MAMMALS IN WHICH FEMALES ARE LARGER THAN MALES

BY KATHERINE RALLS

Division of Mammals, Smithsonian Institution, Washington, D.C. 20560

ABSTRACT

Females are larger than males in more species of mammals than is generally supposed. A provisional list of the mammalian cases is provided. The phenomenon is not correlated with an unusually large degree of male parental investment, polyandry, greater aggressiveness in females than in males, greater development of weapons in females, female dominance, or matriarchy.

The phenomenon may have evolved in a variety of ways, but it is rarely, if ever, the result of sexual selection acting upon the female sex. The most common selective pressures favoring large size in female mammals are probably those associated with the fact that a big mother is often a better mother and those resulting from more intense competition among females for some resource than among males. It appears that, in general, more than one such pressure must affect the females of a species, and that their combined effects must not be countered by even stronger selective pressures favoring large size in males, before the result is that of larger size in the female sex. Sexual selection may often be operating upon the male sex in mammals even when it is the smaller.

Present knowledge about the species of mammals in which females are larger than males is quite rudimentary. Much more information is needed before we will be able to speak of the selective pressures accounting for the phenomenon with any reasonable degree of certainty. Perhaps the most fruitful approach would be a series of field studies of groups of related species in which females are larger in some species and males are larger in others.

INTRODUCTION

FEMALES ARE probably larger than males in most species of invertebrates. Females are also larger in many species of fish and in some species of amphibians and reptiles. Many biologists are aware that the phenomenon occurs in birds, perhaps because phalaropes are a frequent, and often the only, example mentioned in elementary texts. Few, however, seem to be aware that it occurs in mammals.

The purpose of this paper is to make available, for the first time, a list of the mammalian cases as far as they can be determined, and to call attention to the interesting biological problems they pose. Due to the lack of a list of the mammalian cases, and indeed, a general lack of awareness that any do exist, discussions and speculations as to the selective advantages and behavioral correlates of a larger size in the female sex in vertebrates have been based on the cases in other taxa (Williams, 1966; Trivers, 1972). The views of ethologists have been particularly influenced by the avian cases, as much attention has been paid to the phenomenon both in hawks and other raptors (Snyder and Wiley, in press) and the species showing reversed sex roles (Jenni, 1974).

This paper explores the extent to which current views as to the selective pressures responsible for a larger size in females seem to apply to the mammalian cases. Males are thought to be larger in most mammals, and it is generally believed that Darwin's concept of sexual selection is a satisfactory explanation for this. One possible explanation for a larger size in the female sex in mammals is that it results from the reverse situation, that is, from sexual selection acting upon the females of a species rather than the males. Other possible selective pressures are the advantages of female

dominance over males, the reduction of intersexual competition for food, more intense competition for some resource, such as food, by females than by males, and the various advantages associated with the fact that a big mother is often a better mother. I will discuss each in turn, although they are clearly not mutually exclusive: more than one of them may affect a single species.

METHODS AND PROBLEMS

I collected weights and linear measurements; both have been used by others as measures of size. Weight might seem to be the best measure of size in mammals, but mammalian weights are subject to many sources of variation which often make them less reliable than linear measurements. A major problem is that the weight of females varies with their reproductive condition. I have attempted to include only weights from non-pregnant females. Weights also vary according to the amount of food an animal has recently eaten. This problem is particularly acute in carnivores: a spotted hyena has been observed to eat an amount equal to one-third of its body weight in a single meal (Kruuk, 1972). Weights also depend on the general condition of the animal, which in some cases, varies seasonally. If the sexes do not put on or lose weight in proportionate amounts, a seasonal difference in the ratio of weights of the sexes results. For example, in the horseshoe bat, *Rhinolophus ferrumequinum,* the females gain proportionately more weight than the males over the summer. In early spring, when the bats are relatively lean, the ratio of female to male weight is 1.02, while in October, after a summer of feeding, it is 1.21 (Ransome, 1968).

Many of the arguments for considering weight a more reliable measure of size than linear measurements in birds (Amadon, 1943) do not apply to mammals. The total length of a bird is difficult to measure at best because the neck is often relatively long and curved, and the degree to which curvature is eliminated is considerably affected by the condition of the specimen and the technique of the measurer. Total lengths taken from skins are even more subject to error, as their length depends to a great extent on the amount the skin was stretched during skinning and stuffing. Finally, total length, as usually defined by ornithologists, includes the bill and tail feathers, both of which often vary independently of body size.

Linear measurements of mammals are less variable and less subject to error than those of birds. The problem of a long, curved, and flexible neck is encountered less frequently. External measurements are traditionally taken before the specimen is skinned. The problem of bill length is not encountered, except in *Ornithorhynchus,* and that of variable tail length may often be avoided by the use of the head and body length or other long linear measures excluding the tail.

Where allometry is not marked and the bodily proportions of the sexes are similar, the average female value for any large linear measurement divided by the corresponding average male value gives a rough estimate of sexual dimorphism in size which is close to that obtained by using the corresponding ratio of other large linear measurements. For example, in a small antelope, the dik-dik, the mean head and body length is 61.5 cm for females and 59.5 for males, yielding a ratio of 1.03; the mean height at the shoulders is 40.8 cm for females and 39.2 for males, yielding a ratio of 1.02; and the mean skull length is 11.7 cm for females and 11.5 for males, yielding a ratio of 1.02 (Kellas, 1955).

In compiling the linear measurements, head plus body length was chosen if available, although other measurements such as total length often had to be used. The standard length used for pinnipeds and cetaceans is measured to the point between the hind flippers or flukes and thus is comparable to the head and body length of a terrestrial mammal. The length of the forearm is a standard measure for bats and is generally regarded as a good indicator of relative size.

Most of the female/male ratios in Table 1 are based on linear measurements for two reasons. First, more linear measurements than weights are available. Second, I chose linear measurements in preference to weights if both were available for a species, in order to avoid the problems associated with the use of weight discussed above. When weights were the only data available for a species, I used the cube roots of the weights in order to make these ratios more comparable to those based on linear measurements. Both weights and linear measurements were available for some species. In

most of these, ratios based on the cube roots of the weights approximated those based on linear measurements quite well. Although several sources of data were found for many species, only one ratio is given for each species, based on the data I thought were best. The data used in calculating the ratio were obtained from the first reference listed for each species.

Each species was assigned to one of five status categories according to my judgment of the data. Category 1 species are those in which there seems little question that females are larger than males; the data are statistically significant. Category 2 is the most heterogeneous. It includes all species for which the best data available seemed to indicate that females are larger, but the data could not be statistically tested. The quality of the data available for species in this category varies widely. Females are almost certainly larger than males in some of these species; in others, it only seems possible that females are larger than males. One reason that data could not be statistically tested was that they were given only as growth curves for the two sexes. Another common reason was a format used by many authors for presenting data in which only the mean, range, and sample size for each sex were given. It was impossible to calculate the standard deviations, medians, ranks, or other measures of central tendency and dispersion needed to test the difference between the means in these cases. Category 3 contains species for which statements exist in the literature that females are larger, but for which few or no data are available. Category 4 contains species for which statements exist in the literature that females are larger, but the difference is not, or probably not, significant. Category 5 contains species for which statements exist in the literature that females are larger, but the best available data indicate that the males are actually larger. Where the literature is conflicting, sources indicating that the females are larger are listed under (a) and those indicating that there is no difference or that males are larger under (b).

The taxonomic system of Anderson and Jones (1967) has been followed. Species whose scientific names are given in Table 1 are referred to in the text only by their common names.

In cases where large amounts of data exist, it quickly becomes clear that it is impossible to calculate a single ratio of female to male size dimorphism which is valid for all populations of a given species. It is not uncommon for the degree of sexual dimorphism in size to vary considerably between populations of a species, particularly those which differ in total body size (Hall, 1951; Davis, 1938). In many cases, such as that of the spotted hyena, it is impossible to judge to what extent different estimates of the degree to which females are larger reflect real geographical variation in sexual dimorphism in size and to what extent they reflect sampling differences.

When the degree of sexual dimorphism is slight, females may be larger in some populations and not in others. For example, females are heavier than males in many, but not all, populations of feral rabbits and hares. The evidence with regard to *Lepus* has been reviewed by Flux (1967), who concluded that in most of the studies where females were heavier than males a marked seasonal variation in body weight was found, with females heaviest and males lightest in spring, and that in studies where no sexual dimorphism in weight was found there was also no significant seasonal variation in weight.

The extent to which females exceed males in size depends also upon the age structure of the population sampled, which in turn depends upon such factors as the degree of predation or hunting pressure. This problem is well illustrated by the family Balaenopteridae. The abundant data available make it possible to calculate diverse estimates of the degree to which females are larger for most of the species, depending upon the geographical location and the year in which the sample was taken and upon the criteria of maturity used. Estimates of sexual dimorphism in size based on recent catches are sometimes smaller than those based on earlier catches. Perhaps this is because intensive whaling has lowered the average age and size of individuals in these populations (Laws, 1962): one would expect the dimorphism to be less in younger, smaller whales. The effects of human activities upon the degree of sexual dimorphism in a particular population are complex, however, and not always easily predicted (Laws, 1973; Gambell, 1973; Sergeant, 1973).

