

Empirical and Theoretical Constraints on the Evolution of Lactation

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ABSTRACT

For 829 mammalian species, data on age at weaning or age at first solid food were analyzed with respect to body mass, phylogeny, habitat, diet, length of gestation, basal metabolism, and neonatal development. The primary influence on lactation length is female mass, but phylogenetic constraints are important. Thus, lactation can be characterized as short (earless seals and baleen whales), long (marsupials, bats, and primates), or average (remaining eutherians). Among average mammals, lagomorphs have short lactations.

Lactation may have different functions, evolutionary constraints, and physiological control depending on whether young first eat solid food near weaning or well before it. First solid food eaten near weaning occurs in polytocous species with altricial young; in this case, lactation has a clear energetic role. In contrast, first solid food well before weaning is common for mammals with single, precocial offspring. For these species, the energetic and nutritional constraints on lactation may be less important than the benefits of maintaining contact between mother and young, such as reduced juvenile mortality and increased opportunities for learning social or foraging patterns. Thus, the age at first solid food relative to the age at weaning may indicate the function of lactation within the reproductive biology of a given mammal.

Delayed development and implantation alter the timing of energetic invest-

ment during gestation, so too, the age at first solid food may alter or reflect the rate of energetic investment during lactation. Thus, the age at first solid food relative to the age at weaning may indicate the function of lactation within the reproductive biology of a given mammal. Testing these hypotheses will require data from diverse species on the nutritional and energetic value of milk before and after first solid food as well as on the mechanics and consequences of nursing or suckling during the course of lactation.

(Key words: evolution of lactation, allometry, reproductive effort, parental investment)

Abbreviation key: BMR = basal metabolic rate.

INTRODUCTION

Lactation is the quintessence of mammals. Like the evolution of mammals, the evolution of lactation has incorporated many organizational changes. Biochemical changes involve carbohydrate, fat, and protein synthesis in the female and their catabolism in her young. Gland structure and location are anatomically and developmentally modified in females, as are cheek musculature and tooth growth in young. Physiological changes include modifications not only of hormonal control and metabolism, but also of the behaviors of mothers and their young in order to implement and to integrate nursing and suckling. Lactation alters the timing of reproduction to mesh ecologically, energetic demands with seasonal resource abundance. To achieve this organizational integration, the genetic framework supporting lactation and other reproductive traits is likely to be replete with pleiotropy and polygeny. Thus, the selection pressures on lac-

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tation are, and have been, numerous and complex.

Most mammalian traits (e.g., body length, number of toes, and dentition) are characteristics of individuals, but lactation and other reproductive characteristics are not. In particular, the length of lactation is not determined solely by the mother or by the young but rather depends on their interaction. Selection acts on at least two genetic complements simultaneously. Reproductive characteristics, such as lactation, are characteristics of family groups, not of individuals. The evolutionary processes that affect reproductive characteristics have not been delineated, but trait group or interdemographic (between populations) selection may be important (11). The study and characterization of lactation solely on the molecular, cellular, or individual level miss the essential character of this phenomenon.

This paper explores lactation across mammalian species and assesses the relative importance of diverse biological aspects (for example, habitat, diet, body mass, and phylogenetic history) to the temporal and energetic characteristics of lactation. Temporal aspects will be emphasized because the energetic aspects (milk quality and quantity) have already received extensive analysis and, more importantly, because time itself is a limiting resource and a potent evolutionary pressure. Reproduction must fit into a seasonal climatic cycle, where such a cycle exists. Additionally, reproductive success depends on the production of as many viable offspring as possible over a lifetime; the sooner that these offspring can be produced, the greater is the selective advantage (2). Time is essential for parents, for offspring, and for populations during periods of exponential growth and in saturated environments. Thus, the duration of lactation is an important aspect of the reproductive biology of mammals. An additional advantage of this particular analysis is to provide the means to estimate the lactation lengths of extinct, rare, or unstudied mammals based on maternal mass and phylogeny.

MATERIALS AND METHODS

Data on lactation lengths have been recorded for about one-fifth of the known mammals, representing 19 or 20 taxonomic orders. Of these 829 species, age at weaning

(lactation length) is available for 753 species, and age at first solid food is available for 419 species. These and additional data on milk composition, length of gestation (including diapause and implantation delays), development at birth, litter size, and adult female mass were synthesized from over 12,000 sources (1, 5, 7). Common log transformations were performed on the age at weaning, age at first solid food, length of gestation, and adult female mass to improve the symmetry of each distribution across species and the uniformity of spread across orders (8). Not all data were available for each species. The age at first solid food is more precisely and uniformly defined than the age at weaning. Unfortunately, the age at first solid food is recorded about half as often. More observations of the age at first solid food are needed.

Operational definitions of the length of lactation (the age of weaning) vary according to the needs of the investigator. Unless this variability is correlated with a more natural aspect of mammalian biology (for instance, body mass or phylogeny), subsequent analysis of relationships, although not biased, will be more difficult to elucidate. In some cases, the needs of investigators probably are confounded with phylogeny (e.g., primatologists study primates; the whaling industry studies whales). Unfortunately, the biases inherent in these different approaches to mammalian groups have not been precisely delineated. Thus, their effect on comparative analyses are unknown.

Several temporal units are used to record the length of reproductive stages: days, weeks, months, and years. As units, weeks and months have little biological relevance because most species are unaware of our human measurement of time. Measurement of lactation and other reproductive stages in these units is not biologically meaningful and should be avoided. The use of months as a unit is especially problematic because the measure cannot be accurately rescaled into another time frame. A single month can range from 28 to 31 d. For this report, all temporal measures have been converted to days, and a month is assumed to be 30 d.

For this paper, lactation length is considered to be a dependent variable, and description of its variance with respect to a variety of other variables is the major goal. Statistical treat-

ment was by least squares regression or analysis of covariance (5, 9). Least squares regression was chosen over reduced major axis regression to maintain a constant dimensionality of slopes across different data sets. Statistics for significant regression analyses are reported. For each set of regressions, a significance of .05 across sets was approximated by reducing the significance for individual regressions by the number of regressions performed for that analysis. Thus, to be reported, individual regressions for analysis by infraclass needed $P < .0167$ (.05/3 infraclasses), whereas ordinal comparisons needed $P < .0025$ (.05/20 orders), and familial regressions needed $P < .0004$ (.05/136 families).

Several dimensionless ratios were calculated to explore mammalian lactation. Although they are not amenable to rigorous parametric analysis, these ratios, nevertheless, are extremely useful for illustrating multidimensional trends. The ratio of age at first solid food to age at weaning may be an estimate of the relative nutritional dependency of the offspring on lactation. The ratio of lactation length to the period between conception and weaning (gestation plus lactation) is an estimate of the relative contribution of lactation to a female's temporal investment in reproduction. Although the energetic costs of construction and maintenance of placental structures are not included, the ratio of litter mass at birth to female mass is an estimate of the energetic investment into a given reproductive effort before lactation begins. Similarly, the ratio of an individual neonate's mass to maternal mass is an estimate of the energetic investment into a single offspring before lactation begins and an estimate of the reliance on lactation for the physical growth of an individual offspring. Of course, for single litters, litter mass and neonatal mass are identical.

Taxonomic Representation

The ordinal representation of the species in this data set is roughly similar to that for mammals. Small mammals (Insectivora, Chiroptera, and Rodentia) are underrepresented by 5 to 10%, whereas marsupials, primates, and carnivores are overrepresented by similar amounts. For each mammalian order, the number of species with data on the age at weaning

or first solid food and the common names of representative species follow: infraclass Prototheria, order Monotremata (3 species; echidnas and platypus); infraclass Metatheria, order Marsupialia (89 species; opossums, phalangers, kangaroos, wombats, and koala); infraclass Eutheria, orders Xenarthra or Edemata (9 species; anteaters and sloths), Insectivora (38 species; hedgehogs, shrews, and moles), Scandentia (3 species; tree shrews), Dermoptera (no data; flying lemur), Chiroptera (75 species; bats), Primates (64 species; lemurs, monkeys, apes, and humans), Carnivora (128 species; wolves, bears, raccoons, weasels, genets, mongooses, hyena, cats, fur seals, walrus, and earless seals), Cetacea (28 species; dolphins, porpoises, and whales), Sirenia (3 species; dugong and manatees), Proboscidea (2 species; elephants), Perissodactyla (9 species; zebras, tapirs, and rhinoceroses), Hyracoidea (3 species; hyraxes), Tubulidentata (1 species; armadillo), Artiodactyla (82 species; swine, camels, hippopotamus, deer, giraffe, cattle, antelope, sheep, and goats), Pholidota (3 species; pangolins), Rodentia (270 species; squirrels, gophers, kangaroo rats, beaver, voles, hamsters, gerbils, mice, rats, and porcupines), Lagomorpha (15 species; pikas, hares, and rabbits), and Macroscelidea (4 species; elephant shrews). The infraclasses Metatheria and Eutheria are referred to jointly as the taxon Theria. The Appendix provides selected familial common names.

RESULTS AND DISCUSSION

Univariate Statistics

Age at Weaning. The length of lactation in mammals (Figure 1) ranges almost three orders of magnitude, from 4 to 5 d in hooded seals (*Cystophora cristata*, family Phocidae, order Carnivora), spiny rats (*Proechimys guairae*, family Echimyidae, order Rodentia), and elephant shrews (*Macroscelides proboscideus*, family Macroscelididae, order Macroscelidea) to over 900 d in some of the great apes (chimpanzees, *Pan troglodytes*, and orangutan, *Pongo pygmaeus*, family Pongidae, order Primates). Although extremely short lactation lengths (<10 d) are rare, long lactation lengths (>500 d) are common for large-bodied species with singleton offspring, such as kangaroos, great apes, walruses, whales, sirenians, elephants, and

rhinoceroses. Overall, 50% of known lactation lengths range from 29 to 135 d. The median lactation length is 60 d, the geometric mean is 64.56 d ($1.81 \log_{10}$ d, $SD = .428$), and the arithmetic mean is 108.4 d ($SD = 132.1$). The peak at about 30 d may be an artifact of using human-biased units such as weeks or months rather than more biologically meaningful units such as days.

