

# Variation in growth form and precocity at birth in eutherian mammals

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## SUMMARY

Using the flexible Chapman–Richards model for describing the growth curves from birth to adulthood of 69 species of eutherian mammals, we demonstrate that growth form differs among eutherian mammals. Thereby the commonly used Gompertz model can no longer be considered as the general model for describing mammalian growth. Precocial mammals have their peak growth rate earlier in the growth process than altricial mammals. However, the position on the altricial–precocial continuum accounts for most growth-form differences only between mammalian lineages. Within mammalian genera differences in growth form are not related to precocity at birth. This indicates that growth form may have been associated with precocity at birth early in mammalian evolution, when broad patterns of body development radiated. We discuss four non-exclusive interpretations to account for the role of precocity at birth on the observed variation in growth form among mammals. Precocial and altricial mammals could differ according to (i) the distribution of energy output by the mother, (ii) the ability of the young to assimilate the milk yield, (iii) the allocation of energy by the young between competing functions and (iv) the position of birth between conception and attainment of physical maturity.

## 1. INTRODUCTION

Classically, it is assumed that sigmoid curves offer the best compromises for studying mammalian growth from birth to adulthood (Zullinger *et al.* 1984; Georgiadis 1985). However, variation in growth form among mammals has not yet been investigated, despite the importance of growth patterns in population dynamics and life history evolution (Williams 1966; Sadleir 1969; Charlesworth 1980; Stearns & Koella 1986; Gaillard *et al.* 1989; Roff 1992; Stearns 1992). Most previous work has focused on growth rates in the first part of growth curves, generally before weaning (Case 1978; Millar 1981; Zullinger *et al.* 1984; Georgiadis 1985; Pontier *et al.* 1989). Because age at first reproduction is determined by a body weight threshold in most mammals (Sadleir 1969), and because growth patterns covary with mortality patterns independently of body size (Read & Harvey 1989; Promislow & Harvey 1990; Pontier *et al.* 1993), we may expect natural selection to play a role in shaping mammalian growth. In this paper we present a first study of the variability in shape among mammalian growth curves.

According to current theories of resource allocation (Williams 1966; de Jong & Van Noordwijk 1992) the amount of energy received by an individual offspring from its mother must be partitioned between growth and maintenance. Thus the proportion of energy allocated to growth over the lactation period may vary if thermoregulation constraints or time budgets change as age increases (Hull 1973). Because these physiological constraints are greater in altricial than in precocial species (Eisenberg 1981), we would expect different patterns of energy allocation and differences in the timing of peak growth rates according to the precocity at birth of offspring. We therefore looked for answers to two questions (i) are Gompertz-like models suitable for describing growth curves in all eutherian mammals?; and (ii) is there a relationship between precocity at birth and growth form among mammals?

## 2. METHODS

### (a) Data collection

We obtained mammalian growth curves from the literature for 69 species. We restricted our dataset to species for which (i) age is known (recorded from birth), (ii) the initial stage of growth is described in detail (measured at least once a week from birth for large species and almost daily for small species

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Table 1. *Modelling growth curves of 69 eutherian mammal species, using the Chapman–Richards model*

(The form parameter,  $m$  ( $\pm 1$  s.e.) indicates the position of the inflexion point, when maximal growth occurs. The consistency of  $m$  estimates with monomolecular (M,  $m = 0$ ), Gompertz (G,  $m$  approaches 1) and logistic (L,  $m = 2$ ) models is given (+, consistent with) as well as whether or not an inflexion point significantly occurs in the growth curve (+, significant inflexion point ; –, initial growth rate significantly higher than predicted under the monomolecular model.)