Cetologists customarily calculate the mean length of each sex at both sexual and physical maturity (epiphyses of entire vertebral column

fused). Estimates based on length at physical maturity are usually the largest, but since few physically mature animals are taken, the sample sizes are small. Estimates based on length at sexual maturity under-represent the mean size difference between adult females and males and are not comparable to the data on terrestrial mammals. The ratios I calculated myself are marked with a "+"; they are based on all adults longer than the mean length at sexual maturity [according to Mackintosh and Wheeler (1929) for the blue and fin whales and Bryden (1972) for the others] in relatively early catches.

Estimates of sexual dimorphism in size based on breeding adults would be best to use when attempting to find physiological, behavioral, or ecological correlates of a larger size in female mammals. However, such data are unavailable for most species. Comparison of mean weights or measurements of samples of individuals classified as mature may give a misleading picture of the actual mean difference in size between breeding adults. In some species, the individuals of one or both sexes which actually breed are larger than sexually mature but non-breeding adults. This problem is most serious when the social system of a species is such that only a small proportion of the adults of one sex participate in breeding, because the larger, breeding adults of this sex will inevitably be under-represented if animals are collected randomly. In polygynous mammals it is the size of the breeding males which is likely to be underestimated, and failure to appreciate this can lead to a miscalculation of the direction, as well as the magnitude, of the sexual dimorphism in size in breeding adults. In many populations of feral rabbits, for example, the mean weight of females slightly exceeds that of males. Since only dominant individuals breed, however, and social status is significantly correlated with weight in males but not in females, the mean weight of breeding males exceeds that of breeding females (Mykytowycz, 1966; Mykytowycz and Dudzinski, 1972). Because of this possibility, it is safest to exclude from consideration polygynous species in which available data indicate that females are only slightly larger than males.

It may be argued that the best approach to use when searching for correlations of larger size in female mammals would be to exclude from consideration all but the more extreme cases. Indeed, it would be simplistic to expect marked differences in behavior, physiology, and ecology between species in which the males are only slightly larger than the females and those in which the females are only slightly larger than the males. According to this line of reasoning, inclusion of the many cases in which the females are only slightly larger than males would tend to decrease the likehood of finding correlations. Although this may be true to some extent, deciding to use such a procedure after the list was compiled would produce a hand-picked sample, and in any case it is difficult to decide on a size-difference criterion. Other evidence argues against this approach. The females of some species of birds, such as tinamous, which show presumed correlations with larger size in the female sex such as reversed sex roles and brighter plumage in females, are only slightly larger than males. The best-known mammalian species in which female dominance over males and a matriarchial social system are thought to be related to the larger size of the females, the spotted hyena, is by no means an extreme case, for there is a female/male ratio of about 1.04 in head and body length at most. Some evidence exists that small degrees of sexual dimorphism in size can be highly adaptive. House sparrow males averaged only 1.1 per cent larger than females in humerus length and 3.7 per cent larger in sternal length in one sample, taken after a severe storm. Survivors showed normal sexual dimorphism, but non-survivors were monomorphic with regard to skeletal characters (Johnston, Niles, and Rowher, 1972).

COMMENTS ON TABLE 1 AND FIGURE 1

Table 1 shows that present knowledge about the species of mammals in which females are the larger sex is rudimentary. Males are actually larger than females in some species in which it is commonly supposed that females are larger, such as the hippopotamus (category 5). In many cases, females probably are larger but the data are not conclusive (category 2). In others, statements that females are larger are accompanied by little or no data or are based on earlier reports that contain no data (category 3). The list is biased in favor of species of fairly large size; there may well be more cases among small mammals, especially the rodents and bats, which

together comprise at least 60 per cent of living mammalian species, which are not included. Numerous workers have reported that a variety of female vespertilionids tend to be slightly larger than males, but that the differences are not statistically significant. See, for example, Wilson (1971). It is probable that in many of these species the differences are real but are so small that very large sample sizes would be needed to demonstrate statistical significance. There also appear to be many species among the bats where the females may be larger in only some subspecies or populations of a species. See, for example, Handley (1959), Gardner (1966), and Pine (1972). This intraspecific variation may also account for the conflicting reports in the literature regarding some of the species which are listed in the table.

A more complete listing would probably do little to change my conclusions regarding the possible behavioral correlations and selective advantages of a larger size in the female sex in mammals, since very little is known about the social behavior and ecology of the majority of species in these orders.

In spite of the shortcomings of the data, it is clear that females are of greater average size than males in many more species of mammals than is generally supposed. To judge from the taxa in categories 1 and 2 of Table 1, the phenomenon occurs in about 12 (60%) of the 20 orders and in about 30 (25%) of the 122 families of living mammals. It is characteristic of several taxa: a family of bats, the Vespertilionidae; the rabbits and hares, family Leporidae; three families of baleen whales, the Eschrichtidae, Balaenopteridae, and Balaenidae; a subfamily of seals, the Lobodontinae; and two tribes of antelopes, the Cephalophini and Neotragini. It would be interesting to compare the relative frequency of the phenomenon in mammals with that in birds. It might be true that it is better known that the phenomenon occurs in birds simply because it is more common in birds. However, it is impossible to do this because, although Amadon (1959) pointed out the major taxa of birds in which the phenomenon occurs, a more detailed list has never been compiled.

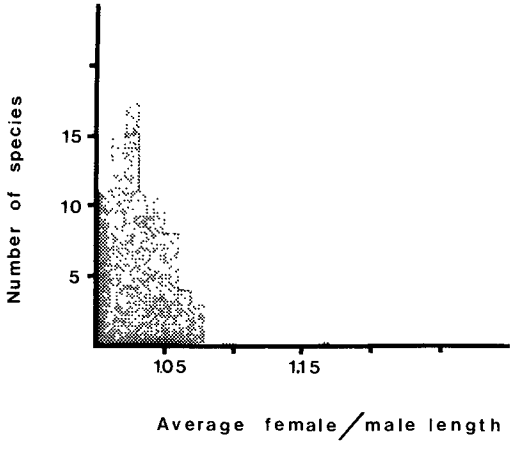

FIG. 1. FREQUENCY DISTRIBUTION OF FEMALE/MALE LENGTH RATIOS FOR MAMMALS IN WHICH FEMALES ARE OF A LARGER AVERAGE SIZE THAN MALES

The figure is based on the 84 species in Table 1 for which ♀/♂ ratios are given.

In considering the magnitude of the ratios in the table, it may be helpful to keep in mind, as a standard of reference, that the ratio of average male to female height in most populations of *Homo sapiens* is about 1.07 (Altman and Dittmer, 1972). Thus the value of 1.07 for the golden hamster indicates that the average difference in length between the sexes of this species is about the same as in our own, but in the opposite direction. It is important to note that the ratios are based on linear measurements or the cube roots of weights, a procedure which minimizes the numerical difference between females and males, since a given ratio of linear measurements corresponds to a much larger ratio by weight. For example, if the females of a species are 3 to 4 per cent larger than males by linear measurements, nonpregnant females are usually about 9 to 13 per cent greater than males in weight.

A frequency distribution of these ratios for the species for which suitable data were found is shown in Fig. 1. It is based on all cases in category 1 together with all cases in category 2 for which ratios are given in Table 1. The sample is biased in favor of cases in which there is a relatively high degree of size dimorphism favoring females. An exhaustive search was not made for species in which females were only slightly larger than males. Nevertheless, it can be seen that in the majority of mammalian cases the females are only slightly larger than males. This is probably also true of the majority of avian cases; but again, an accurate comparison

TABLE 1.

Mammals in which females have been reported to be larger than males

Status categories: 1, females larger than males; 2, females possibly larger than males; 3, statements in literature that females are larger than males but with few or no data; 4, difference in size between females and males not or probably not significant; 5, although statements exist that females are larger than males, best data available show that males are larger or probably larger.

Where the literature is conflicting, sources stating that females are larger are given under (a) and those stating that there is no difference or males are larger under (b).

