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Allochrony: A new way of analysing life histories, as illustrated with mammals

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ABSTRACT

Many life-history features of animals can be scaled to body size. This allometric approach has provided important insights into the evolution of life histories. Here we propose a new approach which involves scaling life-history features in relation to life span or other life-history time periods. We illustrate this 'allochronic method' using life-history data from 190 species and 14 orders of mammals provided by *Asdell's Patterns of Mammalian Reproduction* (Hayssen *et al.*, 1993). Among these species, the durations of gestation, lactation and the post-weaning juvenile period were scaled to age at sexual maturity (first conception). Gestation time and lactation time both tended to show negative allochrony (slope < 1.0) with increasing age at first conception, whereas the juvenile period showed positive allochrony (slope > 1.0). These trends appear to be robust, as they are seen within various orders and families, body-size classes, dietary types and foraging modes. These data suggest that species differences in the age at sexual maturity depend more on differences in developmental time during the post-weaning juvenile period than during the pre-weaning period. Ecological comparisons further reveal that faunivorous mammals tend to spend a greater percentage of their maturation time as post-weaning juveniles than omnivores, granivore/frugivores or herbivores. Arboreal mammals also have proportionately longer juvenile periods than scansorial and terrestrial species. These trends appear to be related to the greater time required for the young of faunivorous and arboreal species to develop foraging and locomotor skills sufficient to permit reproduction. We conclude that the ability of the allochronic method to reveal new interesting patterns warrants its further use as a basic tool for analysing life histories.

Keywords: allochrony, body size, diet, foraging mode, gestation time, juvenile period, lactation time, life histories, mammals, maturation time, reproduction, scaling.

INTRODUCTION

A fundamental question in evolutionary ecology is 'Why are there so many kinds of life histories?' (to paraphrase Hutchinson's, 1959, famous query regarding the plethora of animal species). The diversity of life histories (i.e. age-specific schedules and patterns of growth, reproduction and mortality) has been analysed in several ways: by experiments, by modelling and by taxonomic comparisons. Often a first step taken in taxonomic

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comparisons is to scale the life-history trait(s) in question to body size. This allometric approach has revealed intriguing regularities between life histories and body size that have promoted much discussion (reviewed by Peters, 1983; Calder, 1984, Lindstedt and Swain, 1988; Reiss, 1989). These relationships are quantified by power functions of the form:

$$L = aM^b$$

where L is a life-history trait such as longevity or litter mass, M is adult mass, and a and b are empirical constants. These power functions are linear when plotted on a double logarithmic scale, the slope being b, which often approximates 0.25, 0.75 or 1.0. Allometric relationships also serve as bases of reference when exploring the effects of other factors on life-history variation (e.g. Western, 1979; Eisenberg, 1981; Harvey and Zammuto, 1985; Read and Harvey, 1989; Harvey and Pagel, 1991; Stearns, 1992).

Here we propose a new approach that involves scaling life-history features in relation to life span or other life-history time periods. This ‘allochronic method’ parallels the traditional allometric method in being based on power functions, for example:

$$L = aT^b$$

where T is lifetime or a well-defined portion of lifetime (e.g. age at sexual maturity). In short, allometry scales life-history features to size, whereas allochrony scales them to time.

Others have examined how various life-history traits co-vary with the duration of specific life-history periods. For example, in comparisons of various bird species, Lack (1968) has shown how egg mass and fledgling period vary in relation to incubation period. Similarly, Eisenberg (1981) has explored how newborn mass correlates with gestation time, and how litter size correlates with maximum longevity. Harvey and his co-workers have shown how gestation time, age at maturity, life expectancy and other life-history periods co-vary in mammals once the effects of body size are removed (Harvey and Zammuto, 1985; Read and Harvey, 1989). Similar relationships have been examined in birds (Saether, 1988). Charnov and Berrigan (1990) have also discovered interesting, but puzzling, taxonomic differences in how life span and age at maturity relate to each other (see also Charnov, 1993). Bronson (1989) has even claimed that mammalian reproductive traits are better scaled against life span than body size, although he presented no data to support this contention.

Here we suggest that these aforementioned patterns are special cases of a more general approach that we call ‘allochrony’. This term and its adjective should not be confused with the term ‘allochronic speciation’ coined by Alexander and Bigelow (1960) to refer to speciation by temporal reproductive isolation. Since the use of the word ‘allochronic’ in the sense intended by Alexander and Bigelow is not well-known and little used, we feel justified in re-coining the term to refer to our method of temporal scaling of life-history features.

As an introduction to the allochronic method, we shall restrict our analyses to scaling relatively short life-history periods in relation to longer ones. The method will be illustrated with mammals because of the abundance of data on life-history periods in this well-known group. In addition, we shall focus on the age at sexual maturity, rather than on life span, as the standard metric for this allochronic analysis, because it is more easily and accurately measured, and thus more data are available on it than is the case for life span. However, since life span encompasses all of the events of a life history, it is being used as the standard metric in other allochronic work presently being carried out by the senior author’s research group.

