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Source: *Functional Ecology*, Vol. 6, No. 1 (1992), pp. 57-65

Published by: British Ecological Society

Stable URL: <http://www.jstor.org/stable/2389771>

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Comparative reproductive strategies of altricial and precocial eutherian mammals

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Summary

Mammals produce neonates of varying degrees of development described by the terms altricial and precocial. I rank eutherian mammals by a comprehensive measure of development in which neonates are scored in four areas of independence: thermoregulatory, sensory, locomotory and nutritional. The association between neonatal development and nine life-history traits is examined in 239 species. The distribution of neonatal developmental rankings is associated with adult mass and is related to taxonomic level, with precocial neonates more common among orders, and altricial neonates more common among genera and species. When the effect of adult mass is controlled, precocial mammals produce heavier neonates and heavier litters, possess longer gestation periods, attain adult mass more slowly, and have smaller litter sizes. Mass at weaning, length of the total reproductive interval, and age at first parturition do not differ among developmental categories. Although the continuous nature of development is intuitively appealing, mammalian development patterns do not map onto predictable, continuous changes in life-history patterns. Length of the lactation period is extended in precocial primates but shortened in precocial rodents. Neonate mass varies continuously with stage of neonatal development, while litter size varies dichotomously, and age at first parturition and litter mass differ uniquely in only one developmental category. Thus, neonatal developmental patterns do not appear to result from one continuous axis of selection.

Key-words: Altricial, eutherian mammals, life history, neonatal development, precocial

Functional Ecology (1992) **6**, 57–65

Introduction

The offspring of eutherian mammals differ in their degree of neonatal development. For example, rabbits, cricetid rodents and canids all produce dependent, poorly developed neonates whereas hares, hystricomorph rodents and bovids produce relatively independent, well-developed neonates. These contrasting stages of neonatal development are characterized by the terms altricial and precocial respectively. Ancestral mammals were small in size and are presumed to have produced altricial offspring (Hopson 1973; Case 1978a). Although the majority of extant mammal species produce altricial neonates, precocial forms occur in many orders. The scattered distribution of precocial species among taxa indicates that the timing of birth in relation to stage of development has been modified often during mammalian evolution. This shift in timing may affect

changes in other related phenomena such as size and life-history traits (Gould 1977; Bonner & Horn 1982). Among birds, variation in neonatal maturity is associated with variation in physiological anatomical and behavioural traits (Nice 1962; Lack 1968; Ricklefs 1973). For example, precocial birds grow at only 25% of the rate of altricial species (Ricklefs 1973; Case 1987b).

Previous research on the evolution of neonatal development in mammals has focused primarily on prenatal life-history correlates. Precocial species have been shown to have relatively heavier neonates (Martin & MacLarnon 1985), longer gestation periods (Zaveloff & Boyce 1980; Martin & MacLarnon 1985), and smaller neonatal litter sizes (Zaveloff & Boyce 1980; Eisenberg 1981). Altricial and precocial mammals exhibited no difference in the rate of growth to 50% of adult mass (Case 1978b). Precociality has been interpreted as a correlate to increased length of the gestation period resulting in increased development of the central nervous system (Sacher & Staffeldt 1974) and as resulting from an

Table 1. Neonatal development within 16 orders of eutherian mammals. Developmental categories 0–3 represent neonatal independence in four areas (thermoregulatory, sensory, locomotory, and nutritional), with a rank of 0 representing the most altricial species. Total numbers of genera and families differ from the sum of developmental categories because some taxa may be represented in more than one developmental category