TAXON	COMMON NAME	STATUS	MEASURE	♀/♂ MEAN	SOURCES AND NOTES
ORDER MARSUPALIA					
Family Dasyuridae					
"carnivorous marsupials"		3			Jones, 1923; Kurtén, 1969
Dasyurus viverrinus	Quoll	5			Green, 1967
D. hallucatus	Satanellus	5			Johnson, 1948
Sarcophilus harrisi	Tasmanian devil	5			Green, 1967
Antechinus flavipes	Yellow-footed marsupial mouse	5			Wakefield & Warneke, 1967; Marlow, 1961
A. bellus	Fawn marsupial mouse	5			Taylor & Horner, 1970
A. stuartii	Stuart's marsupial mouse	5			Wakefield & Warneke, 1967; Horner & Taylor, 1959; Wood, 1970
A. godmani	Godman's marsupial mouse	5			Wakefield & Warneke, 1967
A. swanisonii	Swanison's marsupial mouse	5			Wakefield & Warneke, 1963; Green, 1972
A. minimus	Little Tasmanian marsupial mouse	5			Wakefield & Warneke, 1963; Green, 1972
A. apicalis	Dibbler	5			P. Wooley, pers. commun.
A. macdonnellensis	Fat-tailed marsupial mouse	5			P. Wooley, pers. commun.
Sminthopsis leucopus	White-footed dunnart	5			P. Wooley, pers. commun.
Antechinomys spenceri	Wuhl-wuhl	5			P. Wooley, pers. commun.
Dasycercus cristicauda	Mulgara	5			P. Wooley, pers. commun.
Dasyuroides byrnei	Kowari	5			P. Wooley, pers. commun.; Aslin, 1974
Family Phalangeridae					
Phalanger maculatus	Spotted cuscus	2			Jentink, 1885; Thomas, 1888; subspecies *maculatus* only, according to Tate, 1945

Family Phascolomyidae					
"wombats"		3			Krumbiegel, 1955; Wunschmann, 1970
Lasiorhinus latifrons	Hairy-nosed wombat	4			Crowcroft, 1967
Vombatus ursinus	Common wombat	4			J. McIlroy, unpubl.
ORDER INSECTIVORA					
Family Erinacidae					
Echinosorex gymnurus	Moon rat	2			Findley, 1967
Family Soricidae					
"some shrews"		3			Krumbiegel, 1955
Crocidura hirta	Lesser red musk shrew	2	total length	1.02	Smithers, 1971; mean weight of females less than that of males
Family Macroscelididae					
Elephantulus brachyrhynchus	Short-snouted elephant shrew	2	total length	1.03	Smithers, 1971; mean weight of females less than that of males
E. intufi	Bushveld elephant shrew	2	total length	1.05	Smithers, 1971
Family Tupaiidae					
Anthana ellioti	Madras tree shrew	3			Napier & Napier, 1967; Crook, 1972
Tupaia glis	Common tree shrew	5			(a) Schultz, 1969; (b) Kay, 1973; R. Thorington, unpubl.
ORDER CHIROPTERA					
Family Emballonuridae					
Saccopteryx bilineata	Greater sac-winged bat	1	forearm length	1.04	B. Tannenbaum, unpubl.
S. leptura	Lesser sac-winged bat	1	weight	1.08	B. Tannenbaum, unpubl.
Peropteryx kappleri	Greater doglike bat	2			M. Thomas, pers. commun.
Balantiopteryx plicata	Peter's bat	2	forearm length	1.01	Villa-R, 1966
Coleura afra		2	forearm length	1.02	Kock, 1969
Taphozous perforatus		1	head plus body length	1.02	Gaisler, Madkour, & Pelihan, 1972; Kock, 1969
Family Nycteridae					
Nycteris thebaica		2	head plus body length	1.02	Gaisler, Madkour, & Pelihan, 1972
N. hispida		2	forearm length	1.02	Kock, 1969
N. luteola		3			Verschuren, 1957
Family Megadermatidae					
Lavia frons	Yellow-winged bat	2	forearm length	1.02	Kock, 1969

TABLE 1. (Continued)

TAXON	COMMON NAME	STATUS	MEASURE	♀/♂ MEAN	SOURCES AND NOTES
Family Rhinolophidae					
Rhinolophus ferrumequinum	Greater horseshoe bat	2	weight	1.01	Ransome, 1968
Family Hipposideridae					
Hipposiderus cyclops		2	forearm length	1.04	Verschuren, 1957
Family Phyllostomatidae					
Micronycteris megalotis	Little big-eared bat	2	forearm length	1.01	Villa-R, 1966
Macrotus waterhousi	Waterhouse's leaf-nosed bat	2	forearm length	1.02	Villa-R, 1966
Glossophaga morenoi	Long-tongued bat	2	forearm length	1.03	Villa-R, 1966
Anoura geoffroyi	Geoffroy's long-nosed bat	2	forearm length	1.01	Villa-R, 1966
Artibeus jamaicensis	Lesser Trinidad fruit bat	2	forearm length	1.06	(a) Goodwin & Greenhall, 1961; ratio based on midpoints of ranges; (b) Davis, 1970
A. lituratus	Greater Trinidad fruit bat	2	forearm length	1.05	Goodwin & Greenhall, 1961; ratio based on midpoints of ranges
Ardops nichollsi	Lesser Antillean tree bat	2	forearm length	1.05	Jones & Schwartz, 1967
Stenoderma rufum	Red fruit-eating bat	1	forearm length	1.05	Jones, Genoways, & Baker, 1971
Ametrida centurio	Gray's lesser wrinkled-face bat	1	head plus body length	1.17	Peterson, 1965
			forearm length	1.26	
Hylonycteris underwoodi	Underwood's long-tongued bat	2	forearm length	1.01	Gardner, LaVal, & Wilson, 1970
Family Desmodontidae					
Desmodus rotundus	Vampire bat	2	forearm	1.07	(a) Goodwin & Greenhall, 1961; (b) Wimsatt, 1969
Family Thyropteridae					
Thyroptera tricolor	Disk-winged bat	1	forearm length	1.03	Findley & Wilson, 1974
Family Vespertilionidae					
Myotis lucifugus	Little brown bat	2	weight	1.02	Bruce & Weibers, 1970
M. longipes		1	head plus body length	1.04	Gaisler, 1970
Pipistrellus pipistrellus	Pipistrelle	1	forearm length	1.03	Stebbings, 1968
P. hesperus	Western pipistrelle	1	forearm length	1.05	Findley & Trout, 1970
P. nanus		2	forearm length	1.04	Verschuren, 1957
P. subflavus	Eastern pipistrelle	2	total length	1.06	Golley, 1966

Nyctalus noctula	Noctule	2	weight	1.02	D. Kleiman, unpubl.
Eptesicus fuscus	Big brown bat	1	forearm length	1.03	Patterson & Davis, 1968
E. capensis	Cape serotine bat	2	total length	1.08	Smithers, 1971
E. faradjius		2	head plus body length	1.06	Allen, Lang, & Chapin, 1917
E. nasutus		1	head plus body length	1.03	Gaisler, 1970
Nycticeius humeralis	Evening bat	2	total length	1.05	Golley, 1966; Jones, 1967
Scotophilus nigrita	Yellow house bat	2	total length	1.02	Smithers, 1971
S. gigas		2	forearm	1.05	De Vree, 1973
Chalinolobus		2			Koopman, 1971
Lasiurus borealis	Red bat	1	total length	1.10	Golley, 1966
Plecotus auritus	Long-eared bat	2	weight	1.08	Stebbings, 1966
P. rafinesqui	Rafinesque's long-eared bat	2	total length	1.05	Golley, 1966; Barbour & Davis, 1969; Pearson, Koford, & Pearson, 1952
Antrozous pallidus	Pallid bat	2	forearm length	1.03	Orr, 1954; Davis, 1969
Family Molossidae					
Tadarida pumila	Little free-tailed bat	2	total length	1.05	Smithers, 1971
T. aegyptiaca	Bocage's free-tailed bat	2	total length	1.03	Smithers, 1971
ORDER PRIMATES					
Family Lorisidae					
Perodicticus potto	Potto	4			(a) Napier & Napier, 1967; Crook, 1972; (b) Kay, 1973; A. Walker, pers. commun.
Family Cebidae					
Ateles—all species	Spider monkeys	5			(a) Napier & Napier, 1967; Crook, 1972; Schultz, 1966; (b) Eisenberg, 1975; J. Froelich, unpubl.
Family Callithricidae					
Callithrix jacchus	Common marmoset	1	ventral sterno-pubic length	1.02	Wettstein, 1963
Saguinus	Tamarins	3			Crook, 1972
S. fuscicollis	Brown-headed tamarin	4			G. Epple, unpubl.
S. oedipus	Cotton-top tamarin	4			(a) Schultz, 1956; (b) P. Warner, in press; G. Dawson, unpubl.; R. Cooper, unpubl.; S. Hampton, unpubl.
Family Pongidae					

TABLE 1. (Continued)

TAXON	COMMON NAME	STATUS	MEASURE	♀/♂ MEAN	SOURCES AND NOTES
Hylobates concolor	Black gibbon	3			Schultz, 1969
ORDER LAGOMORPHA					
Family Leporidae					
Entire family—about 9 genera, 63 species		2			Layne, 1967; Hall & Kelson, 1959
Lepus townsendii	White-tailed jack rabbit	1	total length		James & Seabloom, 1969; Orr, 1940
L. californicus	Black-tailed jack rabbit	1	total length		Tiemeier, 196[illegible]; Bronson, 1958; Orr, [illegible]940; Griffing, 1974
L. americanus	Snowshoe hare	2	weight	1.02	Severaid, 1942
Sylvilagus nuttallii	Nuttall's cottontail rabbit	2	total length	1.04	Orr, 1940
S. bachmani	Brush rabbit	2	total length	1.02	Orr, 1940; Hall & Kelson, 1959
S. idahoensis	Pigmy rabbit	2	total length	1.01	Orr, 1940
S. floridanus	Eastern cottontail	1	total length	1.01	Chapman & Morgan, 1973
S. transitionalis	New England cottontail	1	total length	1.01	Chapman & Morgan, 1973
Oryctolagus cuniculus	Domestic rabbit	1	total length	1.03	Lattimer & Sawin, 1955, 1957, 1959
ORDER RODENTIA					
Family Sciuridae					
Glaucomys volans	Southern flying squirrel	1	total length	1.03	Golley, 1966; Madden, 1974
Family Cricetidae					
Blarinomys breviceps	Brazilian shrew mouse	1	total length	1.07	Abravaya & Matson, 1975
Mesocricetus auratus	Golden hamster	1	head plus body length	1.07	Swanson, 1967; Gaskin & Kitay, 1970; data in Altman & Dittmer (1972) is for animals too young to show dimorphism
Cricetulus griseus	Chinese hamster	5			G. Yerganian, unpubl.; M. Festing, unpubl. Much of the greater length and weight of the male is due to his relatively enormous testis.
Cricetus cricetus	European hamster	5			Eibl-Eibesfeldt, 1953; Petzsch, 1952