MATERIALS AND METHODS

The mammalian life-history periods examined in this paper are gestation time, lactation time, fetal-infancy period, juvenile period and maturation time (Fig. 1). Gestation encompasses the time from conception (i.e. egg fertilization and zygote formation) until birth. Lactation lasts from birth to weaning. Fetal-infancy period equals gestation time plus lactation time. The juvenile period starts at weaning and ends at the age of sexual maturity (defined as the age at first conception). Maturation time equals the time from when an individual is conceived to when it first conceives its own offspring.

Data on these life-history periods (expressed as days) were collected for 190 species in 14 orders of mammals from Hayssen *et al.* (1993). Only data on females were used. Data on gestation and lactation times and age at first conception were taken directly from Hayssen *et al.* (1993). The end of lactation was determined by only using data designated as 'wean'. The juvenile period was calculated as the age at first conception minus lactation time. Maturation time was calculated by adding together the fetal-infancy period and the juvenile period. Mean values for a life-history period were used whenever more than one value for a species was listed. If only a range of values was available in an entry, we used the mean of the upper and lower bounds of the range.

We scaled gestation time, lactation time, fetal-infancy time and juvenile time in relation to maturation time for the whole sample and for subsamples classified according to taxonomic affiliation (family and order), body mass, diet and foraging mode (Tables 1 and 2). These categories were examined because they are all well-known features that have been shown to be related to life-history variation in mammals. The ordinal classification followed Hayssen *et al.* (1993); the rodent family classification followed Alderton (1996); the data on body mass were from Silva and Downing (1995); and the data on diet and foraging mode were from Nowak and Paradiso (1983). Although 14 orders of mammals were represented, data from only four (Primates, Carnivora, Artiodactyla and Rodentia) with sufficient sample sizes ($n > 15$) were analysed separately. Similarly, although eight kinds of foraging mode were recognized, only three (arboreal, scansorial and terrestrial) with sufficient sample sizes ($n > 15$) were analysed separately. Arboreal species forage in trees and/or bushes, scansorial species forage in trees and/or bushes and on the ground, and terrestrial species forage mainly on the ground (following Eisenberg, 1981). The four diet groups analysed were faunivorous (animal-eating), omnivorous (animal and plant-eating), granivorous/frugivorous (seed- and fruit-eating) and herbivorous (vegetation-eating).

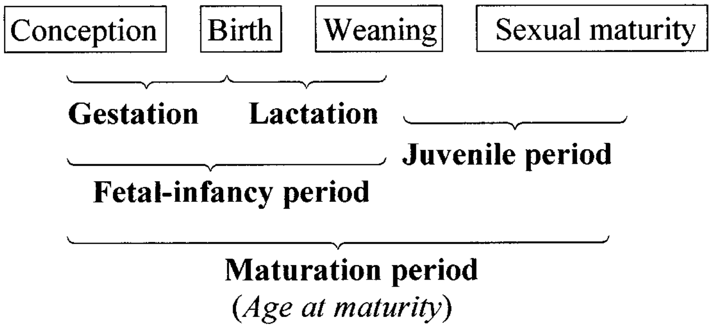

Fig. 1. Major events in a mammal's life history that are analysed in this paper.

Table 1. Numbers of mammal species in different taxonomic, diet and foraging-mode categories that were used in the present allochronic analyses[a]

Order, diet or foraging mode	Number of species
Order	
Marsupialia	9
Insectivora	6
Scandentia	1
Chiroptera	8
Primates	24
Carnivora	37
Cetacea	1
Proboscidea	2
Perissodactyla	4
Hyracoidea	1
Artiodactyla	39
Rodentia	56
Lagomorpha	1
Macroscelidea	1
Diet	
Faunivores	46
Granivore/frugivores	18
Omnivores	43
Herbivores	83
Foraging mode	
Volant	8
Arboreal	19
Scansorial	30
Terrestrial	103
Semi-fossorial	10
Fossorial	2
Semi-aquatic	5
Aquatic	13
Total	190

[a] The categories follow Eisenberg (1981), Nowak and Paradiso (1983) and Hayssen *et al.* (1993).

Allochronic relationships were determined using least-squares regressions expressed as linear equations of the form:

$$\ln L = \ln a + b \ln T$$

which is equivalent to the power function $L = aT^b$ described in the Introduction.