Order	Number of genera (families) within development category				Total
	0	1	2	3	
Insectivora	9(2)	1(1)	—	—	10(3)
Macroscelidae	—	—	—	1(1)	1(1)
Chiroptera	7(2)	1(1)	3(2)	—	10(3)
Scandentia	—	1(1)	—	—	1(1)
Primates	—	2(2)	18(9)	—	20(9)
Edentata	1(1)	—	2(1)	1(1)	4(3)
Pholidota	1(1)	—	—	—	1(1)
Lagomorpha	2(1)	2(2)	—	1(1)	4(2)
Rodentia	58(9)	5(3)	4(4)	17(12)	83(19)
Cetacea	—	—	—	2(1)	2(1)
Carnivora	12(5)	14(5)	2(2)	1(1)	27(7)
Pinnipedia	—	—	—	4(3)	4(3)
Tubulidentata	—	—	1(1)	—	1(1)
Proboscidea	—	—	—	1(1)	1(1)
Hyracoidea	—	—	—	1(1)	1(1)
Artiodactyla	—	—	1(1)	12(5)	13(6)
Total	90(21)	26(15)	31(20)	41(27)	183(62)

interaction between metabolic rate and length of the gestation period (Thompson & Nicoll 1986). Postnatal correlates to neonatal development, such as differences in the length of the lactation period, have received little attention, although many hypotheses suggesting ecological correlates have focused on the benefits of precociality and early offspring independence. Resource availability (Daly 1975; Neal 1984), low water availability (Layne 1986), and increased social interactions (Gould 1975) have been proposed as possible factors selecting for increased precociality.

Two questions relating to the evolution of neonatal development in mammals remain unresolved. First, does the dichotomy implied by the terms altricial and precocial accurately reflect the patterns of neonatal development exhibited by mammals? Although previous research is inconclusive about the nature of the distribution of neonatal development in mammals, the persistence of the terms altricial and precocial suggests that a dichotomy exists and that some meaning is implied by these terms. Secondly, is variation in neonatal development correlated with other life-history traits? Although neonatal development is strongly correlated with prenatal life-history traits, the relationship to other traits has not been carefully examined.

Materials and methods

CRITERIA FOR DETERMINING NEONATAL DEVELOPMENT

Data were collected on the appearance of neonates at birth for 239 eutherian mammals in 183 genera, 62

families and 16 orders. Species were assigned to one of five categories based on the stage of neonatal development in four areas. Species were recorded for presence or absence of a trait based on reports in the literature on neonate appearance within the first 2 days of birth. Neonatal independence was measured in four areas: thermoregulatory, sensory processing, locomotor independence, and nutritional independence. Each of these encompasses several developmental stages; for example, nutritional independence is gained gradually as neonates shift from a milk diet to solid food, and, in the case of carnivores, finally gain the ability to capture their solid food source. The degree of development of neonates in these four areas of independence was estimated by using developmental stages which were commonly reported in the literature. The following traits were used to determine which level of independence a neonate had achieved: hair covers the body (thermoregulatory), eyes open (sensory), move independent of parent (locomotory), and eat solid food (nutritional). These were generally acquired during development in the order listed, but exceptions to this exist. The presence or absence of these traits was summed over the four areas of independence producing five categories (0–4), with category 0 representing the most altricial species. Because of small sample sizes, it was necessary to lump species in categories 3 and 4.

The distribution of observations by developmental category at the family level is shown in Table 1. Each category includes representatives from many different orders; however, more than 50% of the genera in category 2 are primates, which may strongly influence the characteristics of this rank.

Little variation in neonatal development occurs within genera (1.03 developmental categories/genus), moderate variation within families (1.34 categories/family), and considerable variation within orders (1.94 categories/order). The family level of analysis was chosen. The choice of an appropriate level of taxonomic analysis was a compromise between maintaining an adequate sample size and avoiding increasing sample with closely related and, therefore non-independent, observations (see Harvey & Mace 1982).

