

SEXUAL DIMORPHISM IN MAMMALS: AVIAN MODELS AND
UNANSWERED QUESTIONS

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The degree of sexual dimorphism found in mammals ranges from species in which females are larger than males (Ralls 1976a) to those in which males are much larger than females and possess striking secondary sexual characteristics which females lack. Although some work has been done on mammals, principally pinnipeds (Bartholomew 1970; Stirling 1975) and primates (Crook 1972), current theories as to the ultimate causes of this variation in sexual dimorphism were developed largely by workers most familiar with the natural history of passerine birds (Verner and Willson 1966; Orians 1969).

Sexual selection is generally believed to be the principal cause of sexual dimorphism. Trivers (1972) extended earlier ideas and proposed that parental investment is the key factor influencing sexual selection. According to his model, the sex which makes a smaller parental investment in its offspring will compete for mates and be subject to sexual selection. If most sexual dimorphism is due to sexual selection, the degree of sexual dimorphism should in turn be correlated with the relative parental investments of the sexes. Ecological factors, such as the abundance and distribution of food, which influence the degree of sexual selection are pictured as operating mainly by influencing parental investment.

Recent reviews apply this body of theory to all vertebrates (Wilson 1975; Brown 1975). This paper points out some reasons why it applies less well to mammals than to passerines, attempts to evaluate the importance of parental investment in governing the degree of sexual selection in mammals, and makes some alternative predictions as to the probable relative importance of various factors in influencing the evolution of mating systems and sexual dimorphism in mammals. It also discusses the difficulty of measuring male parental investment and contribution to zygotes.

VARIABLES

Sexual Dimorphism

I will consider primarily sexual dimorphism in size, as this is the most common form in mammals and the one most often implied when the term is used without explicit definition. Some of the difficulties of measuring sexual dimorphism are discussed in Ralls (1976a).

It is important to distinguish between sexual dimorphism in size and in other secondary sexual characteristics. The degree of sexual dimorphism in coloration and in structures used in displays or as weapons may be more closely related to the intensity of sexual selection than is the degree of sexual dimorphism in size. While sexual selection may well be the most important pressure affecting color or structures in males, it is but one of the pressures affecting size. These other pressures and those affecting female size, such as neonate and/or litter size, all contribute to the final degree of sexual dimorphism in size.

Studies of the extent to which sexual dimorphism in size correlates with sexual dimorphism in other secondary sexual characteristics are badly needed. The strength of this correlation appears to vary a great deal. Lowther (1975) found no correlation between the degree of sexual dimorphism in size and in plumage in the avian family Icteridae. A preliminary report by Leutenegger and Kelly (1975) on the anthropoid primates indicates that in this group sexual dimorphism in canine tooth size is indeed more closely related to the presumed intensity of sexual selection on males than is sexual dimorphism in body size. However, Gautier-Hion (1975) found a good correlation between sexual dimorphism in size and canine length in several cercopithecids as did Orlosky (1973) in cebids. Geist (1974) states that horn size and body size tend to evolve in parallel in ungulates.

The modal size and degree of sexual dimorphism in each of the mammalian orders is shown in table 1. Although a tabulation at this level is necessarily an oversimplification, it is nevertheless of heuristic value. Most species of mammals are small and not extremely dimorphic.

In 16 of the 20 orders, the degree of sexual dimorphism shown by most species is small to moderate. When dimorphism occurs, males are usually larger than females except in the Mysticeti and Lagomorpha, in which females are larger than males in all or the majority of species, and the Chiroptera, in which a larger size in females is very common (Ralls 1976a).

The orders in which extreme cases of sexual dimorphism favoring males, defined as a ratio of average male to female weights greater than 1.6, occur are marked with an asterisk in table 1. Some cases occur in orders in which the modal degree of sexual dimorphism is small to moderate; usually these cases are concentrated in only a single family of the order. Examples include the Macropididae in the Marsupialia, Pteropidae in the Chiroptera, Physteridae in the Odontoceti, and Mustelidae in the Carnivora. The most extreme cases in these families are probably the great red kangaroo, *Megaleia rufa* (Frith and Calaby 1969), the hammer-headed bat, *Hypsignathus monstrosus* (J. Bradbury, personal communication, 1976), the sperm whale, *Physeter catodon* (Bryden 1972), and weasels such as *Mustela erminea* (Hall 1951).

Most of the extreme cases, however, occur in the four orders in which it is difficult to specify a prevailing mode of sexual dimorphism: Primates, Pinipedia, Proboscidea, and Artiodactyla. Examples are the baboons, *Papio*, the orangutan, *Pongo pygmaeus*, and the gorilla, *Gorilla gorilla* (Crook 1972; Eckhardt 1975; Schaller 1963); the fur seals and sea lions (Otariidae) and elephant seals, *Mirounga* (Bryden 1972); the African elephant, *Loxodonta*