Generally, lactation lengths for prototherians (monotremes) and metatherians (marsupials) are longer than those for eutherians (median lactation length: prototherians, 150 d, 3 species; metatherians, 120 d, 75 species; eutherians, 50 d, 675 species), although lactation lengths are longest in eutherians. Lactation in monotremes and marsupials, but not eutherians, encompasses the exponential period of offspring growth. Additionally, lactation in marsupials is distinctly biphasic. During the phase of continuous teat attachment, marsupial milk is high in carbohydrates and low in lipids, whereas the reverse holds when suckling is intermittent (3, 10). Occasionally, the teat attachment phase of marsupial lactation is equated with the chorioallantoic phase of eutherian gestation. Superficial similarities exist, but this synonymy ignores the vastly different proximate mechanisms (metabolic and physiological control) and ultimate causes (selective pressures and evolutionary constraints) that distinguish gestation and lactation from each other.

Age at First Solid Food. Fewer data exist for the age at first solid food. Solid food is

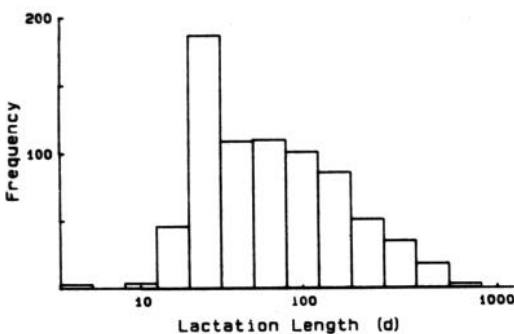


Figure 1. Frequency of lactation lengths in 753 species of mammals. The peak at 30 d may be an artifact of the use of anthropocentric units (e.g., weeks or months) rather than biologically meaningful units (e.g., days).

eaten within wk 1 after birth (occasionally on the day of birth) in hystricomorph rodents, such as guinea pigs, porcupines, coypus, and agoutis, as well as in other mammals, such as sloths, zebras, hyraxes, and bovids. In contrast, first solid food is nearly coincident with weaning in many sciurid (e.g., squirrels) and muroid (e.g., rats or gerbils) rodents and may even occur after weaning, as with earless seals. Age at first solid food ranges from 1 to 300 d; 50% of the observations are from 14 to 50 d. The median age is 30 d, the geometric mean is 27.54 d ($1.44 \log_{10}$ d, $SD = .455$), and the arithmetic mean is 45.1 d ($SD = 50.9$). The median age at first solid food is later for metatherians (75 d, 72 species) than for eutherians (22 d, 345 species). Sufficient data on first solid food for prototherians are lacking.

Comparisons and Analysis. For both age at weaning and age at first solid food, the median and the geometric mean are within 10% of each other, but the arithmetic mean is at least 50% larger. Thus, the \log_{10} -transformed data more closely approximate Gaussian distributions for both variables.

The interquartile range of the age at first solid food (36 d, 419 species) is about a third that of the age at weaning (106 d, 753 species). The smaller sample size for age at first solid food may account for its smaller range, or the age at first solid food may be less flexible and more uniform across mammals than the age at weaning.

Age at weaning and age at first solid food are positively correlated (regression statistics: $r = .58$; $R^2 = .34$; $F = 176$; sample size, 343 species). Species that are older at weaning are also older at first solid food. Age at weaning and age at first solid food are both positively correlated with female mass, although the effect is weak for age at first solid food (see Table 1, Equation [1] for age at weaning statistics; regression statistics age at first solid food: $r = .19$; $R^2 = .03$; $F = 15$; sample size, 408 species).

Analysis of the ratio of age at first solid food to age at weaning effectively removes the confounding influence of body mass. In general, the longer the lactation length, the sooner first solid food occurs relative to weaning. For eutherians with lactation lengths of at least 1 yr (21 species), most (90%) have an age at first solid food within the first third of the

lactation period. For 62% of these species, solid food is eaten within the first fifth of lactation. In contrast, for eutherians with lactation lengths <50 d (123 species), few (11%) have an age at first solid food within the first third of lactation. For 48% of these species, first solid food occurs during the last third of lactation. Thus, infants depend completely on maternal resources for a larger proportion of the lactation period in species with short lactations, whereas offspring may be less reliant on maternal nutrients when lactation lengths are long. The timing of first solid food relative to weaning is also correlated with litter size and with neonatal development as described more fully later.

Allometry of Lactation: The Relationship of Lactation to Maternal Mass

For mammals, the length of lactation is positively correlated with adult female mass (Figure 2; Table 1, Equation [1]). In general, larger species have longer lactation lengths, although several interesting exceptions to this pattern exist.

Earless seals (family Phocidae) and baleen whales (infraorder Mysticeti), but not other marine mammals, have much shorter lactation lengths than expected for their body masses. The extremely short lactation lengths of earless seals appear to be related to the unpredictable and short existence of the ice floes where they breed. The relatively short lactation lengths of baleen whales may reflect the timing of their annual migrations, because a lactation length appropriate to their large mass would not be synchronized with the seasonal nature of their

food and activity. Both groups (especially the baleen whales) exert great statistical influence on the computed relationship between lactation length and body mass. Removal of these two groups from the calculations generates a more representative numerical relationship for mammals in general (Table 1, Equation [2]).

The remaining mammals are still not a homogeneous group, because several mammalian taxa have distinctly long lactation lengths for their mass. Bats, primates, and marsupials together form a homogeneous group of mammals with lactation lengths longer than those of other mammals with similar maternal mass. Covariance analysis confirms this observation (Table 1, Equations [3] and [4]). The slopes of the two regression lines are not statistically distinguishable; thus, the relationship between lactation length and body mass is not different between the two groups. However, the intercepts of the equations are different. Bats, marsupials, and primates, as a group, have lactation lengths 50% longer (on a \log_{10} scale) than other therians of comparable masses. The Prototheria (monotremes) are intermediate. Although the reproductive biology of marsupials is generally different than that of eutherians (6), marsupials are indistinguishable from bats and primates with respect to lactation length. Thus, for lactation length, infraclass comparisons are not appropriate.

Why should mammals with long and average lactation lengths have similar allometric relationships? One explanation is that the similarity of slope between long and average mammals is accidental. In other words, bats, marsupials, and primates each have a separate, selective advantage for long periods of lacta-

TABLE 1. Allometric relationships between the age at weaning (days) and adult female mass (grams) for various mammalian groups.¹

	Slope SE	Constant SE	R ²	n	F
Mammalia ₂	.184 .008	1.275 .026	.43	732	543
Mammalia ² (no short)	.214 .008	1.212 .025	.51	705	743
Long lactations ³	.227 .012	1.501 .033	.62	201	329
Average lactation ⁴	.250 .006	.977 .021	.75	504	1517

¹All variables are \log_{10} -transformed. Sample size is number of species.

²Therian mammals without earless seals (Phocidae), baleen whales (Mysticeti).

³Includes marsupials (Marsupialia), primates (Primates), and bats (Chiroptera) only.

⁴Eutherians, excluding primates (Primates), bats (Chiroptera), earless seals (Phocidae), and baleen whales (Mysticeti).

tion, but, because the three taxa are adjacent and slightly overlapping with respect to body mass, they form a single group with the same slope as that for other mammals. However, if the slope is regarded as a true biological phenomenon (i.e., that an ancestral allometry of mass with lactation length exists for mammals), then the convergence of marsupials, bats, and primates needs explanation.

Given the fetal state of their neonates, the relatively long lactation lengths of metatherians (marsupials) are not surprising; however, neither bats nor primates have such tiny offspring relative to maternal mass. Some metabolic parameter or growth rate may possibly explain the allometric convergence. The lengthy primate lactations may be related to the more extensive psychosocial growth and development characteristic of the order. A similar developmental phenomenon may occur in bats that is related to the extensive neuromuscular coordination required for food acquisition in flight. Perhaps newborn bats and primates are as "fetal" in their neurological development relative to their adult needs as

neonatal marsupials are physically. Comparative data on the developmental similarities of marsupials, bats, and primates and on the quality and quantity of milk over the course of lactation in these groups, especially bats, are needed to explore this empirical relationship.

Thus, mammalian lactation lengths relative to maternal mass can be characterized as short (earless seals and baleen whales), long (marsupials, bats, and primates), or average (the remaining eutherians). For this last (average) group, 75% of the variation in the length of lactation is related to maternal mass. The correlation of lactation length with body mass is stronger for larger species (>1 kg vs. <=1 kg), but this result is confounded by phylogeny, because about 75% of the small mammals with average lactation lengths are rodents.