LIFE-HISTORY CHARACTERISTICS

Nine life-history characteristics were recorded for each species:

1. *K*: growth rate constant *K* of the Gompertz equation, the rate of attaining asymptotic adult mass (*A*). *K* is inversely related to the time taken to reach any proportion of adult mass. It was calculated for each species from growth data in the literature. The method used to calculate *K* was described by Zullinger *et al.* (1984). Asymptotic adult mass (*A*) was also estimated by this procedure and compared to published values of adult mass.
2. *LS*: mean litter size
3. *Mn*: neonate mass, the mean mass of offspring on the day of birth.
4. *G*: gestation period, the time period from fertilization to birth. For species with delayed implantation, the quiescent stage was subtracted from the length of the gestation period.
5. *L*: Lactation period, the period from birth until the termination of lactation.
6. *Mw*: Weaning mass, mass at the termination of active nursing. Estimates were taken from the literature, if available, or estimated from the actual growth curve based on known length of the lactation period.
7. *AFP*: Age at first parturition, the earliest common age at which females first gave birth (that experienced by 20% of the population). If these data were not published, the mean age at first estrus plus the length of the gestation period was used.
8. *MI*: Litter mass, a compound variable estimated by multiplying mean litter size (*LS*) by neonate mass (*Mn*).
9. *RI*: Reproductive interval, a compound variable estimated by adding the length of the gestation period (*G*) to the length of the lactation period (*L*).

These reproductive traits often vary among populations of animals. Whenever possible, values for all variables were taken from the same source and from original publications. Because the analyses of several reproductive traits could be biased by using different data sets for different analyses, I included only species for which information was available for most variables. On average, information was available for 6.3 of the seven baseline life-history traits (excluding

the compound variables *MI* and *RI*) for species included in the data set.

DATA ANALYSIS TECHNIQUES

Adult mass appears to be positively correlated with the degree of neonatal development and is known to be strongly correlated with many life-history traits. To examine the relationship between neonatal development and other life-history characteristics, the effect of adult mass on these variables must be controlled (Read & Harvey 1989). Residual values were calculated for each observation from the common least squares regression line estimated from the mean values of the log transformed life-history traits (dependent variable) and adult mass (independent variable). Because adult mass is not measured without error, these data do not satisfy assumptions of least squares analysis; however, the degree of error around each mass measurement is small compared to the range of adult mass values and should not substantially affect the analysis. The mean values of these residuals then were calculated at the family level by developmental category. Analysis of variance using SAS-GLM procedures was used to test the effect of neonatal maturity on life-history traits (SAS Institute 1985). The LSMEANS procedure was used to test for differences between specific developmental categories.

This methodology assumes that the different developmental categories all exhibit the same slope relationship between the life-history traits and adult mass. The sum of squares associated with the interaction term (neonatal development by adult mass) was calculated to test this assumption.

LEVEL OF ANALYSIS

All data were logarithmically transformed prior to analysis. Family means for each variable were calculated by averaging species values within genera, then, calculating residual values for each generic value of the life-history trait from the regression of the life-history trait on adult mass, and finally, averaging the residual values within families by neonatal developmental category. The effect of adult mass was removed before family means were calculated because sample size was not identical for adult mass and each life-history trait. Because mass can vary considerably within families, calculating family means before calculating residuals would result in mean family values for adult mass which were inappropriate for the mean family values for life-history traits represented by smaller sample sizes.

The robustness of these results was explored by analysing subsets of the original data set. First, the order Primates contributes nine of the 20 families within developmental category 2. This order shows little variation in neonatal development; 90% of the

Table 2. Proportion of observations in each developmental category at different taxonomic levels. The restricted data set only included observations in which adult mass was greater than 100 g and less than 10 kg. This mass range was examined because it lies within the range of observed values of small precocial species and large altricial species. Sample size is shown in parentheses

Taxonomic level	Developmental Category			
	0	1	2	3
<i>Total data set</i>				
Orders	0.22(7)	0.22(7)	0.22(7)	0.32(10)
Families	0.25(21)	0.18(15)	0.24(20)	0.33(27)
Genera	0.48(90)	0.14(26)	0.16(31)	0.22(41)
<i>Restricted data set</i>				
Orders	0.26(5)	0.32(6)	0.21(4)	0.21(4)
Families	0.28(13)	0.23(11)	0.23(11)	0.26(12)
Genera	0.43(39)	0.18(16)	0.20(18)	0.20(18)

genera exhibit the same stage of neonatal development. To reduce inflation of sample size on this developmental category and to separate the taxonomic and developmental correlates with life-history traits, observations for this order were calculated as mean residuals at the order level within developmental category. Secondly, the analyses were repeated within the Rodentia at the family level. Rodentia is the only order which provides a reasonably good sample within each of the four developmental categories.