TABLE 1
NUMBER OF GENERA AND SPECIES, SIZE, AND SEXUAL DIMORPHISM IN SIZE
IN MAMMALIAN ORDERS

Order*	No. of Recent Genera†	No. of Recent Species†	Modal Size Category‡	Modal Degree of Sexual Dimorphism§
Monotremata	3	6	S	M
Marsupialia*	81	242	S	M
Insectivora	77	406	S	M
Dermoptera	1	2	S	M
Chiroptera*	173	875	S	M, ♀♀?
Primates*	47	166	L	V
Edentata	14	31	L	M
Pholidota	1	8	S	M
Lagomorpha	9	63	S	M, ♀♀
Rodentia	354	1,687	S	M
Mysticeti	5	10	L	M, ♀♀
Odontoceti*	33	74	L	M
Carnivora*	96	253	S	M
Pinnipedia*	20	31	L	V
Tubulidentata	1	1	L	M
Proboscidea*	2	2	L	V
Hyracoidea	3	11	S	M
Sirenia	3	5	L	M
Perissodactyla	6	16	L	M
Artiodactyla*	75	171	L	V

* Orders in which extreme cases of sexual dimorphism favoring males have evolved. Extreme dimorphism is defined as a ratio of male to female weight exceeding 1.6.

† After Anderson and Jones 1967.

‡ After Bourlière (1975), with the addition of the nonterrestrial orders. Size categories: S = adult weight less than 3 kg; L = adult weight more than 5 kg.

§ Dimorphism categories: M = small to moderate in all or the majority of species, males probably larger in most cases of dimorphism; M, ♀♀ = small to moderate in all or the majority of species, females larger in most cases of dimorphism. V = variable, degree of dimorphism so variable that it is difficult to specify a prevailing mode.

africanus (Laws, Parker, and Johnstone 1975); and the nyala, *Tragelaphus angasi* (Tello and Van Gelder 1975). The most extreme cases in mammals, such as the northern fur seal, *Callorhinus ursinus* (Scheffer and Wilke 1953), far exceed those in birds (Ralls 1976b).

Sexual Selection

Sexual selection is usually divided into two processes: intrasexual selection, in which members of one sex compete to mate with members of the other, and intersexual or epigamic selection, in which members of one sex choose to mate with members of the other. In practice, the two aspects cannot always be separated and Fisher (1930) argued that, when a selective advantage is linked to a secondary sexual characteristic, there will be simultaneous selection on the other sex in favor of those who prefer the advantageous type. However, most discussions of sexual selection in mammals have stressed the importance of intrasexual selection, e.g., "among mammals the role of aggressive male behavior tends to be more important than that of female choice" (Brown 1975, p. 160).

A variety of field and laboratory observations suggest that the importance of epigamic selection in mammals may have been underestimated. Female mountain gorillas, chimpanzees, *Pan troglodytes*, and African wild dogs, *Lycyaon pictus*, transfer between groups more frequently than males, reversing what is thought to be the usual mammalian pattern (Harcourt, Steward, and Fossy 1976; Kawanaka and Nishida 1975; Frame and Frame 1976). Apparently, the female chooses whether to stay with a particular male or group of males or join another group. Both wild and captive female gorillas initiate sexual activity, males being relatively passive, and captive females are selective in their choice of sexual partners (Schaller 1963; Nadler 1976). Richard (1974) presents evidence on female choice in sifaka, *Propithecus verreauxi*.

Lincoln and Guinness (1973) claim that female red deer, *Cervus elaphus*, play an active role in forming the rutting groups and that a hind in estrus may select a particular stag and move to it. Female bighorn sheep, *Ovis canadensis*, seem to prefer to mate with large-horned males (Geist 1971). Estrous domestic ewes allowed to choose between several tethered rams most often approached those with the best mating records (Lindsay and Robinson 1961). Female fallow deer, *Dama dama*, congregate around territorial rutting bucks (Chaplin and White 1970; Chapman and Chapman 1975). Female pronghorn antelope, *Antilocapra americana*, prefer to mate with territorial rather than nonterritorial males (Kitchen 1974). Female Uganda kob, *Adenota kob*, and Kafue lechwe, *Kobus leche* presumably choose particular territorial males on the lek (Buechner 1974; Schuster 1976) and the same may also occur in other antelope in which the territories are less tightly concentrated.

In deer mice, *Peromyscus leucopus*, each sex is caught most readily in traps baited with the odor of the other sex, indicating that mate selection may not be entirely an active seeking process on the part of males but may involve some male seeking by females (Mazdzer, Capone, and Drickamer 1976). Laboratory data on "proceptivity" (female initiative in sexual behavior) in female rodents suggest that this may be true for other species as well (Beach 1976). Female preference for particular males has been experimentally demonstrated in domestic dogs (Beach and Le Boeuf 1967) and macaques, *Macaca* (Dixson et al. 1973; Eaton 1973; Lindburg 1975). However, workers who have studied pinnipeds almost unanimously report that there is no evidence for female choice in this order (Peterson 1968) and there is some quite strong evidence against it in northern fur seals (R. Gentry, personal communication, 1977). Cox and Le Boeuf (1977) have suggested a mechanism by which female elephant seals may increase their chances of mating with dominant males without directly choosing such males. Females protest vigorously when males attempt to copulate, thus inciting competition among all nearby males.

Brown (1975) suggests that it is possible to distinguish a group of species in which sexual selection consists primarily of intrasexual selection (the "male dominance and competitive mating" type) and a group in which it consists primarily of epigamic selection (the "male adornments and female choice" type). Female preferences for individual males are supposedly weak or difficult to detect in the first group. It seems unlikely that a clear-cut dichotomy really

exists, as much of the evidence suggesting female choice in mammals is from species where intrasexual selection appears to be quite strong.

