

## METATHERIAN REPRODUCTION: TRANSITIONAL OR TRANSCENDING?

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Recent papers (Morton et al. 1982; Russell 1982*a,b*) have renewed the debate regarding the evolutionary interpretation of the divergence in metatherian ("marsupial") and eutherian ("placental") patterns of reproduction. These authors disagreed with the conclusions of earlier papers, in particular those of Low (1978) and Parker (1977). We believe this disagreement rests on (1) differing views of what constitutes primitive and derived character states within the therian mammals, (2) imprecisely developed concepts in the earlier papers of the selective pressures that would favor either the metatherian or eutherian modes of reproduction, and (3) a confusion between points of similarity and difference between metatherian and eutherian patterns of reproduction. In this paper we discuss briefly the first two points and treat the third at greater length.

The metatherian and eutherian lineages have each been evolving for approximately 100 million years since diverging from their shared pantotherian ancestors (Clemens 1979; Kielan-Jaworowska et al. 1979). (None of the conventional terms for the two infraclasses is accurate and without bias. Not all marsupials have a marsupium, and all marsupials have a placenta of one form or another. *Metatherian* mammals may not be an intermediate mammalian grade, and *eutherian* species are no more true mammals than are any other members of the class. Although none of these terms accurately describes its taxon, all are well entrenched in the literature, and we will not propose more-appropriate terms here.) Aside from systematic tradition and from evolutionary interpretations of the reproductive systems of marsupial and placental mammals, the subject of this paper, marsupials are best regarded as alternative to, rather than primitive to, eutherian mammals (Tyndale-Biscoe 1973; Moeller 1975; Renfree 1981). The changeover from a mixed marsupial-placental mammalian fauna in North America

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in the late Cretaceous to an almost wholly placental fauna in the Paleocene has been cited as evidence of the ability of placental mammals to competitively replace marsupials (e.g., Lillegraven 1974). Since much of the terrestrial vertebrate fauna became extinct for as-yet-unknown reasons at the end of the Cretaceous, however, faunal replacements at the Cretaceous-Tertiary boundary should not be interpreted as strong evidence for ecological competition.

The environments in which the therian infraclasses arose are unknown. It is likely that eutherian mammals arose and radiated in the Northern Hemisphere, while marsupials radiated in the south (Kielan-Jaworowska et al. 1979; Woodburne and Zinsmeister 1982). These early environments may have been sufficiently distinct to favor two discrete modes of therian reproduction. Canalization of these early differences may have set separate reproductive patterns in the metatherian and eutherian lines, followed by later selective pressures on certain groups within each infraclass that produced instances of apparent convergence in reproductive patterns. For example, by giving birth to tiny young that suckle for long periods, bears converge on the metatherian pattern, whereas the chorioallantoic placenta of bandicoots may converge on that of eutherians. (It is also possible that the use of a chorioallantoic placenta by bandicoots is an ancestral trait retained from the earliest therians; see below.)

Metatherian and eutherian reproduction differ most consistently and strikingly with respect to the duration of gestation and the size of the neonate. In comparison with placental mammals, marsupials have, on the average, a shorter duration of gestation relative to lactation (fig. 1). Gestation accounts for an average of only 12% of the time from conception to weaning in marsupials (mean of 32 species), whereas for eutherians gestation averages almost three times as long and constitutes over one-half (56%) of the average developmental period (135 eutherians, data from the references for fig. 1). In addition, lactation lengths of marsupials average about 40% longer than those of similarly sized eutherians. Related to their short gestations, parental investment at birth for marsupials is much less than for placental mammals. For marsupials, the litter weight at birth is, on the average, only 0.09% ( $\pm .03\%$  SE,  $n = 33$  species) of the female's adult body mass; average litter mass at birth in eutherians is 170-fold greater ( $15.51\% \pm 0.84\%$  SE,  $n = 198$  species; references as for fig. 1). Because of the relatively short gestation in marsupials and their small size at birth, the extent of fetal influence over maternal physiology may be less than in placental mammals.

These essential differences between the Metatheria and the Eutheria in the reproductive effort apportioned to gestation versus lactation sometimes obscure similarities between the infraclasses concerning the total energetic investment in reproduction. Small marsupials produce somewhat larger litters at weaning than do small eutherians, but over most of the range of body masses the total mass of offspring generated at the end of weaning is not different between the infraclasses (see below; fig. 2; Russell 1982a).

Parker (1977) and Low (1978) suggested that a possible selective advantage of the marsupial mode of reproduction may arise from the ability of marsupial females to terminate reproduction easily and safely at any time during the period of parental investment. Of course, termination of a reproductive attempt would be

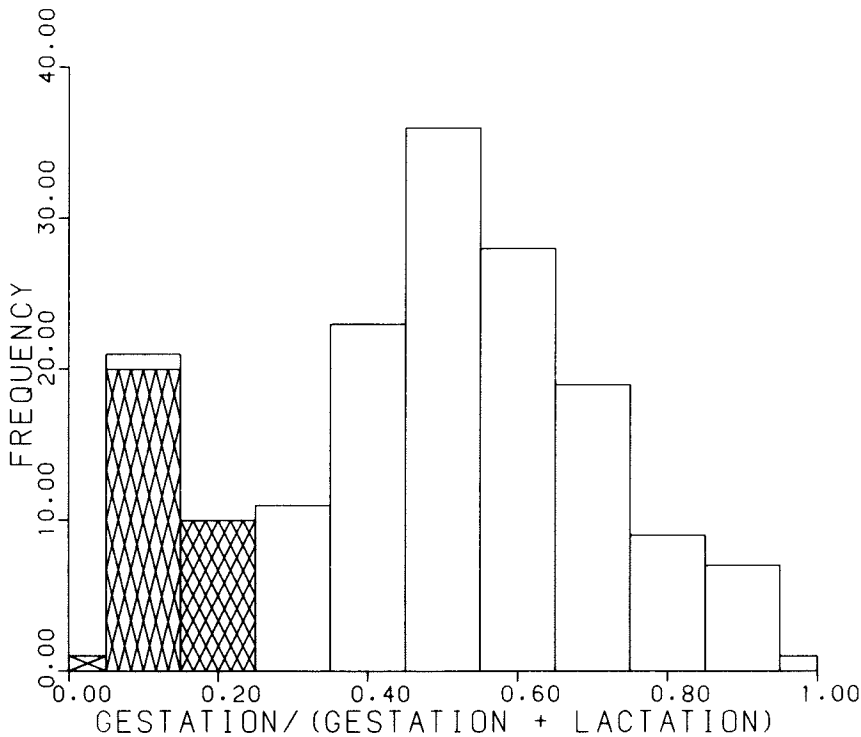


FIG. 1.—Proportion of the period between conception and weaning allocated to in utero development in metatherians (cross-hatched bars) and eutherians (open bars). Bars indicate number of species in increments of 0.1. The metatherian data encompass 32 species in 22 genera and 6 families; the eutherian data include 135 species in 105 genera, 40 families, and 9 orders (all orders with more than 20 extant species). Data were compiled from the following sources (numbers refer to the Literature Cited): 2, 3, 4, 5, 8, 9, 16, 17, 18, 19, 20, 21, 22, 24, 26, 28, 29, 30, 31, 32, 33, 34, 35, 36, 39, 40, 41, 42, 44, 49, 52, 53, 55, 62, 63, 65, 66, 67, 68, 69, 74, 83, 84, 85, 88, 90, 91, 94, 97, 99, 100, 103, 104, 105, 106, 108, 109, 111, 114, 116, 117, 118, 119, 123.