Lagurus lagurus	Steppe lemming	4			(a) M. Festing, unpubl.; (b) Pogosiciuz, 1972
Peromyscus polionotus	Old-field mouse	2	total length	1.06	Golley, 1966
P. crinitus	Canyon mouse	2	total length	1.04	Hall, 1946
P. maniculatus	Deer mouse	2			Hall, 1946; subspecies *oreas* according to Sheppe, 1961
Onychomys leucogaster	Northern grasshopper mouse	2			Hall, 1946
O. torridus	Southern grasshopper mouse	2			Hall, 1946
Family Muridae					
Praomys shortridgei	Shortridge's mouse	2	total length	1.02	Smithers, 1971
Family Gliridae					
Graphirus murinus	African dormouse	2	total length	1.03	Smithers, 1971
Family Dasyproctidae					
Myoprocta pratti	Acouchi	2	weight	1.04	Weir, 1967; D. Kleiman, unpubl.
Family Chinchillidae					
Chinchilla laniger	Chinchilla	1	weight	1.03	Gorgas, 1967; Weir, 1967; Bellamy & Weir, 1972
Lagidium peruanum	Moutain viscacha	4			Pearson, 1948
Lagostomus maximus	Viscacha	5			Bellamy & Weir, 1972
Family Myocastoridae					
Myocastor coypu	Coypu or nutria	5			(a) Wilson & Dewees, 1962; Weir, 1967; (b) M. Gosling, unpubl.; the difference of opinion seems due to the fact that captive females gain proportionately more weight than males
ORDER MYSTICETI					
Family Balaenidae					
Balaena—2 species	Right whales	1			Omura et al, 1969
Caperea marginata	Pigmy right whale	2			R. Brownell, pers. commun.
Family Eschrichtidae					
Eschrichtius glaucus	Gray whale	1	standard length	1.04	Rice & Wolman, 1971
Family Balaenopteridae					
Balaenoptera acutorostrata	Minke whale	1	standard length	1.05+	Int. Whal. Stat., 1973; South Georgia
B. borealis	Sei whale	1	standard length	1.06+	Int. Whal. Stat., 1959; total Antarctic
B. physalus	Finback whale	1	standard length	1.06+	Mackintosh & Wheeler, 1929

TABLE 1. (Continued)

TAXON	COMMON NAME	STATUS	MEASURE	♀/♂ MEAN	SOURCES AND NOTES
B. musculus	Blue whale	1	standard length	1.06+	Mackintosh & Wheeler, 1929
B. edeni	Bryde's whale	1	standard length	1.04+	Int. Whal. Stat., 1973; USSR
Megaptera novaeangliae	Humpback whale	1	standard length	1.07+	Int. Whal. Stat., 1937; Antarctic pelagic
ORDER ODONTOCETI					
Family Ziphiidae					
Berardius bairdi	Baird's beaked whale	2			Omura, Funjino, & Kimura, 1955
Ziphius cavirostris	Cuvier's beaked whale	2			Omura, Funjino, & Kimura, 1955
Family Platanistidae					
Pontoporia blainvillei	Franciscana	1	standard length	1.10	Harrison & Brownell, 1971; R. Brownell, unpubl.; ratio based on largest recorded specimens of each sex
Inia geoffrensis	Amazon dolphin	5	standard length		Layne, 1968
Platanista gangetica	Ganges dolphin	2			Kasuya, 1972
All 4 species in family		2			Rice, 1967
Family Phocoenidae					
Phocoena phocoena	Harbor porpoise	2			Van Bree, 1973
ORDER CARNIVORA					
Family Canidae					
Atelocynus microtus	Small-eared zorro	3			Kurtén, 1969; Herschkovitz, 1961
Family Viverridae					
Some mongooses, in particular *Suricata* and *Crossarchus*		3			Ewer, 1973
Suricata suricata	Suricate	5			C. Wemmer, unpubl.
Herpestes ichneumon	Egyptian mongoose	5			C. Wemmer, unpubl.
H. saguinus	Slender mongoose	5			C. Wemmer, unpubl.
H. auropunctatus	Small Indian mongoose	5			P. Quentin Tomich, unpubl.
Helogale parvula	Dwarf mongoose	2	total length	1.01	Smithers, 1971; C. Wemmer, unpubl.; A. Rasa, unpubl.
Atilax palidinosus	Marsh mongoose	5			C. Wemmer, unpubl.

Mungos mungo	Banded mongoose	5			C. Wemmer, unpubl.; J. Rood, unpubl.
Crossarchus obscurus	Kusimanse	5			C. Wemmer, unpubl.
Ichneumia albicauda	White-tailed mongoose	2			C. Wemmer, unpubl.
Cynictus penicillata	Yellow mongoose	5			C. Wemmer, unpubl.
Paracynictis selousi	Selous's mongoose	5			C. Wemmer, unpubl.
Family Hyaenidae					
Proteles cristatus	Aardwolf	2	total length	1.03	Smithers, 1971
Crocuta crocuta	Spotted hyena	1	head and body length	1.04	Matthews, 1939; Kruuk, 1972; Wilson, 1968; Buckland-Wright, 1969
Hyaena hyaena	Striped hyena	4			C. Wemmer, unpubl.
H. brunnea	Brown hyena	4			C. Wemmer, unpubl.
ORDER PINNIPEDIA					
Family Phocidae					
Hydrurga leptonyx	Leopard seal	1	standard length	1.10	Laws, 1957; Bryden, 1972
Leptonychotes weddelli	Weddell seal	1	standard length	1.06	Lindsey, 1937; Bertram, 1940; Mansfield, 1958
Lobodon carcinophagus	Crabeater seal	2	standard length		(a) Bertram, 1940; (b) Bryden, 1972
Ommatophoca rossi	Ross seal	2			
Monachus—3 species	Monk seals	2			(a) Scheffer, 1958; King, 1964; Stains, 1967; (b) Bryden, 1972
ORDER SIRENIA					
Family Dugongidae					
Dugong dugon	Dugong	2			(a) Norris, 1960; Heinsohn, 1972; (b) Bertram & Bertram, 1973
Family Tricheidae					
Trichechus manatus	West Indian manatee	3			D. S. Hartman, pers. commun.
ORDER PERISSODACTYLA					
Family Tapiridae					
Tapirus—4 species	Tapirs	3			Krumbiegel, 1955
Family Equidae					
Equus burchelli	Burchell's zebra	5			(a) Selous, 1899; (b) Sachs, 1967; P. Gogan, unpubl.

TABLE 1. (Continued)

TAXON	COMMON NAME	STATUS	MEASURE	♀/♂ MEAN	SOURCES AND NOTES
ORDER ARTIODACTYLA					
Family Hippopotamidae					
Hippopotamus amphibius	Hippopotamus	5			(a) Krumbiegel, 1955; (b) Verheyen, 1954; Ledger, 1968
Family Tragulidae					
Hyemoschus aquaticus	African water chevrotain	1	head plus body length	1.05	G. Dubost, unpubl.
Tragulus—3 species	Mouse deer	3			B. Dalzell, pers. commun.
Family Giraffidae					
Okapia johnstoni	Okapi	3			MacClintock, 1973
Family Bovidae					
Cephalophus monticola	Blue duiker	1	head plus body length	1.04	G. Dubost, unpubl.
C. maxwelli	Maxwell's duiker	1	head plus body length	1.03	Baudenon, 1952
Cephalophus—about 12 species	Duikers	2			Ansell, 1971; Haltenorth, 1963; Malbrant & Maclatchy, 1949; Dittrich, 1972; Baudenon, 1952
Sylvicapra grimmia	Common duiker	1	total length	1.03	Smithers, 1971; Wilson & Clark, 1962; Wilson, 1968
Oreotragus oreotragus	Klipspringer	2	weight	1.01	Wilson, 1968
Ourebia orebia	Oribi	2			(a) Baudenon, 1952; Haltenorth, 1963. (b) Wilson, 1968
Raphicerus sharpei	Sharpe's grysbok	2	weight	1.02	Wilson, 1968
R. campestris	Steenbok	2	weight	1.01	Smithers, 1971
R. melanotis	Cape grysbok	2			
Nesotragus moschatus	Suni	3			G. Dubost, pers. commun.
Neotragus—2 species	Royal antelope, Bates Pygmy antelope	2			G. Dubost, pers. commun.
Madoqua kirki	Kirk's dikdik	1	head plus body length	1.03	Kellas, 1955
Madoqua—six other species	Dikdiks	2			

cannot be made since the needed data for birds have never been compiled.