Results

Adult mass differs significantly among developmental categories. Analysis of variance of log-transformed mass measures indicates that individuals in developmental category 3 are significantly heavier than those in categories 2 and 1 which, in turn, are heavier than individuals in category 0 ($F=35.11$, $P<0.0001$, $n=193$). The average of log-transformed mass for each category was 9300, 1840, 1034 and 105 g respectively. In addition to mean mass differing among developmental categories, the proportion of families with geometric mean mass greater than 1000 g also increases with neonatal maturity. Twenty-eight per cent of families in category 0, 40% in category 1, 45% in category 2 and 70% in category 3 exceeded a geometric mean mass of 1000 g.

Altricial species are more abundant at the generic level compared to higher taxonomic levels. At the order and family levels of analysis, developmental categories 0, 1, and 2 are observed approximately equally while category 3 (most precocial) is most common (Table 2). However, at the generic level of analysis, altricial species become more common (48% of observations). If observations are restricted to the mass range in which representatives from each

developmental category occur (100–10000 g), the relative representation of developmental ranks differs depending on level of analysis. The pattern of increasing proportion of altricial representatives at lower taxonomic levels is again observed with 43% of the observations falling in category 0.

The estimated regression equations for the relationship of each life-history trait on adult mass are shown in Table 3. Each life-history variable shows a significant regression on adult mass with r^2 -values ranging from 23 (LS) to 97% (Mw). No life-history traits except neonate mass (Mn), litter mass (Ml), and weaning mass (Mw) exhibit significant interaction terms between developmental category and adult mass. The interaction terms for Mn ($F=8.33$, $P=0.0001$), Ml ($F=5.14$, $P=0.003$), and Mw ($F=4.56$, $P=0.005$) accounted for 1.2, 0.6 and 0.5% of the total sum of squares. The estimated slopes for the regression equations calculated by developmental category for the traits Mn, Ml, and Mw increase in slope in the more precocial mammals (Table 4). Generally, these results are attributable to the life-history characteristics of a few species. For example, two bats, which have very low adult mass measures, have relatively large neonates, while the bear, which has a very heavy adult mass, has a relatively small neonate. These three points jointly serve to lower the estimate of the slope for the most altricial group.

ANALYSIS OF RESIDUAL VARIATION

Analysis of variance of the residual variation of the life-history traits calculated from a common slope shows that nearly all traits exhibit some differences among developmental categories (Table 5). Only weaning mass (Mw), age at first parturition (AFP), and length of the reproductive interval (RI) do not vary with neonatal maturity (Table 5). However, contrary to the ANOVA results, the LSMEANS

Table 3. Regression equations for life-history variables. The slope (m) and the intercept ($\log b$) were estimated by least squares linear regression of log-transformed values. Regression equations were calculated assuming a constant slope among developmental categories. Life-history variables analysed were growth rate constant (K), neonate mass (Mn), litter mass (Ml), gestation period (G), lactation period (L), weaning mass (Mw), litter size (LS), age at first parturition (AFP), and reproductive interval (RI)

Variable	$m \pm SE$	$\log b \pm SE$	r^2
K	-0.335 ± 0.014	-0.797 ± 0.044	0.72
Mn	0.892 ± 0.016	-0.938 ± 0.051	0.93
Ml	0.801 ± 0.014	-0.330 ± 0.043	0.94
G	0.222 ± 0.012	1.163 ± 0.038	0.62
L	0.229 ± 0.013	1.062 ± 0.040	0.52
Mw	0.935 ± 0.012	-0.261 ± 0.035	0.97
LS	-0.095 ± 0.012	0.628 ± 0.037	0.23
AFP	0.274 ± 0.017	1.652 ± 0.055	0.64
RI	0.230 ± 0.012	1.414 ± 0.036	0.67

