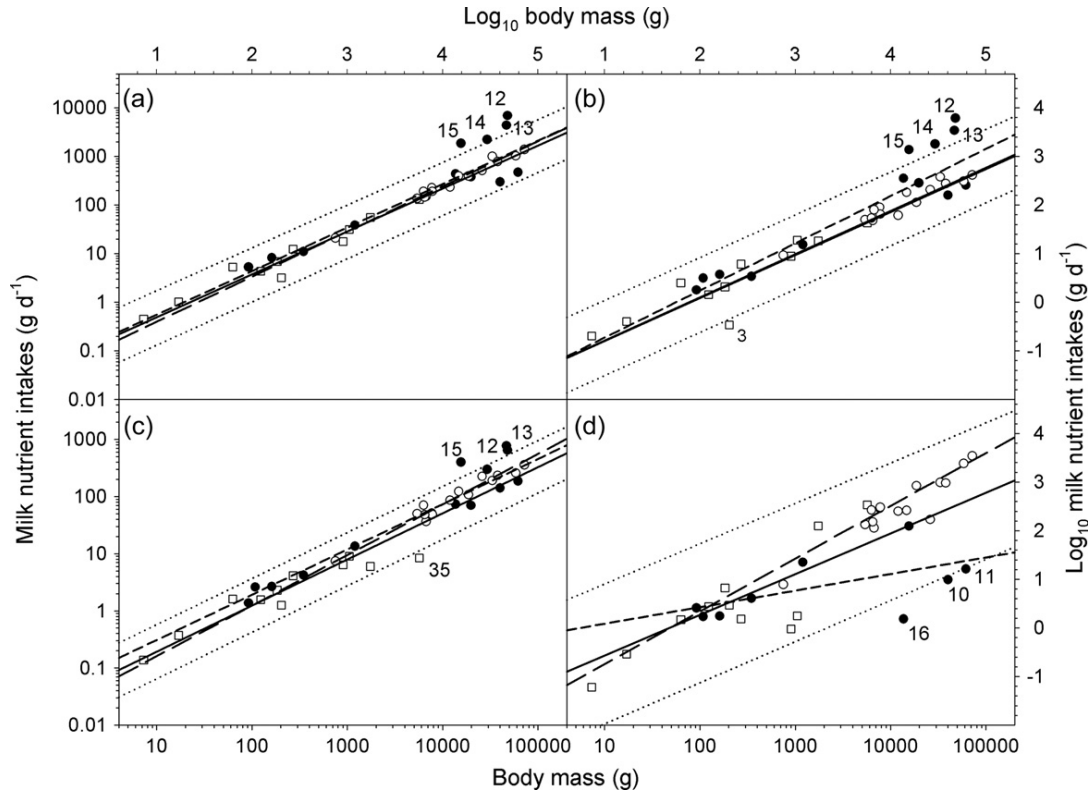


Fig. 3. Relationship between daily intake of milk nutrients (a: solids, b: fat, c: protein and d: sugar) and body mass at peak lactation in suckling carnivores (closed circles, short dashed line), artiodactyls (open circles, long dashed line) and other mammals (open squares). The solid line describes 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.
						<i>a</i>		<i>b</i>		
						Lower	Upper	Lower	Upper	
All	Milk	0.299 M ^{0.881 ± 0.052}	39	0.943	< 0.001	0.100	0.895	0.885	0.877	1
	Solids	0.064 M ^{0.884 ± 0.045}	38	0.930	< 0.001	0.017	0.229	0.888	0.879	2
	Fat	0.021 M ^{0.884 ± 0.062}	39	0.872	< 0.001	0.004	0.145	0.889	0.879	3
Artiodactyla	Protein	0.030 M ^{0.808 ± 0.042}	39	0.945	< 0.001	0.010	0.090	0.812	0.805	4
	Sugar	0.032 M ^{0.713 ± 0.106}	35	0.710	< 0.001	0.002	0.582	0.720	0.705	5
	Milk	0.123 M ^{1.012 ± 0.088}	14	0.956	< 0.001	0.062	0.245	1.014	1.010	6
	Solids	0.047 M ^{0.928 ± 0.044}	14	0.978	< 0.001	0.031	0.071	0.929	0.927	7
	Fat	0.021 M ^{0.890 ± 0.083}	14	0.934	< 0.001	0.010	0.040	0.891	0.888	8
Carnivora	Protein	0.021 M ^{0.885 ± 0.050}	14	0.961	< 0.001	0.012	0.036	0.886	0.884	9
	Sugar	0.014 M ^{0.923 ± 0.136}	14	0.862	< 0.001	0.004	0.049	0.926	0.921	10
	Milk	0.684 M ^{0.756 ± 0.112}	12	0.883	< 0.001	0.092	5.070	0.793	0.719	11
	Solids	0.071 M ^{0.895 ± 0.129}	11	0.848	< 0.001	0.002	0.301	0.951	0.839	12
	Fat	0.020 M ^{0.971 ± 0.136}	12	0.863	< 0.001	0.001	0.348	1.016	0.926	13
	Protein	0.050 M ^{0.792 ± 0.101}	12	0.927	< 0.001	0.029	0.089	0.825	0.758	14
	Sugar	0.305 M ^{0.290 ± 0.222}	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).