The most extreme mammalian case known appears to be that of the bat *Ametrida centurio,* in which the ratio of female to male head and body length is 1.17 and of forearm length 1.26. In fact, the females are so much larger than the males in this species that each sex was classified as a separate species for many years (Peterson, 1965). The degree of dimorphism in size in this species seems comparable to the more extreme avian cases of larger size in females (Ralls, in press). The leopard seal would be almost as extreme if one used the figures for mean length at physical maturity given in Bryden (1972); they yield a female/male length ratio of 1.15. However, Bryden took his figures from Laws (1957): they are asymptotic limits of the growth curves for each sex rather than true means and to use them results in an overestimate of the sexual dimorphism in size. Laws stated that the average adult female is only about 10 per cent longer than the average adult male. I have calculated my ratio of 1.10 from all seals over five years of age listed by Laws.

Since females are the larger sex in the blue whale, the largest species which has ever lived on the earth, the largest individual animal was or is undoubtedly a female. Records of blue whales over 30.5 m in length are probably spurious (Gilmore, 1960). One of the largest individuals known to have been measured properly is specimen number 667 of the Discovery investigations (Mackintosh and Wheeler, 1929). This specimen, a female, was 28.5 m in length.

POSSIBLE SELECTIVE ADVANTAGES AND BEHAVIORAL CORRELATIONS

The degree of sexual dimorphism in size in a mammalian species is the result of the difference between the sum of all the selective pressures affecting the size of the female and the sum of all those affecting the size of the male. There may even be selective pressures for both larger and smaller size on each sex. In order to understand the probable selective pressures which have produced a given degree of sexual dimorphism in size in a particular species, then, one must consider all the selective pressures affecting size in both sexes. Since so many selective pressures affect size, it is unlikely that any single selective pressure lies behind all the mammalian cases of a larger size in the female sex. It is clear that no single selective pressure lies behind all the avian cases, as there are two separate groups of theories which attempt to account for the phenomenon in birds, one for each of the two major groups in which it occurs: the species showing reversed sex roles (Jenni, 1974); and the hawks and other raptors (Snyder and Wiley, in press). Most of the recent theories dealing with raptors are based on specialized aspects of food habits, hunting strategies, and the time in the reproductive cycle at which each parent hunts for the young. They apply only to carnivorous, monogamous species in which both parents hunt for the young. Since none of the mammalian cases of larger size in females meets these requirements, it does not seem possible to generalize such theories to mammals.

Sexual Selection

Although the phrase "sexual selection" was coined by Darwin, there is as yet no general agreement as to exactly which selection processes it includes and how they are to be distinguished from natural selection. This is pointed out by Maynard Smith (1973) in his witty review of a recent collection of essays celebrating the centenary of Darwin's *The Descent of Man and Selection in Relation to Sex.* A good discussion of current views on sexual selection appears in E. O. Wilson's *Sociobiology* (1975).

Sexual selection may be divided into two processes: intrasexual selection, in which members of one sex compete to mate with members of the opposite sex; and intersexual or epigamic selection, in which members of one sex choose to mate with certain members of the opposite sex rather than others. In practice, the two aspects cannot always be separated. Fisher (1930) pointed out that when a selective advantage is linked to a secondary sexual characteristic, there will be simultaneous selection on the opposite sex in favor of those who prefer the advantageous type, and female choice is likely to be important in mammals. However, discussions of sexual selection in mammals have largely been limited to consideration of the causes and effects of intrasexual selection. The result of intrasexual selection upon the male

sex in mammals has traditionally been viewed as the evolution of large size and, in some species, such weapons as antlers and large canine teeth. Males are visualized as competing to mate with as many females as possible. Large size is generally thought to be an advantage in this competition, the larger males mating with more females and leaving more offspring. Since males are consequently subject to a selection pressure for large size which does not affect the females, the result is a larger size in the male sex. Competition among males for mates is thought to account for masculine tendencies toward courtship initiation, polygamy, dominance, and aggressiveness, as well as large size.

It is possible that a larger size in the female sex in mammals might result if the usual situation were reversed, that is, if females competed for males and sexual selection operated upon the females of a species rather than the males. Trivers (1972) has proposed a general model which predicts which sex will compete for mates and be subject to sexual selection. According to this model, the sex which makes a smaller parental investment in its offspring will compete for mates. 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." In mammals, the females of most species make a much larger parental investment than the males, so males should compete for females.

The model predicts that in those comparatively rare cases where the male's parental investment is larger than the female's, females should compete with each other for mates and intrasexual selection should act upon the females. If a larger size in the female sex in mammals is usually owing to intrasexual selection, and if it is true that the key variable determining the sex upon which sexual selection will act is the relative parental investment of the sexes in their young, one would expect to find that males make an unusually large parental investment in those species where females are the larger sex.

Unfortunately, parental investment is impossible to measure. Male parental investment in mammals may take several forms, such as the direct care or provisioning of the young; the defense of the young or of the group to which it belongs, against predators; or the indirect provision of resources by the exclusion of conspecific competitors from an area used by the female and young. It is difficult to quantify any of these forms of parental investment and it is impossible to add together the amount of each performed by the males of a given species in order to arrive at a measure of total male parental investment. The best that can be done is to survey the distribution of the various forms of parental investment in mammals so as to see if the males of the species in which the females are larger seem to contribute a greater than average amount of any or all of them.

As in many other mammals, the males of many species in which females are larger, such as the golden hamster, most of the bats, and the seals, appear to make little parental investment of any kind after copulation. Direct male parental care is uncommon in mammals (Spencer-Booth, 1970). The species in which the greatest degree of male parental care has been described belong to the New World primates and the mongooses, but there seems to be no direct correlation between a larger size in females and male parental care in either group. Males of titi monkeys, *Callicebus moloch*, night monkeys, *Aotus trivergatus*, and common marmosets, pygmy marmosets, *Cebuella pygmaea*, and tamarins, *Saguinus oedipus* and *S. fuscicollis*, spend much time caring for the young (Spencer-Booth, 1970; Christen, 1974, Epple, 1975). Females are slightly larger than males in common marmosets but apparently not in *Aotus*, *Cebuella*, and *Saguinus*. Male banded mongooses, *Mungos mungo*, spend considerable time guarding the young at the den while the lactating females forage (Rood, 1974). Male dwarf mongooses also frequently "baby-sit" (A. Rasa, pers. commun.). It appears that dwarf mongoose females average slightly larger than the males, but banded mongoose males are clearly larger than the females. Defense of the young against predators is not particularly striking in males of any of the species in which females are larger. However, males of many species in which they are the larger sex do defend the young, for example, some large ungulates and Old World primates (Klingel, 1967; DeVore, 1963; Jarman, 1974). Males of several of the species in which females are larger do provide resources by maintaining a territory

for the female and young. This has been documented for dik-diks (Hendrichs and Hendrichs, 1971) and is probably true of other small species of antelopes as well. However, males of many species in which they are the larger sex make a similar contribution; this has been particularly well described for mustelids (Lockie, 1966).

The males of the mammalian species in which females are larger do not in general make an unusually large parental investment. This finding suggests that the phenomenon is not due to intrasexual selection on the female sex. Several other lines of evidence lead to the same conclusion. A species in which females competed for males might be expected to have a polyandrous mating system. However, this mating system is unknown among mammals except for a few human societies (Leach, 1955; Peter, 1963). Birdsall and Nash (1973) found that individual young of a single litter of deer mice often had different fathers and described this as the result of polyandry. However, multiple inseminations probably result more from male competition for females than from female competition for males. In fact, the phenomenon of larger size in females is not associated with any particular form of social organization. Some of the species, such as the golden hamster, are essentially solitary, the largest social unit being a female and her litter. Others, such as the common marmoset, the dwarf mongoose, and the dik-dik, have long-term pair-bonds and are monogamous (Epple, 1967; Rasa, 1972; Hendrichs and Hendrichs, 1971). The spotted hyena lives in clans composed of both females and males (Kruuk, 1972). Some species, such as the bats *Saccopteryx bilineata* and *Nyctalus noctula* (Bradbury, in press) and the Weddell seal (Erickson and Hoffman, 1974) have even been reported to live in "harems," a form of social organization commonly believed to be associated with an extreme degree of sexual dimorphism in size favoring males.

Furthermore, the mammalian cases do not in general show the expected behavioral correlations of intrasexual selection on females: that is, they do not exhibit a sex role reversal. The term "sex role reversal" has been used in various ways by different authors, but it has usually implied one or more of the following aspects of behavior: the male performs all or most of the care of the eggs or young; the female is more aggresive than the male; the female initiates courtship. In polyandrous birds all these aspects of sex role reversal tend to appear together and are often accompanied by a larger size in the female sex (Jenni, 1974).

The male certainly does not perform all or most of the care of the young in the mammalian species in which the females are larger. When one attempts to answer the question of whether or not the females are more aggresive than the males in most of these species, one immediately encounters the problem that, as with so many terms used by those interested in social behavior, satisfactory definitions and measures of aggressiveness applicable to a wide range of species have never been agreed upon. Possible measures of aggressiveness, such as the frequency with which an individual threatens, attacks, or fights, may or may not correlate well with each other in a particular species. In large part, this is because aggressiveness is not a unitary phenomenon. There are several kinds of aggressiveness, such as inter-male and maternal aggressiveness, each of which probably has a separate neural and hormonal basis (Moyer, 1968; Gerattini and Sigg, 1969; Jolly, 1972; Floody and Pfaff, 1974). Because of this, the degree of aggression shown by each sex varies with reproductive state as well as with experimental techniques and environmental conditions such as population density.