Special attention was also given to rodent genera of the family Muridae (*sensu* Alderton, 1996) to check whether the patterns seen for mammals as a whole apply to groups of related

Table 2. Least-squares linear regression statistics for gestation time, lactation time, fetal-infancy period and juvenile period in relation to age at sexual maturity (all expressed as natural logarithms of numbers of days)[a]

			Life-history period							
			Gestation		Lactation		Fetal-infancy period		Juvenile period	
Category	Group	*n*	Slope	*r*	Slope	*r*	Slope	*r*	Slope	*r*
Body mass (kg)	<0.1	39	**0.44**	0.77***	**0.39**	0.75***	**0.42**	0.84***	**1.38**	0.98***
	0.1–5.0	38	0.83	0.77***	**0.66**	0.74***	**0.77**	0.91***	**1.13**	0.98***
	5.0–50.0	29	**0.25**	0.33	1.15	0.81***	**0.71**	0.74***	**1.25**	0.93***
	>50.0	38	**0.47**	0.57***	0.82	0.35*	**0.63**	0.62***	**1.34**	0.87***
Order	Artiodactyla	39	**0.36**	0.55***	0.91	0.52***	**0.59**	0.59***	**1.62**	0.78***
	Carnivora	37	0.86	0.65***	**0.37**	0.22	**0.77**	0.71***	**1.23**	0.76***
	Primates	24	**0.39**	0.86**	1.20	0.86***	**0.85**	0.92***	**1.07**	0.98***
	Rodentia	56	**0.31**	0.49***	**0.38**	0.69***	**0.36**	0.65***	**1.36**	0.97***
Family	Muridae	41	**0.08**	0.23	**0.45**	0.65***	**0.26**	0.58***	**1.61**	0.98***
Diet	Faunivores	46	0.96	0.79***	**0.45**	0.37*	0.82	0.81***	1.07	0.96***
	Granivore/frugivores	18	**0.62**	0.96***	0.99	0.96***	**0.86**	0.96***	**1.12**	0.98***
	Omnivores	43	**0.67**	0.71***	**0.72**	0.84***	**0.72**	0.88***	**1.18**	0.96***
	Herbivores	83	**0.80**	0.87***	**0.85**	0.87***	**0.83**	0.91***	**1.15**	0.95***
Foraging mode	Arboreal	19	0.75	0.55*	1.15	0.80***	0.95	0.82***	1.02	0.98***
	Scansorial	30	**0.71**	0.83***	**0.74**	0.88***	**0.74**	0.92***	**1.19**	0.96***
	Terrestrial	103	**0.83**	0.88***	**0.85**	0.87***	**0.85**	0.91***	**1.12**	0.95***

[a] Groups of mammal species are analysed separately according to their body size, taxonomic affiliation, diet and foraging mode. The slope, Pearson's product–moment correlation coefficient (*r*) and sample size (*n*) are given for each regression. Note that gestation time, lactation time and fetal-infancy period generally show 'negative allochrony' (slopes < 1.0), whereas juvenile period shows 'positive allochrony' (slope > 1.0).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Slopes with **bold** numbers are significantly different from 1.0.

species. The family Muridae is especially suitable for such an analysis because it has a large number of species and genera with pertinent life-history data.

RESULTS

For the whole sample of 190 species, gestation time, lactation time, fetal-infancy period and juvenile period all show significant positive correlations with maturation period (Fig. 2). Moreover, the slopes for gestation time, lactation time and fetal-infancy period in relation to maturation period are all significantly less than 1 (0.795 ± 0.079, 0.768 ± 0.090 and 0.813 ± 0.059, respectively), whereas the slope for juvenile period in relation to maturation period is significantly greater than 1 (1.138 ± 0.050) (i.e. the 95% confidence limits of the slopes, indicated in parentheses, did not overlap 1.0). This means that, as maturation time increases, juvenile period not only increases but also takes up a greater proportion of maturation time. However, although fetal-infancy period and its components also increase with increasing maturation time, they take up a decreasing proportion of maturation time. Following terminology used in allometric analyses (Huxley, 1932), the juvenile period shows 'positive allochrony', whereas gestation time, lactation time and the fetal-infancy period show 'negative allochrony'.

These patterns are robust as they occur repeatedly no matter how we subdivide the whole sample (Table 2). The rodent family Muridae and each of four orders (Primates, Carnivora, Artiodactyla and Rodentia) all show this pattern, with only one exception (primate lactation time shows positive rather than negative allochrony, although not significantly so). All four body-mass classes generally show the pattern, except that lactation time for the 5.0–50.0 kg class shows positive (non-significant) allochrony rather than negative allochrony. In addition, all four diet classes show the overall pattern. And all three foraging-mode classes obey the pattern, although lactation time for the arboreal mammals shows positive (non-significant) allochrony rather than negative allochrony. Looking at Table 2 as a whole, gestation time and fetal-infancy period show negative allochrony in all 16 classified groups, lactation time shows negative allochrony in 13 of these groups, and juvenile period shows positive allochrony in all 16 groups.

To further examine possible effects of ecology on these allochronic patterns, we compared the proportions of maturation time spent in the fetal-infancy and juvenile periods among four diet classes and three foraging-mode classes. These analyses revealed significant differences. Faunivorous mammals tend to spend a greater percentage of their maturation time as post-weaning juveniles than omnivores, granivore/frugivores and herbivores (Fig. 3). In addition, arboreal species tend to have proportionately longer juvenile periods than scansorial and terrestrial species (Fig. 3).