Table 4

Summary of allometric relationships between average daily gain (g) (ADG) 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.
						<i>a</i>		<i>b</i>		
						Lower	Upper	Lower	Upper	
All	Milk	5.714 ADG ^{0.948 ± 0.054}	38	0.920	< 0.001	1.431	26.91	0.956	0.94	16
	Solids	1.270 ADG ^{0.943 ± 0.047}	37	0.940	< 0.001	0.374	4.295	0.951	0.936	17
	Fat	0.380 ADG ^{0.959 ± 0.067}	38	0.911	< 0.001	0.071	2.042	0.969	0.960	18
	Protein	0.440 ADG ^{0.873 ± 0.043}	38	0.965	< 0.001	0.168	1.104	0.878	0.867	19
	Sugar	0.272 ADG ^{0.849 ± 0.106}	34	0.692	< 0.001	0.014	5.309	0.862	0.837	20
Artiodactyla	Milk	4.021 ADG ^{1.058 ± 0.084}	14	0.941	< 0.001	1.837	8.790	1.062	1.053	21
	Solids	1.214 ADG ^{0.960 ± 0.054}	14	0.963	< 0.001	1.000	2.109	0.963	0.958	22
	Fat	0.516 ADG ^{0.910 ± 0.099}	14	0.883	< 0.001	0.210	1.268	0.915	0.905	23
	Protein	0.488 ADG ^{0.910 ± 0.066}	14	0.952	< 0.001	0.274	0.867	0.913	0.906	24
	Sugar	0.327 ADG ^{0.970 ± 0.137}	14	0.867	< 0.001	0.099	0.923	0.977	0.964	25
Carnivora	Milk	9.023 ADG ^{0.792 ± 0.067}	12	0.967	< 0.001	3.350	24.27	0.817	0.767	26
	Solids	2.080 ADG ^{0.884 ± 0.092}	11	0.931	< 0.001	0.435	10.19	0.922	0.845	27
	Fat	0.639 ADG ^{0.982 ± 0.109}	12	0.930	< 0.001	0.092	4.416	1.022	0.941	28
	Protein	0.849 ADG ^{0.792 ± 0.080}	12	0.953	< 0.001	0.251	2.877	0.823	0.761	29
	Sugar	0.367 ADG ^{0.526 ± 0.164}	8	0.599	n.s.	0.044	3.055	0.588	0.463	30