avoided if there were a high probability of successfully raising the young. In times of stress, however, a female mammal can terminate a reproductive attempt that has a low probability of success and threatens future reproduction by blocking implantation, resorbing embryos, aborting fetuses, or ceasing lactation. The termination of lactation is among the simplest and least risky of these processes in terms of the possible secondary effects on the female. Thus, when there is high resource variability, and when a female can increase her chances of reproducing successfully in the future by terminating her current parental investment in a failing reproductive attempt, the marsupial mode of reproduction (with short in utero development and prolonged lactation) may be favored by selection. Since the eutherian mode of reproduction provides a longer fetal period, which is hormonally mediated by a secretory trophoblast of fetal origin, the termination of gestation may involve a costly conflict between placental mother and young

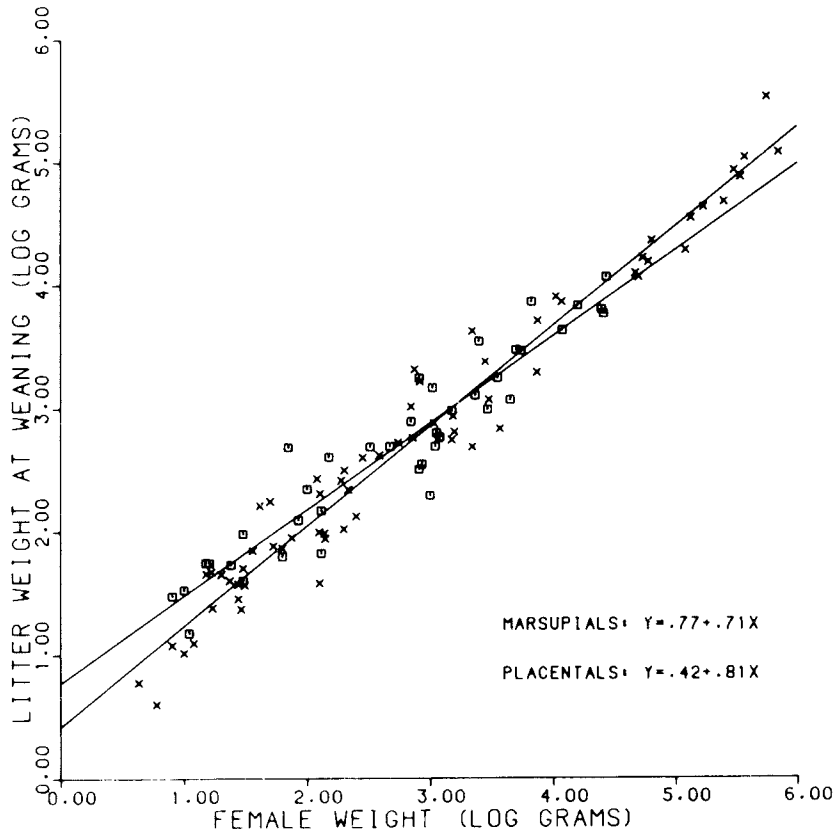


FIG. 2.—The allometry of parental effort as measured by litter weight at weaning in metatherians (squares enclosing dot,  $n = 40$  species in 29 genera and 6 families) and eutherians (crosses,  $n = 67$  species in 54 genera, 16 families, and 6 orders). Litter weight is tightly correlated with female mass in both infraclasses (Metatheria,  $\log_{10}$  (litter mass, g) =  $.775 (\pm .113 \text{ SE}) + .706 (\pm .039)\log_{10}$  (female mass, g),  $r = .95$ ; Eutheria,  $\log_{10}$  g =  $.422 (\pm .066) + .815 (\pm .020)\log_{10}$  g,  $r = .98$ ). Covariance analysis indicates that the slopes are significantly different ( $F = 6.392$ ;  $df = 1, 103$ ;  $P < .05$ ), and thus the factors that determine the weight of a litter at weaning relative to maternal weight may differ for the two infraclasses. However, since the intersection of the two lines is near the midpoint of the range of each, the biological effect of this difference will be significant only for comparisons of very large or small species, not for the majority of the species in the two infraclasses. Sources as in fig. 1.

(Hayssen 1984a). When resources are predictable, the eutherian pattern would seem as adaptive as that of marsupials, since females seldom experience unexpected stress after conception.

Morton et al. (1982) and Russell (1982a,b) questioned the contention of Parker (1977) and of Low (1978) that environmental unpredictability favors the marsupial reproductive pattern. In rejecting the conclusions of the previous authors, Russell viewed the metatherian pattern either as primitive or as a result of undetermined selective pressures. Morton et al. contended that marsupials are restricted to

relatively slow growth and reproduction by low metabolic rates adapted to conditions of periodic resource scarcity, whereas the eutherian mode of reproduction and high metabolic rates enable rapid reproduction and growth when resources are abundant.

DURATION AND MAGNITUDE OF REPRODUCTIVE EFFORT  
IN MARSUPIAL AND PLACENTAL MAMMALS

Both Morton et al. and Russell relied on Braithwaite and Lee's (1979) paper to support their claim that small marsupials have a prolonged period between conception and weaning relative to comparable eutherians. The statistically untested "trend" in Braithwaite and Lee's data rests, however, on a comparison of six small dasyurids (<100 g) with 3 insectivores and 12 myomorph rodents. The remaining marsupials (>100 g) are bracketed on both sides by eutherian data. Our statistical analysis of data on 32 marsupial species, compared with data on 135 eutherian species (well representative of the taxonomic diversities of the two infraclasses), reveals a rather different pattern (fig. 3). Covariance analysis indicates that the lines do not differ significantly in slope ( $F = .96$ ;  $df = 1, 163$ ;  $P > .05$ ), but they differ significantly in elevation ( $F = 17.03$ ;  $df = 1, 164$ ;  $P < .01$ ).