Eutherian Ordinal Analyses. Although lactation is strongly correlated with maternal mass across mammalian species, within individual eutherian orders, the relationship between female mass and lactation length is less obvious (Figure 3). Many systematically distinctive orders (tree shrews, sirenians,

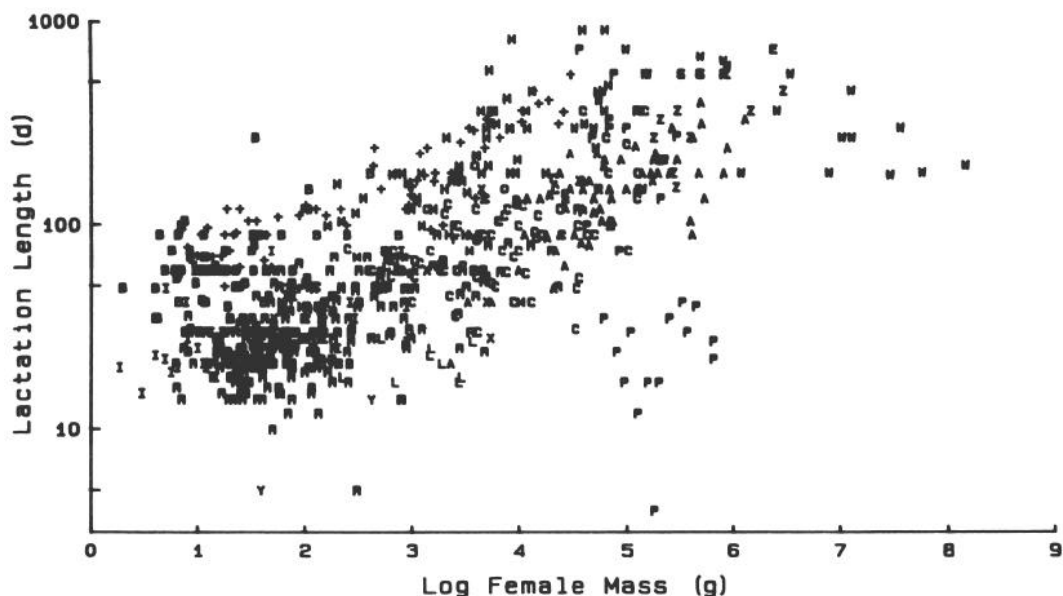


Figure 2. Allometric relationship of lactation length with female mass (732 species). Marsupials, bats, and primates form a homogenous group with long lactations. Baleen whales and earless seals have unusually short lactations. Key to orders: infraclass Prototheria; order Monotremata (P), infraclass Metatheria, order Marsupialia (+); infraclass Eutheria, orders Artiodactyla (A), Chiroptera (B), Carnivora (C), Proboscidea (E), Pholidota (F), Hyracoidea (H), Insectivora (I), Scandentia (K), Lagomorpha (L), Primates (M), Rodentia (R), Sirenia (S), Tubulidentata (T), Cetacea (W), Xenarthra (X), Macroscelidea (Y), and Perissodactyla (Z). Common names are given in Materials and Methods.

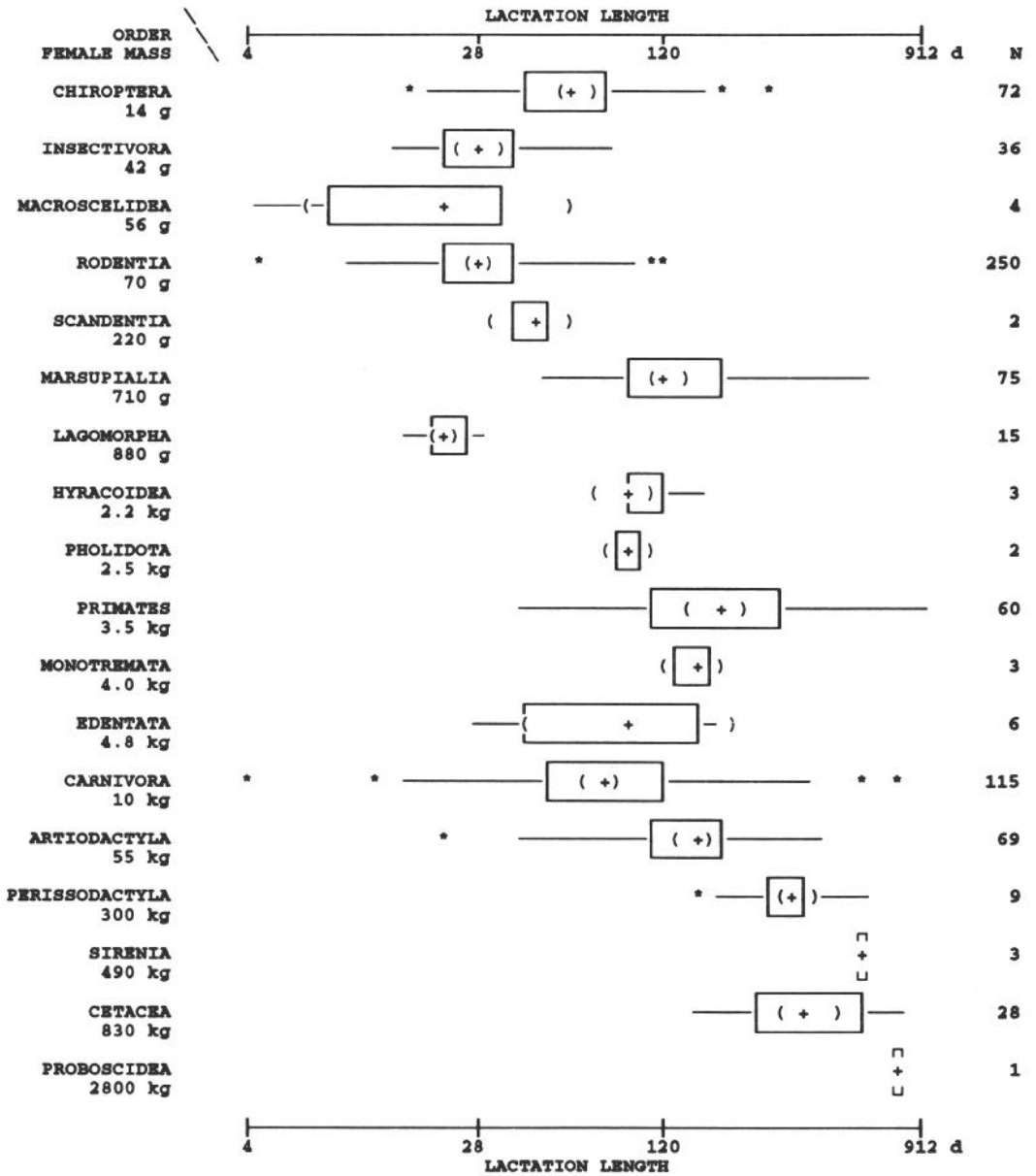


Figure 3. Box plots of lactation length (\log_{10} -transformed age at weaning in d) for 753 mammalian species grouped by order and ranked by median maternal mass (provided beneath name of order). Sample size in number of species is listed in the right column. Lagomorphs have relatively uniform and short lactations. Carnivore lactation lengths have the broadest range. Median (+), interquartile range (\bullet), approximate 95% confidence interval for median (\square), outliers, the values distant from the median by >1.5 times the interquartile range (*), and "whiskers", the range excluding outliers (—). Names of common representatives of each order are given in Materials and Methods.

elephants, hyraxes, aardvarks, pangolins, and elephant shrews) have too few species for analysis. For others, such as xenarthrans, perisodactyls, and lagomorphs, the absence of a statistical relationship between lactation length and female mass may be an artifact of the narrow range of body masses present across species within these orders. However, the range of body masses in each of several other orders (insectivores, bats, carnivores, and cetaceans) spans three to four orders of magnitude; however, for these groups, lactation length also is not correlated with maternal mass. Only for primates, artiodactyls, and rodents is lactation significantly related to maternal mass, and only for primates and artiodactyls does body mass explain >50% of the variance in lactation length (Table 2). For eutherian orders represented in the data set by at least 3 families or 15 species, descriptions of the allometry of lactation length follow (Figures 4 to 7).

The four families of xenarthrans (which includes anteaters, two- and three-toed sloths, and armadillos) are each remnants of previously diverse taxa. Data for 6 of the 29 species (21%) are available. Although lactation lengths are highly varied among species with similar female mass (Figure 4a), overall, they are near those expected for average mammals of equivalent size.

The six families of the order Insectivora (which includes hedgehogs, tenrecs, shrews, moles, etc.) are a taxonomic mixture with little close phylogenetic relationship. Data for 36 of the 379 species (10%) are available. Maternal mass varies over almost three orders of magnitude, but lactation lengths are nearly all between 20 and 50 d (median 28 d). Thus, within this order, the duration of lactation and female mass are not correlated (Figure 4b). However, phylogeny confounds this analysis: shrews (family Soricidae) tend to be small; moles (family Talpidae) are larger; tenrecs (family Tenrecidae) are intermediate; and hedgehogs (family Erinaceidae) are often the largest. Although Insectivora generally have lactations of average duration for mammals of their mass, the small soricids (shrews <10 g) tend to have longer lactation lengths than expected.

With at least 17 families, 175 genera, and over 900 species, bats (order Chiroptera) are second only to rodents in phylogenetic diversity. Unfortunately, data on lactation are available for only 8% of the species (representing 37 genera and 10 families). For 85% of these limited observations, lactation length is between 30 and 90 d. Maternal mass spans nearly three orders of magnitude but accounts for only 8% of the variation in the length of

TABLE 2. Regression statistics for significant allometric relationships between the age at weaning (days) and adult female mass (grams) for various mammalian taxa.¹

	Slope	SE	Constant	SE	R ²	n	F
Infraclass							
Metatheria	.197	.017	1.628	.047	.64	74	129
Eutheria	.191	.008	1.210	.026	.48	655	608
Order							
Marsupialia	.197	.017	1.628	.047	.64	74	129
Primates	.334	.043	1.104	.148	.51	59	61
Artiodactyla	.271	.032	.831	.154	.51	69	73
Rodentia	.150	.015	1.153	.032	.30	242	103
Fissipedia ²	.180	.026	1.238	.098	.36	85	49
Family							
Dasyuridae	.137	.020	1.771	.038	.64	27	46
Macropodidae	.340	.038	1.172	.141	.85	15	82
Mustelidae	.168	.031	1.314	.100	.53	25	28
Bovidae	.237	.040	1.001	.195	.45	42	34

¹For each set of regressions, a significance level of .05 was approximated by reducing the significance for individual regressions by the number of regressions performed for that analysis: infraclass regressions ($P < .0167$); ordinal regressions ($P < .0025$); and familial regressions ($P < .0004$). Sample size is number of species. All variables are \log_{10} -transformed.

²Carnivora, excluding the Pinnipedia (Otariidae, Odobenidae, Phocidae).