Table 4. Regression equations calculated by development category (AP) for life-history traits with significant differences in slope among development categories. Neonate mass (Mn) and litter mass (MI) are based on a sample size of 76 while weaning mass (Mw) is based on a sample size of 75

Variable	AP	$m \pm SE$	$\log b \pm SE$
Mn	0	0.69 ± 0.05	-0.65 ± 0.20
	1	0.67 ± 0.07	-0.40 ± 0.24
	2	0.78 ± 0.04	-0.54 ± 0.21
	3	0.94 ± 0.03	-0.92 ± 0.14
MI	0	0.65 ± 0.04	-0.10 ± 0.16
	1	0.72 ± 0.06	-0.16 ± 0.20
	2	0.77 ± 0.04	-0.32 ± 0.18
	3	0.85 ± 0.03	-0.31 ± 0.12
Mw	0	0.84 ± 0.04	-0.06 ± 0.16
	1	0.87 ± 0.05	-0.07 ± 0.20
	2	0.90 ± 0.04	-0.16 ± 0.17
	3	1.01 ± 0.03	-0.48 ± 0.12

procedure of pairwise comparison of mean values indicates that age at first parturition occurs earlier in the most precocial mammals compared to other developmental categories (Table 6).

Neonate mass is significantly different among developmental categories, with precocial neonates being relatively heavier (Table 6). Gestation period also varies significantly among categories with relatively longer gestation periods associated with precocial development. Litter mass differs significantly with the most precocial mammals (category 3) producing the heaviest litters (Table 6). Litter size also differs with more altricial mammals tending to have larger litters (Table 6). Lactation period differs significantly, and is longest in the semi-precocial mammals (category 2). Finally, rate of attaining adult mass varies among developmental categories with precocial mammals tending to attain adult mass more slowly (Table 6).

ANALYSIS OF RESIDUALS WITHIN THE RODENTIA

In most aspects, the analysis within the Rodentia shows similar patterns to that seen within the total sample. Neonate mass ($F=7.75$, $P<0.001$, $n=27$), litter mass ($F=3.56$, $P<0.03$, $n=27$), and gestation period ($F=4.72$, $P<0.01$, $n=27$) differ significantly with precocial species exhibiting relatively greater values for each trait. Length of the lactation period differs ($F=2.94$, $P<0.05$, $n=28$); unlike the previous analysis, lactation period is relatively shorter among more precocial rodents. No difference in rate of attaining adult mass ($F=0.26$, NS, $n=27$), weaning mass ($F=0.08$, NS, $n=27$), litter size ($F=0.79$, NS, $n=27$), age at first parturition ($F=1.27$, NS, $n=22$), or total length of the reproductive interval ($F=0.55$, NS, $n=27$) is exhibited among developmental rankings with the Rodentia.

THE EFFECT OF PRIMATES ON THE ANALYSES

The influence of primates on the results was examined by comparing the analyses with primates represented at the family or order level of variation. When the representation of primates in the analyses is reduced, significant variation among developmental rankings is discovered only for neonate mass ($F=8.65$, $P<0.0001$, $n=69$), litter mass ($F=9.81$, $P<0.0001$, $n=69$) and gestation period ($F=3.16$, $P=0.03$, $n=69$). With this modified analysis, differences no longer exist in the rate of attaining adult mass ($F=1.35$, NS, $n=72$), litter size ($F=0.77$, NS, $n=72$), or length of the lactation period ($F=0.34$, NS, $n=72$). As in the complete sample, no significant differences existed between developmental rankings in the length of the reproductive interval, mass at weaning, or age at first parturition.