Large macropodids, which often nourish several successive offspring simultaneously (an intrauterine embryo, a pouch young, and a joey at heel), spend more time from conception to weaning than do many similarly sized eutherians. If the macropodids are dropped from the statistical analysis, however, the remaining marsupials do not differ significantly from eutherians ( $F$  slope = 0.26,  $df = 1, 148$ ,  $P > .05$ ;  $F$  intercept = 3.85,  $df = 1, 149$ ,  $P > .05$ ). Dasyurids spend more time from conception to weaning than the average eutherian (or other marsupials), but peramelids have relatively short developmental times. (In both infraclasses, some species—some bats, seals, weasels, and macropodids—delay implantation, such that there may be a period of time after conception during which development is not proceeding. Thus, although conception-to-weaning times correctly measure the speed with which independent offspring can be produced, they do not always reflect the rate of development of the young. We include periods of delayed implantation in the conception-to-weaning times for those species in which the delay is obligatory.)

Russell (1982 *a,b*) indicated that some marsupials (small dasyurids) make a large investment in reproduction. These marsupials produce a litter weighing 322%–373% of the female's body mass at the time the young are weaned. Russell claimed that this pattern of reproduction precludes the putative ease of termination of reproductive investment in marsupials discussed by Low and Parker. In presenting data on litter weights at weaning, however, Russell overlooked a main point of the Parker and Low hypothesis, namely, that maternal investment is low at *parturition*, allowing an early termination of reproductive effort subsequent to birth at a low cost to the marsupial female.

In spite of her acknowledgment of the issue, Russell still committed the "Concorde Fallacy" (Dawkins and Carlisle 1976) when she claimed, "By the time the litter is large enough to be worth deserting, it is too costly to replace" (1982*b*, p.

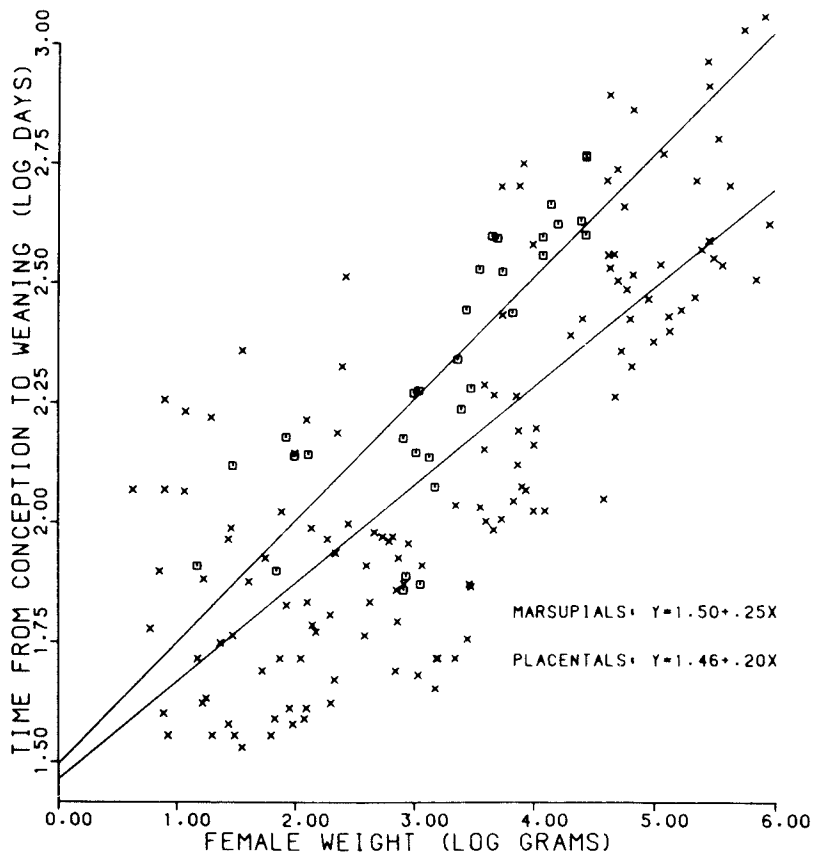


FIG. 3.—The allometry of parental effort as measured by time from conception to weaning in metatherians (squares enclosing dot,  $n = 32$  species in 22 genera and 6 families) and eutherians (crosses,  $n = 135$  species in 105 genera, 40 families, and 9 orders). The scatter around both lines is large (Metatheria,  $\log_{10}$  days =  $1.496 (\pm .114) + .252 (\pm .034)\log_{10} g$ ,  $r = .81$ ; Eutheria,  $\log_{10}$  days =  $1.464 (\pm .052) + .204 (\pm .015)\log_{10} g$ ,  $r = .77$ ). Data compiled from sources in fig. 1.

468). The selective cost of terminating a currently failing reproductive attempt is not the size of the lost reproductive investment at weaning, or even the lost investment at the time a prenatal or postnatal litter is discarded. Rather, the costs and benefits resulting from the early desertion of a litter are to be measured by the effect that the loss has on the probability of successful reproduction both then and in the future. Thus, a litter is most "worth deserting" when the greatest amount of resources remain to be invested and can still be diverted to a future reproductive attempt with a higher probability of success, not when the largest investment has already been committed. Selection would favor earlier rather than later cessation of a reproductive attempt that has little or no chance of successful completion, and a less risky (to the mother) rather than more dangerous mode of termination, because these mechanisms would minimize the delay in reinitiat-

ing reproduction when conditions improve and maximize the probability that future reproductive attempts would be successful.

#### EVOLUTION OF REPRODUCTIVE PATTERNS IN OPPORTUNISTIC AND SEASONAL BREEDERS

Morton et al. (1982) suggested that Low, Kirsch (1977*a,b*), and Parker overgeneralized from the example of the opportunistically breeding Macropodidae that clearly illustrates the Low and Parker hypothesis. Morton et al. contended that because other marsupials, such as some dasyurids, petaurids, phalangerids, and didelphids, are seasonal breeders and live in predictable environments, nonmacropod marsupials do not conform to the ideas of Parker and Low. That many marsupials presently live in environments in which the more facile termination of reproductive investment would seem of lesser benefit does not refute the hypothesis that the basic marsupial pattern of reproduction arose to counter the risks of breeding in unpredictable environments. Even if those marsupials now inhabiting more-benevolent environments have had sufficient evolutionary time to reverse the characteristically marsupial trend toward exceptionally low investment in their young at birth, it is not clear that there would be any selective advantage in their doing so. *Antechinus stuartii* would seem the extreme example of a seasonally breeding marsupial that invests in large litters in a predictable environment. Yet, even in this "semelparous" (Braithwaite and Lee 1979) dasyurid, females can survive to breed a second year (Wood 1970), thus leaving open a role for selection to conserve reproductive resources for a subsequent reproductive event. We contend that marsupial reproductive patterns are not maladaptive in seasonal or predictable environments. The metatherian mode of reproduction would seem to offer scope for considerable ecological and evolutionary flexibility, rather than leading to the evolutionary stagnation suggested by Lillegraven (1979).