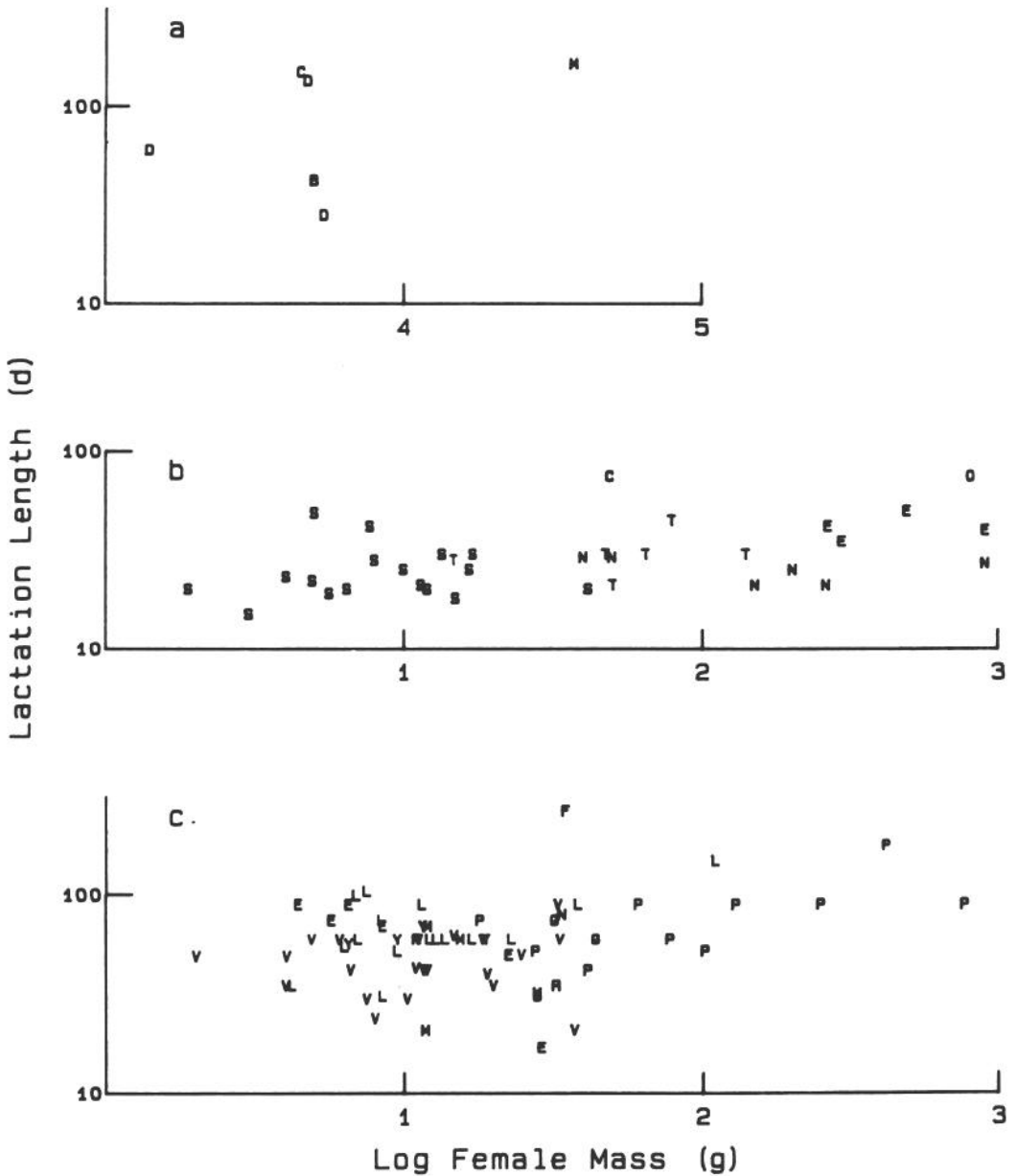


Figure 4. Allometric relationships of age at weaning with maternal mass for a) edentates, b) insectivores, and c) bats. Species from the same family have the same letter code. Key to families within each order: a. Edentata or Xenarthra: Bradypodidae (B), Choloepidae (C), Dasypodidae (D), and Myrmecophagidae (M); b. Insectivora: Chrysochloridae (C), Erinaceidae (E), Tenrecidae (N), Solenodontidae (O), Soricidae (S), and Talpidae (T); c. Chiroptera: Emballonuridae (E), Phyllostomidae (F), Megadermatidae (G), Rhinolophidae (L), Molossidae (M), Noctilionidae (N), Pteropodidae (P), Rhinopomatidae (R), Vespertilionidae (V), and Nycteridae (Y). Familial common names are given in the Appendix.

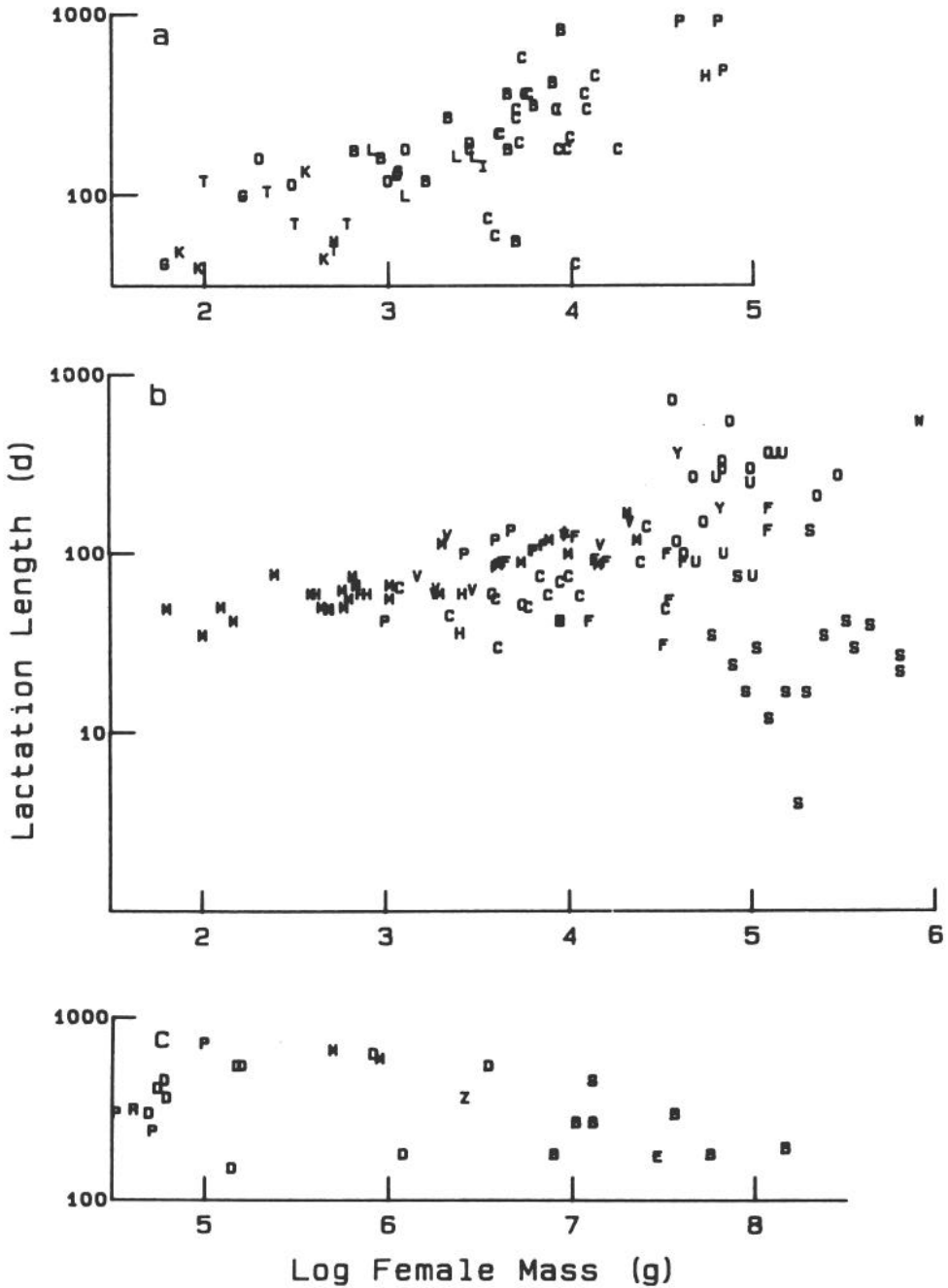


Figure 5. Allometric relationships of age at weaning with maternal mass for a) primates, b) carnivores, and c) Cetaceans. Species from the same family have the same letter code. Key to families within each order: a. Primates: Cebidae (B), Cercopithecidae (C), Daubentoniidae (D), Galionidae (G), Hominidae (H), Indridae (I), Cheirogaleidae (K), Lemuridae (L), Callimiconidae (M), Lorisidae (O), Pongidae (P), and Callitrichidae (Y); b. Carnivora: Protelidae (A), Canidae (C), Felidae (F), Herpestidae (H), Mustelidae (M), Otariidae (O), Procyonidae (P), Phocidae (S), Ursidae (U), Viverridae (V), Odobenidae (W), and Hyaenidae (Y); c. Cetacea: Balaenopteridae (B), Delphinidae (D), Eschrichtidae (E), Monodontidae (M), Phocoenidae (P), Platanistidae (R), Physeteridae (S), and Ziphiidae (Z). Familial common names are given in the Appendix.

lactation (Figure 4c). Insectivora and Chiroptera have a similar range of female mass, and both orders exhibit little correlation of body mass with lactation length; however, the median lactation length for bats (60 d) is over twice that of the Insectivora (28 d).

Primates also lactate for long periods relative to most mammals. Maternal mass is strongly and positively correlated with lactation length (Figure 5a) and accounts for >50% of the variation in the length of lactation (Table 2). Although the ordinal trend (based on 33% of the known species) is clear, no strong correlation between mass and lactation length exists within any primate family.

