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## PARENTAL INVESTMENT AND MATING SYSTEMS IN MAMMALS

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Theory on mating system evolution (e.g., Darwin, 1874; Orians, 1969; Trivers, 1972; Williams, 1975; Borgia, 1979) suggests that females should choose mates which confer maximum fitness. If males contribute significantly to the care of the offspring, both male and female fitness may be maximized in monogamy. We expect monogamy to be more prevalent in mammals bearing altricial than precocial young since opportunities for male investment (*sensu* Trivers, 1972) are greater. High paternal care has been noted among many species of monogamous mammals, and several authors suggest that male investment in offspring is one of the principal advantages of a monogamous mating system (Clutton-Brock and Harvey, 1977, 1978; Crook, 1977; Kleiman, 1977; Ralls, 1977; Daly and Wilson, 1978; Thomas and Birney, 1979).

Parental investment is defined by Trivers (1972) as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." The sum of the parental investment received by each offspring in a given time has been defined as the parental effort (Low, 1978). Together, parental effort and mating effort comprise reproductive effort (Low, 1978; Alexander and Borgia, 1979).

In this paper we demonstrate that indeed mating systems in mammals are correlated with the degree of maternal investment in offspring at birth. Females of different species expend variable time and energy and incur different risks in producing offspring of varying states of maturation, thus the stage of development of neonates directly reflects maternal investment. The relative maturity of the neonate

is commonly described by the terms altricial and precocial. Unfortunately, there is not the dichotomy that these terms imply and definitional problems have arisen as a result. Certainly, there is a considerable range of variation within both categories (Ewer, 1968). For example, it has been suggested that all species in the Bovidae bear precocial young (Ralls, 1977), whereas Estes (1974) claims that only those in the bovid tribe *Alcelaphini* bear precocial young. Because of this ambiguity, in addition to altricial and precocial classifications of the young, we examine two relative measures of maternal investment at birth: gestation period, and neonate weight divided by litter size, both standardized for body weight by regression analysis.

### METHODS

Data on litter size, neonate weight, body weight, gestation period, neonate status, and mating system for 556 placental mammals (14.5% of all such species) representing 17 orders were collected from 110 literature sources. Complete data are not available for some species. Body weights are often averages of adult male and female weights (e.g., Sacher and Staffeldt, 1974) but whenever available we used weights of nonpregnant adult females. Occasionally, litter sizes are approximations since they might be based on averages from small samples. For species exhibiting delayed reproduction, gestation period was defined as the time between implantation and parturition; otherwise these mammals were omitted from appropriate analyses.

The null hypothesis that no relationship exists between the level of maternal investment at birth and the type of mating system was tested in three ways. First, the

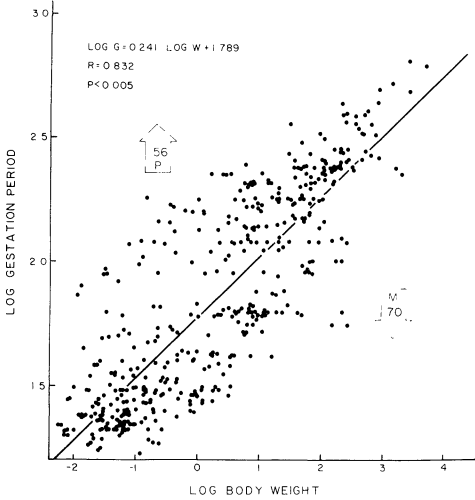


FIG. 1. Gestation period ( $G$ , in  $\log_{10}$  of days) vs. adult body weight ( $W$ , in  $\log_{10}$  of kg) for 451 species of mammals, excluding cetaceans. A least squares regression line characterizes the average or "expected" gestation period for a particular body weight. For species in which the mating system is known, the values inside the arrows equal the proportion of polygynous ( $P$ ) species possessing longer than average gestation periods ( $N = 89$ ), and the proportion of monogamous ( $M$ ) species with shorter than expected gestation periods ( $N = 50$ ).

association of altriciality with monogamy, and precocity with polygyny was assessed by a  $2 \times 2$  contingency table analysis. Monogamy is defined as a reproductive unit of one male and one female; polygyny occurs when one male is either serially or simultaneously bonded with several females (Barash, 1977).