At least at the present level of knowledge, it is not possible to predict the roles played by the sexes either from the social system or the degree of sexual dimorphism. For example, both hamadryas, *Papio hamadryas*, and gelada (*Theropithecus gelada*) baboons are extremely dimorphic and live in stable harems. However, young gelada males may start to cultivate the attention of juvenile females within a harem without attracting the attention of the adult harem male, while the young hamadryas male has to begin by kidnapping young females. Similarly, gelada harem males do not solicit new females; rather, it is the females that choose harems to join (Gartlan 1973; Dunbar and Dunbar 1975). The hamadryas females appear to be captured by males and do not have the opportunity to express a preference (Kummer 1968).

The indiscriminate use of the terms harem and harem master (Brown 1975; Wilson 1975) is a legacy of early misconceptions of the social structure of most highly polygynous mammals. Several field observers have stressed that it is extremely misleading to use harem and harem master with respect to pinnipeds (Peterson 1968; Gentry 1975*a*, 1975*b*; Marlow 1975) and the same is true with respect to most antelopes (Estes 1974). Peterson (1968, p. 36) comments on pinniped breeding groups:

The misconceptions regarding the harems of pinnipeds seem to be a result of superficial investigations. To a casual observer, the males of several species do indeed seem to have stable groups of females within their territories. . . . In the otarids, especially, it might appear that each male is controlling one of the aggregations of females. When the animals are individually marked, however, it soon becomes clear . . . that females may move through these harems fairly easily, and that the groups result more from the gregariousness of the females than from the efforts of the "harem master." . . . Bulls of several species chase females that attempt to leave the aggregations within their territories, and in dimorphic species, such as fur seals where the male is much larger than the female, a bull may lift a female and throw her back into his territory. . . . But there are too many females per territory and they are too agile for the bulls. I have watched female fur seals move through five harems in less than one hour.

Early casual observations of antelopes also suggested that most species formed stable harems. However, field studies of such species as the impala, *Aepyceros melampus*, have usually shown that their breeding groups consist of a mosaic of male territories through which female groups of unfixed membership wander almost at will (Jarman 1974; Jarman and Jarman 1974). The home range of a typical female impala covers about 10 male territories. Female mobility has also been described in the rutting groups of the red deer: "In contrast to the restricted movements of the stags controlling the harems, the hinds are able to move between the different rutting groups" (Lincoln and Guinness 1973, p. 486).

Although ethologists have not formally defined the scientific meaning of harem, two dictionaries define it as a "group of females led by and mated to one male" (Random House Unabridged Dictionary) and a "group of females controlled by one male" (Webster's Third New International Dictionary). These definitions suggest that the term might properly be applied to a mammalian social unit that consisted of a stable group of one dominant male and several

females persisting throughout at least one breeding season. Mammalian breeding groups meeting these criteria do exist; for example, those of the hamadryas baboon (Kummer 1968) and the vicuna, *Vicugna vicugna* (Franklin 1974). Those of most polygynous mammals do not, however, due to the movement of females between groups and the lack of male control. It would seem best to use a neutral term with no behavioral implications, such as breeding group or one-male group in most cases and restrict the use of harem to those few species in which long-term group stability and male control actually exist.

The terms monogamy and polygyny are presently used in two distinct senses. They may be defined by the nature of the bonds between the sexes, as follows: polyandry = one female has bonds with several males; monogamy = one female has a bond with one male; polygyny = several females have bonds with one male; promiscuous = no bonds between the sexes. This system is much used by ornithologists; Selander (1972) offers a more elaborate version. It is difficult to use when discussing the mammals as a whole, however, due to the large number of nonmonogamous species, the lack of agreement on an operational definition of a bond in these species, and the lack of detailed studies of their social behavior. Alternatively, the terms may be part of a classification based on genetic criteria, as follows: polyandry = more males than females contribute gametes to zygotes; monogamy = males and females contribute gametes to zygotes in equal numbers; polygyny = more females than males contribute gametes to zygotes (Wiley 1974a). I will follow this classification. Fortunately, it is the relative genetic contributions of the sexes which presumably affect the evolution of sexual dimorphism, regardless of the exact nature of the bonds between the sexes. Under this system, promiscuous species are considered polygynous. Birdsall and Nash (1973) claim that deer mice, *Peromyscus maniculatus*, are polyandrous, since the individual young in a litter often have different fathers. However, they did not establish that more males than females contribute gametes to zygotes.

The intensity of intrasexual selection in a species should be proportional to the ratio of the lifetime number of offspring sired by a highly successful male compared to the number born by a highly successful female in her lifetime. Although the data needed to calculate this ratio are available for only a few mammalian species, such as the northern elephant seal, *Mirounga angustirostris* (Le Boeuf 1974), it is clear that it will tend to be smallest in monogamous species and tend to increase with increasing degrees of polygyny. Due to the lack of adequate data on the actual contributions of individual males to zygotes in most species, it is necessary to estimate this from behavioral observations. The use of observations such as long-term association and bonding between individual males and females to identify the monogamous species is probably not a serious source of error. Estimating the degree of polygyny from behavioral observations, however, is often exceedingly difficult and may lead to large errors.