Morton et al. also claimed that Parker and Low overlooked the extent to which placental mammals can terminate a pregnancy in response to stress. They presented data on the postimplantation loss of young in 12 rodents, 1 lagomorph, and 1 artiodactyl. The mean fetal mortality of the nonlaboratory animals was 7.4% (range, 0.1%–25%). From these data, Morton et al. concluded that metatherians and eutherians do not differ greatly in their ability to terminate reproductive effort. Postimplantation mortality in eutherians is not necessarily related to environmental stress, however.

We cannot accept the evidence of Morton et al. that Parker (1977) and Low (1978) understated the extent of postimplantation losses in eutherians resulting from environmental causes. Morton et al. (1982, pp. 129–130) stated

most of the studies cited, together with other reports (Brambell 1948; Macfarlane et al. 1957; Perry 1960; Hanly 1961), suggest that resorption and abortion are linked to environmental stress. Food shortage, poor quality of food, high temperatures, and increased population densities are factors affecting continued pregnancy. Environmental variation is responsible for differences in the extent of resorption or abortion within species between localities and years (table 1).

Unfortunately, most of the studies cited do not concur with the summary of their results by Morton et al. Some do not address the effects of food shortage, poor quality of food, high temperatures, increased population densities, or environ-

mental variation between localities and years, nor do they present data in which such factors can be examined (Watson 1950; Osborn 1953; Beer et al. 1957; Perry 1960). Most of the data presented by Morton et al. come from papers in which the authors specifically state that these factors are *not* implicated as the cause of postimplantation mortality (Perry 1945; Brambell 1948; Adams 1960; Hanly 1961; Krebs 1964, discussed in Keller and Krebs 1970, p. 291; Batten and Berry 1967; Keller and Krebs 1970). In three studies, the authors suggested that these factors may be causal but conceded that statistically significant data demonstrating relationships are lacking (Robinette et al. 1955; Tomich 1962; Myers and Poole 1962).

Only the two experimental studies carried out on laboratory rats constitute documented examples of resorption induced by environmental stress (Macfarlane et al. 1957; Woodside et al. 1981). Environmental stress probably does induce the resorption of some eutherian embryos; yet the studies cited by Morton et al. provide no evidence that it is a frequent occurrence in natural populations, and several of the studies suggest that genetic defects are the probable cause of the postimplantation losses (Perry 1960; Hanly 1961; Batten and Berry 1967; Keller and Krebs 1970).

#### REPRODUCTION AND MAMMALIAN METABOLIC RATES

Morton et al. made another claim: low metabolic rates in marsupials are an adaptation to life with limited resources, and as a consequence, marsupials have slow rates of growth and development. Therefore, even when resources are abundant, marsupials cannot produce large numbers of young quickly because of the constraints imposed by their basal metabolic rates. Irrespective of the possibility that basal metabolic rates may show no consistent relationship with the metabolic rates of reproductive animals (Hayssen 1984*b*), the weight of young at weaning relative to maternal weight is no less in marsupials than in placental mammals (fig. 2). Development of young from conception to weaning is slower among the macropodids (fig. 3), but they often simultaneously nurse successive offspring. Thus, if marsupials do have lower metabolic rates during reproduction than do eutherians of similar weight, their mode of reproduction must be more efficient energetically than that of eutherians. The common assumption that the marsupial mode of reproduction would be energetically less efficient because most nutrients are transferred to offspring via milk rather than directly across a placenta overlooks the added cost of placental growth and maintenance for eutherians with long gestations.

The view that metabolic rate constrains reproductive adaptations in any obvious way is not supported by data. Fleming et al. (1981) examined the reproductive energetics of the North American opossum, *Didelphis virginiana*, and found that the resting metabolic rate of lactating females is 92% higher than that of nonlactating females. More important, their data also show that the rate of energy transfer to offspring is not different between this didelphid marsupial and eutherian mammals. Hennemann (1983) attempted to compare the basal metabolic rates (BMR) of mammals with reproductive output as estimated by the intrinsic rate of increase, in order to test McNab's (1980) hypothesis that metabolism constrains



TABLE 1

THE EFFECT OF BODY MASS AND METABOLIC RATE ON THE DURATION OF REPRODUCTION IN EUTHERIAN MAMMALS, ANALYZED BY MULTIPLE REGRESSION

| Independent Variable  | Intercept <i>a</i> | <i>B</i> <sub>1</sub> (SD)<br>(incremental <i>R</i> <sup>2</sup> ) | <i>B</i> <sub>2</sub> (SD)<br>(incremental <i>R</i> <sup>2</sup> ) | No. of Species<br>(total <i>R</i> <sup>2</sup> ) |
|-----------------------|--------------------|--|--|--|
| Gestation             | 1.22               | .150***(.036)<br>(59.5%)   | -.265*(.122)<br>(2.5%)   | 75<br>(62.0%)                                    |
| Lactation             | 0.97               | .221***(.046)<br>(36.4%)   | .268 (.159)<br>(2.8%)  | 65<br>(39.2%)                                    |
| Conception to weaning | 1.34               | .213***(.032)<br>(71.3%)   | -.010 (.109)<br>(0.0%)   | 59<br>(71.3%)                                    |

NOTE.—The regression parameters are for the following model:  $\log_{10}(\text{days}) = a + B_1(\text{mass in } \log_{10} \text{ g}) + B_2(\text{basal metabolic rate in } \log_{10} \text{ ml O}_2/[\text{g} - \text{h}])$ . The coefficient of determination (*R*<sup>2</sup>) gives the percent of variance in the dependent variable accounted for by its relationship to the independent variables. Standard metabolic rates are from McNab (1966, 1969, 1979*a,b*, 1980). There seems to be a slight effect of metabolic rate on gestation, such that animals of a given body size with higher metabolic rates may have shorter gestations, but the reverse may be true for lactation. Over the entire period of maternal dependence, metabolic rate appears to have no relation to the duration of the growth period.

\* *P* < .05.

\*\*\* *P* < .001.

reproduction. The six marsupials included in Hennemann's (1983) data averaged only 65% of the BMR expected for mammals of their body size (based on the Kleiber 1961 curve), compared with an average of 121% of expected for 36 eutherian mammals. Yet, those same marsupials averaged 154% of the expected intrinsic rate of increase (based on an allometric relationship calculated by Hennemann), compared with an average of 128% for the eutherians. In addition, multiple-regression analyses of gestation and lactation length versus adult weight and basal metabolic rate suggest that metabolic rate shows little correlation with the variation in these reproductive states even within the Eutheria (table 1).

MARSUPIAL REPRODUCTIVE PATTERN AS A DERIVED,  
NOT PRIMITIVE, CHARACTER

It has often been suggested (e.g., Lillegraven 1979; Russell 1982*a*) that the marsupial characters of short gestation lengths, long periods of lactation, and immature young at birth are a remnant of the ancestral condition of the mammalian stock that gave rise to both marsupials and placentals. Rather than considering the marsupial mode as primitive, we would suggest that the marsupial mode can be viewed equally well as an extremely derived state.