Discussion

CHARACTERIZATION OF MAMMALIAN NEONATAL DEVELOPMENT PATTERNS

Large mammals are more likely to produce a well-developed neonate than small mammals. Large mammals develop at an absolute slower rate compared to small mammals (e.g. absolutely longer time period to attain weaning at a relatively lower weaning mass). In general, large mammals require a longer period of time to attain any proportion of adult mass compared to small mammals (Zullinger *et al.* 1984). However, larger mammals develop relatively more quickly (i.e. greater development/% adult body mass). Mechanisms of growth, defined as increase in mass, and mechanisms of development, as restricted to differentiation of cells and tissues, are independent processes. Thus, the stage of neonatal development exhibited by a species appears to be less dependent on actual size and more a function of time, thus making it more likely that a large mammal would produce a more well-developed neonate as a consequence of its longer gestation period.

Table 5. Analysis of variance of the effect of neonatal development on residual variation of life-history variables

Variable	n	F	Prob $F >$	r^2
K	80	2.91	0.04	0.103
Mn	78	8.20	0.0001	0.25
MI	78	10.68	0.0001	0.302
G	78	3.77	0.014	0.132
L	80	3.23	0.027	0.113
Mw	75	0.61	NS	0.025
LS	81	3.13	0.030	0.109
AFP	62	2.38	0.079	0.110
RI	76	2.36	0.078	0.090

Abbreviations for the life-history variables are given in Table 3

Table 6. Mean residual values for life-history variables by developmental category

Variable	Developmental category			
	0	1	2	3
K	0.07 (0.06) ^a	0.10 (0.07) ^a	-0.15 (0.07) ^b	-0.05 (0.06) ^{ab}
Mn	-0.18 (0.06) ^a	-0.07 (0.08) ^{ab}	0.05 (0.06) ^b	0.22 (0.06) ^c
MI	-0.12 (0.05) ^a	-0.06 (0.06) ^a	-0.10 (0.05) ^a	0.20 (0.04) ^b
G	-0.07 (0.06) ^a	-0.01 (0.06) ^{ab}	0.16 (0.05) ^c	0.11 (0.04) ^{bc}
L	0.00 (0.05) ^a	0.01 (0.06) ^{ab}	0.16 (0.06) ^b	-0.06 (0.05) ^a
Mw	-0.04 (0.04) ^a	0.00 (0.06) ^a	0.00 (0.04) ^a	0.04 (0.04) ^a
LS	0.05 (0.05) ^a	0.01 (0.06) ^a	-0.16 (0.05) ^b	-0.04 (0.04) ^{ab}
AFP	0.16 (0.07) ^a	0.16 (0.08) ^{ab}	0.14 (0.07) ^{ab}	-0.05 (0.06) ^b
RI	-0.02 (0.05) ^a	-0.00 (0.06) ^a	0.15 (0.05) ^b	0.04 (0.04) ^{ab}

Means ($\pm$ SE) with the same superscript were not significantly different among developmental categories. Abbreviations for the life-history variables are given in Table 3.

Although precocial neonates are generally produced by larger mammals, there are obvious exceptions to this. The rufous elephant shrew (*Elephantulus rufescens*, order Macroscelidae) and the spiny mouse (*Acomys cahirinus*, order Rodentia) produce young which are well furred and have open eyes though both of these species only weigh 50–60 g (Rathbun, Beaman & Maliniak 1981; E.M. Derrickson, unpublished data). Conversely, large mammals do not always produce well-developed neonates; black bears (*Ursus americanus*) and giant anteaters (*Myrmecophaga tridactyla*) produce young with closed eyes and sparse fur though the parents weigh in excess of 75 and 25 kg respectively (Ewer 1973; Merrett 1983).

The characteristics of neonatal development and reproduction in eutherian mammals can be defined further when the effect of adult mass is statistically controlled. Life-history traits associated with prenatal effects differ greatly among developmental categories. Precocial mammals produce well-developed neonates that are relatively heavy. These neonates are born after a long gestation period and have relatively few litter mates. Neonatal litter mass also is heaviest in the most precocial mammals; this appears to differ from Eisenberg (1981) who found no correlation between average gain in foetal mass during the last half of gestation and neonatal development.