To further examine the relationship between maternal investment at birth and the mating system, we examined variation in gestation period and neonate weight/litter size. Our choice of neonate weight/litter size is based upon (1) the proportionality between the weight of an individual newborn and maternal investment, and (2) the inverse relationship between possible maternal investment in each offspring and the number of young in each litter. Both gestation period and neonate weight/litter size increase with body weight (see Millar, 1971; Weir and Rowlands, 1973; Millar, 1975; Blueweiss et al.,

1978; Case, 1978*b*), thus we employ regression analysis to statistically normalize for variation in body weight (see Atchley, 1978). A least squares linear regression between an investment parameter (either  $\log_{10}$  gestation period or  $\log_{10}$  neonate weight/litter size) and  $\log_{10}$  body weight provides the average or expected distribution of maternal investment. Data points lying above the regression line are treated as indicating species with a relatively high maternal investment at birth, whereas observations lying below this line of expectation represent species possessing relatively low maternal investment at birth. Again, we employ contingency tables to test the associations of high maternal investment at birth with polygyny and low initial maternal investment with monogamy.

Cetaceans were excluded from the above regressions since they display atypical patterns in the parameters which we used to reflect maternal investment (Kihlström, 1972). For both investment parameters, the number of cases used for computing the regression lines exceeds the totals for which neonate status and mating system are known.

We also examined the relationship between neonatal status and litter size since Ewer (1968) hypothesized that large litters ( $>2$ ) are characteristic of altricial species and small litters ( $\leq 2$ ) are found among precocial species. Finally, we tested the null hypothesis of random association among mating systems and litter size by contingency table analysis.

## RESULTS

As predicted, species with altricial young tend to be monogamous and those with precocial young tend to be polygynous ( $P < .005$ ; Table 1). From the analysis of variation in gestation period (Fig. 1), the association between altricial and monogamous species with low maternal investment at birth, and between precocial and polygynous species with high female investment at birth are both highly significant ( $P < .005$ ; Table 1). Our observation that precocial mammals tend to have longer gestation periods than those

TABLE 1. Proportions of species with a particular neonatal status exhibiting monogamy or polygyny and proportions of species with a relative level of female investment at birth or litter size exhibiting certain mating systems and neonatal statuses.

	Neonatal status		Gestation period		Neonate wt /Litter size		Litter size	
	Altricial	Precocial	<Expected	>Expected	<Expected	>Expected	≤2	>2
Monogamy	0.79	0.31	0.70	0.44	0.64	0.46	0.38	0.76
Polygyny	0.21	0.69	0.30	0.56	0.36	0.54	0.62	0.24
N =	68	87	50	89	28	54	85	49
Altriciality	—	—	0.82	0.37	0.81	0.37	0.22	0.87
Precocity	—	—	0.18	0.63	0.19	0.63	0.78	0.13
N =			174	171	101	115	166	173

bearing altricial young is supported by the analysis of Sacher and Staffeldt (1974). Our Figure 1 is similar to one in Blueweiss et al. (1978) but is based upon a sample size over four times as large.

Variation in the  $\log_{10}$  of a ratio of neonate weight to litter size also appears to reflect variation in developmental status at birth since altricial species occur predominantly below the expected distribution line, whereas precocial species are most frequent in the region of high maternal investment at birth ( $P < .005$ , Table 1). As before, monogamous species tend to possess low neonate weight/litter size and polygynous species tend to have high neonate weight/litter size values, but this relationship lacks statistical significance ( $P = .13$ , Table 1). However, if this analysis is repeated omitting primates and hystricomorph rodents as well as cetaceans, the above relationship is statistically significant ( $P < .025$ ; Fig. 2). This may be expected since Huggett and Widdas (1951) found the relation between birth weight and gestation period to be atypical for cetaceans, hystricomorphs, and primates. Thus, in all three tests, a low maternal investment at birth is associated with monogamy whereas a high female investment at birth is associated with polygynous mating systems.

To ascertain if outliers were affecting the outcome of the regressions (Figs. 1 and 2), residuals were examined. One data point on the plot of gestation against body weight differed from the expected line by 3 standard deviations; that of the tarsier

(*Tarsius* sp.). This outlier probably does not appreciably affect the regression. No outliers of significance were found in either plot of neonate weight/litter size against body weight.

As suggested by Ewer (1968), altricial young are most common in large ( $>2$ ) litters and precocial young predominate in mammal species bearing small ( $\leq 2$ ) litters ( $P < .005$ ; Table 1). Similarly, monogamous mating systems are more frequently found in species bearing large ( $>2$ ) litters ( $P < .005$ ; Table 1).

Several taxonomic patterns of maternal investment appear. The Rodentia, Lagomorpha, and fissiped Carnivora consistently possess less than expected female investment at birth. In contrast, greater than expected female investment at birth is typical in the Primates, pinniped Carnivora, Perissodactyla, and Artiodactyla. Biases in some of our analyses may exist due to differential representation of various taxa. Therefore, in Table 2 we provide a breakdown of the proportionate representation of various orders in each of the contingency table analyses.