To investigate potential phylogenetic effects, we also examined how juvenile period, as a percentage of maturation time, varies with diet and foraging mode in different orders with sufficient samples sizes (Table 3). Faunivorous bats and carnivores have proportionately long juvenile periods, whereas herbivorous rodents and ungulates have relatively short juvenile periods. Volant bats and arboreal/scansorial primates also spend more of their maturation time as juveniles than terrestrial rodents and ungulates. However, within orders, the effects of diet and foraging mode are not readily apparent. Only two significant differences were found: relative juvenile period was significantly longer in scansorial versus arboreal primates ($t = 2.84$, $P = 0.011$; data normalized by arcsine square-root transformation, following Zar, 1984) and relative juvenile period was longer in terrestrial carnivores

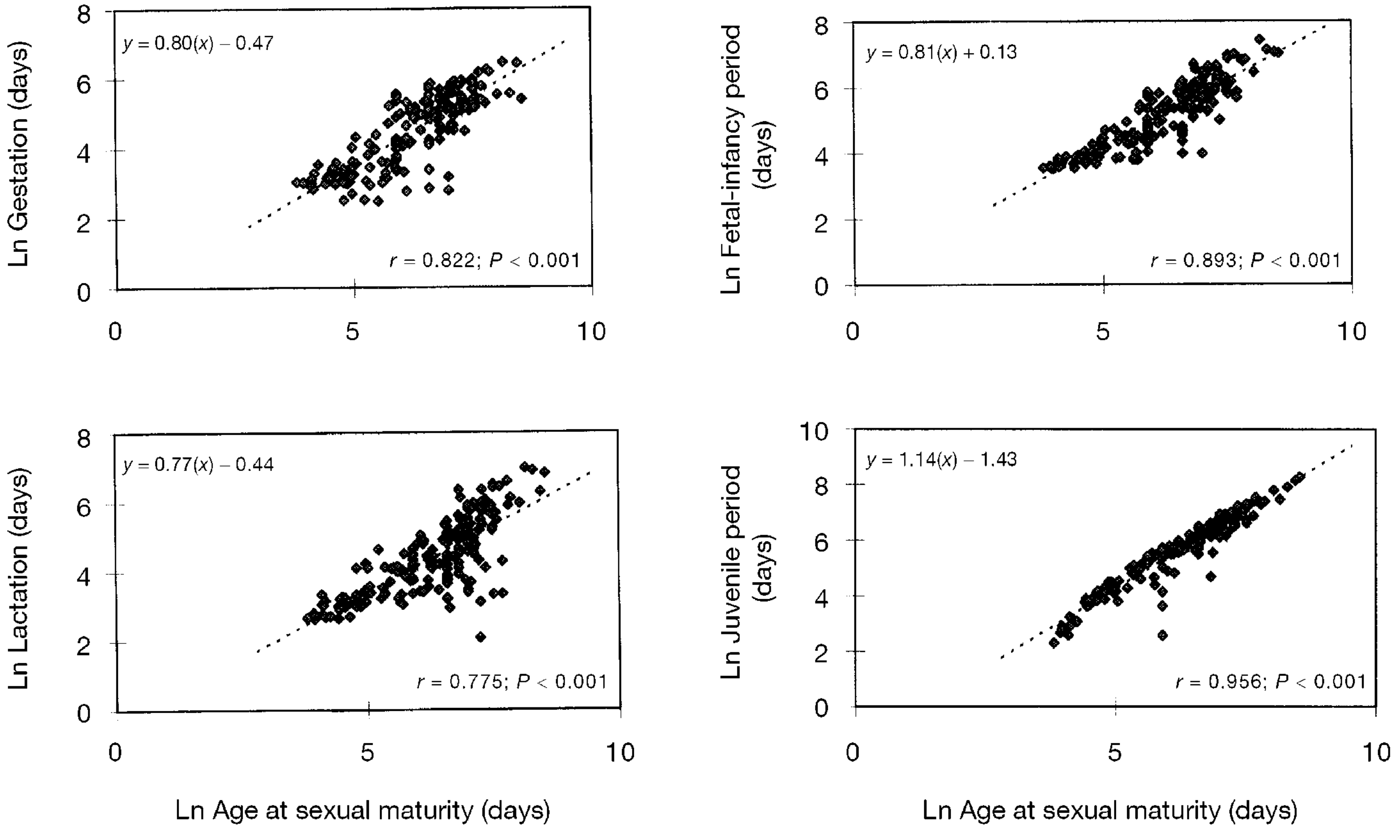

Fig. 2. Allochronic relationships of gestation time, lactation time, fetal-infancy period and juvenile period with age at sexual maturity in 190 mammal species (all expressed as natural logarithms of numbers of days). Shown are least-squares regression lines and their equations and Pearson's product–moment correlation coefficients and their level of significance. Note that gestation time, lactation time and fetal-infancy period show 'negative allochrony' (slopes < 1.0), whereas juvenile period shows 'positive allochrony' (slope > 1.0).