Despite these findings, some mammals can produce precocial offspring without an increase in gestation period and/or a decrease in litter size. The capybara (*Hydrochoerus hydrochoeris*) produces an average litter size of 3.1 young after a gestation period of 152 days (Zara 1973); based on an adult mass of 64 kg it is predicted to have a litter size of 1.5 and gestation period of 170 days. The coypu (*Myocaster coypus*) has an average litter size of 5.6 (Newson 1966) which is three times greater than that predicted for an animal of 6.4 kg. Hares (*Lepus*) have on average a gestation period of 39 days (Haskell & Reynolds 1947; O'Farrell 1965) which is considerably

less than the 77 days predicted for a 1860-g mammal. Primates, which have the longest relative gestation periods, do not produce extremely precocial young.

Fewer differences existed between developmental categories during the postnatal period. Neonatal development is not clearly related to the amount of parental care required during the postnatal period. Mass at weaning and length of the lactation period show no differences among mammals producing well-developed or poorly developed neonates. Length of the lactation period shows an association with neonatal development in only two groups. The Primates have exceptionally long periods of lactation for their size and they produce somewhat precocial neonates; the average primate in category 3 has a mean mass of 2480 g, an expected lactation period of 69 days and a mean observed period of 166 days. Conversely, the Rodentia tend to show a decrease in the length of the lactation period in species producing more precocial offspring; mean residual values of the most precocial rodents are 30% lower than those of the most altricial rodents.

The timing of other postnatal events also exhibits little correlation with neonatal development. Age at first parturition tends to be earlier in the most precocial species (category 4). A previous analysis of this trait by Hennemann (1984) indicated that age at first parturition was shorter in altricial species; differences in the results between the two studies may be due to differences in sample content (more pinnipeds and fewer rodents in Hennemann's study) or sample size (49 vs 64 in the present study). Rate of attaining adult mass tends to be slightly more rapid in species with more altricial neonates. This differs slightly from Case's findings (1978b) that no difference existed in growth rate between altricial and precocial mammals during the first half of the growth; however, these two studies examined different aspects of growth which may not be comparable. Total length of the reproductive interval showed no consistent association with neonatal development.

Neonatal development can affect parental invest-

ment both at the level of the individual offspring and the litter. Zeveloff & Boyce (1980) found that mammals with monogamous mating systems tend to produce altricial offspring; one hypothesis used to explain this correlation was that altriciality presents increased opportunities for male investment. The results of this study and others demonstrate that more altricial neonates are present and provide opportunities for male investment; however, these poorly developed neonates do not require a longer period of postnatal care. Further differences in parental investment in altricial and precocial neonates may exist. Altricial young do not generally require longer periods of lactation but do attain similar weaning mass, perhaps as a consequence of more rapid postnatal growth. This suggests that altricial mammals would require more energy on a daily basis to support the growth of the individual. Altricial and precocial young may also differ in the types of investment required during the lactation period. The period of time from first intake of solid food until termination of lactation appears to be longer in more precocial rodents and may be related to an increased period of socialization (Kleiman 1972; Derrickson 1989). Thus, different measures of nutritional independence, such as first intake of solid food, may change the interpretation of the relationship between neonatal development and length of the lactation period.

NEONATAL DEVELOPMENT IN MAMMALS: DICHOTOMY OR CONTINUUM

Development does not appear to be strongly correlated with any composite dimension of life-history traits. The best predictors of neonatal development were relative neonate mass and relative neonatal litter mass. Species producing precocial neonates give birth to individual offspring and to litters which are heavier than predicted by adult mass. Although mammalian development is often considered as bimodal (altricial and precocial mammals) (Portmann 1941; Martin & MacLarnon 1985, 1986; Vaughan 1986; Flowerdew 1987), this study shows the dichotomous interpretation to be weak for many life-history traits. Examination of the mean trait residual values show that some traits (e.g. Mn) decline continuously, some appear dichotomous (e.g. LS, K), while others uniquely differ in only one developmental category (e.g. Ml, AFP). Although viewing mammalian neonatal development as dichotomous may distort the interpretation of results, it can improve the statistical significance of analyses examining the difference between developmental categories. The data set used in this study produces similar, but more striking, results if observations are separated into altricial (including categories 0 and 1)

and precocial groupings (categories 2 and 3) (E. M. Derrickson, unpublished data). Although, grouping development into two categories may be artificial, because it increases the sample size in each category, overall significance improves. Thus, our view of development as dichotomous is reinforced, though often unwarranted.