species	$m$	s.e. ( $m$ )	consistent with			significant inflexion occurrence	sources	ABW	BW	$r^2$
			M	G	L					
artiodactyls										
<i>Aepyceros melampus</i>	1.207	0.788	+	+	+		1			0.97
<i>Capreolus capreolus</i>	0.342	0.158	+				2	23000	1500	0.98
<i>Pudu pudu</i>	−0.226	0.118	+				3	6250	780	0.99
<i>Sylvicapra grimmia</i>	0.043	0.181	+				4	20430	1640	0.99
<i>Taurotragus oryx</i>	−0.241	0.189	+				5	454000	31500	0.97
bats										
<i>Antrozous pallidus</i>	0.499	0.191				+	6	20	3	0.99
<i>Eptesicus fuscus</i>	0.253	0.988	+	+	+		7			0.90
<i>Eptesicus serotinus</i> (P4 fixed)	−0.203	0.453	+				8	25	5.8	0.96
<i>Myotis lucifugus</i>	7.070	4.360	+	+	+		9			0.87
<i>Pipistrellus pipistrellus</i>	−1.334	0.622				−	8	5	1.4	0.98
<i>Vespertilio superans</i>	−0.775	0.435	+				10	18.3	2.33	0.99
fissipeds										
<i>Alopex lagopus</i>	0.714	1.326	+	+	+		11			0.57
<i>Bassariscus astutus</i>	0.574	0.168				+	12	870	28	0.99
<i>Felis catus</i>	−0.363	0.390	+				13	3100	115	0.86
<i>Gulo gulo</i> (P4 fixed)	0.996	0.075		+		+	14	10350	99.2	0.99
<i>Ictonyx striatus</i>	1.454	0.248		+		+	15	630	15.2	0.99
<i>Lynx lynx</i>	0.861	0.261		+		+	16	17800	311.5	0.99
<i>Mustela putorius</i>	1.120	0.142		+		+	17	800	8.4	0.99
<i>Poecilogle albinocha</i>	2.730	0.387			+	+	15	250	4	0.99
<i>Vulpes vulpes</i>	0.298	0.040				+	18	5000	105	0.99
hyracoids										
<i>Procavia capensis</i>	0.391	0.012				+	19	2600	165	0.99
insectivores										
<i>Crocidura russula</i>	0.132	0.190	+				20	7.8	0.8	0.99
<i>Crocidura suaveolens</i>	−0.530	0.300	+				21	7.8	0.5	0.80
<i>Neomys fodiens</i>	−0.310	0.114				−	22	12	1	0.99
<i>Sorex cinereus</i>	2.265	0.319			+	+	23	4	0.3	0.99
<i>Suncus murinus</i>	0.123	0.146	+				24	28	2.1	0.99
lagomorphs										
<i>Lepus americanus</i>	1.167	0.135		+		+	25	1437	52	0.99
<i>Lepus californicus</i>	0.634	0.041				+	26	2300	110	0.99
<i>Lepus europaeus</i>	0.460	0.190				+	27	4250	107	0.95
<i>Ochotona princeps</i>	0.565	0.290	+	+			28, 28'	169	11.7	0.99
<i>Ochotona rufescens</i>	0.755	0.185		+		+	29	250	11.4	0.99
<i>Sylvilagus aquaticus</i>	0.336	0.193	+				30	2200	61.4	0.99
<i>Sylvilagus floridanus</i>	1.006	0.360		+		+	31	1300	25.6	0.95
primates										
<i>Arctocebus calabarensis</i>	0.818	0.548	+	+			32	310	30	0.99
<i>Callimico goeldii</i>	0.492	0.193				+	33	530	40	0.99
<i>Macaca mulatta</i>	0.274	0.044				+	34	9000	472	0.99
<i>Papio cynocephalus</i>	1.065	0.278		+		+	35	15000	854	0.99
<i>Saguinus nigricollis</i>	0.747	0.143		+		+	36	464	43	0.99
rodents										
<i>Aethomys chrysophilus</i>	0.259	0.150	+				37	80	4.1	0.99
<i>Apodemus argenteus</i>	0.376	0.184				+	38	18	1.8	0.99
<i>Arvicanthis niloticus</i>	1.100	0.213		+		+	39	(89)	(3.75)	0.99
<i>Atherurus africanus</i>	−0.076	0.167	+				40	2500	150	0.97
<i>Clethrionomys gapperi</i>	0.581	0.250		+		+	41	26.8	1.81	0.99
<i>Clethrionomys glareolus</i> (P4 fixed)	6.590	8.490	+	+	+		42			0.96
<i>Dipodomys stephensi</i>	3.471	0.603				+	43	42	4	0.97
<i>Eothenomys smithi</i>	0.679	0.284		+		+	44	(22.5)	(2.61)	0.99
<i>Eutamias palmeri</i>	2.263	0.321			+	+	45	60	4.3	0.99
<i>Eutamias panamintinus</i>	3.464	0.503				+	45	50	5.8	0.99
<i>Glaucomys volans</i>	0.698	0.439	+	+			46	50	3.4	0.77
<i>Hystrix africaeaustralis</i>	0.518	0.166				+	47	12000	480	0.99

Table 1—cont.