Of mammalian orders with >20 species, carnivores and artiodactyls are the best known. Each has lactation length data recorded for 43% of its species. The increasing variance in lactation length with body mass in carnivores is distinctive. Nearly all female carnivores <10 kg lactate from 30 to 130 d. However, of those carnivores >10 kg, some ursids (bears), most otarids (fur seals), and odobenids (walruses) have lactation lengths >130 d, whereas many phocids (earless seals) wean their young <30 d after birth. Exclusion of the pinnipeds improves the homoscedasticity and generates a significant allometric equation (Fissipedia, Table 2). Lactation lengths for mustelids (e.g., weasels, skunks, and badgers) are strongly and positively correlated with maternal mass (Table 2), and the few data for procyonids (raccoons) and viverrids (genets) also suggest a positive correlation with female mass. For the remaining carnivore families, lactation length appears to be relatively independent of maternal mass (Figure 5b).

Few of the data on cetacean lactation lengths are from direct observations of live mother and calf pairs over the course of lactation. Most data are estimates from the seasonal presence of milk in adult females and in calves killed by the commercial whaling industry. These data represent 36% of the known species and suggest that the large baleen whales lactate for shorter periods than the smaller toothed whales. Because smaller cetaceans have lactation lengths more in keeping with their body mass, the overall trend is an inverse relationship of lactation with body mass (Figure 5c). Like bats, toothed whales must catch individual food items in a dynamic, three-

dimensional environment, and their longer lactation lengths may reflect this developmental constraint. Clearly, more precise data are needed to confirm the unusual negative correlation of lactation and body mass in cetaceans.

Like the xenarthrans, the three families of perissodactyls (which include zebras, tapirs, and rhinoceroses) are remnants from previously more diverse taxa. Lactation data are available for 9 of 18 species (50%). The larger rhinoceroses have the longest lactation lengths, but, overall, the duration of milk production is only weakly correlated with female mass (Figure 6a).

In contrast, over 50% of the variation in lactation length is correlated with maternal mass for artiodactyls (which include pigs, peccaries, camels, hippopotamuses, deer, giraffes, and antelope; Figure 6b; Table 2). Bovids (antelope, cattle, sheep, and goats) constitute 60% of the artiodactyla data set, and lactation lengths of bovids are strongly and positively correlated with maternal mass (Table 2).

Lagomorphs come in three sizes (100- to 500-g pikas, 500- to 1500-g rabbits, and 2- to 3-kg hares), but lactation ranges only between 17 and 28 d for the entire order, represented by 15 of 62 species (24%). Not only do lagomorphs tend to have relatively invariant periods of lactation, they also have short lactation lengths compared with other mammals of similar mass (Figure 7a). The leporids (hares and rabbits) have neonates widely divergent in developmental condition at birth; the larger hares produce precocial young, whereas the smaller rabbits produce altricial young. Perhaps as a result, first solid food is about 1 wk earlier for precocial hares than for altricial rabbits. Hares have shorter lactations than expected given their mass, but whether this difference is due to the production of precocial young or to a general trend toward short lactation lengths within lagomorphs is not clear. Delineation of the differences between hares and rabbits in the physiology and ecology of lactation could be especially useful because the two groups are both polytocous, they have similar diets and phylogenetic ancestry, and they can have sympatric populations (i.e., they coexist in the same location). Thus, the two groups form a natural control for the effects of diet, habitat, and phylogeny on the production of altricial versus precocial young.

Rodents are the largest mammalian order, and lactation data are available for about 15% of the >1700 species. Maternal mass ranges from 6 g to 35 kg, but almost 90% of the lactation lengths are between 10 and 50 d, and half are between 21 and 38 d (Figure 7b). Thus, for rodents, lactation is only modestly correlated with maternal mass (Table 2). Sciurid (e.g., squirrels) rodents have long lactation lengths relative to maternal mass. Cricetids (e.g., hamsters, gerbils, and deermice) may have shorter lactation lengths than murids (e.g., rats and house mice) of similar size, although the overlap between them is large.

Reproductive Effort and the Length of Lactation

Temporal Investment. Time and energy are two components of maternal investment. Mammals can dissociate the temporal and energetic components of reproductive investment during gestation, through diapause and delayed implantation, and during lactation, via early first solid food and altered milk composition or production. Although the energetic demands of a current reproduction effort clearly affect future reproductive success, temporal aspects are also important, especially in temperate or other climatically seasonal environments. Appropriate timing of the energetic demands of

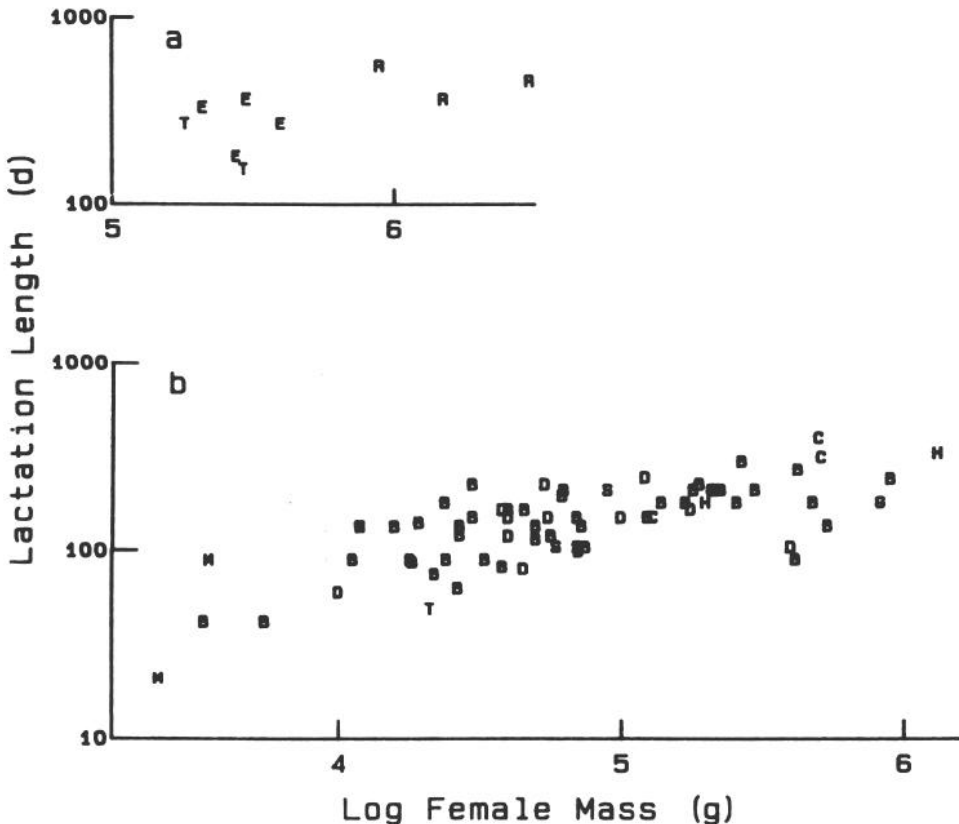


Figure 6. Allometric relationships of age at weaning with maternal mass for a) odd-toed ungulates (perissodactyls) and b) even-toed ungulates (artiodactyls). Species from the same family have the same letter code. Key to families within each order: a. Perissodactyla: Equidae (E), Rhinocerotidae (R), and Tapiridae (T); b. Artiodactyla: Bovidae (B), Camelidae (C), Cervidae (D), Giraffidae (G), Hippopotamidae (H), Tragulidae (M), Suidae (S), and Tayassuidae (T). Familial common names are given in the Appendix.

reproduction to coincide with periods of resource abundance and environmental suitability increases reproductive success. The length of lactation is determined by the timing of weaning. Yet, mothers and their offspring may be in conflict regarding the timing of weaning relative to the seasonality of resource abundance. The energetic demands on females usually are largest before weaning, but the period after weaning is the most demanding for offspring. The length of lactation and the timing of weaning may reflect the relative

importance of females and offspring in the evolution of a particular reproductive pattern.

A female's investment in her offspring begins at conception; thus, lactation is only one component of reproductive effort, and the timing of weaning depends, in part, on the length of gestation. Marsupials may spend >90% of the period between conception and weaning on lactation, and phocid seals may devote <5% of their temporal investment on lactation, but these groups are exceptional (Figure 8). Given that mammalian gestation and lactation lengths