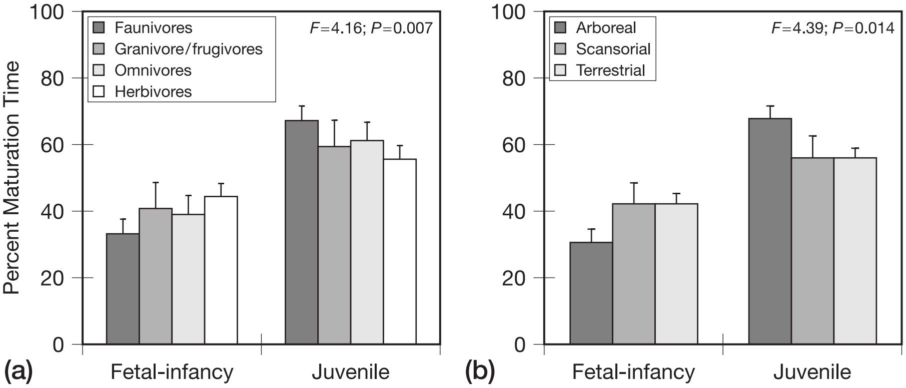

Fig. 3. Percentage of maturation time (mean ± 95% confidence limit) spent in the fetal-infancy and juvenile periods for mammals with different diets (a) and foraging modes (b). Shown are the results of analyses of variance based on data normalized by the arcsine square-root transformation (Zar, 1984).

than in scansorial or aquatic ones ($F = 6.00$, $P = 0.0061$). Both of these trends were counter to the trends shown by all mammals collectively.

To control for body-size, foraging mode and phylogenetic effects more carefully, we carried out allochronic analyses on a group of related scansorial/terrestrial genera of similar body size within the rodent family Muridae. As already stated, murid gestation time, lactation time and fetal-infancy period all show negative allochrony in relation to maturation time, whereas juvenile period shows positive allochrony. In addition, an ecological classification of murid rodents into ‘grazers’ (vegetation-eaters) and ‘hunters’ (faunivores, omnivores and granivore/frugivores) reveals significant differences in the timing of their life-history periods (Fig. 4). Hunters not only have longer fetal-infancy and juvenile periods than grazers, but also their juvenile periods take up disproportionately larger fractions of the maturation period. Indeed, most of the differences in maturation time between grazing and hunting murids appears to be due to differences in the length of the juvenile period. Unfortunately, insufficient data were available to test whether allochronic differences exist between arboreal and scansorial/terrestrial murids.

DISCUSSION

Given that life histories are fundamentally about time schedules, it is surprising that the allochronic technique has not been applied systematically before now. On the other hand, allochronic relationships may have been neglected because life-history periods tend to scale similarly with body size (slope ~ 0.25; see Lindstedt and Calder, 1981; Calder, 1984). Hence, isochrony, rather than allochrony, is to be expected. Therefore, it is surprising to find that gestation time, lactation time and the fetal-infancy period show negative allochrony when scaled against age at sexual maturity (first conception), whereas juvenile period shows positive allochrony.

What causes these allochronic patterns? We suggest that they are the result of age at sexual maturity being more dependent on differences in developmental time during the post-weaning juvenile period than during the pre-weaning period. That is, juvenile period is positively allochronic with age at sexual maturity because its variation has a greater effect

Table 3. Juvenile period as a percentage of maturation time (mean ± 95% confidence limit; $n \geq 5$) in various mammalian orders categorized by diet and foraging mode (sample size in parentheses)

	Diet				Foraging mode				
Order	F	G/F	O	H	V	A	S	T	AQ
Marsupialia			58.6 ± 16.9 (6)						
Chiroptera	73.7 ± 13.7 (8)				73.7 ± 13.7 (8)				
Primates			69.9 ± 4.8 (12)	72.2 ± 5.3 (8)		68.4 ± 4.2 (15)	75.5 ± 3.9 (6)		
Carnivora	66.9 ± 5.6 (28)		56.0 ± 27.0 (7)				52.7 ± 24.3 (6)	74.4 ± 4.4 (17)	63.2 ± 9.4 (12)
Artiodactyla				53.4 ± 5.6 (40)				52.3 ± 5.5 (38)	
Rodentia		57.1 ± 10.4 (13)	57.4 ± 10.3 (15)	51.6 ± 8.5 (25)			54.9 ± 10.6 (15)	54.2 ± 6.2 (34)	

Abbreviations: F, faunivores; G/F, granivore/frugivores; O, omnivores; H, herbivores; V, volant; A, arboreal; S, scansorial; T, terrestrial; AQ, aquatic.