species	<i>m</i>	s.e. ( <i>m</i> )	consistent with			significant inflexion occurrence	sources	ABW	BW	<i>r</i> <sup>2</sup>
			M	G	L					
<i>Microtus agrestis</i>	0.620	0.170				+	48	35.5	2.9	0.99
<i>Microtus montebelli</i>	0.027	0.126	+				49	40	2.63	0.99
<i>Microtus pinetorum</i>	0.106	0.265	+				50	29.4	2.35	0.99
<i>Neotoma cinerea</i>	0.412	0.876	+	+	+		51			0.95
<i>Orchotomys nuttalli</i>	0.020	0.460	+				52	25	2.7	0.97
<i>Ondatra zibethica</i> (P4 fixed)	0.943	0.046		+		+	53	1090	22	0.99
<i>Peromyscus gossypinus</i>	0.666	0.170		+		+	54	29	2.2	0.99
<i>Peromyscus leucopus</i>	1.785	0.375			+	+	55	25	1.8	0.99
<i>Peromyscus maniculatus</i>	0.991	0.130		+		+	56	20	1.7	0.99
<i>Peromyscus polionatus</i>	1.936	0.234			+	+	57	15	1.6	0.99
<i>Peromyscus yucatanicus</i>	1.670	0.380		+	+	+	58	28	2.5	0.96
<i>Pseudomys novaehollandiae</i>	0.621	0.159				+	59	(15.9)	(2.38)	0.99
<i>Rattus exulans</i>	0.695	0.038				+	60	72	3	0.99
<i>Rattus rattus</i>	1.080	0.287		+		+	61	90	4.5	0.99
<i>Spermophilus lateralis</i>	1.625	0.241			+	+	62	300	6.1	0.99
<i>Spermophilus leucurus</i>	6.760	1.820				+	63	111.1	3.5	0.99
<i>Spermophilus mohavensis</i>	2.860	1.104		+	+	+	63	195.6	4.44	0.99
<i>Spermophilus mollis</i>	2.820	0.458			+	+	64	150.3	3.87	0.99
<i>Spermophilus saturatus</i>	2.430	0.265			+	+	65	200	6	0.99

ABW, adult body weight; BW, birth weight.  
See appendix 2 for full reference details.

such as rodents), (iii) a monotonic increasing curve is a good descriptor of growth and (iv) measurements of weight until adulthood are available. We therefore considered only those studies in which monitoring encompasses the total length of the growth period (see figure 1 for examples).

### (b) Data analysis

To account for possible variation in growth form we fitted the general Chapman–Richards model (Richards 1959) to the growth curves according to the following equation:

$$W_t = K / \{1 + (m-1) \exp(a(t_0-t))\}^{1/(m-1)},$$

where  $W_t$  is the body weight at age  $t$ ,  $K$  is the asymptotic body weight (adult body weight),  $m$  is a form parameter that locates the inflexion point (on the weight axis),  $a$  is the relative growth rate and  $t_0$  is the age at which the inflexion point occurs.

This parameterization differs slightly from Richards's original parameterization; we used the age at which growth rate is maximal rather than when body weight is at the origin (see Nelder (1962) for the same modification). The Chapman–Richards model allows a flexibility in form, ranging from a monotonic concave increase (no inflexion point, peak growth at birth, illustrated by the monomolecular model) to a monotonic convex increase (no inflexion point, peak growth at maturity, illustrated by a truncated exponential model). Between these extreme cases any sigmoid curve can be found. Such variability in growth form is encoded by the form parameter,  $m$ . Thus,  $m = 0$  when growth follows the monomolecular model (no inflexion point), approaches 1 when growth follows the Gompertz model (inflexion point at about 36.8% of the asymptotic body weight) and equals 2 when growth follows the logistic model (inflexion point at 50% of the asymptotic body weight). We fitted the Chapman–Richards model to growth data by ordinary least squares criterion, using the Marquardt algorithm (Marquardt 1963).

To answer the first question, whether or not the monomolecular, Gompertz or logistic model was acceptable for a

given growth curve, we simply checked whether or not the 95% confidence interval of  $m$  included 0, 1 and 2 respectively. To answer the second question, whether or not growth form among mammals is related to precocity at birth, we first looked for a measure of precocity at birth in mammals. Following recent analysis (Derrickson 1992), we log-transformed the weight data and we used the relative birth weight (i.e. the deviation from the regression line between birth weight and female adult body weight after correcting for phylogeny) for ranking species on a precocial–altricial continuum. Then we assessed the relationship between this precocity index and growth form using regression after accounting for phylogeny. To avoid statistical problems caused by the non-independence between species points (Felsenstein 1985; Harvey & Pagel 1991) we used the independent contrasts method (Harvey & Purvis 1991; Garland *et al.* 1992). This method, assuming a Brownian motion model of evolution and accuracy in phylogenetic information (Purvis *et al.* 1994), is currently the best way to account for phylogenetic inertia. However, it makes certain assumptions about the rate of evolution, i.e. that it should be constant and identical in both traits under study. We used nested ANOVA with the taxonomic levels of order, family and genus (Gittleman & Luh 1992) to check this assumption. When the distribution of variance over the taxonomic levels was similar in both traits, we then used the method of independent contrasts to account for phylogeny. To do this, we inferred phylogeny from taxonomy (Nowak 1991) and branch length was considered unknown. When the distribution of variance over the taxonomic levels differed markedly between traits, we assessed the relationship between traits by using two procedures:

1. Using Nee *et al.*'s recent work (Nee *et al.* 1991) we analysed relationships across and within taxa by considering correlations across species within genera, across generic means (calculated from species points) within families, across family means (calculated from generic means) within orders and across order means (calculated from family means) within eutherian mammals. We then tested for positive or negative trends using binomial tests.

2. We replicated the analysis at each of the taxonomic levels (considering them as distinct datasets). At each step we used the independent contrasts method to account for phylogenetic inertia. In analyses performed on the species points, on the generic points (calculated from the species points) and on the family points (calculated from the generic means), phylogeny was inferred from taxonomy (Nowak 1991), and branch length was considered as unknown. In the analysis performed on the order points (calculated from family means) we used the phylogeny proposed by Novacek (1993). Phylogenies corresponding to all these analyses are presented in Appendix 1.

### 3. RESULTS

#### (a) Modelling growth curves in eutherian mammals

All curves fit the Chapman–Richards model ( $r^2$  higher than 0.95 in 63 out of 69 cases, table 1; see figure 1 for examples). For six species the modelling of growth curves could not distinguish between monomolecular, logistic and Gompertz models (table 1); we eliminated these from subsequent analyses. Among the remaining 63 growth curves we could identify two broad types: (i) curves with a growth rate decreasing from birth to adulthood (no significant inflexion point in the growth curve as described by the monomolecular model in 21 out of 63 species); (ii) curves with a growth rate first increasing after birth and then decreasing to maturity (significant inflexion point in the growth curve as described by Gompertz and logistic models in 42 out of 63 species). Phylogeny seems to be strongly involved in this dichotomy: more than 70% of rodents (23 out of 27), fissipeds (7 out of 8), lagomorphs (5 out of 7) and primates (4 out of 5) have curves with peak growth rates well after birth, whereas all ungulates (4 out of 4) and 75% of bats (3 out of 4) have curves with peak growth rates at birth (table 1). The Gompertz model fits only one third of the growth curves (21 cases out of 63, table 1).

#### (b) Assessing the relationship between precocity at birth and growth form in eutherian mammals

Adult body weight and birth weight (after log-transformation) have similar distributions of variance over the taxonomic levels (table 2) and are closely related after accounting for phylogenetic inertia ( $r = 0.947$ ,  $p < 0.0001$ ). We therefore used the slope estimated by the independent contrasts method (0.814) to remove the allometric effect of body weight on birth weight. We then obtained a precocial–altricial continuum at the species level that accounts for phylogeny. However, this precocity at birth index and the growth-form parameter have contrasting distributions of variance over the taxonomic levels (table 2); most variation in precocity at birth occurred among orders, whereas the variation in growth form is more regularly spread over the taxonomic levels. We therefore used both Nee *et al.*'s method and the independent contrast method at each of the taxonomic levels (species, genus, family and order).

Using Nee *et al.*'s approach there is a trend for a negative within-taxon association between precocity at