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

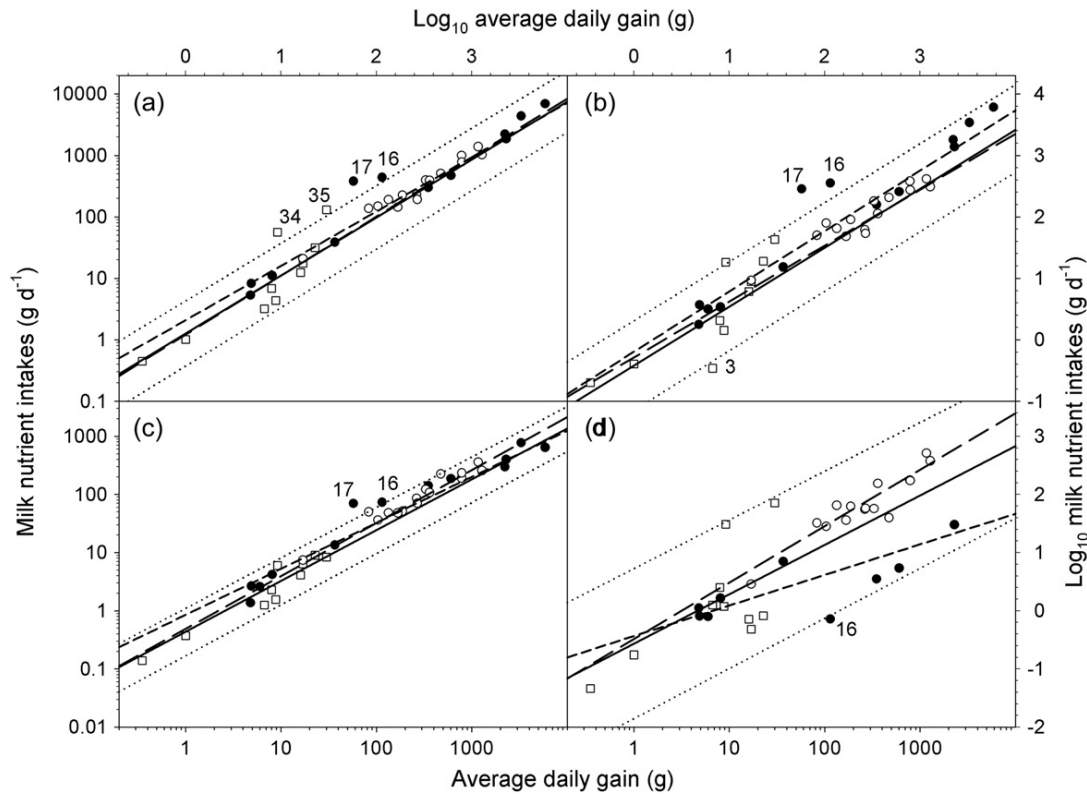


Fig. 4. Relationship between daily intake of milk nutrients (a: solids, b: fat, c: protein and d: sugar) and average daily gain at peak lactation in suckling carnivores (closed circles, short dashed line), artiodactyls (open circles, long dashed line) and other mammals (open squares). The solid line 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).

However, the slope for the relationship between body mass and milk intake was significantly ($F_{1,22}=3.74$; $P=0.043$) lower in carnivores (0.76) than in artiodactyls (1.01), the same was the case for ADG and milk intake (carnivores, 0.79; artiodactyls, 1.06; $F_{1,22}=5.05$, $P=0.035$). The two regression lines for artiodactyls and carnivores intersect at 806 g body mass (Fig. 2a) and 21 g

ADG (Fig. 2b), respectively. This suggests that suckling carnivores weighing up to approximately 800 g at the time of peak lactation ingest more milk on a mass-specific basis compared to similar sized artiodactyls. This relationship between carnivores and artiodactyls seems to be the opposite when body mass of suckling young at peak lactation is exceeding 800 g. Furthermore, the

scaling factor for solid intake in suckling young for all mammals (0.88, CI: 0.83–0.94) was substantially higher compared to the scaling factor derived for dry matter intakes in adult mammals (0.74) (Nagy 2001), emphasising that scaling factors derived from adult mammals cannot be used for suckling young. A similar observation was found for energy intakes (Riek 2008). It needs to be determined, if the same holds true for fat, protein and sugar intakes until more comparative published data on these nutrients for adult mammals become available.