Even a small change in experimental method can reverse one's conclusion as to which sex is more aggressive. For example, if a technique in which each pair fights only once is used, male and female golden hamsters would be judged equally aggressive, as there are no significant differences between pairs of males and pairs of females in such measures as the number of encounters per test, the number of tests without fights, or the number of decisive interactions per test (Payne and Swanson, 1970). However, if pairs are tested repeatedly, males might be judged more aggressive than females, since fighting between pairs of males is more frequent and intense than between pairs of females (Johnston, 1970; 1975). After reviewing pertinent examples from the primate literature, Jolly (1972) sensibly concluded that "any description of the level of aggression in a primate individual or species must specify which level in which circumstances." This is true for mammals other than primates and for the category of sex as well as those of individual and species.

In spite of these difficulties, it is possible to gain some idea of the relative aggressiveness of the sexes in many mammalian species if one adopts the criterion that the more aggressive sex is the one in which intrasexual agonistic encounters are the more frequent or severe. This seems the most pertinent definition of aggressiveness to use in the present context, as the extent of competition within a sex for mates would be expected to be related more closely to the intensity of intrasexual encounters than intersexual encounters. Measures used by various authors include frequency of attacks, threats, and fights, numbers and severity of wounds, and general "vigor" of fighting. Even these measures may not agree within a species: for example, Bernstein (1972) found that female pig-tailed macaques showed a greater frequency of aggressive responses, although the results of male aggression tended to be more severe.

However, using this criterion, it is apparent that the males are probably the more aggressive sex in the majority of the mammalian cases in which females are the larger sex. Examples of species in which females are larger but inter-male aggression is more frequent or severe include dik-diks and duikers (Hendrichs and Hendrichs, 1971; Ralls, 1975), the African water chevrotain (Dubost, 1975), the golden hamster (Johnston, 1970, 1975), the Weddell seal (Smith, 1966; Fenwich, 1973), and the bat *Saccopteryx bilineata* (Bradbury and Emmons, 1974). However, Mykytowycz and Hesterman (1975) report that female rabbits are just as aggressive as males and may be more aggressive toward juveniles. The assumption that the larger sex is the sex upon which sexual selection is operating has led to the generalization that there is a strict association between body size and aggression, the larger sex being the more aggressive (Trivers, 1972; Rodman, 1973; Goldberg, 1973). This generalization does not hold for mammals.

The remaining aspect of a possible "sex role reversal" syndrome is initiation of courtship by females. It is often somewhat arbitrary to decide which sex initiates courtship in mammals. For example, the sexual invitation signals of the well-studied female rhesus macaque, *Macaca mulatta,* went unnoticed for years until pointed out by a perceptive female observer (Michael and Zumpe, 1970). In fact, if one interprets the deposition of chemical signals as an initiation of courtship, then courtship initiation by females is probably the usual case in mammals. However, in many species males are constantly checking for such secretions and one could perhaps say that this checking is an initial form of courtship, which again shows the rather arbitrary nature of decisions on this point. However one chooses to view these matters, the important point is that the females of the species in which they are larger do not in general appear to play a different role than in other mammals. Since the possible components of a "sex role reversal" syndrome in mammals do not covary, the use of the term only leads to confusion and it would be preferable, when describing the behavior of particular mammalian species, to state simply that the female initiates courtship, that females are more aggressive than males, or that males care for the young.

A final line of evidence indicates that a larger size in the female sex in mammals is not the result of intrasexual selection acting upon females. It is usually not accompanied by secondary sexual characters of the type associated with intrasexual selection upon males, such as antlers or large canine teeth.

In sum, intrasexual selection on females is either non-existent or very rare in mammals. Once female mammals became committed to internal gestation and lactation, their parental investment was so great that the likelihood of evolving a social system in which the relative parental investment of males exceeded that of females and males became a limiting resource for females became exceedingly slim.

Intrasexual selection may often be operating upon the male sex even in those mammalian species in which males are the smaller, as predicted by the greater parental investment of the females. Although this is a somewhat novel idea with respect to mammals, there is ample precedent for it elsewhere in the animal kingdom. Females are larger than males in the majority of invertebrates, yet there is evidence that intrasexual selection operates upon males in many instances (Ghiselin, 1974). Other cases occur in fish. For example, the female guppy is much larger than the male, yet it is the male which is more aggressive and brightly colored. The situation in some of the mammalian species in which females are larger seems comparable.

For example, in the dik-dik the females are slightly larger but are hornless whereas the males are more aggressive and possess small horns.

In such species, it seems possible that either: (1) large size is an advantage in inter-male competition for females but does not result in males exceeding females in size either because large size is disadvantageous to males in some other respect, or because there are even stronger selective pressures for large size on females; or (2) large size is not an advantage in inter-male competition. At the present stage of knowledge, it is not possible to determine which of these possibilities applies to each of the species in question.

It does seem likely, however, that the second possibility is sometimes true, and even that small males may be more successful than large ones in competing for females. In some species, perhaps most often in aquatic or aerial forms, attributes associated with small size, such as greater agility or speed, may be advantageous in inter-male competition. It is known that the importance of relative body size in determining the outcome of agonistic encounters varies widely in mammals. For example, Fleming (1974) studied two species of Costa Rican heteromyid rodents in this respect and found that dominance in dyadic encounters was positively related to size in both sexes of one, *Liomys salvani*, but not of the other, *Heteromys desmarestianus*; and Meese and Ewbank (1973) found that rank was not correlated with weight in domestic pigs. Almost nothing is known, however, about the circumstances in which intrasexual selection on male mammals might favor smaller rather than larger individuals. Ghiselin (1974) has made a first attempt, mainly with regard to taxa other than mammals, to discuss possible circumstances in which small males may be at an advantage.

Perhaps if the males of a species begin reproducing or cease growth earlier than the females it indicates that the species is one in which large size is not an important advantage in competition between males for females. In mammals in which males are considerably larger than females, the females typically cease growth at an earlier age than the males, and also begin breeding sooner. The most extreme examples are polygynous pinnipeds such as the elephant seal *Mirounga angustirostris* (LeBoeuf, 1971; LeBoeuf, Whiting, and Gantt, 1972). Large size is such an advantage in inter-male competition in these species that males defer reproduction for several years while growing to a large size. In several of the mammalian species in which males are smaller, however, it is known that males stop growing at an earlier age than females. This is true for the dik-dik (Kellas, 1955), the spotted hyena (Matthews, 1939), and the golden hamster (Swanson, 1967). Male common marmosets apparently reach sexual maturity earlier than females (Hearn, in press), and data of Bryden (1972) suggest that this may also be true in some cetaceans in which males are smaller.

Little is known about the control of growth in mammalian species in which males are smaller. It is known that the golden hamster does not show the typical mammalian pattern. It is generally believed that androgens stimulate growth, whereas estrogens depress it. Castrated young male golden hamsters grow as large as females: hence in this species testosterone seems to inhibit rather than stimulate growth (Swanson, 1967).

The general anabolic and myotrophic effects of androgens have probably been overestimated, however, because of the use of the levator ani muscle of the rat in many studies. The levator ani is part of the perineal musculature of the rat and is probably important in its male sexual activity. Testosterone has been found to stimulate growth in the levator ani but not in other muscles of the male rat; this muscle was also the only one in which the effect of growth hormones was enhanced by testosterone (Scow and Hagen, 1965). Similarly, castration of male rats greatly decreased growth in the levator ani but not in 29 other skeletal muscles of the male rat (Kochakian, Tillotson, and Endahl, 1956). The response of skeletal muscle to androgens obviously varies from species to species and from muscle to muscle within a species. Cock (1966) has pointed out that systemic (humoral or neural) mechanisms are likely to play a relatively unimportant role in the control of growth in systems in which one cell type occurs throughout the body but has a characteristically different growth rate in each location, such as the muscular and skeletal systems. In contrast, systemic mechanisms are generally sufficient to control growth in organs which are relatively simple in gross anatomical form but are highly specialized in metabolic function, such as the liver and endocrine organs. I have been unable to find any studies of the hormonal control of muscle

growth in a species in which females are the larger sex. It is probable that in a given species only those muscles which are relatively larger in males than females, such as the temporal muscles of the guinea pig and the neck muscles of horned ungulates, or those which are important for sexual activity in the male, such as the levator ani of the rat, show a marked increase in growth in response to testosterone (Scow and Hagen, 1957; Russell and Wilhelmi, 1960; Szirmai, 1962; Scow and Hagen, 1965).

The physiology of sex and aggression in male golden hamsters shows several departures from the usual mammalian pattern. It is not known, however, whether these are shared by the males of some of the other species in which females are larger or whether they may prove to be characteristic of species in which males do not compete intensely for females. Androgens typically promote aggression in male mammals whereas estrogens do not. Work on the effects of steroid hormones on aggressive behavior in golden hamsters has been summarized by Floody and Pfaff (1974). Ovarian implants or exogenous estradiol benzoate facilitate fighting between pairs of castrated males. Estradiol benzoate seems to be at least as effective as testosterone propionate.