Many reptilian orders, as well as other vertebrate classes, include members that provide intrauterine nourishment to their young and bear live young (Fitch 1970; Wake 1977; Wourms 1981; Blackburn 1982*a,b*; Blackburn et al. 1984). Thus, the completion of development within the uterus is not a uniquely mammalian character.

Like all living reptiles, the ancestors of mammals probably produced young that were well developed at birth or hatching and required little or no postpartum or

posthatching maternal care (Case 1978*a*). Lactation probably evolved in the mammallike reptiles or early mammals as a nutritional supplement for well-developed young. As progressively greater reliance on milk obtained, the birth of less-developed young would have been possible. In this respect marsupials, relative to eutherians, seem farther from the reptilian mode of reproduction, since they are strongly altricial, with young whose development is highly modified in sequence and timing for a prolonged period of growth supported by lactation.

This assessment of marsupial reproduction is not generally advanced, probably because of the apparent similarity in certain features of monotreme and marsupial reproduction. Yet, monotremes and therians are less closely related than are metatherians and eutherians (Lillegraven et al. 1979), and many features of monotreme biology are distinct from those shared by marsupial and placental mammals (Griffiths 1978). The mosaic nature of evolutionary change precludes the facile assumption that, because some features of marsupials appear to be remnants of the ancestral mammalian condition, other unrelated features must also be ancestral characteristics that have persisted since monotremes and therians diverged. There is insufficient evidence to distinguish clearly between shared reproductive characters in monotremes and marsupials that were retained through common ancestry and those obtained through convergent evolution, perhaps in response to similar environments. If the marsupial reproductive pattern of short gestation and long postbirth parental care was ancestral to that of placental mammals, then the reproductive pattern of placental mammals that places less reliance on lactation and greater emphasis on internal production of well-developed young must be an evolutionary reversal, converging on the characters of their reptilian ancestors.

The one reproductive adaptation unique to mammals, lactation, is most elaborated in the marsupials (Renfree 1981). In marsupials, lipid and protein concentrations in the milk increase severalfold during lactation, accompanied by changes in the primary constituents of these fractions (Tyndale-Biscoe 1973). These modifications of milk composition keep pace not only with the changing nutritional requirements of the developing young, but also with the ability of its digestive tract to absorb complex molecules. Furthermore, some macropodids are able to produce simultaneously milk of two different compositions from adjacent mammary glands to support the development of both a neonate pouch young and a joey (Lincoln and Renfree 1981). Such intricately controlled lactation is unmatched in the Eutheria.

Another complex of adaptations involved in the marsupial mode of reproduction is the mosaic of developmental precocity, which allows for birth and suckling while body size is extremely small and the developmental state of the young is immature. As Sharman (1973) observed, the marsupial neonate is not developmentally equivalent to a premature eutherian but rather is adapted to sustain growth and development via lactation. Specific fetal adaptations in marsupials include a cervical swelling in the least-developed marsupial young (which serves to position the body while suckling), deciduous claws functionally attached to extensor and flexor muscles of the forelimbs at the same time that the skeletal tracts of the hindlimbs are represented only by condensed mesenchyme without formed muscle primordia, a precociously functional olfactory system, and a

functional mesonephric kidney at birth (Sharman 1973). These unique adaptations of marsupials to the immature condition of their neonates support the view that their reproductive patterns are highly derived.

Prolonged gestation in eutherians depends on the development of a secretory chorioallantoic placenta, which prevents the potential allograft rejection by maternal tissues. The secretory activity of the marsupial placenta is suggested by hybrid crosses among macropodids, in which gestational length is altered from what is characteristic of the maternal species (Kirsch and Poole 1972; Poole 1975), and by findings that the yolk-sac placenta of some marsupials can synthesize progesterone and other steroids (Bradshaw et al. 1975; Heap et al. 1980). Among the Metatheria, the greatest similarity to the eutherian character of a highly invasive chorioallantoic placenta is found in the bandicoots (Peramelidae; see Padykula and Taylor 1976). Peramelids develop a chorioallantoic placenta in which the fetal-maternal barrier is reduced to maternal stroma and thin cytoplasmic extensions of syncytial cells (possibly of joint maternal and fetal origin), which together separate the maternal and fetal capillaries. The elaborate development of the endoplasmic reticulum and Golgi complex in the syncytial cells indicates that the secretory potential of this marsupial placenta is large; as yet, however, no one has looked for direct evidence of protein or steroid synthesis.

Thus, bandicoots give evidence of the marsupial evolutionary potential for achieving a eutherian mode of gestation. Nevertheless, it will be difficult to determine whether the chorioallantoic placenta of bandicoots is convergent on that of eutherians or simply retained from a common therian ancestor. On the one hand, the frequency with which chorioallantoic placentas have evolved in independent reptilian lineages (Luckett 1977) attests to the possibility of convergence in the placental structures. On the other hand, the approximately equal development of chorioallantoic and choriovitelline membranes (presumably functioning in gas exchange) in the monotreme platypus egg (Luckett 1977), as well as the finding of a highly vascularized chorioallantois in the koala (Hughes 1974) and the uncertain phylogenetic position of the bandicoots (Kirsch 1977c), leaves open the possibility that the dual use of choriovitelline and chorioallantoic placentas is the ancestral condition in the Theria. Having attained, or retained, a chorioallantoic placenta, bandicoots do not exploit it to extend the length of gestation as do eutherians; rather, they retain and condense still further an essentially marsupial character of short internal gestation. Bandicoots produce young that are developmentally and physically similar to those of other marsupials but that are produced in an even shorter time (12 days).

#### CONCLUSIONS

We have argued for an evolutionary interpretation of the marsupial pattern of reproduction as an effective alternative to that of eutherian mammals. Whereas the overall investment of resources in reproduction is apparently similar in these two groups, the partitioning of the reproductive investment between internal growth and development (during gestation) and external growth and development (during lactation) differs.

We do not know what environmental conditions predominated at the time the Metatheria and Eutheria diverged. Nor can we be certain whether the central theme of marsupial reproduction, that of short internal gestation and low parental investment at birth, suits marsupials particularly for the diverse environments they currently inhabit. We maintain, however, that the marsupial mode of reproduction must have been favored by selection, perhaps in unpredictable environments. It is not a primitive state in the attainment of a more advanced eutherian mode of reproduction, but rather it represents an alternative adaptation in mammalian reproduction.

#### SUMMARY

The major difference between metatherian and eutherian reproductive patterns is the relative *apportionment* of maternal resources to gestation versus lactation, not the total temporal and energetic investment in each reproductive attempt. Gestation accounts for an average of 12% of the time from conception to weaning in marsupials, whereas in placental mammals it accounts for 56% of this period of development. Parental investment at birth is less in marsupials (litter weight averages 0.09% of female body mass) than in eutherians (average 15.5%). However, total maternal effort is comparable in the two groups, since the litter weight at weaning is similar for metatherians and eutherians of equivalent adult weight. Metabolic rate does not seem to constrain reproductive adaptations.