## DISCUSSION

Mammal species exhibiting high maternal investment at birth tend to possess polygynous mating systems, whereas species bearing relatively less developed offspring tend to possess monogamous mating systems. The mating system may be a result of potential opportunity by males for investment in rearing their offspring. In species bearing altricial off-

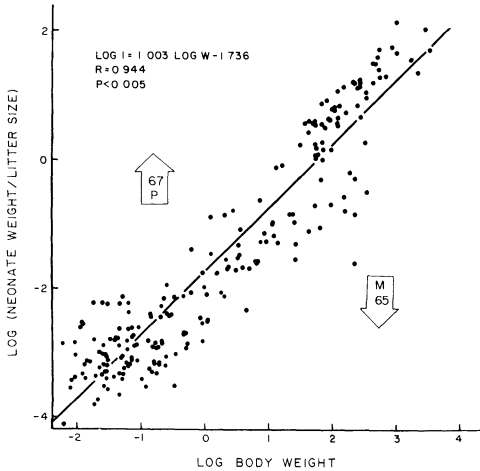


Fig. 2. Neonate weight/litter size ( $I$ , in  $\log_{10}$  of kg/no.) vs. adult body weight ( $W$ , in  $\log_{10}$  of kg) for mammals, excluding cetaceans, primates and hystricomorph rodents ( $N = 223$ ). For species in which the mating system is known, the values inside the arrows equal the proportion of polygynous ( $P$ ) species possessing higher than average female investment at birth ( $N = 36$ ), and that of monogamous ( $M$ ) species in the region of low female investment at birth ( $N = 26$ ).

spring, the ability of the male to contribute to the survival of the young is greatest. Opportunities for paternal care of young are lower in species bearing precocial offspring, and sexual selection may provide greater benefits to females that choose to mate with the most fit but polygynous male (Orlans, 1969).

An alternative hypothesis is maternal investment being a consequence rather than a cause of the mating system. A trend towards altriciality may be accelerated under monogamy, and similarly the advantages of precocial young may increase in a polygynous mating system (R. D. Alexander, pers. comm.). But the two interpretations need not be mutually exclusive especially since the "mating-rearing" system (Crook, 1977) probably responds to selection in a unitary fashion. Parental investment and the mating system are also individually shaped by a variety of ecological pressures (Downhower and Armitage, 1971; Alexander, 1974; Smith and Fretwell, 1974; Low, 1978; Alexander et

al., 1979; Borgia, 1979; Capinera, 1979). Because the mating system is strictly a behavioral attribute, it may possess greater phenotypic plasticity than the physiological and morphological adaptations which constitute maternal investment at birth. Therefore, it seems probable that the mating system is often a consequence rather than a cause of maternal investment at birth.

We have demonstrated a distinct association between the mating system and offspring number. Thus, ecological pressures which are influential in the evolution of reproductive patterns such as litter size may indirectly influence mating systems (Emlen and Oring, 1977). Given the same level of reproductive effort, the potential energy and resources expended on each offspring decrease as offspring number increases. The optimal balance between offspring size and number has been shown to vary as a function of several ecological parameters (Smith and Fretwell, 1974) including environmental predictability (Low, 1978; Capinera, 1979). This tradeoff between number and size of offspring almost certainly accounts for our observation that species bearing small litters tend to be precocial and polygynous, whereas, monogamous species tend to bear large litters of altricial young. Our findings conflict with the claims of Eisenberg (1966) and Kleiman (1977) that mammalian monogamy is generally found in species with a low reproductive potential. This discrepancy may be partly due to a lack of agreement as to what constitutes high reproductive potential; six of eight species in Kleiman's (1977, p. 48) sample may produce more than two offspring per litter.

Although our analysis is only of the female's investment in her offspring at birth, our results cannot be properly interpreted without consideration of parental investment by the male (Maynard Smith, 1978a). As the degree of polygyny increases, the possible contribution by a male toward parental care for an individual offspring necessarily decreases (Downhower and Armitage, 1971; Weatherhead and Robertson, 1979) simply because