Adult male rats and mice do not readily show female sexual behavior following castration and treatment with estrogen and progesterone. This resistance seems to be the result of androgens previously secreted during a critical period of brain development, acting on neural structures that are responsible for the expression of sexual behavior. Castrated male golden hamsters, however, readily show lordosis in response to treatment with estrogen and progesterone. If male hamsters are neonatally androgenized, their sensitivity to androgens as adults is increased and will result in the exhibition of behavioral characteristics comparable to those of normal male rats and mice. They show more aggression and respond to changing levels of circulating androgens resulting from castration and treatment with testosterone propionate. Their ability to show lordosis is suppressed. Payne and Swanson (1972) have speculated that "masculinization" of the central nervous system of the normal male golden hamster is somehow incomplete in comparison with that of the males of other rodents. Perhaps either the secretion of androgens by the male hamster is less than in rats and mice, or the threshold for programming the relevant neural structures is higher.

Female Dominance and Matriarchy

The idea that larger size in females tends to be correlated with female dominance over males stems from a combination of sources. In some cases, the supposed advantages of female dominance have been offered as an explanation of the evolution of larger size in females; in others, female dominance is viewed more as a result of the larger size of the female than as a selective pressure producing it. The hypothesis that the advantages of female dominance are responsible for the evolution of a larger size in females has been most thoroughly developed with regard to hawks (Amadon, 1959; Brown and Amadon, 1968; Snyder and Wiley, in press). Female raptors do tend to be dominant to males. It was thought that females "needed" to be dominant for some reason, such as to avoid being treated as a prey item by the male or to protect the young from him, and it has been assumed that females needed to be larger than males in order to be dominant to them. Madden (1974) has expressed a similar view with regard to a mammalian case, the southern flying squirrel: "the males weigh less than the females, as one would expect if the females are territorial and dominant over males." Another source is the association of larger size and dominance in female birds showing reversed sex roles, such as some phalaropes. The fact that females are dominant to males in the three mammalian cases of larger size in the female sex which are best known to ethologists, namely, the golden hamster (Payne and Swanson, 1970), the spotted hyena (Kruuk, 1972), and the dwarf mongoose (Rasa, 1972), has also suggested that such a correlation might exist. The golden hamster is a solitary species, whereas the spotted hyena and the dwarf mongoose are gregarious and have matriarchal social organizations. It therefore seems necessary to explore the possibility that a correlation exists between larger size in female mammals and female dominance, and between larger size in females and matriarchy in the gregarious species.

In everyday language, dominance may be thought of as obtaining what one wants by winning fights or without having to fight, and aggressiveness may be regarded as initiating fights. Although dominance is sometimes confused or even equated with aggressiveness, the two must be distinguished, as they do not always covary. As with aggressiveness, however, satisfactory definitions and measures of dominance applicable to a wide range of species have never been agreed upon. Possible measures of domi-

nance, such as priority of access to food or sexual partners, the frequency with which other animals avoid or retreat from an individual, and the percentage of fights won, may or may not correlate well with each other in a particular species (Gartlan, 1968; Drews, 1973; Syme, Pollard, Syme, and Reid, 1974; Rowell, 1974). Workers familiar with primate behavior in the field have concluded that no such unitary property as dominance exists (although the old concept of dominance as a fundamental structuring mechanism of mammalian societies lingers on in some quarters) and that the term is no longer useful except as a form of shorthand to indicate that the outcome of an agonistic or competitive interaction between two animals is predictable at some practical level of certainty (Gartlan, 1968; Rowell, 1974).

I will use dominance in the limited sense advocated by Rowell (1974): one sex is termed dominant if it usually wins intersexual agonistic encounters. Criteria of winning vary with species and author, but one animal is usually said to have won if the other adopts submissive postures, persistently avoids or flees from it, or is killed. It is not possible simply to assume that the more aggressive sex is the dominant sex, as there are species, such as the ring-tailed lemur, *Lemur catta* (Jolly, 1966), in which intermale aggression is much more frequent and severe than inter-female aggression, and males may therefore be judged the more aggressive, but in which females usually win intersexual agonistic encounters and therefore may be considered dominant.

The outcome of intersexual agonistic encounters may depend so strongly on the reproductive condition of the participants as to make it impossible to generalize as to which sex usually wins. Pregnant or lactating females are often dominant to males in species where males are usually dominant to non-pregnant females. If females are not pregnant or lactating, the usual outcome often depends upon the stage of their estrous cycle. For example, non-pregnant female golden hamsters characteristically fight with, and defeat, males on the three days of their cycle when they are not receptive, but on the fourth day, when they are in estrus, their interactions with males are sexual and no agonistic behavior is seen, at least if a single brief test period is used (Payne and Swanson, 1970). It has been claimed that female chimpanzees are dominant to males only when in estrus (Yerkes, 1943; Herschberger, 1963). The reproductive condition of the male may also be decisive, particularly in seasonally breeding species.

It is also possible for one sex to be judged dominant in group situations, but the other in paired encounters. The highest ranking animals in groups of squirrel monkeys, *Saimiri sciureus,* and talapoin monkeys, *Miopithecus talapoin,* are usually females (Baldwin, 1968; Dixson, Scruton, and Herbert, 1975; Wolfheim, 1975, in press). However, male squirrel monkeys are dominant to females in dyadic encounters (Clark and Dillon, 1974), and it seems that female dominance in group situations is maintained by coalitions of females.

A final difficulty is that many species cannot be considered within a dominance framework at all, as a model of intersexual relationships based on dominance is neither appropriate for nor applicable to all mammals. For example, some gregarious species, such as the common marmoset, maintain separate dominance hierarchies for each sex. There is a dominant female and a dominant male in each group, but the relationship between the dominant pair is peaceful and neither one is dominant to the other (Epple, 1967). In less gregarious species, agonistic interactions between the sexes may be equally rare and measures of dominance so specific to particular situations as to make them useless as bases for generalization regarding the relative dominance of the sexes. For example, in captive Maxwell's duikers, *Cephalophus maxwelli,* which I observed, males had priority at favored resting places but females could almost always appropriate choice bits of food.

In spite of all the difficulties involved in speaking of the relative dominance of the sexes in a variety of species of mammals, the evidence indicates that the larger sex is not always dominant. There are species in which females are larger but are not dominant to males, for example, the bat *Saccopteryx bilineata* (Bradbury and Emmons, 1974), the African water chevrotain (Dubost, 1975), and many small antelopes such as dik-diks and duikers (Hendrichs and Hendrichs, 1971; Ralls, 1975). There are also species in which females are dominant to but not larger than males, such as the Chinese hamster (Schwentker, 1957), the ring-tailed lemur (Jolly, 1966), the pygmy marmoset, *Cebuella pygmea* (Christen, 1974), the otters *Amb-*

lonyx cinerea and *Lutrogale perspicilla* (N. Duplaix-Hall, pers. comm.), beavers, *Castor canadensis* (Hodgdon and Larson, 1973), and nutria (Warkentin, 1968).

Additional evidence that female mammals do not always need to be larger than males to dominate them is provided by the facts that females of the golden hamster (Payne and Swanson, 1970), the spotted hyena (Kruuk, 1972), and the dwarf mongoose (A. Rasa, pers, commun.) are usually dominant to males even in those occasional cases where an individual male is larger than an individual female.

Matriarchy may be viewed as a special form of female dominance found in gregarious species. In attempting to assess whether matriarchy is particularly common in the gregarious species of mammals in which females are the larger sex, one must be aware of the fact that the term is at present being used in two quite distinct senses by ethologists. Some use matriarchy to describe social systems such as that of the spotted hyena (Van Lawick-Goodall, 1971), in which both males and females are normally present in a group and the females are both dominant to the males and also are the usual leaders of progressions (Kruuk, 1972). Others use the term in a more general way to cover any society consisting of a related group of females and their young, with no explicit implications regarding leadership roles or intersexual dominance relationships. For example, Eisenberg (in press) states: "One of the more common forms of social organization repeatedly evolved within the Class Mammalia consists of a matriarchy. This is essentially a female and a series of daughters or sisters, age graded, who participate mutually in the rearing of their collective progeny." By this definition, red deer and elephant societies are matriarchies, and lion society can be viewed as a matriarchy with an attached male or males. Of course, if a group is composed only of females and their young, status and leadership roles, if any, will be carried out by females. In the red deer, females and males live in separate groups for much of the year, but when males do join the females during the breeding season, they would certainly be judged to be dominant to them, although old females may retain leadership roles (Darling, 1937). Still other ethologists use the term in both senses (Rasa, 1972).

The term matriarchy stems from anthropology and was used in the nineteenth century to designate the hypothetical form of society in which women were leaders and rulers. Today the term has been discarded by most anthropologists (Gould and Kolb, 1964). The statement that matriarchy is one of the more common types of mammalian society would probably evoke amazement from the average anthropologist or layman, both of whom would tend to interpret the term as implying female dominance or leadership in a bisexual group. In the interests of avoiding such confusion and of promoting interdisciplinary understanding, it would be best to restrict the use of the term in ethology to describe societies, such as those of the spotted hyena, in which both males and females are normally present in a group and females are both dominant to males and also are the leaders of progressions. The term "extended mother-family," which has been used by Eisenberg (in press) in the same sense as he uses matriarchy, could then be used to describe groups of females, in part related by descent, which form social units together with their young. An alternative term for these groups, which would be correctly interpreted by social scientists, is "extended matricentric family." A matricentric family contains a woman and her children. Matricentric families can be grouped into larger units or "hooked on" to a male or group of males to create other kinds of families (Bohannan, 1963).