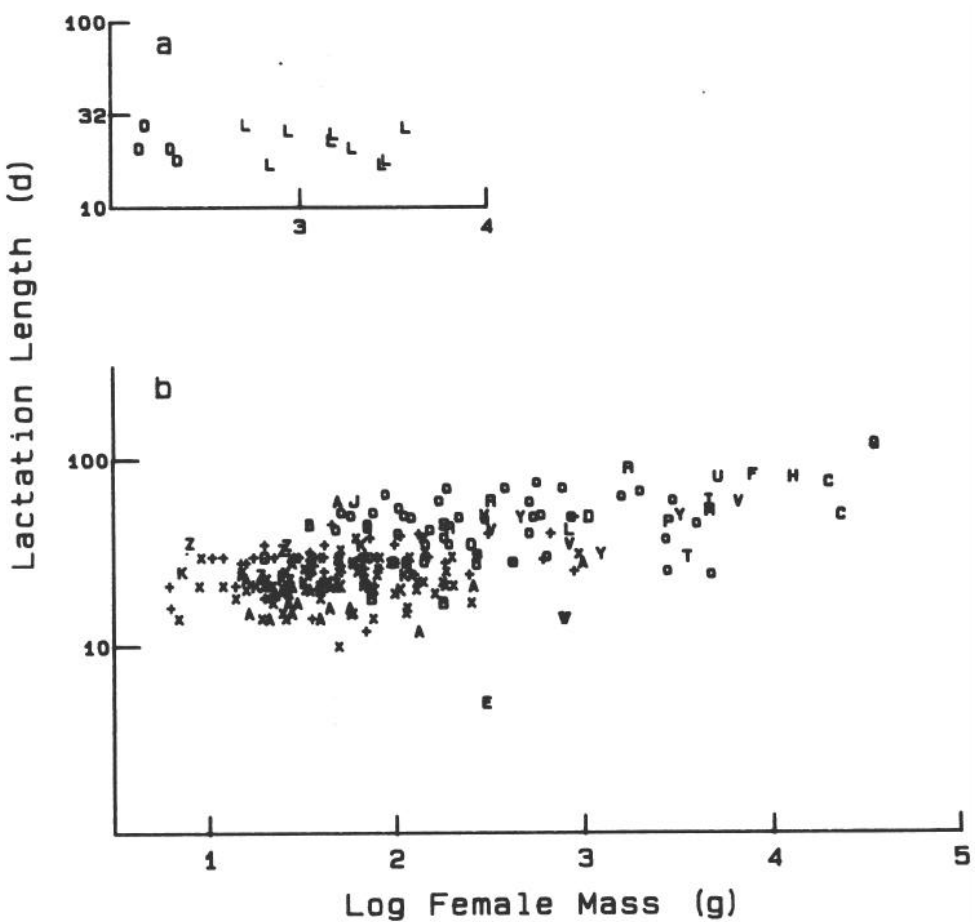


Figure 7. Allometric relationships of age at weaning with maternal mass for a) pikas, hares, and rabbits (lagomorphs) and b) rodents. Species from the same family have the same symbol or letter. Key to families within each order: a. Lagomorpha: Leporidae (L) and Ochotonidae (O); b. Rodentia: Muridae (+), Sciuridae (o), Cricetidae (x), Arvicolidae (A), Bathyergidae (B), Castoridae (C), Dasyproctidae (D), Echmyidae (E), Agoutidae (F), Gliridae (G), Hystricidae (H), Erethizontidae (I), Dipodidae (J), Heteromyidae (K), Aplodontidae (L), Myocastoridae (M), Octodontidae (O), Pedetidae (P), Hydrochaeridae (Q), Rhizomyidae (R), Spalacidae (S), Thryonomyidae (T), Capromyidae (U), Caviidae (V), Chinchillidae (Y), and Zapodidae (Z). Familial common names are given in the Appendix.

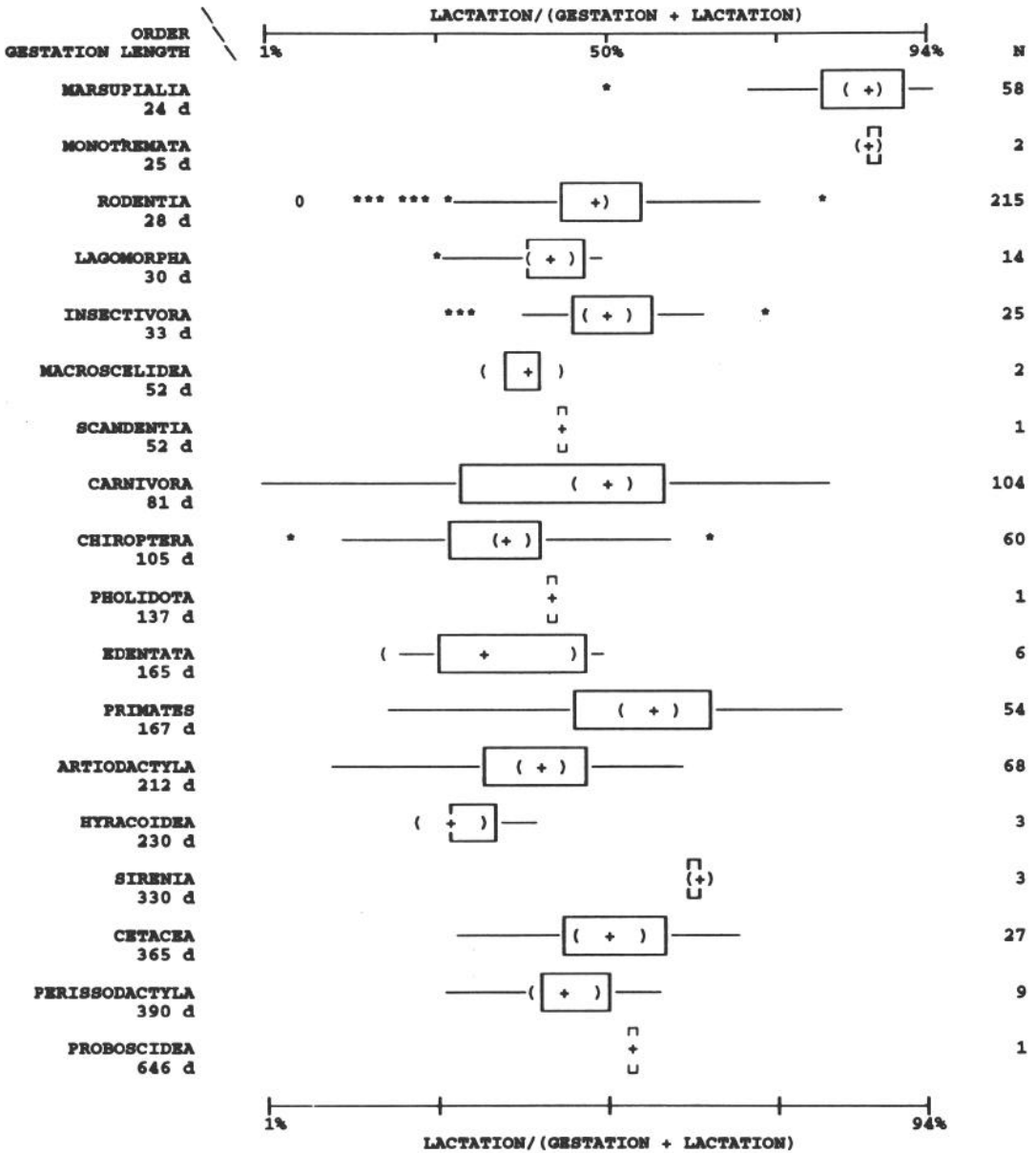


Figure 8. Box plots of the proportion of the period from conception to weaning, which is lactation for 653 mammalian species grouped by order and ranked by median gestation length (provided beneath name of order). Sample size in number of species is listed in the right column. For most eutherians, lactation occupies about half of the period between conception and weaning. For most prototherians and metatherians, lactation is usually over 75% of the parental investment period. Median (+), interquartile range (•), approximate 95% confidence interval for median (), outliers, the values distant from the median by >1.5 times the interquartile range (*), and “whiskers”, the range excluding outliers (—). Names of common representatives of each order are given in Materials and Methods.

range over nearly three orders of magnitude, the percentage of time that a female spends in lactation relative to the total period of reproductive investment is surprisingly constant across mammals. Generally, lactation occupies about half of the period between conception and weaning ($X = 49\%$; $SD = 17\%$; median 48%, 653 species). Approximately 50% of these species have lactation lengths between 40 and 60% of the time between conception and weaning (lower quartile, 39.3%; upper quartile, 57.3%). Thus, most mammals spend approximately the same amount of time in gestation as in lactation. One practical consequence is that the gestation length of a mammal is a rough estimate of its lactation length.

Mammals with extremely long or short lactation lengths do not have consistent patterns of temporal investment. Marsupials have long lactation lengths, and for them lactation is a large percentage (75 to 95%) of the period from conception to weaning. However, bats and primates also have long lactation lengths, but lactation for these groups is not an extraordinary proportion of the time between conception and weaning. Lactation lengths of bats, although relatively long for their mass, are relatively short, <40% of their total parental investment with none >65%. However, lactation lengths of most primates are about 40 to 60% of parental investment, and for about 10 species lactation is >65% of the period between conception and weaning.

Mammals with short lactation lengths are similarly diverse. Earless seals have short lactation lengths (4 to 40 d), and lactation is also a small temporal component of their reproductive investment (gestation lasts about 1 yr). Similarly, baleen whales have short lactation lengths for their mass (.5 to 1 yr), but the contribution of lactation to the period between conception and weaning in these mammals is not relatively small; gestation lasts .8 to 1.2 yr or about the same length as that of earless seals. Although the data are limited, milk composition also appears to be similar between the two groups. Milks from both groups are high in fat and protein. In contrast, the age at first solid food is probably very different. Earless seals first ingest solid food after lactation is over, whereas baleen whale calves probably first ingest krill well before weaning. Thus, the

temporal and energetic demands of lactation are different for the two mammalian groups with the shortest relative lactation lengths.

Although a trade-off between gestation and lactation might be expected, such that long periods of lactation would compensate for short periods of gestation and vice versa, this trend is valid only for marsupials and earless seals. For most mammals, after the effects of female mass are removed, the lengths of gestation and lactation are positively, not inversely, correlated, although the effect is not strong (Table 3). Thus, mammals with long gestation lengths tend to have long periods of lactation, and mammals with short in utero development tend to wean their offspring early.

Energetic Investment at Birth. The timing of first solid food relative to weaning may indicate the extent to which lactation is important to the nutritional or energetic needs of the offspring. Thus, the timing of first solid food relative to weaning may be of greater biological interest in the study of lactation than the absolute age at either weaning or first solid food. When the age at first solid food occurs long before weaning, lactation may have significant functions beyond nutrition or energy.

The relationship of relative nutritional dependency (age at first solid food divided by age at weaning) to the relative mass of offspring at birth (litter mass divided by female mass) can be examined either with respect to litter size (Figure 9a) or neonatal development (Figure 9b). A clear pattern emerges, even though neonatal development and litter size are confounded. (Monotocous eutherians usually have precocial young, whereas polytocous species often have altricial or semi-altricial neonates.)

TABLE 3. Statistics for the multiple regression of body mass (grams) and the length of gestation (days) on the length of lactation (days).