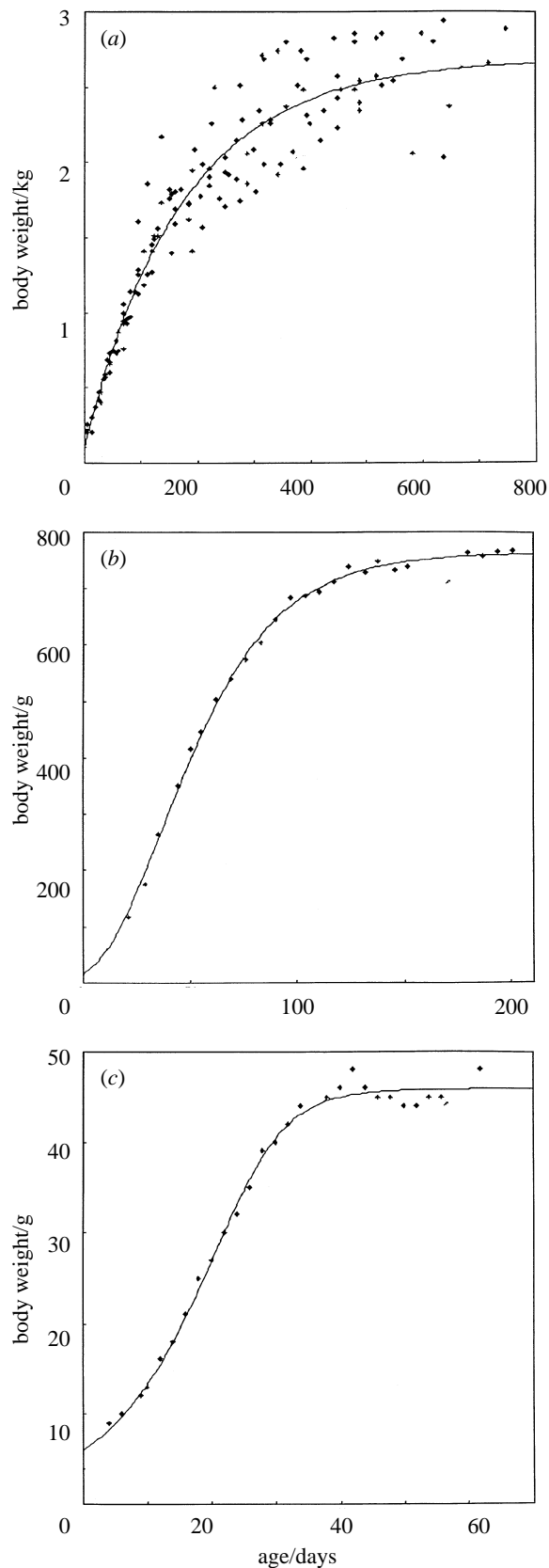


Figure 1. Examples of curve-fitting using the Chapman–Richards model for mammalian growth curves. (a) Monomolecular growth (ex. *Atherurus africanus*), (b) Gompertz growth (ex. *Ondatra zibethica*), (c) logistic growth (ex. *Dipodomys stephensi*).

Table 2. Proportion of the variation in adult body weight, birth weight, precocity index and growth form parameter occurring at order, family, genus and species levels

(The precocity index was defined for each species as birth weight corrected for female adult body weight after removing phylogenetic inertia.)

	order	family	genus	species
adult body weight	39.22	4.11	16.42	7.87
birth weight	68.69	5.92	7.73	1.14
precocity index	71.90	4.69	5.30	0.79
growth form parameter	34.71	31.02	24.06	10.22

Table 3. Correlations between precocity at birth (measured from the regression accounting for phylogeny between female adult body weight and birth weight) and the timing of maximal growth (growth form measured as  $\ln(m+3)$ ) across subtaxa in different taxonomic levels

across	within	number of positive correlate	number of negative correlate
species	genera	7	2
generic means	families	2	11
family means	orders	1	4
orders means	eutherian mammals	0	1
total		10	18

birth and growth form (10 positive and 18 negative associations,  $p = 0.092$ ; table 3). However, there is a trend for a positive association within lower taxa (species within genera, 7 positive and 2 negative,  $p = 0.09$ ; table 3), whereas a strong negative association occurs across taxa within higher taxa (3 positive and 16 negative,  $p = 0.011$ ; table 3). Thus across higher taxa, growth rate peaks consistently earlier in the growth process among precocial taxa than among altricial taxa.

The independent contrast analyses replicated for different taxa after removing phylogeny provide the same results (figure 2). Growth form and the precocity index are more tightly associated at the order ( $r = -0.964$ ,  $p < 0.0001$ ), family ( $r = -0.276$ ,  $p = 0.120$ ) and genus ( $r = -0.324$ ,  $p = 0.0014$ ) levels than at the species level ( $r = -0.123$ ,  $p = 0.168$ ).

#### 4. DISCUSSION

This analysis demonstrates that growth form among mammals is extremely variable. Some mammals have a decelerating growth rate from birth to maturity, whereas others have the more classical sigmoid curve, with peak growth rate occurring after birth. The Gompertz model, often cited as the most appropriate model for describing mammalian growth (Zullinger *et al.* 1984), is therefore unsuitable for describing all growth patterns of eutherian mammals from birth to