Species may be polygynous in the absence of easily recognized groups containing one male and several females. For example, the mountain lion, *Felis concolor*, is usually solitary. Since a male's territory encompasses the territories of several females, however, the species is polygynous (Seidensticker et al. 1973).

This dispersed form of polygyny is much more difficult to detect than that seen in the African lion, *Panthera leo*, in which males and females are often associated; it may be widespread in mammals, however, as it has been reported in a variety of species including rodents (Brown 1966), cervids (Dubost 1970), prosimians (Charles-Dominique 1972), and mustelids (Lockie 1966).

Even if it is established that a species has a breeding sex ratio of one male to some number of females, determining the actual degree to which individual males contribute to zygotes, and the number of offspring a male can potentially sire, may still be very difficult. Changes in the membership of a group of females associated with a given male may be frequent and extensive (Peterson 1968; Jarman 1974; Jarman and Jarman 1974; Lincoln and Guinness 1973; Bradbury, in press). The relationship between the degree of turnover in female groups and the expected degree of sexual dimorphism is unexplored.

Estimating male contribution to zygotes is further complicated in many species because of the turnover in males holding territories. In the impala, for example, about one-third of the adult males hold territory at a time. Females spend most time in territories containing the best resources; this places strenuous demands on the males holding these territories and turnover on them is more frequent than on other territories (Jarman and Jarman 1974). Males who lose territories join bachelor groups and work their way up the hierarchy in these groups before attempting to regain territory. Similar problems arise with pinnipeds. For example, the observed ratio of breeding males to females in the northern fur seal of about 1:20 has led to the characterization of this species as the most highly polygynous pinniped. Since the annual rate of turnover in breeding males is much higher than in females, however, the ratio of zygote-contributing males to females is likely to be lower (Peterson 1968). Furthermore, males are selectively harvested from the population and a ratio lower than 1:20 might have occurred under undisturbed conditions.

When the social group contains several adult males, it is necessary to estimate the proportion of young sired by each. It is usually assumed that the males of such species are arranged in a dominance hierarchy, and that the highest ranking males sire the most offspring (Wilson 1975; Brown 1975), but some workers question this hypothesis (see Kolata 1976).

A common technique for estimating the proportion of young sired by each male is to count the number of times each male copulates during some period of observation. Difficulties arise, however, because males of high and low status are often not equally visible to a human observer. For example, it has often been reported that high-ranking rhesus macaques, *Macaca mulatta*, mate more frequently than low-ranking males. But an observer may easily fail to note some of the copulations of low-ranking and solitary males because they tend to be more secretive and peripheral than high-ranking males. Drickamer (1974) found that when he corrected his data on copulation frequencies to account for the relative observability of males of high and low status there were no significant differences between them. Similarly, Missakian (1973) suggests that mating activity of mother-son pairs may often be overlooked because it is less conspicuous than typical consort behavior. Eaton (1974) found no relationship

between dominance scores and several measures of sexual behavior in the males of a captive troop of Japanese macaques; Enomoto (1974) found no correlation between number of copulations and rank order among the high-status males of a wild troop.

Ascertaining the relationship between frequency of copulation and actual paternity presents additional problems. For example, it is often stated that high-ranking male primates have priority of access to females at the height of estrus and thus sire the majority of young. Rowell (1974, p. 149), however, in an important review of the concept of social dominance, concluded that "the evidence for priority of access to receptive females is equivocal, especially when access to ripe ova rather than access to receptive females is considered, since the latter do not always contain the former. . . . Estrus is not necessarily associated with ovulation in rhesus monkeys (Loy 1970) and Conaway and Koford (1965) found that high ranking males preempted the more attractive older females in the group for most of the breeding season—continuing to consort with them exclusively while they were already pregnant, and so siring fewer offspring than their sexual activity might suggest."

The priority of access model was formulated mathematically by Altmann (1962) and has been most carefully tested by Hausfater (1975) on yellow baboons, *Papio cynocephalus*. His data did not support the hypothesis that first-ranking males have higher reproductive success than lower ranking males. However, male rank did account for 56% of the variance in proportion of copulations among males.

The only study which determined the actual number of offspring sired by each male of a primate troop is that of Duvall et al. (1976) on the rhesus monkey, *Macaca mulatta*. Paternity was ascertained by analysis of serum proteins, red cell enzymes, and leucocyte antigens. The alpha male did not father all, or even most, of the 29 infants born during the 2-year study. In fact, he could not have fathered more than seven, which was not significantly different from the number expected by chance. The male which had both the most known (eight) and the most possible (10) offspring was of low rank during 1 year of the study and of middle rank the other.

As with territorial species, it is very difficult to estimate the degree of lifetime differential reproductive success in species with multimale groups, as an individual male does not occupy a given rank for very long. As Hausfater (1975) comments:

. . . data on the total lifetime reproductive success for even a single individual nonhuman primate are not presently available. It may be, for example, that every adult male baboon in his lifetime occupies each dominance rank for the same amount of time as does every other male. If so, then, in the long run, all males would be expected to have an equal total lifetime reproductive success. Even if, as is more likely, males differ in the sequence of ranks that they occupy and in the duration of rank occupancy, the total lifespan reproductive success of all males may still be equal . . . to achieve any given level of reproductive success, a male may either occupy second rank and reproduce at a high rate for a short period of time or occupy fifth rank and reproduce at a low rate for a longer period of time.