Resorption of postimplantation embryos in placental mammals is not closely linked to environmental conditions. Embryonic resorption, when it does occur, would seem to be more costly and risky than terminating reproduction by cessation of lactation. Metatherian reproduction may confer advantages to the female in unpredictable environments by protecting her ability to reproduce in the future. Metatherian reproduction is best regarded as alternative, not inferior, to eutherian reproduction. In fact, the reproductive mode of marsupials may be more derived than that of eutherians.

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#### LITERATURE CITED

1. Adams, C. E. 1960. Prenatal mortality in the rabbit *Oryctolagus cuniculus*. *J. Reprod. Fertil.* 1:36-44.
2. Asdell, S. A. 1964. Patterns of mammalian reproduction. Cornell University Press, Ithaca, N.Y.
3. Banfield, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Toronto.
4. Baranga, J. 1980. The adrenal weight changes of a tropical fruit bat, *Rousettus aegyptiacus* E. Geoffroy. *Z. Säugetierkd.* 45:321-336.
5. Barnes, R. D. 1968. Small marsupials as experimental animals. *Lab. Anim. Care* 18:251-257.
6. Batten, C. A., and R. J. Berry. 1967. Prenatal mortality in wild-caught house mice. *J. Anim. Ecol.* 36:453-463.
7. Beer, J. R., C. F. MacLeod, and L. D. Frenzel. 1957. Parental survival and loss in some cricetid rodents. *J. Mammal.* 38:392-402.
8. Bekoff, M. 1977. *Canis latrans*. *Mamm. Species* 79:1-9.

9. Bekoff, M., J. Diamond, and J. B. Mitton. 1981. Life history patterns and sociality in canids: body size, reproduction, and behavior. *Oecologia (Berl)*. 50:386-390.
10. Blackburn, D. G. 1982a. An evolutionary analysis of vertebrate viviparity. *Am. Zool.* 21:936.
11. ———. 1982b. Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphib.-Reptilia* 3:185-205.
12. Blackburn, D. G., L. J. Vitt, and C. A. Beuchat. 1984. Eutherian-like reproductive specializations in a viviparous reptile. *Proc. Natl. Acad. Sci. USA* 81:4860-4863.
13. Bradshaw, S. D., I. R. McDonald, R. Hahnel, and H. Heller. 1975. Synthesis of progesterone by the placenta of a marsupial. *J. Endocrinol.* 65:451-452.
14. Braithwaite, R. W., and A. K. Lee. 1979. A mammalian example of semelparity. *Am. Nat.* 113:151-155.
15. Brambell, F. W. R. 1948. Prenatal mortality in mammals. *Biol. Rev. Camb. Philos. Soc.* 23:370-405.
16. Brosset, A. 1962. La reproduction des chiroptères de l'ouest et du centre de l'Inde. *Mammalia* 26:176-213.
17. Brosset, A., and H. St. Girons. 1980. Cycles de reproduction des microchiroptères troglodiphiles du nord-est du Gabon. *Mammalia* 44:225-232.
18. Bryden, M. M. 1972. Growth and development of marine mammals. Pages 1-79 in R. Harrison, ed. *Functional anatomy of marine mammals*. Academic Press, New York.
19. Burt, W. H. 1957. *Mammals of the Great Lakes region*. University of Michigan Press, Ann Arbor.
20. Canivenc, R. 1966. A study of progestation in the European badger (*Meles meles* L.). *Symp. Zool. Soc. Lond.* 15:15-26.
21. Carrick, R., S. E. Csordas, and S. E. Ingham. 1962. Studies on the southern elephant seal *Mirounga leonina* (L.). IV. Breeding and development. *CSIRO Wildl. Res.* 2:161-197.
22. Carter, D. 1970. Chiropteran reproduction. Pages 233-246 in B. H. Slaughter and D. W. Walton, eds. *About bats*. Southern Methodist University Press, Dallas.
23. Case, T. J. 1978a. Endothermy and parental care in the terrestrial vertebrates. *Am. Nat.* 112:861-874.
24. ———. 1978b. On the evolution and adaptive significance of post-natal growth rates in the terrestrial vertebrates. *Q. Rev. Biol.* 53:243-282.
25. Clemens, W. A. 1979. Marsupialia. Pages 192-220 in Lillegraven et al. 1979.
26. Corbet, G. B., and H. N. Southern, eds. 1977. *The handbook of British animals*. Blackwell, Oxford.
27. Dawkins, R., and T. R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. *Nature (Lond.)* 262:131-133.
28. Dryden, G. L. 1968. Growth and development of *Suncus murinus* in captivity on Guam. *J. Mammal.* 49:51-62.
29. Dwyer, P. D. 1963. The breeding biology of *Miniopterus schreibei blepotis* (Temminch) (Chiroptera) in northeastern New South Wales. *Aust. J. Zool.* 11:219-240.
30. Eisenberg, J. F. 1981. *The mammalian radiations: an analysis of trends in evolution, adaptation and behavior*. University of Chicago Press, Chicago.
31. Eisenberg, J. F., and E. Gould. 1970. The tenrecs: a study in mammalian behavior and evolution. *Smithson. Contrib. Zool.* 27:1-138.
32. Erickson, A. W. 1959. The age of self-sufficiency in the black bear. *J. Wildl. Manage.* 23:401-405.
33. Ewer, R. F. 1973. *The carnivores*. Cornell University Press, Ithaca, N.Y.
34. Fadem, B. H., G. L. Trupin, E. Maliniak, J. L. VandeBerg, and V. Hayssen. 1982. Care and breeding of the gray, short-tailed opossum (*Monodelphis domestica*). *Lab. Anim. Sci.* 32:405-409.
35. Fenton, M. B. 1975. Observations on the biology of some Rhodesian bats, including a key to the Chiroptera of Rhodesia. *Life Sci. Contrib., R. Ont. Mus. J.* 104:1-27.
36. Fenton, M. B., and R. M. R. Barclay. 1980. *Myotis lucifugus*. *Mamm. Species* 142:1-8.
37. Fitch, H. S. 1970. Reproductive cycles in lizards and snakes. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* 52:1-247.
38. Fleming, M. W., J. D. Harder, and J. J. Wukie. 1981. Reproductive energetics of the Virginia