Whichever definition one uses, it is clear that larger size in female mammals is not always associated with matriarchy in gregarious species. If the more general definition is used, there are many matriarchal species in which males are the larger sex. Even if the more restricted definition suggested above is used, the ring-tailed lemur may be cited as an example of a matriarchal society in which males are larger (Jolly, 1966); and there are many species where the females are larger that do not have this form of social organization.

Females are not dominant to males in the majority of species of mammals in which they are larger, so the advantages of female dominance cannot provide a general explanation of larger size in female mammals, although they may be involved in a few instances. The existence of species in which females are dominant, although smaller than males, shows that female dominance can be achieved by mechanisms

other than large size, such as hormonal regulation. As mentioned with regard to competition between males, however, the importance of relative body size in determining the outcome of agonistic encounters varies widely in mammalian species.

Differential Niche Utilization

The total niche of a species may be partitioned or even expanded if the sexes come to occupy differing subniches. The idea that sexual dimorphism may often arise primarily because of the advantages of decreased intersexual competition for food has been most extensively developed by Selander (1966, 1972) with regard to birds. However, examples of sexual dimorphism related to differences in the nature of the food consumed by the two sexes have also been noted in fish (Keast, 1966), skates (Feduccia and Slaughter, 1974), lizards (Schoener, 1967; 1968), and even a primate (Kummer, 1971).

Several authors have interpreted the larger size of female raptors as a means of reducing intersexual competition for food (Rand, 1952; Selander, 1966, 1972; Earhart and Johnson, 1970). It seems plausible that some of the species of mammals in which females are the larger sex may be reducing intersexual competition for food and exploiting a wider range of resources than would be possible if the sexes were equal in size. However, I will not discuss this hypothesis in detail, both because it does not deal directly with the question of why the female sex should be the larger, that is, it predicts a difference between the sexes but not which, if either, should be larger, but also because the data necessary to examine it closely are largely unavailable.

Little work has been done on the question of possible differential niche utilization by the sexes in mammals. In birds, differential niche utilization can be accomplished primarily by sexual dimorphism in size, by sexual dimorphism in the feeding apparatus, by a combination of both, or by differences in foraging behavior unaccompanied by much sexual dimorphism in either (Morse, 1968: Robins, 1971; Williamson, 1971). The circumstances under which differential niche utilization in mammals might be expected to be accomplished by the evolution of sexual dimorphism in size are as yet unclear.

Even if sexual dimorphism in size in mammals is found to be accompanied by differences in the nature or size of the food eaten by the sexes, this does not clarify the degree to which advantages of reducing intersexual competition for food have been responsible for the evolution of the sexual dimorphism. If the sexes are of different sizes primarily because of some other selective pressure, such as sexual selection, they still might tend to differ in food habits simply because they are of different sizes. It does seem possible to exclude this selection pressure as a contributing factor, however, in species where the feeding habits of the sexes appear identical.

More Intense Competition by Females

Another possible selective pressure tending to result in a larger size on the part of the females of a species would arise if females compete more intensely for some resource, such as food, than do the males. An alternative way of describing this situation is to say that the lack of some resource is more critical to female than to male reproductive success. Because of the heavy energy demands of female reproduction in mammals, it seems reasonable to expect that this sometimes occurs. For example, the increased energy requirements above normal for the bank vole, *Clethrionomys glareoulus*, averaged 32 per cent per day during pregnancy and 92 per cent per day during lactation (Kaczmarski, 1966); the corresponding figures for the European common vole, *Microtus arvalis*, are 24 per cent and 133 per cent (Migula, 1969) and for the deermouse, *Peromyscus maniculatus*, 28 per cent and 98 per cent (Sadleir, Casperson, and Harling, 1973).

However, this possible cause of a larger size in female mammals remains to be demonstrated. A likely example of a species in which it may be important is the southern flying squirrel, in which larger size in the females is accompanied by female territorial defense, while the males do not defend territories (Madden, 1974). Females are clearly competing for the resources contained in the territories rather than for males. Several other species in which females are larger, such as the acouchi, the golden hamster, and the duikers, have a dispersed social organization which may involve

intense competition by females for resources. Precise comparison is difficult, but females of these and some other species in which they are larger seem unusually aggressive compared to the females of most mammalian species (but not necessarily when compared to the males of their own species). Intense female competition for resources may be correlated with this aggressiveness. However, the likelihood of this being true depends upon the strength of the correlation between large size and success in agonistic encounters in each species.

The "Big Mother" Hypothesis

A bigger mother is often a better mother, that is, larger females may produce a greater number of surviving offspring. This is known to be the case, for example, in some domestic animals such as sheep (Grubb, 1974) and in humans. The correlation between tallness in women and reproductive success remains even when nutritional effects are taken into account: "Women who are genetically short, whose growth has *not* been stunted, are on the whole less efficient at reproduction than women who are genetically tall." (Thomson, 1959; see also World Health Organization, 1965, and Thomas and Hytten, 1973). A larger mother may produce a larger baby with greater chances of survival, she may enable it to grow more rapidly by providing more or better milk, and she may be better at such aspects of maternal care as carrying or defending her baby.

In many cases in which females are larger, the total weight of the baby or babies is relatively large compared to that of the mother, for example, in the common marmoset, many of the bats, and the cetaceans and pinnipeds. However, many species of marmosets, bats, cetaceans and pinnipeds in which the males are larger also have relatively large babies. In fact, the toothed whales, in which males are usually larger, have relatively even larger babies than do the baleen whales, in which the females are larger (Ohsumi, 1966). The situation is complicated by the fact that within any taxon the relative size of the baby or babies tends to increase with decreasing size of the species (Wettstein, 1963; Ohsumi, 1966; Spencer, 1971; Leutenegger, 1973). All cases of a larger size in females in some taxa, such as primates and bovids, do occur in small species.

An interesting variation of the "big mother" explanation has been suggested for the bat *Pipistrellus hesperus*: "Once embryonic development begins in the spring, it would seem important that it proceed without delay, inasmuch as in the relatively short season of optimal activity and feeding the bats must complete embryonic development, reach adult size and flight capability, and accumulate adequate energy stores to survive the winter season. . . . If pregnant bats entered hypothermia and ceased feeding with every entry into a cool ambient temperature, such as must obtain in many rock crevices, even during the daytime in early spring, the growth of the embryos would be continually interrupted and delayed. The advantages of homeothermy at this time are thus obvious. Homeothermy, of course, may be achieved through several means, but certainly would be simpler to maintain in larger bats." (Findley and Trout, 1970).

Both cetaceans and pinnipeds produce exceedingly rich milk enabling their young to grow very rapidly. It has been suggested that female bats may be larger in species in which females carry infants with them on foraging flights (Phillips, 1966). Surprisingly large weights can be carried by females at such times. A female red bat, *Lasiurus borealis*, was found with four young whose combined weight was almost twice her own (Stains, 1965). The need to defend the young against the cannibalistic males has been suggested as a reason why spotted hyena females are larger than males (Kruuk, 1972).

Selective pressures in favor of larger mothers thus seem to be involved in many of the mammalian cases of larger size in the female sex. However, they would seem to apply to many species in which males are larger as well. Acting alone, they are apparently usually not sufficient to result in larger size in females, but they may often be a contributing factor.

CONCLUSIONS

A larger size in the female sex in mammals is more common than is generally supposed. It may evolve in a variety of ways but is rarely, if ever, the result of sexual selection upon females. It may arise primarily through selective pressures that favor smaller males, primarily through selective pressures that favor larger females, or through a combination of both.

When selective pressures favoring larger females are implicated, it appears that more than one such pressure must affect the females of a species, and that their combined effects must not be countered by even stronger selective pressures favoring larger size in the males, before the result is a larger size in the female sex. For example, the combination of relatively large babies, intense competition by females for resources, and only mild competition by males for mates may be found to account for some cases, such as the acouchi and the duikers.

Much more information is needed before we will be able to speak of the selective pressures accounting for the phenomenon with any reasonable degree of certainty. Perhaps the most fruitful approach would be a series of field studies of groups of related species in which females are larger in some species and males are larger in others. There are many such groups for which the general biology, particularly with respect to behavior and ecology, seems much the same for all of the species at our present level of knowledge. Why, for example, are females larger in only some species of marmosets if all have relatively large babies, a great deal of male parental care, and apparently similar social organizations? Why are the females larger in golden but not in Chinese and European hamsters, if all are solitary species with similar ecologies? Why are females larger in the dolphin *Pontoporia blainvillei* but not in the related *Inia geoffrensis*? Perhaps more detailed field studies, particularly if they are designed and conducted with the problem of sexual dimorphism in mind, will reveal subtle, yet important differences which will help to answer such questions.

A larger size in the female sex in mammals may evolve in a variety of ways, and the problem of determining the selection pressures responsible is exceedingly complex. Sexual selection on male mammals may favor smaller males in some species. Why, then, should we tend to assume that sexual selection is sufficient to account for all the mammalian cases in which males are the larger sex?

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