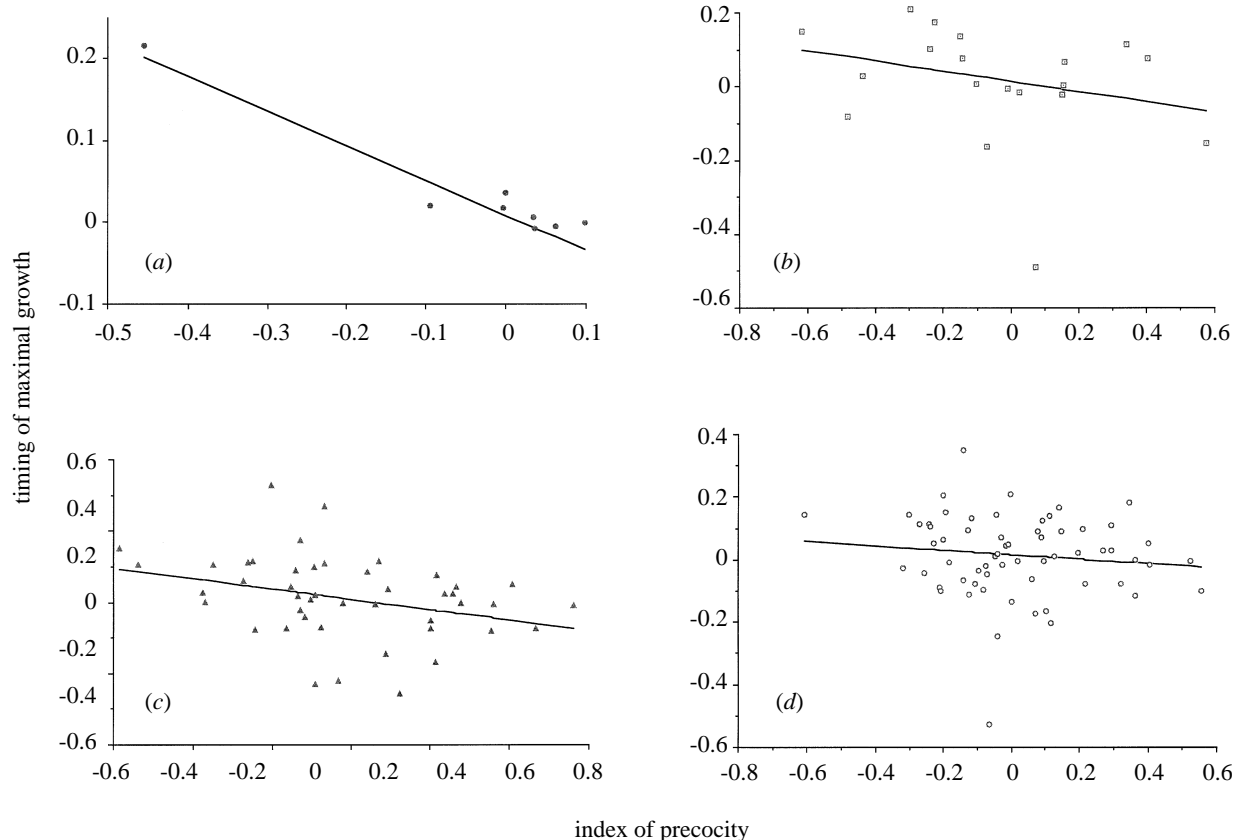


Figure 2. Regression forced through the origin of the contrast scores of timing of maximal growth (growth form measured as  $\log(m+3)$  to account for the log-normal distribution of  $m$  values, where  $m$  is the position of the inflexion point) on the contrast scores of precocity at birth (measured for 63 species of mammals as birth weight corrected for adult female body weight after removing phylogenetic inertia) at order (a), family (b), genus (c) and species (d) levels.

maturity. This variability in growth form is biologically meaningful unless it can be accounted for by methodological problems. For example, sampling biases involving simultaneous over-representation of small animals in altricial species and large animals in precocial species could mimic the observed pattern. Although we cannot demonstrate that this did not occur, such a combination is highly unlikely, especially because our sample size is quite large (more than 60 species). The possibility of a problem of differential growth monitoring according to body size can also be discarded because we only selected species for which the entire length of the growth period had been measured. Lastly, differential size-specific mortality in altricial versus precocial species cannot account for the observed pattern because body growth positively affects survival in species with logistic growth (e.g. ground squirrels; see Rieger 1996) as well as in species with monomolecular growth (e.g. ungulates; see Clutton-Brock *et al.* 1987).