- opossum compared with some eutherians. *Comp. Biochem. Physiol. B, Comp. Biochem.* 70:645–648.
39. Forsyth, D. J. 1976. A field study of growth and development of nestling masked shrews (*Sorex cinereus*). *J. Mammal.* 57:708–721.
  40. Frase, B. A., and R. S. Hoffmann. 1980. *Marmota flaviventris*. *Mamm. Species* 135:1–8.
  41. Funmilayo, O. 1979. Ecology of the straw-coloured fruit bat in Nigeria. *Rev. Zool. Afr.* 93: 594–596.
  42. Gopalakrishna, A., M. S. Kharparde, and V. M. Sapkal. 1976. Parturition in the Indian false vampire bat, *Megaderma lyra lyra* Geoffroy. *J. Bombay Nat. Hist. Soc.* 73:464–467.
  43. Griffiths, M. 1978. *The biology of the monotremes*. Academic Press, New York.
  44. Hahn, E. W., and R. C. Western. 1969. *The biomedical use of ferrets in research: a synopsis of papers published through 1965 with a supplemental bibliography of some papers published but not reviewed*. Marshall Research Animals, North Rose, N.Y.
  45. Hanly, S. 1961. Prenatal mortality in farm animals. *J. Reprod. Fertil.* 2:182–194.
  46. Hayssen, V. 1984a. Mammalian reproduction: constraints on the evolution of infanticide. Pages 105–123 in G. Hausfater and S. B. Hrdy, eds. *Infanticide: comparative and evolutionary perspectives*. Aldine, New York.
  47. ———. 1984b. Basal metabolic rate and the intrinsic rate of increase: an empirical and theoretical reexamination. *Oecologia (Berl.)* 64:419–424.
  48. Heap, R. B., M. B. Renfree, and R. D. Burton. 1980. Steroid metabolism in the yolk-sac placenta and endometrium of the tammar wallaby, *Macropus eugenii*. *J. Endocrinol.* 87:339–349.
  49. Heidt, G. A. 1970. The least weasel *Mustela nivalis* Linnaeus: developmental biology in comparison with other North American *Mustela*. *Publ. Mus. Mich. State Univ., Biol. Ser.* 41:227–282.
  50. Hennemann, W. W. 1983. Relationship among body mass, metabolic rate, and the intrinsic rate of natural increase in mammals. *Oecologia (Berl.)* 56:104–108.
  51. Hughes, R. L. 1974. Morphological studies on implantation in marsupials. *J. Reprod. Fertil.* 39:173–186.
  52. Humphrey, S. R., and T. H. Kunz. 1976. Ecology of a Pleistocene relict, the western big-eared bat (*Plecotus townsendii*), in the southern Great Plains. *J. Mammal.* 57:470–494.
  53. Kekagul, B., and J. A. McNeely. 1977. *Mammals of Thailand*. Kurusapha Ladprao, Bangkok.
  54. Keller, B. L., and C. J. Krebs. 1970. *Microtus* population biology; III. Reproductive changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana, 1965–67. *Ecol. Monogr.* 40:263–294.
  55. Kenneth, J. H., and G. R. Ritchie. 1953. *Gestation periods: a table and bibliography*. Commonw. Bur. Anim. Breed. Genet. Tech. Comm. 5.
  56. Kielan-Jaworowska, Z., T. M. Brown, and J. A. Lillegraven. 1979. Eutheria. Pages 221–258 in Lillegraven et al. 1979.
  57. Kirsch, J. A. W. 1977a. The six-percent solution: second thoughts on the adaptedness of the Marsupialia. *Am. Sci.* 65:276–288.
  58. ———. 1977b. Biological aspects of the marsupial-placental dichotomy: a reply to Lillegraven. *Evolution* 31:898–900.
  59. ———. 1977c. The comparative serology of Marsupialia, and a classification of marsupials. *Aust. J. Zool. Suppl. Ser.* 52:1–152.
  60. Kirsch, J. A. W., and W. E. Poole. 1972. Taxonomy and distribution of the grey kangaroos, *Macropus giganteus* Shaw and *Macropus fuliginosus* (Desmarest), and their subspecies (Marsupialia: Macropodidae). *Aust. J. Zool.* 20:315–339.
  61. Kleiber, M. 1961. *The fire of life*. Wiley, New York.
  62. Kleiman, D. G. 1969. Maternal care, growth rate, and development in the noctule (*Nyctalus noctula*), pipistrelle (*Pipistrellus pipistrellus*), and serotine (*Eptesicus serotinus*) bats. *J. Zool. (Lond.)* 157:187–211.
  63. ———. 1974. Patterns of behavior in hystricomorph rodents. *Symp. Zool. Soc. Lond.* 34:171–209.
  64. Krebs, C. J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959–62. *Arctic Inst. N. Am., Tech. Paper* 15:1–79.
  65. Krohne, D. T. 1981. Intraspecific litter size variation in *Microtus californicus*: variation within populations. *J. Mammal.* 62:29–40.

66. Krott, P. 1959. Der Vielfrass (*Gulo gulo* L. 1758). Monographien der Wildsäugetiere 13. Fischer Verlag, Jena.
67. Kunz, T. H. 1971. Reproduction of some vespertilionid bats in central Iowa. *Am. Midl. Nat.* 86:477-486.
68. Leitch, L., F. E. Hytten, and W. Z. Billewicz. 1959. The maternal and neonatal weights of some mammals. *Proc. Zool. Soc. Lond.* 133:11-28.
69. Leutenegger, W. 1973. Maternal-fetal weight relationships in primates. *Folia Primatol.* 20:280-293.
70. Lillegraven, J. A. 1974. Biogeographical considerations of the marsupial-placental dichotomy. *Annu. Rev. Ecol. Syst.* 5:263-283.
71. ———. 1979. Reproduction in mesozoic mammals. Pages 259-276 in Lillegraven et al. 1979.
72. Lillegraven, J. A., Z. Kielan-Jaworowska, and W. A. Clemens, eds. 1979. *Mesozoic mammals: the first two-thirds of mammalian history*. University of California Press, Berkeley.
73. Lincoln, D. W., and M. B. Renfree. 1981. Mammary gland growth and milk ejection in the agile wallaby, *Macropus agilis*, displaying concurrent asynchronous lactation. *J. Reprod. Fertil.* 63:193-203.
74. Long, C. A. 1973. *Taxidea taxus*. *Mamm. Species* 26:1-4.
75. Low, B. S. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. *Am. Nat.* 112:197-213.
76. Luckett, W. P. 1977. Ontogeny of amniote fetal membranes and their application to phylogeny. Pages 439-516 in M. K. Hecht, P. C. Goody, and B. M. Hecht, eds. *Major patterns in vertebrate evolution*. Plenum, New York.
77. Macfarlane, W. V., P. R. Pennycook, and E. Thrift. 1957. Resorption and loss of fetuses in rats living at 35° C. *J. Physiol. (Lond.)* 135:451-459.
78. McNab, B. K. 1966. The metabolism of fossorial rodents: a study of convergence. *Ecology* 47:712-733.
79. ———. 1969. The economics of temperature regulation in neotropical bats. *Comp. Biochem. Physiol.* 31:227-268.
80. ———. 1979a. Climatic adaptation in the energetics of heteromyid rodents. *Comp. Biochem. Physiol. A, Comp. Physiol.* 62:813-820.
81. ———. 1979b. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. *Ecology* 60:1010-1021.
82. ———. 1980. Food habits, energetics, and the population biology of mammals. *Am. Nat.* 116:106-124.
83. Medway, L. 1972. Reproductive cycle of the flat-headed bats *Tylonycteris pachypus* and *T. robustula* (Chiroptera: Vespertilioninae) in a humid equatorial environment. *Zool. J. Linn. Soc.* 51:33-61.
84. Millar, J. S. 1977. Adaptive features of mammalian reproduction. *Evolution* 31:370-386.
85. ———. 1981. Pre-partum reproductive characteristics of eutherian mammals. *Evolution* 35:1149-1163.
86. Moeller, H. 1975. Sind die Beutler den plazentalen Saugern unterlegen? *Säugetierkd. Mitt.* 23:19-29.
87. Morton, S. R., H. F. Recher, S. D. Thompson, and R. W. Braithwaite. 1982. Comments on the relative advantages of marsupial and eutherian reproduction. *Am. Nat.* 120:128-134.
88. Müller, H. 1970. Beiträge zur Biologie des Hermelins, *Mustela erminea* Linné, 1758. *Säugetierkd. Mitt.* 18:293-380.
89. Myers, K., and W. E. Poole. 1962. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. *Aust. J. Zool.* 10:225-267.
90. Noll, U. G. 1979. Postnatal growth and development of thermogenesis in *Rousettus aegyptiacus*. *Comp. Biochem. Physiol. A, Comp. Physiol.*, 63:89-93.
91. O'Gara, B. W. 1978. *Antilocapra americana*. *Mamm. Species* 90:1-7.
92. Osborn, D. J. 1953. Age classes, reproduction, and sex ratios of Wyoming beaver. *J. Mammal.* 34:27-44.
93. Padykula, H. A., and J. M. Taylor. 1976. Ultrastructural evidence for loss of the trophoblastic layer in the chorioallantoic placenta of Australian bandicoots (Marsupialia: Peramelidae). *Anat. Rec.* 186:357-386.