Despite the strong relationship between body mass and milk intake and intake of milk nutrients for all mammals, outliers existed for milk (Fig. 2a: black bear, brown bear), solid (Fig. 3a: hooded seal, bearded seal, gray seal, harp seal), fat (Fig. 3b: hooded seal, bearded seal, gray seal, harp seal, common ringtail possum), protein (Fig. 3c: hooded seal, bearded seal, harp seal, human) and sugar intake (Fig. 3d: brown bear, black bear, Northern fur seal). Outliers existed also for the relationship between ADG and milk (Fig. 2b: human, baboon), solid (Fig. 4a: human, baboon, Northern fur seal, South American fur seal), fat (Fig. 4b: South American fur seal, Northern fur seal, ringtail possum), protein (Fig. 4c: South American fur seal, Northern fur seal) and sugar intake (Fig. 5d: Northern fur seal). In the following an attempt is made to explain some of these outliers.

The black and brown bear (Table 1, nr. 10 and 11) were the only two species outside the 95% CI of prediction for the relationship between body mass and milk intake (Fig. 2a). In relation to their body mass they ingested significantly less milk at peak lactation compared to other mammals included in the present study. However, the milk of bears is more concentrated than that of most other carnivores (with the exception of marine carnivores) with high solid (33%), fat (18–19%), and protein (7%) concentrations (Farley and Robbins 1995). Thus although cubs consume less milk on a body mass basis compared to other mammals in general and carnivores in particular, they receive adequate amounts of solids, fat, and protein for growth due to the high concentrations of these nutrients in the milk. Unlike to fat and protein concentrations sugar concentrations in bear milk are low (1–3%) and thus sugar intakes via milk are lower than in most other carnivores (Fig. 3d).

The present data set included 4 phocid seal species (species 12–15, Table 1). In relation to body mass, phocid seals ingested more solids (Fig. 3a) and fat (Fig. 3b) via milk compared to all other species included in the analysis. A similar trend was observed for protein intakes (Fig. 3c), although less pronounced than for solids and fat (only hooded seal, bearded seal and harp seal outside 95% CI of prediction). These high intakes can be explained by the fact, that phocid seals have very short but intense lactation periods (4–45 days) with high milk energy transfer rates (Bowen et al. 1992) due to high fat and protein concentrations in the milk which can surpass 50% for fat and 10% for protein (Oftedal 1984a). In contrast, sugar concentrations in seals are usually below 1% (Arnould and Hindell 1999) and thus sugar intakes in suckling seals are one of the lowest compared to all other mammals (Fig. 3d).

The ring-tailed possum, the smallest folivorous marsupial in Australia, ingested less fat in relation to its body mass (Fig. 3b) than other mammals, which can be explained by the very low fat concentrations of 1.5% (Munks et al. 1991) in the milk. McNab (1980) suggested that the low nutrient content in leaves and the low absolute energy intake in that aboreal folivore may affect milk quality.

Relating milk intake and intake of milk nutrients to ADG revealed that the two primate species included in the present study (baboon, human) have approximately 7- to 8-times higher milk (Fig. 2b) and 4- to 5-times higher solid intakes (Fig. 4a) than expected (Table 4, eqs. 16, 17). However, primates have atypical

mammalian growth patterns (Payne and Wheeler 1968; Oftedal 1981) with slow growth rates compared to similar sized mammals. The only other species that also stand out in this regard are the otariid seals (South American fur seal, Northern fur seal) with generally higher solid, fat, and protein intakes than expected from regression analysis. In contrast to phocid seals, otariid seals have long lactation periods (4–36 months) with lactating mothers alternating between short nursing periods ashore (2–3 days) and long foraging trips at sea (3–28 days) (Georges and Guinet 2000). Thus, pups lose considerable amount of body mass fasting, while the mother is absent resulting in reduced growth efficiency (Arnould et al. 1996).

Conclusion

The present study is the first that investigated milk intake and intake of milk nutrients in suckling mammalian young employing PIC analysis. The outcomes suggest a consistent phylogenetic pattern for milk and intake of milk nutrients. The developed allometric equations can be used to predict milk intake and intake of milk nutrients at peak lactation from body mass or ADG for species that have not been studied yet, providing that the body mass falls inside the range of masses used to derive the equations. However, these equations need to be used with caution to predict values of missing species, as the fit-lines are not accounted for the phylogenetic history of missing species. Nevertheless, in the absence of any published comparative data on milk and milk nutrient intakes in suckling mammalian young at peak lactation, the range of animals included in the present study gives a starting point for estimates of closely related species, thus making these equations a useful tool for zoo keepers, animal nutritionists, veterinarians and wildlife zoologists.

Acknowledgements

The study was supported by a research fellowship from the Alexander von Humboldt-Foundation to the author.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.mambio.2010.03.004.

References

- Arnould, J.P.Y., Hindell, M.A., 1999. The composition of Australian fur seal (*Arctocephalus pusillus doriferus*) milk throughout lactation. *Physiol. Biochem. Zool.* 72, 605–612.
- Arnould, J.P.Y., Hindell, M.A., 2002. Milk consumption, body composition and pre-weaning growth rates of Australian fur seal (*Arctocephalus pusillus doriferus*) pups. *J. Zool.* 256, 351–359.
- Arnould, J.P.Y., Boyd, I.L., Socha, D.G., 1996. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Can. J. Zool.* 74, 254–266.
- Baker, B.E., Cook, H.W., Teal, J.J., 1970. Muskox (*Ovibos moschatus*) milk. I. Gross composition, fatty acid, and mineral constitution. *Can. J. Zool.* 48, 1345–1347.
- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., et al., 2007. The delayed rise of present-day mammals. *Nature* 446, 507–512.
- Blomberg, S.P., Garland, T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: behavioural traits are more labile. *Evolution* 57, 717–745.
- Bowen, W.D., Oftedal, O.T., Boness, D.J., 1992. Mass and energy-transfer during lactation in a small Phocid, the harbor seal (*Phoca vitulina*). *Physiol. Zool.* 65, 844–866.
- Buss, D.H., Voss, W.R., 1971. Evaluation of four methods for estimating the milk yield of baboons. *J. Nutr.* 101, 901–909.

- Carl, G.R., Robbins, C.T., 1988. The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. *Can. J. Zool.* 66, 239–246.
- Coward, W.A., Sawyer, M.B., Whitehead, R.G., Prentice, A.M., Evans, J., 1979. New method for measuring milk intakes in breast-fed babies. *Lancet* 2, 13–14.
- Cowie, A.T., 1969. Variations in the yield and composition of the milk during lactation in the rabbit and the galactopoietic effect of prolactin. *J. Endocrinol.* 44, 437–450.
- Degen, A.A., Elias, E., Kam, M., 1987. A preliminary report on the energy intake and growth rate of early weaned camel (*Camelus dromedarius*) calves. *Anim. Prod.* 45, 301–306.
- Dobenecker, B., Zottmann, B., Kienzle, E., Zentek, J., 1998. Investigations on milk composition and milk yield in queens. *J. Nutr.* 128, 2618S–2619S.
- Donohue, M.J., Costa, D.P., Goebel, E., Antonelis, G.A., Baker, J.D., 2002. Milk intake and energy expenditure of free-ranging northern fur seal, *Callorhinus ursinus*, pups. *Physiol. Biochem. Zool.* 75, 3–18.
- Dove, H., Axelsen, A., 1979. Estimation of milk consumption in beef calves using a tritiated water dilution technique. *Aust. J. Exp. Agric.* 19, 666–672.
- Dove, H., Cork, S.J., 1989. Lactation in the tammar wallaby (*Macropus eugenii*). I. Milk consumption and the algebraic description of the lactation curve. *J. Zool.* 219, 385–397.
- Farley, S.D., Robbins, C.T., 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Can. J. Zool.* 73, 2216–2222.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *Am. Nat.* 125, 1–15.
- Fortun-Lamothe, L., Gidenne, T., 2000. The effects of size of suckled litter on intake behaviour, performance and health status of young and reproducing rabbits. *Ann. Zootech.* 49, 517–529.
- Garland, T., Harvey, P.H., Ives, A.R., 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* 41, 18–32.
- Garland, T., Dickerman, A.W., Janis, C.M., Jones, J.A., 1993. Phylogenetic analysis of covariance by computer-simulation. *Syst. Biol.* 42, 265–292.
- Garland, T., Ives, A.R., 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* 155, 346–364.
- Gittleman, J.L., Oftedal, O.T., 1987. Comparative growth and lactation energetics in carnivores. *Symp. Zool. Soc. London* 57, 41–77.
- Gjostein, H., Holand, O., Weladji, R.B., 2004. Milk production and composition in reindeer (*Rangifer tarandus*): effect of lactational stage. *Comp. Biochem. Physiol. A* 137, 649–656.
- Georges, J.-Y., Guinet, C., 2000. Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology* 81, 295–308.
- Green, B., 1984. Composition of milk and energetics of growth in marsupials. *Symp. Zool. Soc. London* 51, 369–387.
- Hackländer, K., Tataruch, F., Ruf, T., 2002. The effect of dietary fat content on lactation energetics in the European hare (*Lepus europaeus*). *Physiol. Biochem. Zool.* 75, 19–28.
- Harvey, P.H., Pagel, M.D., 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Hendriks, W.H., Wamberg, S., 2000. Milk intake of suckling kittens remains relatively constant from one to four weeks of age. *J. Nutr.* 130, 77–82.
- Iverson, S.J., Bowen, W.D., Boness, D.J., Oftedal, O.T., 1993. The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). *Physiol. Zool.* 66, 61–88.
- Jordan, G.E., Piel, W.H., 2008. PhyloWidget: web-based visualization for the tree of life. *Bioinformatics* 24, 1641–1642.
- Kametaka, M., Inaba, J., Ichikawa, R., 1974. Estimation of daily milk intake of suckling rat using turnover rate of potassium. *J. Nutr. Sci. Vitaminol.* 20, 421–429.
- Kleiber, M., 1975. *The Fire of Life*. Robert E. Krieger Publishing Company, Huntington, New York.
- Knight, C.H., Maltz, E., Docherty, A.H., 1986. Milk yield and composition in mice: effects of litter size and lactation number. *Comp. Biochem. Physiol. A* 84, 127–133.
- Langer, P., 2008. The phases of maternal investment in eutherian mammals. *Zoology* 111, 148–162.
- Linzell, J.L., 1972. Milk yield, energy loss in milk, and mammary gland weight in different species. *Dairy Sci. Abstr.* 34, 351–360.
- Lydersen, C., Kovacs, K.M., Hammill, M.O., 1997. Energetics during nursing and early postweaning fasting in hooded seal (*Cystophora cristata*) pups from the Gulf of St Lawrence, Canada. *J. Comp. Physiol. B* 167, 81–88.
- Lydersen, C., Kovacs, K.M., Hammill, M.O., Gjert, I., 1996. Energy intake and utilisation by nursing bearded seal (*Erignathus barbatus*) pups from Svalbard, Norway. *J. Comp. Physiol. B* 166, 405–411.
- Maltz, E., 1979. Productivity in the desert: Bedouin goat, ibex and desert gazelle. Ph.D. Thesis, Tel Aviv University.