Variable	Coefficient	SE
Constant	.911	.057
Log female mass	.122	.012
Log gestation	.295	.040

¹For 634 species, after the effects of female mass are removed gestation and lactation lengths are positively correlated ($R^2 = .47$; $F = 285$). All variables are \log_{10} -transformed.

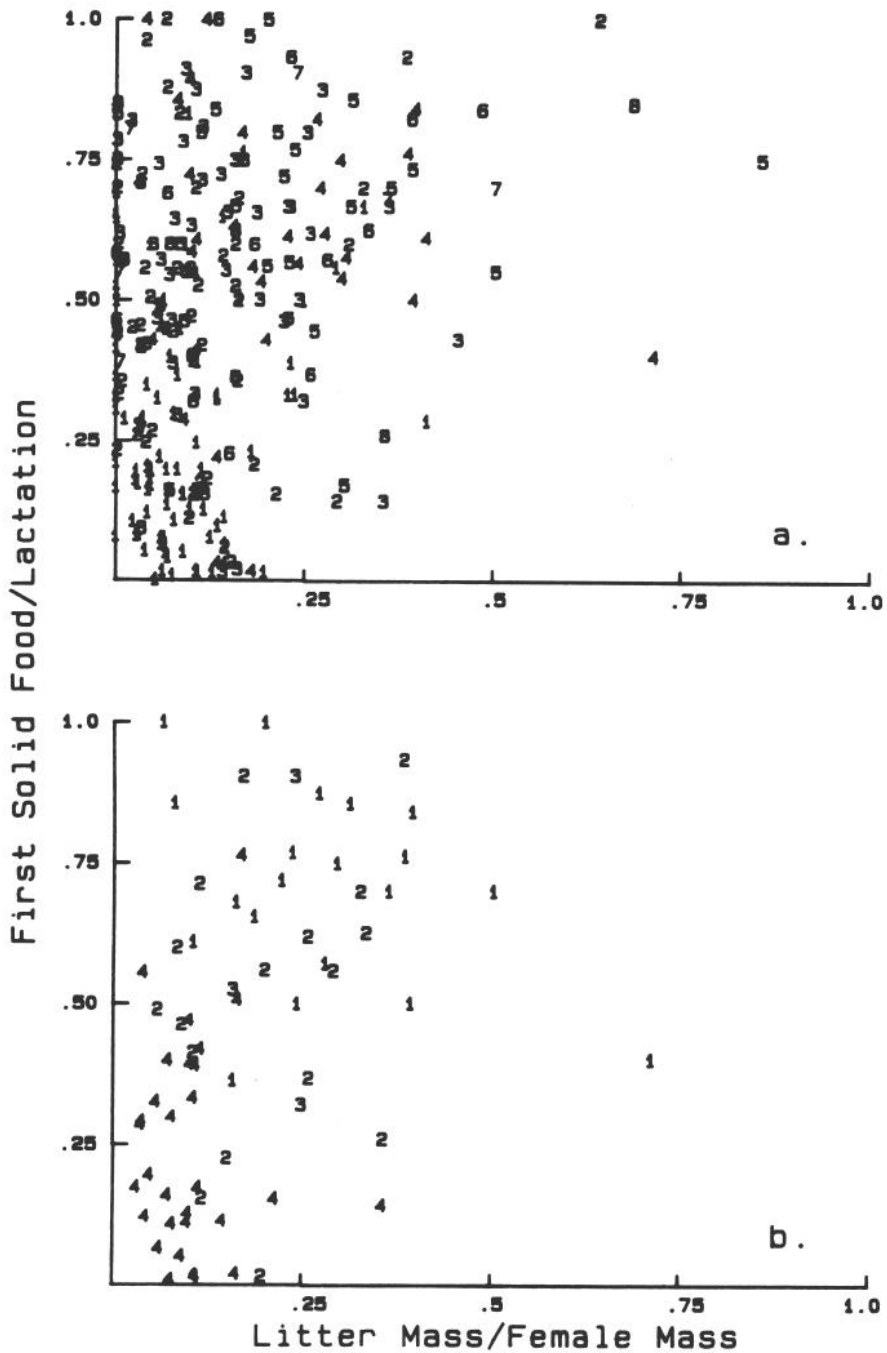


Figure 9. Relative nutritional dependency (age at first solid food divided by age at weaning) versus relative energetic investment at birth (litter mass at birth divided by maternal mass) broken down by a) litter size (litter sizes of 8 or more are coded as 8; 280 species) for all mammals or b) developmental state at birth for eutherians (70 species). Key to developmental state: altricial (1), semi-altricial (2), semi-precocial (3), and precocial (4). Single, precocial young are a smaller proportion of maternal mass at birth and rely less on lactation for nutritional support than the altricial young of polytocous species.

Monotocous, precocial eutherians have relatively small offspring at birth (small percentage of adult mass), and these offspring eat solid food early in lactation. The young are furred, mobile, and complete in sensory function (eyes and ears open) soon after birth, but they remain with their mothers for long periods. For these species, concurrent gestation and lactation seldom occurs. Overall, the relationship among these reproductive characteristics—early first solid food, precocial singleton young, and small relative mass at birth—is distinctive and may be a highly derived condition.

Conversely, polytocous species with altricial or semi-altricial young are far more variable. Litter mass can be a small or large proportion of female mass, and age at first solid food can occur early or late in lactation but usually occurs closer to weaning. In addition, gestation and lactation are commonly concurrent. The production of multiple offspring with a large litter mass at birth, altricial development, and late first solid food may be the ancestral eutherian condition.

The consequences of each constellation of reproductive characteristics are varied. The litter mass at weaning of muroid rodents (altricial litters with late first solid food) is often larger than that of the mother, whereas a calf or a human infant at weaning (single precocial offspring with early first solid food) is only a small fraction of maternal mass. In addition, the mouse and vole weanlings have relied almost entirely on their mothers for nutrients and energy during lactation, whereas the human infant and the calf supplement their diets with solid food for a large portion of lactation. Not only are the demands of lactation enormous when multiple young are dependent for all their nutritional and energetic needs on milk, as with mice and voles, but, with concurrent gestation, the female may also be meeting the nutritional needs of a second, in utero, litter. Such a mother's energetic budget and potential for future reproductive success might be tightly constrained.

For species with single precocial offspring, lactation may play a far different role in the allocation of temporal and energetic resources than it does in polytocous species with altricial young. Milk production may not be the primary function of lactation; instead, selective pressures may operate on other aspects of off-

spring growth and development via maintenance of the parent and offspring bond. Subsequent benefits include predator defense, educational opportunity, and social facilitation. Predators may be less apt to attack a small juvenile if a large adult is nearby, because that adult may directly intervene to protect the juvenile. Extended parental care can also provide an opportunity for young to learn from their parents about the location and quality of food, nest sites, or potential threats. Finally, few mammals with single precocial young are solitary. Most are born into a larger social arena of colony, troop, tribe, or herd. The survival and reproductive success of these mammals depends on their integration into appropriate social roles. Long lactations that continue after nutritional or energetic needs are met facilitate this social integration.

Differences in the energetic demands, evolutionary constraints, and functional role of lactation between altricial, polytocous species that have late first solid food and precocial, monotocous species that have early first solid food suggest additional differences in the control of lactation, its resistance to environmental change, and the composition and output of milk over time. For example, the frequency of suckling and the duration of lactation may be under maternal control in polytocous species with late first solid food, whereas offspring are more apt to control nursing and weaning when solid food is ingested early in lactation. The cost to a mother of continuing to nurse a single offspring a fraction of her size that already obtains a proportion of its nutritional requirements on its own is much less than that associated with nursing multiple young that collectively weigh as much or more than she does. Thus, the cost to benefit ratios associated with weaning are different.

Although lactation often extends or delays gestation when the two are simultaneous, the duration of lactation is also determined by gestation, because the birth of a subsequent litter forces the weaning of the first. Not only are successive litters in conflict regarding the timing of weaning, but littermates compete throughout lactation for current maternal resources. Maternal control over milk composition and production over the course of lactation allows females to fine tune their energetic investment as environmental conditions vary.

The composition of milk over the course of lactation may be more closely tied to the needs of the offspring when milk is the sole source of energy and nutrients than when milk supplements metabolic intake. In sum, maternal control over the timing of weaning and the allocation of metabolic resources may reduce intralitter and interlitter competition and, thus, allow a more selectively advantageous distribution across current and future reproductive investment.

Lactation may be under tighter genetic control (lower heritability) in species for which age at first solid food occurs close to weaning rather than close to birth because heritabilities are small for traits of critical importance to reproductive fitness, and appropriate allocation of resources during reproduction is more critical to survival and to reproductive success for polytocous species with ingestion of solid food late in lactation. Thus, lactation may be less responsive to current offspring demands in species for which age at first solid food is near weaning. Responses to changing environmental conditions may be more important to fitness in these mammals. Lactation may be most tied to the survival of current offspring in monotocous species with precocial young through the physiological regulation of gestation (including the timing of birth) and the flexibility of its genetic program across species.

To test these hypotheses, data on the nutritional and energetic value of milk before and after first solid food and data on suckling frequency, duration, initiation, and biochemical consequences over lactation and in a variety of environmental conditions are needed for an array of species. The captive breeding populations of diverse mammals in various zoos, especially those near research institutions that can analyze milk composition, provide an opportunity not only to collect these data but also to facilitate interdisciplinary exchange.

Other Influences on the Length of Lactation

Habitat and Diet. Preliminary analyses of the relationships of habitat and diet to the length of lactation (4) suggest that, when they are broadly defined, habitat and diet do not influence the length of lactation across mammals (Table 4). However, many taxonomic orders of mammals have distinctive habitats (e.g.,

TABLE 4. Analysis of the variance in lactation length (380 species) with habitat and diet when broadly defined habitat and diet have little influence on the length of lactation.¹

Independent variable	Cumulative		
	F	df	R ²
Adult mass	595.93	1	.45
Infraclass	96.91	2	.59
Order (infraclass)	13.58	13	.72
Habitat	1.85	5	.73
Diet	2.19	2	.73

¹For further details, see the study by Hayssen (4).

volant and marine) as well as specific diets (e.g., herbivores and carnivores); thus, habitat and diet analyses are confounded with phylogeny. The effects of habitat or diet on lactation may be more apparent within orders or families rather than across higher phylogenetic categories. Such detailed analysis is outside the realm of this review. Overall, for mammals, body mass and phylogenetic ancestry have greater influence on lactation length than do current habitat and diet.