It does not seem likely that the total life-span reproductive success of all males is equal; the point is that evidence to rule out this hypothesis in primates is still lacking.

In mammals which have more than one offspring at a time, the problem of ascertaining paternity is further complicated because the members of a single litter may have different fathers. Birdsall and Nash (1973) have shown that this occurs in a large proportion of litters in the deer mouse.

Parental Investment

Parental investment is defined 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" (Trivers 1972, p. 139). Male parental care is relatively rare in mammals (Spencer-Booth 1970) and the overall variation in male parental investment from species to species is greater than that of female parental investment, making it particularly important to assess the degree of male parental investment. Unfortunately, parental investment is presently impossible to measure.

The magnitude of a given parental investment is proportional to the degree to which it decreases the parent's ability to invest in other existing or hypothetical future offspring. For some forms of parental investment, such as feeding or transporting the young, measures of the time or energy devoted to the activity may reflect the amount of investment rather well. In other cases some fraction of the time and energy devoted to an activity would seem an appropriate measure of the parental investment it represents. For example, territorial defense by males is an indirect form of parental investment when it preserves resources for females rearing young sired by the male. Because territorial defense is usually a multipurpose activity, however, and provides other benefits to the male performing it, only some unknown proportion of the time and energy devoted to it should be considered parental investment. It is clearly not possible to measure some forms of parental investment, such as defense of the young, in time or energy units at all. The magnitude of a parental investment involving defense of the young would seem to be related to the degree of risk of injury or death rather than to the amount of time or energy required for the actual behavior.

Trivers's model will remain untestable in any precise way until some agreement is reached on the best way to quantify each type of parental behavior and on how to estimate the degree of parental investment a given amount of each behavior represents. It is therefore important to devise some system to estimate the amount of male parental investment shown by a given mammalian species. Kleiman (1977) has made a first attempt.

It seems unlikely, however, that the degree of male parental investment can be considered a unitary variable with regard to the evolution of sexual dimorphism. Some forms of male parental investment, such as direct care of the young, do seem to set limits to the degree of sexual selection upon males and thus favor little or no sexual dimorphism. Both defense of the young and defense of a territory often involve selective advantages for large size in males and may be associated with pronounced sexual dimorphism favoring males. Indeed, the role of the male in defense has often been considered the primary

reason that males of many Old World primates are considerably larger than females (DeVore 1963).

RELATIONSHIPS AMONG THE VARIABLES

If there are associations among the degrees of sexual dimorphism, parental investment, and sexual selection (as implied from the breeding system) in mammals, they should be very evident in the extreme cases. I will therefore briefly review present knowledge of the associations between the extreme forms of these variables.

Sexual Dimorphism and Male Parental Investment

In general, species in which males make a very large parental investment show little sexual dimorphism, in spite of the advantages of large males in defense (Kleiman 1977), and the males of extremely dimorphic species make small parental investments. However, the males of most mammalian species make small parental investments, and only a small proportion of these species are extremely sexually dimorphic. There are many more species which show little sexual dimorphism in which male parental investment is very small, particularly in the orders Insectivora, Chiroptera, and Rodentia. It can be seen from table 1 that these orders comprise the majority of mammalian species.

Parental Investment and Breeding System

Monogamous species tend to show unusually large male parental investments. Male parental investment also occurs in some nonmonogamous species but it tends to be smaller than in the monogamous species, or it occurs in a highly specific and individualistic way rather than a species-typical one (Kleiman 1977).

The majority of mammalian species are nonmonogamous ones in which males make a small parental investment. The degree of polygyny is not known for most species but is probably modest; relatively few show the extreme degrees of polygyny exhibited by some of the bovids and pinnipeds. In general, the males of highly polygynous species make little parental investment, although interception of sharks, which was interpreted as defense of pups, has been reported in the Galapagos sea lion, *Zalophus californianus wollebaeki* (Barlow 1972, 1974a, 1974b).

Sexual Dimorphism and Breeding System

Monogamous species in general show little sexual dimorphism (Kleiman 1977). The hooded seal, *Cystophora cristata*, is reportedly monogamous yet males are considerably larger than females (Mansfield 1963; Olds 1950; Øritsland 1970). Nonmonogamous species which show little sexual dimorphism are extremely numerous in the orders Insectivora, Chiroptera, and Rodentia (table 1).

The correlation between degree of polygyny and degree of sexual dimorphism is undoubtedly better in some mammalian taxa than others, as is the case in birds (Selander 1972). Unfortunately it has never been evaluated for the three orders which comprise at least 70% of recent mammals: the insectivores, bats, and rodents. There are polygynous species, such as the plains and mountain zebras, *Equus quagga* and *E. zebra*, which are undimorphic, but the ratio of females to males in these species is only about 5:1 (Klingel 1967, 1968). The Weddell seal, *Leptonychotes weddelli* (Erikson and Hofman 1974; Bertram 1940; Mansfield 1958; Stirling 1971), and some bats (Bradbury, in press) are polygynous but females are larger than males.