TABLE 2. A synopsis of the sample sizes used in the seven contingency table analyses; the parameters compared are indicated above each column. The values represent the number of species in an order that were used in a particular test and the total sample size for each analysis is at the bottom of each column. Data from Hamilton (1933), Bradt (1939), Crile and Quiring (1940), Guenther (1948), Altman (1956), Novikov (1956), Spector (ed.) (1956), Fitch (1957), Buechner (1961), Asdell (1964), Davis (1965), Rosevear (1965), Smithers (1966), Harris (1968), Van den Brink (1968), Bartholomew (1970), American Society of Mammalogists (1971-78), Kingdon (1971, 1974), Prater (1971), Wilsson (1971), Crook (1972), Eisenberg et al. (1972), Herter (1972), Kruuk (1972), LeBoeuf et al. (1972), Ewer (1973), Boyce (1974), Estes (1974), Fradrich (1974), Harrison (1974), Klingel (1974), Lott (1974), Owen-Smith (1974, 1977), Sacher and Staffeldt (1974), Moss (1975), Walker (1975), E. O. Wilson (1975), V. J. Wilson (1975), Burt and Grossenheider (1976), Crook et al. (1976), Zeveloff (1976), Bradbury (1977), Geist (1977), Kleiman (1977), Millar (1977), Ralls (1977), Bekoff (1978), Case (1978b), Gunderson (1978), Myers (1978), Whitlow (1978), Yahner (1978), Thomas and Birney (1979).

Order	Neonate status and mating system	Degree of investment (gestation) and neonate status	Degree of investment (gestation) and mating system	Degree of investment (neo. wt / litter size) & neonate status	Degree of investment (neo. wt. / litter size) and mating system	Neonate status and litter size	Mating system and litter size
Insectivora	3	19	1	10	0	19	1
Dermoptera	0	1	0	0	0	1	0
Chiroptera	2	8	3	5	1	8	1
Primates	14	25	25	20	0	23	22
Lagomorpha	0	15	0	8	0	12	0
Rodentia	19	117	21	81	12	106	16
Edentata	0	3	0	1	0	3	0
Pholidota	0	2	0	0	0	0	0
Tubulidentata	0	1	0	1	0	1	0
Carnivora	53	56	32	48	27	66	39
Mysticeti	1	0	0	0	0	3	0
Odontoceti	1	0	0	0	0	6	0
Proboscidea	1	1	2	1	1	1	2
Hyracoidea	3	4	3	2	2	4	3
Sirenia	2	2	2	2	2	2	2
Perissodactyla	6	12	4	4	1	10	3
Artiodactyla	50	79	46	33	16	74	45
Total	155	345	139	216	62	339	134

there is an increasing number of offspring requiring attention. As a consequence, females of some species may "test" the reliability of long-term pair bonds to ensure that their offspring will benefit from high paternal care (Trivers, 1972).

The probability of genetic relatedness may be important in the evolution of paternal care (Hamilton, 1963, 1964*a*, 1964*b*; Maynard Smith, 1964; Alexander, 1974; West Eberhard, 1975; Graul et al., 1977; Alexander and Borgia, 1979; Blumer, 1979; Borgia, 1979; Kurland, 1979; Thornhill, 1979); consequently high confidence of paternity is necessary for high male parental care. For example, monogamous male primates that are confident of paternity exhibit greater parental care than other pri-

mates (Alexander, 1974). Such confidence decreases with long gestation periods and thus males may not be willing to risk the investment of paternal care in precocial offspring (R. D. Alexander, pers. comm.). This effect may contribute to the tendency for monogamy in species with short gestation periods.

Ralls (1977) claims that a large paternal investment is a good predictor of monogamy although Kleiman (1977) states that monogamy implies nothing about the level of male parental investment. Conversely, Ralls (1977) postulates that low paternal investment is a good predictor of extreme polygyny in mammals, and E. O. Wilson (1975) and Orians (1969) argue that precocial young may facilitate polygyny's

evolution in vertebrates by reducing the need for paternal investment. A greater degree of paternal investment should be more evident in monogamy because the evolution of care by both parents is accommodated by a durable pairbond (Williams, 1975). Kleiman's (1977) study suggests that low reproductive potential and delayed sexual maturation may be associated with monogamy, but concludes that monogamy is without other clear-cut reproductive correlates. Yet, our comparative approach shows that a low maternal investment at birth is clearly related to monogamy, accepting that there may be considerable variation in the male's investment (Kleiman, 1977). But it is likely that a high male investment will occur in monogamy, especially since the production of altricial offspring is conducive to the male's sharing of much of the risk and energetic expense associated with parental care (Case, 1978b).