Milk Composition. When the primary role of lactation is social or protective, milk production and composition may be less correlated with the long-term nutritional needs of the offspring than with support of immediate energetic demands. Thus, the low fat and protein and the high sugar content of primate and ungulate milks may reflect the alternative functions of lactation in these mammals.

Milk may have a thermoregulatory function for some mammals. Certainly, the high fat composition of cetacean milk serves a thermoregulatory function in the offspring. More direct thermoregulatory advantages may also accrue. Many altricial offspring are unable to maintain high body temperatures, and milk with high specific heat coming from endothermic mothers may serve to warm the young, especially newborns for which ingested milk can be a relatively large proportion of neonatal mass.

Thus, for some species, the nutritional value of milk may be of least equal importance to the thermoregulatory, social, or protective functions of lactation. Milk quality and quantity may reflect these additional functions of lactation and not be closely tied to offspring growth and development.

Basal Metabolism. The relationship between basal metabolic rate (BMR) and lactation is complicated (Table 5). Data for age at weaning, female mass, and BMR exist for only 180 species, including the three monotremes. After the effects of mass are removed, BMR is negatively correlated with lactation for these species; i.e., a higher resting metabolism is related to an earlier age at weaning. However, separate analyses of species with long (44 species) and average (131 species) lactation lengths indicate no significant relationships of BMR with lactation in either group after the effects of mass are removed. Separate analyses of metatherians (29 species) and eutherians (148 species) suggest that BMR has no relationship to lactation length for marsupials but is inversely related to the age of weaning in placental mammals, again, after the effects of mass are removed.

Basal metabolic rate is defined for non-reproductive, nongrowing, feed-deprived, inactive animals. During lactation, neither mothers nor offspring fit these criteria. Unfortunately, measures of metabolism in mother and offspring pairs during lactation are lacking. Until such estimates are available for an array of mammals, the relationship of metabolism to lactation will remain as opaque as milk.

CONCLUSIONS

Lactation defines mammals. As such, understanding lactation is crucial to understanding the biology of mammals. However, stan-

dard biological texts give scant attention to this central mammalian characteristic, and most studies of the phenomenon itself are on the cellular and molecular aspects. In this comparative investigation, temporal and energetic aspects of lactation have been analyzed using species, not cells or molecules, as units.

For mammals, allometric constraints are the most important determinants of lactation length. Within smaller phylogenetic subsets of mammals (orders and families), allometric constraints are reduced, or they disappear. Apart from female mass, some reproductive characteristics (litter size, neonatal development, and relative nutritional dependency) may operate in concert to influence lactation. For instance, species with single, precocial young have early first solid food relative to weaning regardless of body mass. The age at first solid food may alter the rate or timing of energetic investment during lactation, as do delayed implantation and dispare during gestation.

The coordination and integration of reproductive characteristics have a profound impact on the evolution of unitary phenomena, for example, the lipid content of milk. The amount of fat in milk may be influenced not solely by nutritional needs, but also by the selective pressures on a more varied, yet cohesive, array of reproductive characteristics.

Pleiotropy and polygeny, as well as the social nature of reproduction in general and lactation in particular, weave the molecular and cellular aspects of lactation into the larger fabric of a deme's reproductive biology. Simi-

TABLE 5. Relationship of lactation length to adult female mass (grams) and basal metabolic rate (BMR) (whole body, milliliters of oxygen per hour) for various mammalian groups.¹

	Slope _{MASS}	SE	Slope _{BMR}	SE	Constant	SE	R ²	n	F
Mammalia	.518	.075	-.471	.101	1.528	.077	.40	180	61
Long lactations ²	.206*	.216	-.006*	.276	1.570	.113	.54	44	26
Average lactations ³	.210	.062	-.020*	.086	1.111	.070	.58	131	90
	<i>P</i> = .001								
Marsupialia	.454*	.310	-.354*	.399	1.744	.147	.56	29	19
Eutheria	.332	.075	-.227	.102	1.339	.079	.40	148	49
	<i>P</i> = .027								

¹All variables are log₁₀-transformed. Sample size is number of species. Coefficients followed by an asterisk are not significantly different from zero. Unless separately indicated, all other coefficients are statistically significant (*P* < .0005).

²Includes marsupials (Marsupialia), primates (Primates), and bats (Chiroptera) only.

³Eutherians, excluding primates (Primates), bats (Chiroptera), earless seals (Phocidae), and baleen whales (Mysticeti).

lar patterns (reproductive strategies) may emerge, although the particular threads (specific mechanisms) within the design will vary.

Ancestral features of mammalian lactation (and mammalian reproductive biology in general) are the basis for all other future modifications. Only primitive aspects will be the same across a majority of mammals. Derived (selectively advantageous) aspects of lactation evolve independently in various lineages. To ascertain the general applicability of a particular molecular or physiological process, its ancestry must be determined. If the process is primitive, it may be widespread across mammals; if it is derived, its utility is apt to be specific to that lineage. Parallel modifications may occur independently in other lineages subjected to similar selective pressures. However, the advanced features of lactation in a particular group are germane only for that group, and not of general applicability.

The hormonal and metabolic controls of lactation in species with widely disparate suites of reproductive characteristics (for example, mice and cattle) have evolved under very different selective regimens. On the molecular and cellular levels, only primitive features are expected to be similar among mammals with differing reproductive patterns. Physiological or biochemical processes identified as having adaptive value in mice may not have similar utility for cows or humans. Broad physiological similarities in the hormonal control and metabolism of lactation most likely represent primitive features of milk production rather than recent adaptive modifications.

Lactation is the quintessence of mammals. Mammals are defined by this multifaceted component of their reproduction, which has influenced their biochemistry, physiology, anatomy, behavior, sociality, ecology, and evolution. Understanding how these components are integrated and how they have changed over time offers an unparalleled opportunity for synthesis across biological disciplines that are usually disparate. Bridging disciplinary barriers, as this symposium does, will eventually contribute to a multidimensional understanding of lactation as cohesive and intricate as the phenomenon itself.

ACKNOWLEDGMENTS

This article is dedicated to the memory of my brother, Sandy, whose multifaceted approach to both life and death was as complicated and important to me as the evolution of lactation is to mammals.

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APPENDIX

Familial common names (or the most popularly known representative) are listed for orders presented in Figures 4 through 7.

Edentata or Xenarthra: Bradypodidae (three-toed sloths), Choloepidae (two-toed sloths), Dasypodidae (armadillos), and Myrmecophagidae (anteaters).

Insectivora: Chrysochloridae (golden moles), Erinaceidae (hedgehogs), Solenodonti-

dae (solenodons), Soricidae (shrews) Talpidae (moles), and Tenrecidae (tenrecs).

Chiroptera: Emballonuridae (sheath-tailed bats), Megadermatidae (false vampire bats), Molossidae (free-tailed bats), Noctilionidae (bulldog bats), Nycteridae (slit-faced bats), Phyllostomidae (leaf-nosed bats), Pteropodidae (flying foxes), Rhinolophidae (horseshoe bats), Rhinopomatidae (mouse-tailed bats), and Vespertilionidae (common insectivorous bats).

Primates: Callimiconidae (Goeldi's marmoset), Callitrichidae (tamarins), Cebidae (New-world monkeys), Cercopitheciidae (Old-world monkeys), Cheirogaleidae (mouse lemurs), Daubentoniidae (aye-aye), Galagonidae (galagos), Hominidae (humans), Indridae (sifakas), Lemuridae (lemurs), Lorisidae (lorises), and Pongidae (great apes).

Carnivora: Canidae (dogs) Felidae (cats), Herpestidae (mongooses), Hyaenidae (hyenas), Mustelidae (weasels), Odobenidae (walruses), Otariidae (fur seals), Phocidae (earless seals), Procyonidae (raccoons), Protelidae (aardwolves), Ursidae (bears), and Viverridae (genets).

Cetacea: Balaenopteridae (rorquals), Delphinidae (marine dolphins), Eschrichtidae (grey whales), Monodontidae (white whales), Pho-

coenidae (porpoises), Physeteridae (sperm whales), Platanistidae (river dolphins), and Ziphiidae (beaked whales).

Perissodactyla: Equidae (zebra), Rhinocerotidae (rhinoceroses), and Tapiridae (tapirs).

Artiodactyla: Bovidae (antelope), Camelidae (camels), Cervidae (deer), Giraffidae (giraffes), Hippopotamidae (hippopotamuses), Suidae (pigs), Tayassuidae (peccaries), and Tragulidae (chevrotains).

Lagomorpha: Leporidae (hares) and Ochotonidae (pikas).

Rodentia: Agoutidae (pacas), Aplodontidae (mountain beavers), Arvicolidae (voles), Bathyergidae (African mole rats), Capromyidae (hutias), Castoridae (beavers), Caviidae (guinea pigs), Chinchillidae (chinchillas), Cricetidae (gerbils), Dasyproctidae (agoutis), Dipodidae (jerboas), Echmyidae (spiny rats), Erethizontidae (New-world porcupines), Gliridae (dormice), Heteromyidae (kangaroo rats), Hydrochaeridae (capybaras), Hystricidae (Old-world porcupines), Muridae (rats), Myocastoridae (nutrias), Octodontidae (degus), Pedetidae (spring hares), Rhizomyidae (bamboo rats), Sciuridae (squirrels), Spalacidae (blind mole rats), Thryonomyidae (cane rats), and Zapodidae (jumping mice).