Some pinnipeds such as the gray seal and the walrus, *Odobenus rosmarus*, are more dimorphic than would be expected from their breeding systems. The discrepancy posed by these species has been dealt with by postulating that they now copulate more frequently in the water than they did in the past. A few males can monopolize the females less successfully if copulation occurs in the water, and hence the degree of polygyny in these species may now be less than it was during the period when the sexual dimorphism supposedly evolved (Bertram 1940; Repenning 1976). The orangutan is also much more dimorphic than would be expected from its breeding system, and MacKinnon (1974) accounts for this in a similar manner by postulating that the extreme sexual dimorphism is a relict of former times when large males enjoyed more of a reproductive advantage than they do today. Such hypotheses, while perhaps plausible, are impossible to test, and it might be productive to explore the possible role of selective pressures other than sexual selection in these cases. Several small weasels are extremely dimorphic but modestly polygynous at most. Niche separation may be particularly important in these cases (Brown and Lasiewski 1972) and the tendency toward seasonal geographical segregation of the sexes found in some otariids suggests that this factor may play a role in pinnipeds as well.

Consideration of these associations between the extreme forms of the variables allows an estimate of the chances that one would be correct in predicting that a species exhibited an extreme form of one variable if it were known that it exhibited an extreme form of another. This is instructive because the success with which the first member of such a pair could be predicted from the second is often quite different from the success with which the second could be predicted from the first. For example, monogamy is a good predictor of little sexual dimorphism but little sexual dimorphism is a poor predictor of monogamy, because the set of mammalian species which shows little sexual dimorphism includes but is much larger than the set which is monogamous.

In table 2 the extreme forms of the three variables are listed in pairs and the value of each member of the pair as a predictor of the other is roughly judged as either "very good," "good," or "poor." In light of the lack of knowledge about many mammalian species and the previously discussed difficulties in measuring the variables, it is obvious that some of these judgments may be in error. Nevertheless, I believe they accurately reflect the current state of mammalogical opinion and are of considerable heuristic value.

TABLE 2
ESTIMATES OF THE PREDICTABILITY RELATIONSHIPS AMONG THE EXTREME FORMS OF
MALE PARENTAL INVESTMENT, BREEDING SYSTEM, AND SEXUAL DIMORPHISM IN MAMMALS

<i>a</i>	Predictability	<i>b</i>
Large male parental investment . .	$a-b = \text{good};$ $b-a = \text{very good}$	Monogamy
Monogamy	$a-b = \text{very good};$ $b-a = \text{poor}$	Little sexual dimorphism
Large male parental investment . .	$a-b = \text{good};$ $b-a = \text{poor}$	Little sexual dimorphism
Small male parental investment . .	$a-b = \text{poor};$ $b-a = \text{good}$	Extreme polygyny
Extreme polygyny	$a-b = \text{very good};$ $b-a = \text{very good}$	Extreme sexual dimorphism
Small male parental investment . .	$a-b = \text{poor};$ $b-a = \text{good}$	Extreme sexual dimorphism

NOTE.—E.g., given that a species is known to be monogamous, the likelihood that the prediction that it shows little sexual dimorphism would be correct is very good. However, given that a species shows little sexual dimorphism, the likelihood that the prediction that it is monogamous would be correct is poor.

EVOLUTION OF SEXUAL DIMORPHISM IN MAMMALS

There is a high predictability both from monogamy to little sexual dimorphism and from extreme polygyny to extreme sexual dimorphism. Thus the breeding system, at least in the extreme cases, is a good predictor of the degree of sexual dimorphism and the concept of sexual selection can account for a good deal of the variability in degree of sexual dimorphism found in mammals.

Parental investment, however, does not seem to be the key variable governing the degree of sexual selection in mammals. Although a large male parental investment is a good predictor of both monogamy and little sexual dimorphism, a small male parental investment is a poor predictor of extreme polygyny and sexual dimorphism. There must be other important factors which oppose the evolution of extreme polygyny and sexual dimorphism in mammals. The nature of these factors may vary from taxon to taxon and they have not been investigated for most groups. In general, they appear to act by increasing the spacing or mobility of females or favoring a short breeding season. The quality and dispersion of food resources could plausibly oppose polygyny by favoring dispersion of females. Jarman (1974) argues that the highly nutritious and widely dispersed food items utilized by forest antelopes act in this fashion. Owen-Smith (1975) suggests that dispersed food resources account for the absence of extreme polygyny and sexual dimorphism in the white rhinoceros, *Ceratotherium simum*, a species in which males make a minimal parental investment.

In the pinnipeds, the most important variables seem to be whether or not copulation occurs on land, whether parturition occurs on land, land-fast ice, or pack ice, and the length of the pupping, and hence mating, season. Their influence has been pointed out by Stirling (1975) and his views are summarized

below as an example of the probable importance of factors other than male parental investment.

Male parental investment is very low in the majority of pinniped species, yet some have evolved extreme polygyny and sexual dimorphism while others have not. Extreme polygyny tends to develop only in species, such as the sea lions and fur seals, in which both parturition and copulation occur on land, and the mating season is prolonged. On land, females are often closely spaced because of their reduced mobility and the relatively small amount of suitable pupping habitat. Extreme polygyny has not evolved in species, such as the common seal, *Phoca vitulina*, and the monk seals, genus *Monachus*, which give birth on land but copulate primarily in the water. The mobility of seals in the water and the difficulty of maintaining aquatic territories may be important in these cases.