- Maltz, E., Shkolnik, A., 1984. Lactational strategies of desert ruminants: the Bedouin goat, ibex and desert gazelle. *Symp. Zool. Soc. London* 51, 193–213.
- Martin, R.D., 1984. Scaling effects and adaptive strategies in mammalian lactation. *Symp. Zool. Soc. Lond* 51, 87–117.
- McEwan, E.H., Whitehead, P.E., 1971. Measurement of the milk intake of reindeer and caribou calves using tritiated water. *Can. J. Zool.* 49, 443–447.
- McNab, B.K., 1980. Food habits, energetics, and the population biology of mammals. *Am. Nat.* 116, 106–124.
- Merchant, J.C., Libke, J.A., Smith, M.J., 1994. Lactation and energetics of growth in the brush-tailed bettong, *Bettongia penicillata* (Marsupialia: Potoroidae) in captivity. *Aust. J. Zool.* 42, 267–277.
- Munks, S.A., Green, B., 1997. Milk consumption and growth in a marsupial arboreal folivore, the common ringtail possum, *Pseudocheirus peregrinus*. *Physiol. Zool.* 70, 691–700.
- Munks, S.A., Green, B., Newgrain, K., Messer, M., 1991. Milk-composition in the common ringtail possum, *Pseudocheirus peregrinus* (Petauridae, Marsupialia). *Aust. J. Zool.* 39, 403–416.
- Nagy, K.A., 2001. Food requirements of wild animals: predictive equations for free-living mammals, reptiles, and birds. *Nutr. Abstr. Rev.* 71, 21R–32R.
- Oftedal, O.T., 1981. Milk, protein and energy intakes of suckling mammalian young: a comparative study. Ph.D. Thesis, Cornell University, Ithaca.
- Oftedal, O.T., 1984a. Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symp. Zool. Soc. London* 55, 33–85.
- Oftedal, O.T., 1984b. Lactation in the dog: milk composition and intake by puppies. *J. Nutr.* 114, 803–812.
- Oftedal, O.T., Bowen, W.D., Boness, D.J., 1996. Lactation performance and nutrient deposition in pups of the Harp seal, *Phoca groenlandica*, on ice floes off southeast Labrador. *Physiol. Zool.* 69, 635–657.
- Oftedal, O.T., Hintz, H.F., Schryver, H.F., 1983. Lactation in the horse: milk composition and intake by foals. *J. Nutr.* 113, 2096–2106.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analysis of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Parker, K.L., White, R.G., Gillingham, M.P., Holleman, D.F., 1990. Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. *Can. J. Zool.* 68, 106–114.
- Payne, P.R., Wheeler, E.F., 1968. Comparative nutrition in pregnancy and lactation. *Proc. Nutr. Soc.* 27, 129–138.
- Pluske, J.R., Williams, I.H., Zak, L.J., Clowes, E.J., Cegielski, A.C., Aherne, F.X., 1998. Feeding lactating primiparous sows to establish three divergent metabolic states: III. Milk production and pig growth. *J. Anim. Sci.* 76, 1165–1171.
- Reese, E.O., Robbins, C.T., 1994. Characteristics of moose lactation and neonatal growth. *Can. J. Zool.* 72, 953–957.
- Riek, A., Gerken, M., 2006. Changes in Llama (*Lama glama*) milk composition during lactation. *J. Dairy Sci.* 89, 3484–3493.
- Riek, A., Gerken, M., Moors, E., 2007. Measurement of milk intake in suckling llamas (*Lama glama*) using deuterium oxide dilution. *J. Dairy Sci.* 90, 867–875.
- Riek, A., 2008. Relationship between milk energy intake and growth rate in suckling mammalian young at peak lactation: an updated meta-analysis. *J. Zool.* 274, 160–170.
- Robbins, C.T., Podbielanciknorman, R.S., Wilson, D.L., Mould, E.D., 1981. Growth and nutrient consumption of elk calves compared to other ungulate species. *J. Wildlife Manage.* 45, 172–186.
- SAS Release 9.01., 2001. SAS Inst. Inc., Cary, NC.
- Sawaya, W.N., Khalil, J.K., Alshalhat, A., Almohammad, H., 1984. Chemical composition and nutritional quality of camel milk. *J. Food Sci.* 49, 744–747.
- Scantlebury, M., Russell, A.F., McIlrat, G.M., Speakman, J.R., Clutton-Brock, T.H., 2002. The energetics of lactation in cooperatively breeding meerkats *Suricata suricatta*. *Proc. R. Soc. London B* 269, 2147–2153.
- StatistiXL Release 1.8., 2007. www.statistiXL.com.
- Stern, A.A., Kunz, T.H., Studier, E.H., Oftedal, O.T., 1997. Milk composition and lactational output in the greater spear-nosed bat, *Phyllostomus hastatus*. *J. Comp. Physiol. B* 167, 389–398.
- Taylor, B.A., Varga, G.A., Whitsel, T.J., Hershberger, T.V., 1990. Composition of blue duiker (*Cephalophus monticola*) milk and milk intake by the calf. *Small Rum. Res.* 3, 551–560.
- Withers, P.C., Cooper, C.E., Larcombe, A.N., 2006. Environmental correlates of physiological variables in marsupials. *Physiol. Biochem. Zool.* 79, 437–453.
- Withers, P.C., 2008. Independent Contrasts, version 1.14. Distributed by the Author. Department of Zoology, University of Western Australia, Crawley, WA, Australia.