Zeveloff & Boyce (1986) noted that dichotomous schemes of neonatal development are arbitrary when mammalian species occur along a continuum of neonatal development maturity. Although the continuous nature of development is intuitively appealing, mammalian developmental patterns do not map onto predictable continuous change in life-history patterns. That trends among different life-history traits with neonatal development are quite variable supports this conclusion. For example, although selection on litter size would be expected to result in increased altriciality (Eisenberg 1981; Genoud & Vogel 1990), litter size does not exhibit continuous change with increasing altriciality. The greatly differing life-history characteristics of primates which produce well-developed neonates also support the view that neonatal development does not strongly correlate with other life-history factors. Rate of attaining adult mass, length of the gestation period, length of the lactation period, litter size, age at first parturition and total length of the reproductive interval all differ significantly from that expected given the primates stage of neonatal development. All these findings suggest that neonatal developmental patterns are not the result of one continuous axis of selection and that altricial and precocial forms of neonatal development evolve in response to more than one selection pressure.

PHYLOGENETIC DISTRIBUTION OF PRECOCIALITY

The evolution of the precocial development pattern has occurred often. Primitive mammals exhibited altricial development (Hopson 1973; Case 1978a); however, at the ordinal level most taxa can be characterized as consisting of species that produce well-developed neonates. Although precocial development is common at the ordinal level, the most speciose groups are among altricial mammals. This phenomenon is confounded by the inverse association of body size and species numbers. When the taxonomic distribution of neonatal developmental categories is examined within a narrower size range, a correlation still exists between increased altriciality and more speciose taxa. This association appears particularly strong within the rodents. Hennemann (1984) suggested that few small precocial species exist because they have lower intrinsic rates of natural increase.

Few orders exhibit variation among genera in the stage of neonatal development of their offspring. Only the rodents and Carnivora contain more than five observations in two or more developmental categories. Some of the apparent similarity within orders is due to the coarseness of the classification used in this analysis. Researchers who study particular groups can discern differences in neonatal development not shown by this classification scheme. For example, Dempster & Perrin (1989) studied three species of rodents which would all be classified in category 1 of this study; however, they discovered that *Petromyscus* attained some physical and behavioural developmental stages before *Gerbillus* and could be described as less altricial than the *Gerbillus* species. Similar situations are described within small fields (Tonkin & Kohler 1978), gerbils (Daly 1975), shrews (Genoud & Vogel 1990) and *Pseudomys* (Fox & Kemper 1982).

Classification of development in mammals is a difficult undertaking. The criteria used by Case (1978b) and Eisenberg (1981) have tended to focus more on differences among degrees of altriciality. The classification used in this analysis focuses on the attainment of four different types of developmental independence: nutritional, sensory, locomotory and thermoregulatory. Each of these classification schemes has merit, but all suffer from their categorical nature. The results of this study indicate that relative neonate mass may serve as an alternative measure of neonatal development. It shows continuous, relatively linear change among altricial and precocial categories and is easily measured. Another alternative to categorical measures may be to use the growth trajectory to standardize the appearance of developmental landmarks. Future study on the relative timing of developmental events (rather than presence or absence) may shed more light on the relationship of neonatal maturity to other life-history traits.

Acknowledgements

I am very grateful for the helpful criticisms by J. S. Millar and K. C. Derrickson on a previous version of this manuscript. This work was partially supported by a NATO postdoctoral fellowship (RCD-8854458).

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Received 2 March 1991; accepted 29 April 1991