Another factor, in addition to aquatic copulation, works against the development of polygyny in species such as the harp seal, *P. groenlandicus*, and the crabeater seal, *Lobodon carcinophagus*, which give birth on pack ice: females disperse more on ice than they do on land and the habitat is unstable. Winds and currents suddenly break up the ice and widely disperse groups of females. No pagophilic pinniped is known to show extreme polygyny and some are believed monogamous. There must be strong selection for a brief synchronized period of parturition and copulation in these species. Pups born late would be subject to severe mortality when the ice breaks up and females coming into estrus late in the season might be physically dispersed before they could mate. For those pack-ice species on which good data exist, most mating occurs within a 10-day period. A small number of males might not be physically capable of impregnating the entire female population within such a short period while warding off other males.

Species which give birth on land-fast ice may be expected to be intermediate between those which breed on land and those which breed on the unstable pack ice. The best-studied is the Weddell seal, *Leptonychotes weddelli*. The dispersion of females in this species seems dependent on the number of holes in the ice because only a limited number of females can use a single access hole. Copulation occurs in the water under the ice. Males appear to defend underwater territories but are unable to achieve the degree of polygyny found in species which give birth and copulate on land, and the mating season may last several weeks although it remains highly synchronized on a seasonal basis.

Kleiman (1977) has identified two forms of monogamy in mammals. She classifies monogamous species which are most often seen singly or in pairs as showing Type I or facultative monogamy, and monogamous species typically seen in families as showing Type II or obligate monogamy. A large male parental investment is found only in species showing obligate monogamy and it is only this type which is successfully predicted by models based on passerine data. It seems likely that facultative monogamy evolves when the kinds of factors discussed above, which set constraints on the number of females available to successful males, are exceedingly strong. This seems to be the case in the pinnipeds, in which all of the species and subspecies in which monogamy has been reported show the facultative type.

Although the "Orians-Verner" model for the evolution of polygyny may apply in part to some mammalian species, such as the yellow-bellied marmot, *Marmota flaviventris* (Downhower and Armitage 1971), it is inadequate as a general explanation of the evolution of polygyny in mammals, because most species do not meet one or more of its assumptions. First, it assumes that the need for male parental care is the main factor opposing the evolution of polygyny, which is often not the case. Second, it assumes that females choose to mate with particular males. Although this may be true of more mammalian species than is generally supposed, there is evidence that it is not true in some species, such as the hamadryas baboon and polygynous pinnipeds. Finally, it assumes that a female raises her young on the resources contained in the territory of the male with which she mates and this is not true of many highly polygynous species.

The territories of male antelopes, for example, except for a few small species such as the dik-dik, *Madoqua kirki*, serve only as part of their mating strategy and are thus not functionally equivalent to those of most passerine birds (Hendrichs and Hendrichs 1971; Jarman 1974; Estes 1974). The model might be applicable to pinnipeds if one regarded choice pupping habitat as analogous to abundant food resources (J. Bradbury, personal communication, 1976). Such an interpretation, however, would require that the males arrive first on the rookeries and establish territories before the arrival of the females. Although this occurs in some species, such as the northern fur seal, *Callorhinus ursinus* (Peterson 1968), it does not occur in others such as the grey seal, *Halichoerus grypus* (Hewer 1974), and the California sea lion, *Zalophus californianus* (Odell 1975).

Precocial young are thought to facilitate the evolution of polygyny in vertebrates by reducing the need for male parental investment (Wilson 1975). However, because male parental investment in many mammalian taxa consists only of copulation, it would appear impossible for it to be affected by how precocial the young are. A brief consideration of what is known about the distribution of precocial young in the Mammalia indicates little correlation between the degree of precociality and the degree of polygyny. All species of bovids, cervids, cetaceans, pinnipeds, perissodactyls, and caviomorph rodents have precocial young, yet breeding systems within these groups vary enormously. In pinnipeds, the least precocial young occur in the species with the greatest degree of polygyny, i.e., Otariids (I. Stirling, personal communication, 1977). The most precocial young among the African bovids are found in one of the less dimorphic groups, the Alcelaphini (Estes 1974). Conversely, the young of the Chiroptera are all somewhat more altricial, although the degree of development at birth varies (Gould 1975), yet the species of bats show a full range of breeding systems from monogamy to extreme polygyny (Bradbury, in press). In the family Leporidae, the hares have precocial young while the rabbits do not, yet hares do not tend to be more polygynous than rabbits.

The emphasis on progeny-rearing strategies by the males of many passerine species led ornithologists to develop theories which stressed the influence of the degree of male parental care on the evolution of mating systems and sexual

dimorphism. However, passerines are, in several respects, an unusual group and may not be well suited to serve as models for other vertebrate taxa, particularly those which emphasize mating strategies. The passerine radiation filled a series of niches which could only be occupied by species of small body size. The small size of the females dictated a small egg, which in turn resulted in altricial young. Therefore, females typically require male assistance to rear young successfully and about 90% of living avian species are monogamous (Lack 1968).

In larger birds with herbivorous diets and precocial young, such as grouse, there is much less male parental care, monogamy is less common, and males tend to emphasize mating strategies. Wiley (1974a) points out that the degree of male parental investment is insufficient to explain the evolution of polygyny and sexual dimorphism in these avian taxa.