94. Parker, P. J. 1977. An ecological comparison of marsupial and placental patterns of reproduction. Pages 273–286 in B. Stonehouse and D. Gilmore, eds. *The biology of marsupials*. University Park Press, Baltimore.
95. Perry, J. S. 1945. The reproduction of the wild brown rat (*Rattus norvegicus* Erxleben). *Proc. Zool. Soc. Lond.* 115:19–46.
96. ———. 1960. The incidence of embryonic mortality as a characteristic of the individual sow. *J. Reprod. Fertil.* 1:71–83.
97. Pitcher, K. W., and D. G. Calkins. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. *J. Mammal.* 62:599–605.
98. Poole, W. E. 1975. Reproduction in two species of grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest). II. Gestation, parturition and pouch life. *Aust. J. Zool.* 23:333–353.
99. Powell, R. A. 1982. *The fisher: life history, ecology, and behavior*. University of Minnesota Press, Minneapolis.
100. Ramaswamy, K. R. 1961. Studies on the sex cycle of the Indian vampire bat *Megaderma (Lyroderma) lyra lyra* (Geoffroy). I. Breeding habits. *Proc. Natl. Inst. Sci. India Part B, Biol. Sci.* 27:287–307.
101. Renfree, M. B. 1981. Marsupials: alternative mammals. *Nature (Lond.)* 293:100–101.
102. Robinette, W. L., J. S. Gashwiler, D. A. Jones, and H. S. Crane. 1955. Fertility of mule deer in Utah. *J. Wildl. Manage.* 19:115–136.
103. Russell, E. M. 1982a. Parental investment and desertion of young in marsupials. *Am. Nat.* 119:744–748.
104. ———. 1982b. Patterns of parental care and parental investment in marsupials. *Biol. Rev. Camb. Philos. Soc.* 57:423–487.
105. Sacher, G. A., and E. F. Staffeldt. 1974. Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth. *Am. Nat.* 108:593–615.
106. Scheffer, V. B., and F. Wilkie. 1953. Relative growth in the northern fur seal. *Growth* 17:129–145.
107. Sharman, G. B. 1973. Adaptations of marsupial pouch young for extra-uterine existence. Pages 67–89 in C. R. Austin, ed. *The mammalian fetus in vivo*. Chapman & Hall, London.
108. Smith, E. 1956. Pregnancy in the little brown bat. *Am. J. Physiol.* 185:61–64.
109. Stewart, R. E. A., and D. M. Lavigne. 1980. Neonatal growth of northwest Atlantic harp seals, *Pagophilus groenlandicus*. *J. Mammal.* 61:670–680.
110. Tomich, P. S. 1962. The annual cycle of the California ground squirrel *Citellus beecheyi*. *Univ. Calif. Publ. Zool.* 65:213–282.
111. Tutin, C. E. G. 1980. Reproductive behavior of wild chimpanzees in the Gombe National Park, Tanzania. *J. Reprod. Fertil. Suppl.* 28:43–57.
112. Tyndale-Biscoe, C. H. 1973. *Life of marsupials*. Elsevier, New York.
113. Wake, M. H. 1977. Fetal maintenance and its evolutionary significance in the Amphibia: Gymnophiona. *J. Herpetol.* 11:379–386.
114. Walker, E. P. 1975. *Mammals of the world*. Johns Hopkins University Press, Baltimore, Md.
115. Watson, J. S. 1950. Some observations on the reproduction of *Rattus rattus* L. *Proc. Zool. Soc. Lond.* 120:1–12.
116. Watts, C. H. S., and H. J. Aslin. 1981. *The rodents of Australia*. Angus & Robertson, Sydney.
117. Weir, B. J. 1974. Reproductive characteristics of hystricomorph rodents. *Symp. Zool. Soc. Lond.* 34:265–301.
118. Wemmer, C., and J. Murtaugh. 1981. Copulatory behavior and reproduction in the binturong, *Arctictis binturong*. *J. Mammal.* 62:342–352.
119. Western, D. 1979. Size, life history and ecology in mammals. *Afr. J. Ecol.* 17:185–204.
120. Woodburne, M. O., and W. J. Zinsmeister. 1982. Fossil land mammal from Antarctica. *Science (Wash., D.C.)* 218:284–286.
121. Woodside, B., R. Wilson, P. Chee, and M. Leon. 1981. Resource partitioning during reproduction in the Norway rat. *Science (Wash., D.C.)* 211:76–77.
122. Wourms, J. P. 1981. Viviparity: the maternal fetal relationship in fishes. *Am. Zool.* 21:473–515.
123. Wright, P. L. 1966. Observations on the reproductive cycle of the American badger (*Taxidea taxus*). *Symp. Zool. Soc. Lond.* 15:27–45.