Several authors (Eisenberg, 1966; Orians, 1969; Alexander, 1974; Crook, 1977) have claimed that monogamy is comparatively rare in mammals, at least partly because of the existence of mammary glands which enhance the female's capacity to provide for the offspring after parturition (Trivers, 1972; Eisenberg, 1977; Kleiman, 1977; Millar, 1977; Maynard Smith, 1978b). However, the actual proportion of mammals exhibiting monogamy is not known since the majority of species have not been examined. Kleiman (1977) notes that less than 3% of all mammals have been found to be monogamous, and Crook (1977) found 12.5% to be monogamous in a sample which he studied. Even though our sample clearly contains some taxonomic biases (see Table 2), 52% of the mammals for which the mating system is known are monogamous ( $N = 155$ ). Nevertheless, a bias in the proportion of monogamists sampled should in no way detract from the generality of the maternal investment patterns which we describe.

Although our analysis elucidates distinct trends in mammalian reproduction, there are incongruities. For example, the lagomorphs all exhibit relatively low in-

vestment in offspring at birth and the primates all produce young with long gestation periods and high neonate weight to litter size ratios. However, both orders have members which are altricial, precocial, monogamous and polygynous. Interestingly, large precocious caviomorph rodents do not exhibit the typical patterns of mating system and neonatal status found for other mammals. Case (1978a) notes that the precocity of caviomorphs is largely influenced by the fact that most rear their young on open, exposed areas where predator selection appears to favor an increase in neonate size. In the first test of the association between neonatal status and mating system (Table 1), the six precocious, monogamous caviomorphs contributed to almost twice as many precocious, monogamous mammals ( $N = 27$ ) as altricial, polygynous species ( $N = 14$ ), the two least typical of the four possible combinations. Even though this group is disproportionately represented, it and other exceptions simply add "noise" to the analysis and do not obscure the prevailing statistical patterns.

Humans (*Homo sapiens*) constitute another taxa which requires further discussion. We classify this species as altricial and monogamous although the choice of a definitive mating system is not clear. Various marital customs, sexual dimorphism, and greater variance in male reproductive success have led to the characterization of humans as moderately polygynous (Alexander et al., 1979; Wilson, 1979). Yet, we agree with Bensch and Thornhill (1979) who argue that lifetime or serial monogamy is the major system of human mating since it is the most persistent form of the union of the sexes. Human monogamy may be the consequence of male and female parental investment approaching equality and of male efforts to guarantee paternity (Bensch and Thornhill, 1979); notions consistent with our arguments.

Perhaps body size is related to the associations of polygyny with long gestation periods and high neonate weight/litter size values. Especially large mammals ( $>315$

kg) typically occur above the regression lines in the analyses employing these parameters ( $P < .025$ , Figs. 1 and 2). Leutenegger (1978) argues that because sexual selection is greater in the more polygynous primates natural selection favors larger males. Consequently, he contends that polygyny should also result in an increase in the body size of the species. If larger males favor the evolution of deferred male reproduction and thus sexual bimaturism, larger size may favor polygyny's evolution (Wiley, 1974). Since sexual dimorphism increases with body size in mammals (Ralls, 1977) and polygynous forms are more sexually dimorphic, the association of polygyny with greater than average maternal investment may also be a correlate of larger body size.

Although avian polygyny is more apt to occur among precocial than altricial species (Orians, 1969), other patterns which we have described for mammals are in fascinating contrast to those found in birds. Birds hatching precocial young often lay larger clutches than is typical of species with altricial nestlings (Ricklefs, 1973; Ar and Yom-Tov, 1978). Rahn and Ar (1974) found that incubation length is not significantly different between birds having altricial and precocial offspring, and neither is the length of the fledging period (Ar and Yom-Tov, 1978). Conversely, the longer the gestation period and the smaller the litter size, the more advanced the developmental status in mammalian neonates.

Although we have not quantified male parental investment, this study nevertheless supports the argument that the relative parental investment controls sexual selection (Trivers, 1972); patterns of male investment necessarily reciprocate those of the female. Just as fish mating systems follow from parental care patterns (Perrone and Zaret, 1979), we claim that relative parental investment levels result in certain mating systems in mammals. Crook (1977) emphasizes this relationship between parental investment and mating schemes by referring to them as the "mating-rearing" system. It is clear that an ultimate link in

theory exists between factors shaping some life history tactics (e.g., reproductive effort) and those important in the evolution of mating systems.

#### SUMMARY

Data on litter size, neonate weight, body weight, gestation period, neonatal status, and mating system for 556 species of placental mammals were employed to assess the relationships between mating systems and the degree of maternal investment in the neonate. Three measures of relative maternal investment at birth consistently indicate that when maternal investment is high, polygynous systems prevail, whereas species with low investment in the young at birth tend to be monogamous. We suggest that when female mammals bear precocial young the opportunities are low for male investment in the offspring, thus sexual selection results in polygynous mating systems.

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