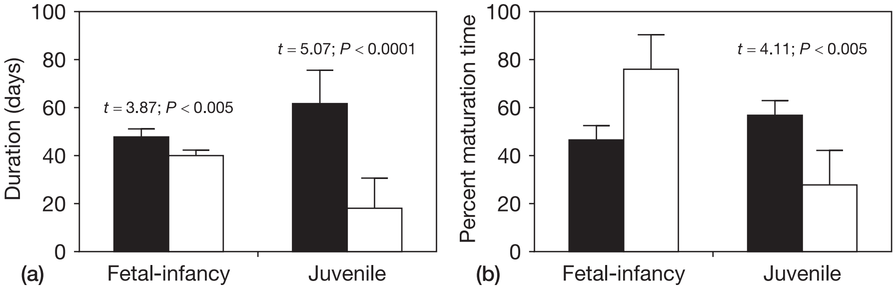

Fig. 4. (a) Duration and (b) percentage of maturation time (mean ± 95% confidence limit) spent in the fetal-infancy and juvenile periods for scansorial/terrestrial murid rodent genera with different diets. 'Hunters' (■) are faunivores, granivore/frugivores or omnivores (= *Acomys*, *Aethomys*, *Akodon*, *Apodemus*, *Meriones*, *Peromyscus*, *Phodopus*, *Praomys*, *Rhabdomys*, *Saccostomus* and *Tatera*, representing five different subfamilies: Cricetinae, Cricetomyinae, Gerbillinae, Hesperomyinae [Sigmodontinae] and Murinae), whereas 'grazers' (□) are herbivores (= *Arvicanthus*, *Calomys*, *Clethrionomys*, *Dicrostonyx*, *Lagurus*, *Lemmus*, *Microtus* and *Phenacomys*, representing three different subfamilies: Hesperomyinae, Microtinae [Arvicolinae] and Murinae; classification follows Alderton, 1996). To control for the effects of body size, only genera with body masses of 20–100 g were analysed (hunting genera averaged 46.6 g; grazing genera averaged 40.8 g). Generic averages were used instead of species values to minimize phylogenetic effects. Shown are the results of *t*-tests comparing hunters versus grazers (the percentage data were normalized by the arcsine square-root transformation, following Zar, 1984).

on maturation time than does variation in gestation time, lactation time or fetal-infancy period. This explanation is consistent with the fact that age at sexual maturity is more highly correlated with juvenile period than with gestation time, lactation time or fetal-infancy period (Fig. 2, Table 2).

The positive allochrony of the juvenile period persists even if slopes obtained by reduced major axis (RMA) regression are examined, rather than slopes based on least-squares regression, as was done here. It can be argued that RMA regression is more appropriate because the independent variable – age at sexual maturity – is measured with some error, as are the other life-history periods (e.g. Sokal and Rohlf, 1981; LaBarbera, 1989; Harvey and Pagel, 1991). For the whole mammal sample, the RMA slopes are 1.19 (juvenile period), 0.91 (fetal-infancy period), 0.97 (gestation time) and 0.99 (lactation period). The interested reader can also calculate RMA slopes for the various subsamples in Table 2 by dividing the least-squares slope by the correlation coefficient *r*.

We have chosen to focus on the least-squares regression results for two reasons. First, we feel that the RMA slopes do not make as much sense as the least-squares slopes, because the positive allochrony of the juvenile period is not matched by an equivalent negative allochrony of the other periods making up maturation time. Second, since neither least-squares nor RMA regression seems to be more valid statistically than the other for all of the relationships examined, we decided to be consistent by focusing only on the least-squares regression results. Differences in appropriateness of the two methods arise because in some cases the *y*-variable is more error-prone than the *x*-variable (favouring least-squares regression), whereas in other cases this is probably not true (possibly favouring RMA regression) (cf. Calder, 1987). For example, least-squares regression seems to be more appropriate for scaling juvenile period against age at sexual maturity because juvenile period is measured with more error than age at sexual maturity. This is because weaning, which marks the beginning of the juvenile period, is a continuous process that is difficult to pinpoint in time, whereas age at sexual maturity (defined as the age at first conception) is a more discrete event that can be measured precisely (see also below). However, RMA regression may be more appropriate for scaling gestation time against age at sexual maturity because both variables probably have relatively similar error, as both are well-defined periods that can be measured precisely.

One may also question the validity of the present regression analyses because the y- and x-variables are not independent. Each developmental period (y) is a part of maturation time, against which it is scaled (x). However, similar allochronic patterns are still generally observed even when each developmental period is scaled against maturation time *minus* the developmental period in question. When this is done, the least-squares and RMA slopes for the whole mammal sample are as follows: gestation time (0.674 *vs* 0.907), lactation time (0.670 *vs* 0.947), fetal-infancy period (0.575 *vs* 0.766) and juvenile period (0.982 *vs* 1.307). In any case, we focused on using maturation time as the scaling factor because we wanted to see how each developmental period varied in proportion to this entire time period, not some segment of it.