The relative importance of progeny rearing and of mating strategies varies among mammalian taxa just as it does among avian taxa. However, mammals as a whole clearly tend to resemble grouse rather than passerines in this respect. Male parental care is relatively rare and fewer than 3% of the species are monogamous (Kleiman 1977). The basic reproductive characteristics of internal gestation and lactation make it possible for a female mammal to rear her young successfully alone under a wide range of environmental conditions and the "mother-family," not the pair, is the fundamental unit of mammalian society (Eisenberg 1966, and in press).

Polygyny in grouse is correlated with later onset of reproduction in males than in females, a condition for which Wiley (1974a) has coined the fitting term "sexual bimaturism." This led him to develop a two-factor theory in which the evolution of polygyny depends on the balance between the advantages of dual parental care and the advantages of sexual bimaturism (Wiley 1974a, 1974b). Because of the relative emphasis on mating strategies in mammals, the advantages of sexual bimaturism may play a correspondingly large role in the evolution of mammalian mating systems. Polygyny is known to be associated with marked sexual bimaturism in many ungulates (Estes 1974) and pinnipeds (Peterson 1968; Bryden 1972). However, the majority of mammals probably show some sexual bimaturism and the relationship between the degree of sexual bimaturism and degree of sexual dimorphism remains to be critically examined. Wiley's model, while more appropriate for most mammals than the Orians-Verner model, is probably still too simple. An adequate model will certainly have to incorporate factors other than a large male parental investment which oppose the evolution of polygyny.

Another factor which will have to be included in an adequate model is body size. Although the influence of this variable is not well understood, it is apparent from tables 1 and 2 that extreme sexual dimorphism evolves much more frequently in large species of mammals than in small ones. Most extremely dimorphic species are large and most occur in orders in which the modal species size is large: Primates, Pinnipedia, Proboscidea, and Artiodactyla. In the Marsupialia and the Chiroptera, the extremely dimorphic species are found in the families which have the largest modal species size in their orders.

The question of whether or not sexual dimorphism in size tends to increase

with increasing body size in individual mammalian taxa has not been systematically investigated. Although Rensch (1950, 1959) claims that this is the general rule in the animal kingdom, he found that it was not true for several pairs of related European mammalian genera and suggested that the hypothesis should be tested on a larger mammalian sample.

In grouse, large body size and greater sexual dimorphism are correlated with sexual bimaturism and the evolution of polygyny is inseparable from the evolution of large body size (Wiley 1974*a*). Wiley argues that larger size might contribute to the evolution of deferred reproduction. Body size has also been shown to be related in some taxa to the nutritional value and dispersion of the food items utilized. The highly nutritious and widely dispersed food items used by forest antelopes favor both a small body size and a dispersed social organization which makes a high degree of polygyny impossible (Jarman 1974). Large body size is generally correlated with long life span (Kurtén 1953; Sacher 1975) and it has also been argued that longevity will favor the evolution of polygyny (Elliott 1975).

Although the predictability between extreme sexual dimorphism and extreme polygyny is good in both directions, the association between degree of polygyny and degree of sexual dimorphism seems loose enough to indicate that sexual selection cannot account for all the variation in sexual dimorphism. An additional paradigm seems needed.

Variations in the degree of sexual dimorphism have traditionally been interpreted in terms of the factors affecting the size of the males. Recently, however, several workers have suggested new approaches by focusing on the factors affecting female size. Downhower (1976), arguing from simple bioenergetic considerations, concludes that, in a fluctuating environment, smaller female birds are likely to breed sooner and more often than larger ones. His hypothesis provides an alternate interpretation of the general condition of larger size in males, at least in temperate species. Sexual selection could then amplify the degree of dimorphism in some species. Hamilton (1975), studying sexual dimorphism in American Indians, concluded that selective pressures affecting female size—pregnancy, lactation, and childbirth—may be more powerful determinants of sexual dimorphism in human populations than those which affect males. She concluded that small size was advantageous to women when food supplies were not ample during lactation. Ralls (1976*a*) considered the mammalian species in which females are larger than males and concluded that selective pressures in favor of larger females, but not sexual selection on females, were involved in many cases. An additional paradigm may already be in the making!

SUMMARY

Current models for the evolution of polygyny and sexual dimorphism are largely derived from data on passerine birds. These models are less appropriate for taxa such as mammals, in which males emphasize mating strategies, than for those such as passerines, in which males emphasize progeny rearing strategies.

The Orians-Verner model is inadequate as a general explanation of the evolution of polygyny in mammals because many species do not meet one or more of its assumptions: that the need for male parental care is the main factor opposing the evolution of polygyny; that females choose to mate with particular males; and that the female raises her young on the resources contained in the territory of the male with which she mates. A two-factor model incorporating the concept of sexual bimaturism, developed by Wiley for grouse, is more appropriate for many mammals but still too simple.

In mammals, large male parental investment is a good predictor of both monogamy and reduced sexual dimorphism, but small male investment is a poor predictor of extreme polygyny and increased sexual dimorphism. Thus, large male parental investment is only one of the important factors which oppose the evolution of polygyny. An adequate mammalian model will have to include another set of factors which oppose the evolution of polygyny by increasing the spacing or mobility of females. It will also have to explain why sexual dimorphism has evolved more frequently in large mammals than in small ones.

Sexual selection cannot account for all the variation in degree of sexual dimorphism found in mammals. An emerging paradigm based on the consideration of bioenergetic constraints and the factors affecting female size promises new insight.

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