The variability in growth form we found in this analysis is most likely to be linked to precocity at birth. Precocial mammals exhibit peak growth rate earlier than altricial mammals. For methodological reasons we did not consider some mammal orders (such as pinnipeds and cetaceans) in our analysis, but available information supports our conclusion. Both precocial pinniped and cetacean species seem to exhibit their highest growth rates near birth (Brown & Lockyer 1984; Bowen 1991; McLaren 1991). However, within mammalian genera, variation in growth form is not related to precocity at birth. This could arise because (i) error variance is likely to be higher at lower taxonomic levels (e.g. Pagel & Harvey 1988) and/or (ii) very little variation in precocity at birth across species occurs within genera (Pélabon *et al.* 1995) and variation in growth form is more widespread over the different taxa. In mammals higher taxa can be considered as separate lineages according to the mammalian radiation (Eisenberg 1981). We propose that lineage-specific physiological and developmental processes have constrained growth patterns to certain broad limits. Within these limits set by precocity at birth, species-specific life histories have then fine-tuned growth patterns.

Four non-exclusive interpretations can be proposed to account for a link between growth form and precocity at birth in eutherian mammals: (i) a differential distribution of energy output by the mother during the lactation period; (ii) a differential ability of the young to ingest and/or to assimilate the milk yield from the mother with increasing age; (iii) a differential energy allocation by the young between maintenance, daily activities and growth with increasing age; and (iv) a delayed birth time in precocial mammals compared to altricial ones.

Lactation in mammals is generally viewed as a multistage process, with various differences between species in the distribution of milk yield and/or milk composition over the lactation period (Oftedal 1984). However, although primates, carnivores and artiodactyls all produce high-protein colostrum (Oftedal 1984), they differ markedly in growth form (see table

1). Although we do not know of any differences in maternal energy allocation between precocial and altricial species, more data are clearly required before we can reject interpretation (i). Differences in suckling efficiency (interpretation (ii)) could account for the observed variability in mammalian growth form. Given the same relative amount of energy provided by the mother to its young, suckling efficiency could be higher in early stages in precocial compared with altricial mammals. This would lead early growth rate to be higher in precocial mammals than in altricial mammals. Suckling efficiency has previously been suspected to explain growth differences (Glücksman 1974; Laviguer & Barrette 1992), with heavy neonates generally growing faster than light ones (Clutton-Brock 1991), and with males growing faster than females in sexually dimorphic species where males are heavier at birth (Clutton-Brock 1991). A differential allocation of energy by young to competing functions (interpretation (iii)) could also account for the relationship between growth form and precocity at birth. The low mobility of young mammals during the first stages of their life (Eisenberg 1981) allows the majority of available energy to be allocated to either maintenance or growth, with activities such as foraging occurring only infrequently. This contrasts with birds, where precocial chicks show high levels of activity, do not receive a large amount of parental care and exhibit lower growth rates than altricial chicks (Olson 1992). Among mammals, active precocial neonates (e.g. follower (*sensu* Lent 1974) ungulates) also have lower growth rates during the first days after birth compared to more passive precocial neonates (i.e. hider (*sensu* Lent 1974) ungulates) (Carl & Robbins 1988). Moreover, the trade-off between maintenance and growth and the higher surface/volume ratio of small altricial neonates should result in a higher energy allocation to maintenance compared to larger precocial neonates (Eisenberg 1981), especially for homeotherms like mammals, for which thermoregulation in the very early stages is a major energy expenditure (Hull 1973). The fact that precocial neonates have thicker fur at birth than altricial neonates may accentuate this difference (Rogowitz 1992). Lastly, if we think of growth as a process that begins not from birth but rather from conception, then altricial and precocial taxa could differ in timing of peak growth rate simply because precocial species are further advanced along the total growth trajectory relative to the point of conception (interpretation (iv)). This is supported by previous findings that report a longer gestation period for precocial mammals (Martin & McLarnon 1985).

Whatever the cause for the observed link between precocity at birth and growth form from birth to adulthood in mammalian higher taxa, our study supports the key role of growth patterns in the evolution of mammalian life histories pointed out by Charnov (1993). It is now well established that mammal species can be ranked from a covariation between precocity at birth, low reproductive output and iteroparity, to a covariation between altriciality, high reproductive output and semelparity (Partridge & Harvey 1988; Stearns 1992). The first strategy is

based on a long reproductive life that requires early maturity (Gaillard *et al.* 1989, Derrickson 1992) and therefore a high initial growth rate (Sadleir 1969; Pontier *et al.* 1993). Energy from the mother is then expected to be channelled into growth and this may jeopardize juvenile survival, particularly under harsh environmental conditions. This evolutionary model is supported by studies of precocial large mammals that have shown that juvenile survival before weaning is often low and highly variable (Fowler *et al.* 1981; Gaillard *et al.* 1993).

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#### APPENDIX 1. Phylogenetic trees inferred from taxonomy

Branch lengths in bold are considered as 0, other branch lengths are considered as unknown. Distance between taxons is calculated as the number of taxonomic levels between them. For example, in Artiodactyla, the distance between Capreolus and Pudu is 1 and the distance between Cervidae (Capreolus/Pudu) and Bovidae (Taurotragus/Sylvicapra) is 2.

(i) *Left-hand column*  
top: Artiodactyla  
centre: Chiroptera  
bottom: Carnivora

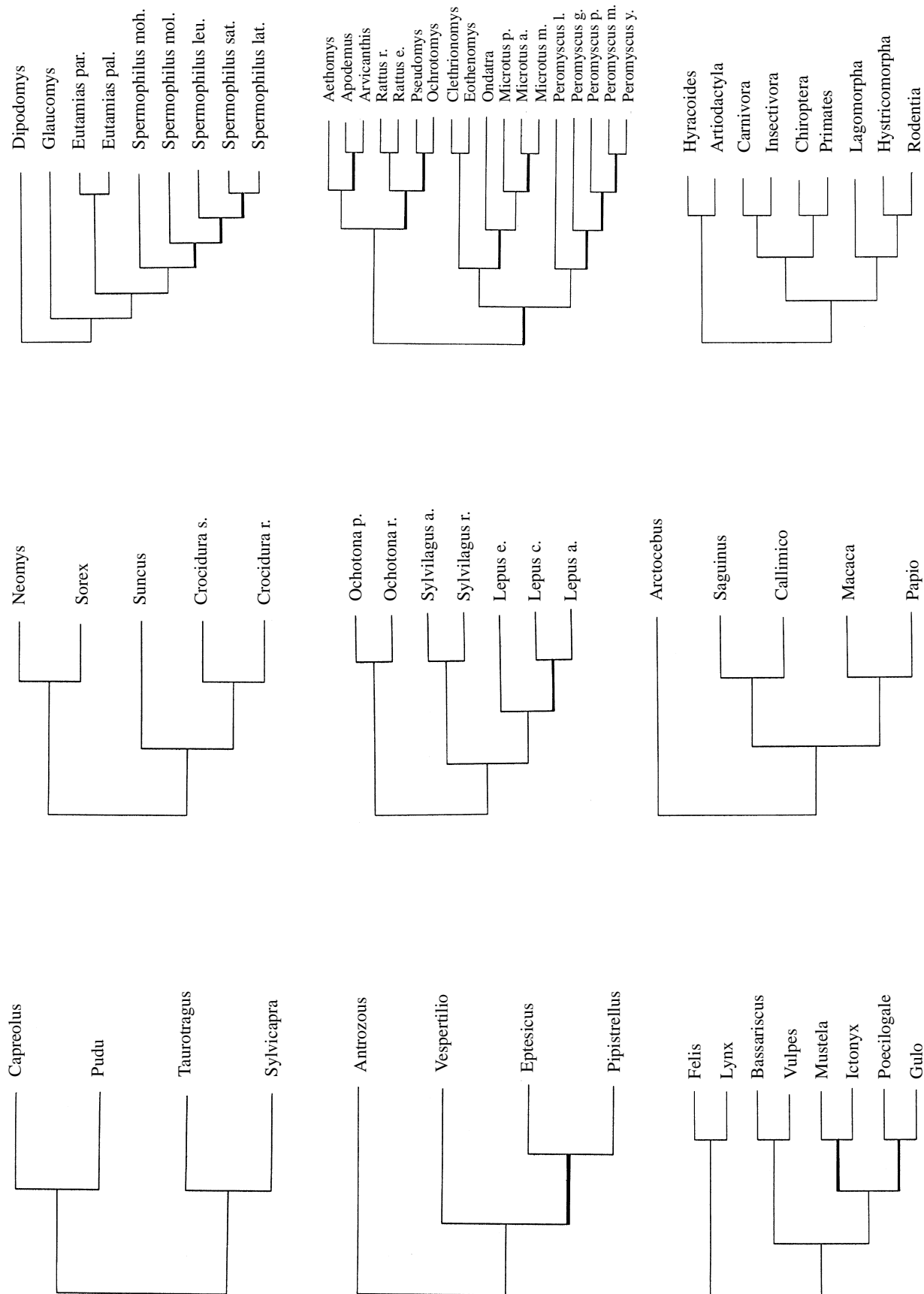
(ii) *Central column*  
top: Insectivora  
centre: Lagomorpha  
bottom: Primates

(iii) *Right-hand column*  
top: Sciuromorpha  
centre: Myomorpha  
bottom: Eutherian orders (in this tree, branch lengths provided by Novacek's phylogeny of mammalian orders have been used).

#### APPENDIX 2

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