Why should the post-weaning juvenile period have a stronger impact on age at sexual maturity than the pre-weaning developmental periods? One explanation is that since the juvenile period is usually longer than the fetal-infancy period, its variation (even if random) will have a greater effect on maturation time for purely statistical reasons. However, this hypothesis does not explain why the juvenile period is still positively allochronic even in taxa with roughly equal juvenile and fetal-infancy periods (e.g. the artiodactyls; see Tables 2 and 3). In any case, the juvenile period is usually not much longer than the fetal-infancy period, averaging only 58.6% of maturation time for the whole mammal sample. The ‘statistical artefact hypothesis’ also doesn’t explain why the allochronic slope of the fetal-infancy period (0.81) is not significantly greater than those of the shorter periods making it up (0.80: gestation time; 0.77: lactation time; see Fig. 2).

Another possibility is that the juvenile period has more of an effect on age at maturity because it is more variable, as a result of relatively large measurement error, than the other developmental periods. Indeed, ln juvenile period shows more residual variation after being regressed against ln body mass ($r^2 = 0.377$) than do ln gestation time ($r^2 = 0.676$), ln lactation time ($r^2 = 0.444$) or ln fetal-infancy period ($r^2 = 0.717$). However, this explanation is also probably not true for the following reason. The most discrete life-history events considered here are conception and birth, whereas the least discrete is weaning, which is essentially a continuous process. Thus, the timing of conception and birth can be measured precisely, whereas weaning is estimated much less precisely. Now, the fetal-infancy period ends with weaning and the juvenile period begins with weaning. Therefore, both of these periods should be affected by the imprecision of measuring weaning time, not just the juvenile period. In addition, although the ‘measurement artefact hypothesis’ predicts that lactation time should be more positively allochronic than gestation time, because lactation time is more imprecisely estimated, no significant difference exists between their slopes for the entire mammal sample (Fig. 2).

All in all, there appears to be little reason to suspect that the allochronic patterns observed here are merely statistical or measurement artefacts. Rather, they appear to be biologically significant, as suggested by the following evidence. Both diet and foraging mode are related to how maturation time is divided between the pre-weaning and post-weaning periods. Faunivorous mammals tend to spend a greater percentage of their maturation time as post-weaning juveniles than omnivores, granivore/frugivores or herbivores (Fig. 3). Arboreal mammals also have proportionately longer juvenile periods than scansorial and terrestrial species (Fig. 3).

Wootton (1987) has further shown that herbivorous mammals tend to mature more quickly than most other trophic types of equivalent body size. However, these dietary effects apparently 'disappear' after order-level phylogenetic effects are removed. Similarly, the present effects of diet and foraging mode on relative juvenile period seem to vanish or to be altered when they are examined within orders (Table 3). However, small sample sizes and the potentially conflicting effects of body size, diet, foraging mode and other factors, which are accentuated by small sample sizes, may explain why the ecological trends observed for mammals as a whole are not seen at lower taxonomic levels. Moreover, it is difficult to separate phylogenetic and ecological effects because taxic boundaries often coincide with ecological differences. Indeed, the ecological factors in question may be ultimately responsible for the phylogenetic differences that one is trying to factor out. Consequently, factoring out taxonomic effects may underestimate ecological effects (cf. McNab, 1992). For example, arboreality may have been an important factor influencing the evolution of not only the relatively long juvenile periods of primates, but also many of the traits that define these animals as a taxon. The strong influence of arboreality may also explain why primates have long juvenile periods regardless of diet (Table 3). Similar conclusions may be applicable to the prolonged juvenile periods of faunivorous carnivores, and to the relatively short juvenile periods of herbivorous rodents and ungulates (see Table 3).

In any case, a more careful attempt at controlling for body size, foraging-mode and taxonomic effects was made by examining the effects of diet on relative juvenile period among genera within the same rodent family, the Muridae. Only scansorial/terrestrial genera with a body mass of 20–100 g were included in the sample. A comparative analysis revealed that murids that hunt for animal prey, seeds and/or fruits have longer juvenile periods, both absolutely and in proportion to maturation time, than murids that graze on vegetation (Fig. 4). Unfortunately, however, not enough data were available to examine the effects of foraging mode on murid juvenile period.

Obviously, more data are needed to test whether diet and foraging mode have significant effects on the timing of life-history events in mammals. However, it is encouraging that the trends that have been detected make sense, and are consistent with other observations. It stands to reason that the young of faunivorous and arboreal mammals will require more time to develop foraging skills sufficient for supporting a family than herbivorous and terrestrial species. Hunting, catching and dispatching prey require more learning than grazing on easily accessible vegetation. Similarly, foraging in three dimensions (arboreal lifestyle) requires more learning than foraging in two dimensions (terrestrial lifestyle). Thus, it should not be surprising that the juvenile period, as a percentage of maturation time, is longer in faunivorous and arboreal species than in herbivorous and terrestrial species.

The 'development-of-foraging-skills hypothesis' is also consistent with two other observations. First, differences in maturation time between murid 'hunters' and 'grazers' are more related to differences in the juvenile period, when the young are foraging on their own, than to differences in the fetal-infancy period, when the young are dependent on their mother (see Fig. 4). This pattern is also consistent with the observation made above that the juvenile period shows more residual variation when scaled against body mass than does the fetal-infancy period. This may be because environmental effects are more pronounced on the juvenile period than on the fetal-infancy period. Second, among small mammals, faunivores more often show declines in growth at weaning than herbivores (D.S. Glazier, unpublished). This is because a newly weaned animal has a more difficult time of maintaining a positive energy balance, let alone obtaining enough energy for reproduction, if it is learning how to capture elusive animal prey than if it is learning how to graze readily available vegetation. Thus, for energetic reasons, it should take faunivores more time to reach reproductive maturity than herbivores.

The greater effect of diet on the juvenile period than on the fetal-infancy period also lends support to our suggestion that the positive allochrony of the juvenile period has biological significance. Indeed, the analyses in this paper suggest that we should be able to go a long way towards achieving an understanding of why age at sexual maturity varies in mammals, once we determine how various ecological factors affect the duration of the juvenile period.

In conclusion, the allochronic method presented here shows that time (like size) is an important scaling dimension for life-history traits. It also reveals new ways by which life-history traits are related to one another and to ecological factors. Therefore, we feel that the allochronic method should be considered as a basic tool for analysing life histories. We have demonstrated the method by focusing on age at sexual maturity as the scaling factor and mammals as the source of life-history data. However, many other kinds of temporal scaling could be done by considering other life-history periods (e.g. life span). In addition, the method should be tried in other animal groups with well-known life histories (e.g. birds). In this way, it will be possible to determine the generality of the allochronic trends observed here, a current objective of the senior author's research group.

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REFERENCES

Alderton, D. 1996. *Rodents of the World*. New York: Facts on File.

Alexander, R.D. and Bigelow, R.S. 1960. Allochronic speciation in field crickets, and a new species, *Acheta veletis*. *Evolution*, **14**: 334–346.

Bronson, F.H. 1989. *Mammalian Reproductive Biology*. Chicago, IL: University of Chicago Press.

Calder, W.A. 1984. *Size, Function and Life History*. Cambridge, MA: Harvard University Press.

Calder, W.A. 1987. Scaling energetics of homeothermic vertebrates: An operational allometry. *Ann. Rev. Physiol.*, **49**: 107–120.

Charnov, E.L. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford: Oxford University Press.

Charnov, E.L. and Berrigan, D. 1990. Dimensionless numbers and life history evolution: Age at maturity versus the adult lifespan. *Evol. Ecol.*, **4**: 273–275.

Eisenberg, J.F. 1981. *The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior*. Chicago, IL: University of Chicago Press.

Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Harvey, P.H. and Zammuto, R.M. 1985. Patterns of mortality and age at first reproduction in natural populations of mammals. *Nature*, **315**: 319–320.

Hayssen, V., van Tienhoven, A. and van Tienhoven, A. 1993. *Asdell's Patterns of Mammalian Reproduction*. Ithaca, NY: Cornell University Press.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.*, **93**: 145–159.

Huxley, J.S. 1932. *Problems of Relative Growth*. London: Methuen.

LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. *Ann. Rev. Ecol. Syst.*, **20**: 97–117.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.

Lindstedt, S.L. and Calder, W.A. 1981. Body size, physiological time, and longevity of homeothermic animals. *Q. Rev. Biol.*, **56**: 1–16.

Lindstedt, S.L. and Swain, S.D. 1988. Body size as a constraint of design and function. In *Evolution of Life Histories of Mammals* (M. Boyce, ed.), pp. 93–106. New Haven, CT: Yale University Press.

McNab, B. 1992. A statistical analysis of mammalian rates of metabolism. *Funct. Ecol.*, **6**: 672–679.

Nowak, R.M. and Paradiso, J.L. 1983. *Walker's Mammals of the World*. Baltimore, MD: Johns Hopkins University Press.

Peters, R.H. 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.

Read, A.F. and Harvey, P.H. 1989. Life history differences among the eutherian radiations. *J. Zool.*, **219**: 329–353.

Reiss, M.J. 1989. *The Allometry of Growth and Reproduction*. Cambridge: Cambridge University Press.

Saether, B.E. 1988. Pattern of covariation between life-history traits of European birds. *Nature*, **331**: 616–617.

Silva, M. and Downing, J.A. 1995. *CRC Handbook of Mammalian Body Mass*. Boca Raton, FL: CRC Press.

Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. San Francisco, CA: Freeman.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Western, D. 1979. Size, life history and ecology in mammals. *Afr. J. Ecol.*, **17**: 185–204.

Wootton, J.T. 1987. The effects of body mass, phylogeny, habitat, and trophic level on mammalian age at first reproduction. *Evolution*, **41**: 732–749.

Zar, J.H. 1984. *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall.