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The Evolution of the Reproductive Unit in the Class Mammalia

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I heard Daniel Lehrman lecture for the first time in 1957. The subject was ring doves and the hypotheses concerned the interrelationship of physical objects (nests and eggs), behavior (courtship), and induction and phasing of hormonal secretions. It was and is an elegant story. Although I have studied mammalian reproduction and social behavior from the perspective of a phyleticist, the paradigm proposed by Lehrman has never been forgotten. Some years later, in 1970, I was invited to present a lecture on the reproduction patterns of tenrecoid insectivores at the Institute of Animal Behavior. Lehrman's interest, penetrating questions, and courtesy made me realize that even though we worked from widely different points of view, a zoologist such as myself had much to gain and perhaps something to offer to the active, experimental group at Rutgers. I am both touched and honored to have been invited to contribute to this first symposium honoring Daniel Lehrman, phyleticist at heart, who founded the active, experimentalist group which hosted us today.

Introduction

Anyone engaged in the process of defining a term is limited by the state of knowledge at the time of formulating the definition as

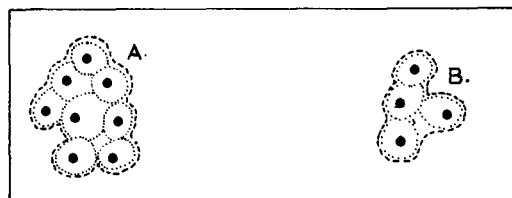
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well as by those philosophical biases the individual may bring to the material. Perhaps one of the most ambitious efforts in animal sociology was made by Deegener (1918), who exhaustively named social units according to recognizable functional and compositional categories. His total reached some 58 social types, not including forms of aggregation or temporary association. All of his terms were developed *de novo* by the appropriate combination of Greek prefixes and suffixes. His terminology was demanding and rather esoteric. In spite of its rigor, I know of only Krumbiegel (1953, 1954), who made extensive use of this scheme for mammals.

Most investigators of animal social behavior attempt to build their definitions of social units around the very important fact that different species show different dispositions in space. We then arrive at a classification based on spatial criteria. Figure 1 refers to a tripartite classification: colonial, communal, and dispersed. Spacing is maintained through the use of threat display and negatively reinforced by agonistic encounters. Presumably such spacing mechanisms involve the partitioning of resources within an environment and vary from species to species as a result of a compromise between (a) the ability to defend and (b) the utility of discrete defense of restricted resources (Brown, 1964). This assumes a center of activity for each individual and, in the case of the dispersed system, an individual's activity areas are for its exclusive use. In a colonial system, exclusive use areas are still present, but the members of each colony are clumped into discrete groupings. In a communal system, all individuals have potentially equal access to resources within the area that the group occupies. This sort of simple classification is useful for species that have a fixed location in space.

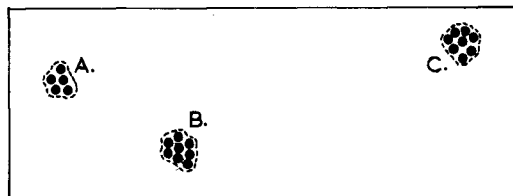
Referring to Figure 1, the colonial system might represent the territories of adult, reproducing yellow-bellied marmot females (*Marmota flaviventris*) (Armitage, 1962). The communal diagram may represent the coterie composing a prairie dog town, such as those described by King (1955) for *Cynomys ludovicianus*. The dispersed system would exemplify the foraging territories of the adult red squirrel (*Tamiasciurus*) described by Smith (1968).

In the case of the red squirrel population studied by Smith, males and females had individually distinct, defended territories. Males only entered females' areas at the time of reproduction. This is an exception rather than the rule, since in most cases a male's home

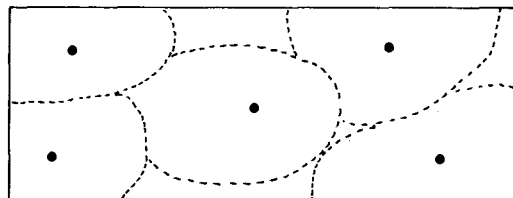


Colonial

Figure 1. Three possible schemes illustrating animal spacing patterns. Black dots equal individuals. Dotted lines equal boundaries of individual or group living areas. Colonial: Individuals are grouped into distinct clumps but each individual has access to an exclusive area. A and B are two colonies. Communal: Several individuals share a home range in common. They may be discretely organized (A, B, C) or clumped into colonies; thus, a communal system may become a special case of a colonial system. Dispersed: Individuals have exclusive use areas which may be true territories under special circumstances.



Communal



Dispersed

range may overlap a female's and he may have access to many parts of it, although perhaps not access to the natal nest at the time of parturition.

This brings us, then, to a consideration of the reproductive unit. The reproductive unit can be considered a social structure organized to replicate itself through births. Spacing mechanisms may be weakly developed in the case of communal species or strongly manifested in the case of species exhibiting a dispersed system. If an area is defended for exclusive use, it is referred to as a territory. If, on the other hand, the foraging area of an individual is shared with others, it is generally referred to as an individual's home range (Burt, 1943). It

should be understood, however, that even with communal use patterns or considerable overlap in foraging areas, each individual in an organized social group may show an individual distance, which means that when it is in a given part of its home range a neighbor can only approach to a certain distance without being threatened or attacked outright (Hediger, 1952). As a result of negative reinforcement, such agonistic bouts can lead to the formation of a hierarchy of individuals that use the same space in common yet exhibit differential access to resources with the space. Even if the individual organisms move about and have no fixed site attachment, individual distance may be shown and hierarchies may be formed. Members of a given social group can have an internal hierarchy and mutually defend themselves against threats from conspecifics in areas of overlap (Ewer, 1968).

Fisler (1969) made a significant advance in classifying social units, approaching the problem by cleanly separating those organizational systems based on individual effort from those based on group efforts. Under each system, he then subdivided according to a basic recognition of two functional classes of behavior: (a) site attachment and (b) capacity to express aggressive behavior. Both types of behavior could vary in step as one passed from an extreme case of high site attachment and low interindividual aggression. At this latter point, group aggressive systems could become an emergent phenomenon. In his system, he makes due allowance for seasonal variation or phases.

In my publication of 1966, I recognized two broad types of social systems. In one type, the individuals are relatively dispersed in space and come into intimate contact only when a male and female mate or during that time when the female is preoccupied in the initial care and rearing of the young. This so-called solitary or asocial system has run into severe semantic difficulties and has been criticized by Anderson (1970). Perhaps the choice of the word *solitary* is unfortunate. Leyhausen (1965a) wrote a very provocative paper titled "The Communal Organization of Solitary Mammals," in which he expounded upon the paradox. Yet I have chosen to retain the term *solitary* for convenience, fully recognizing that, in order to remain apart from one another, adults must know the position of their neighbors, and thus some form of communication or monitoring of conspecifics must take place. I have justified this in arguments elsewhere (Eisenberg, Muckenhirn, & Rudran, 1972; see also Seidensticker, Hornocker, Wiles, & Messick, 1973, p. 54).

In contrast to this, we may have rearing systems composed of several adult animals. Such groupings, when mobile and moving over a wide area that is not uniformly defended, show a great deal of cohesion. A discrete structure can be observed either at certain times or throughout the reproductive cycle. In my own efforts at a synthesis (Eisenberg, 1966, 1967), I duly noted the phasic nature, often tied to reproduction, of social units, and I then developed a scheme to include four major forms of social structure, all ultimately based on variations in the extent of parental care. The evolution of a cohesive social grouping, which exhibits forms of proto-cooperation, is almost always tied to the development of extended families, and thus the group structure has a kinship network as its basis. Other forms of sociality, which are often more ephemeral, do not derive from parental care units.

Using the sex and age composition of such groupings as criteria, I proposed a simple classification: (1) The matriarchy or extended mother family consists of females, in part related by descent, which form a unit for the mutual rearing of their progeny. This is one of the more common types of cohesive social groupings shown in those species of Mammalia which form organizations composed of several adults. (2) Some social systems involve continuous male association but only indirect participation by the male in the rearing of the young. The male, through his activities, aggressively keeps other males out of the living space, thus increasing the carrying capacity of the area in which his females are located. This, then, would be a unimale rearing system generally exhibiting polygyny (e.g., zebra or horse, Klinge, 1972). (3) A rare symptom in the Class Mammalia includes the participation of the male with the female in the initial rearing phase of the young. This, then, is a true parental family. The role of the male is varied and may involve provisioning, such as in many species of the genus *Canis* (Kleiman & Eisenberg, 1973), or carrying of the young, shown uniformly in the New World primate family, Callithricidae. (4) One of the most infrequently evolved social systems in the Class Mammalia is that which includes a relatively permanent, cohesive grouping of several adult reproducing females attended phasically or continuously by several adult males potentially having partial access to the sexually mature females. Such systems have evolved convergently in the lion (Schaller, 1972), some primates (Crook & Gartlan, 1966), some Cetaceans, and a few ungulates (Eisenberg, 1966).

As McBride (1964) points out, one must not think of vertebrate social systems as static entities, either in space or in time. With a simplified diagram (Eisenberg, 1966, p. 15), I tried to indicate that regardless of the form of dispersion in space of the species in question, at least three critical phases occurred in the development of the next generation: (1) the time during which the adult male and female pair and mate, (2) the time of parturition and early maternal care, followed by (3) the time during which the littermate group moves about with the female prior to dispersal. Even in a simple system, where the young disperse early and the male does not consort with the female, these three phases are of paramount importance. Obviously, the phasing of social tolerance, even in the most asocial of species, permits pairing and the constitution of, at the minimum, a mother family. Thus, basically, there will be a period of pair tolerance. The duration of the pair association may in fact be brief since the unique method of neonatal nutrition in the Mammalia makes permissible a maximum parental investment by the reproducing female.

Recently, Anderson (1970) has criticized Fisler and myself, rightly pointing out that both of us have defined a type of social system referred to as "asocial" or "solitary" (Eisenberg, 1966, 1967) or "exclusive territorial" (Fisler, 1969). Although both of us recognize the universality of the parental care unit (in most cases a "mother family"), Anderson focuses on the reality of the deme as the fundamental social unit. He suggests that, in most populations of mammals regardless of the spacing system, the fundamental organization consists of a set or several sets of parents (monogamous or polygynous) with offspring of various ages. Such demes are often divisible into functionally different classes: (a) a stable reproducing unit from which offspring disperse and (b) newly formed units which form from dispersing individuals and serve as colonizers. Not only does such a demic view of populations have much heuristic value for the ecologist, but it is also a fundamental structural concept for understanding the role of kin selection in the differential survival of genetic traits (see Wilson, 1973). Yet, the population structures described by Anderson are not incompatible with the recognition of different degrees of social tolerance as outlined by Fisler and myself, for, undeniably, mammalian species vary with respect to their tolerance for conspecifics and in the forms of spacing mechanisms which they show (Eisenberg, 1967; Crook & Gartlan, 1966).

The Reproductive Unit as a Device for Self-Replication

It is essential to consider survival strategies when attempting to understand the evolutionary histories of mating systems. Survivorship of individual genotypes (or portions of genotypes) is ensured only if the reproducing individual replicates itself through the creation of a viable offspring reproducing in the next generation. Thus, in a species exhibiting a minimum of social tendencies, the reproductive strategy of the male will be to select a female for insemination with the goal of leaving behind his genotype as expressed in the joint progeny reared by the female. This assumes minimal parental investment on the part of the male. Thus, his choice of a female will be critical if he is monogamous and breeds only once in his lifetime. On the other hand, the male may opt for a strategy of inseminating as many females as possible, thus increasing his chances for leaving behind progeny (Orians, 1969).

The female, on the other hand, will be concerned with rearing a litter and producing at least one surviving offspring in the next generation. If the male does not participate in parental care, then her selection of a male may not be nearly as critical. On the other hand, if the male does participate to some extent, either in parental care or in enhancing by his efforts her capacity to rear the litter, then her selection of a male to mate with becomes more critical. In any event, the female will have to have access to resources such as food and water in sufficient quantities to guarantee that she will have the economic means at hand to rear her litter. This is especially critical in species that breed during only one season. In a long-lived species with several chances at reproduction in its life history, such availability of resources may be less critical in any one season but, overall, may have the same impact.

Examination of closely related species, such as rodents of the genus *Marmota*, indicates interesting trends in the evolution of mating systems. For example, in the yellow-bellied marmot, *M. flaviventris*, the adult females are somewhat aggressive toward one another, thus spacing themselves out so that sufficient foraging area is available to each of them in order to guarantee sufficient sustenance to see them through their lactation and rearing phase. In an especially rich habitat with a high carrying capacity, females may in effect defend a rather small foraging area. The net result is that a given male can defend

with very little effort several females and thus approximate a polygynous mating system. In areas of poor carrying capacity with a large home range per female, a male may find it economically impractical to defend an area that encompasses more than one female. In this case, the system appears monogamous. Yet the potentiality for expressing a polygynous mating system is there, but in this case its expression is a function of habitat (see Armitage, 1962; Downhower & Armitage, 1971). In this species, there is little direct participation on the part of the male in the rearing of the young; nevertheless, through his own activities, he ensures that a number of adult males do not occupy the same area as the female. Thus, he enhances, through his territorial activities, the reproductive success of a female within his range. This sort of indirect benefit that a female can derive through the defensive presence of a male is widespread in mammalian species that do not show a permanent family unit.

Lest one think that this system typifies reproduction in the genus *Marmota*, however, it should be pointed out that *M. monax*, the woodchuck, shows even less structure in its social unit. The young woodchucks mature very rapidly during the spring of their birth and, through aggressive activities between the adults and themselves, they disperse to establish independent foraging areas prior to their autumnal hibernation (Bronson, 1964). On the other hand, *M. flaviventris* does not show such a quickened rhythm in dispersal of littermates, and the young remain with the female, feeding in her core area and entering hibernation, only to disperse in the following spring.

Barash (1973) has demonstrated yet a more complex social structure in the Olympic marmot, *M. olympus*, where the young of the year do not disperse until their second or third year. Thus, in the Olympic marmot, there is an extended family occupying a defended area with an adult male, one or two adult females, and young of two generations. This unit shows the beginnings of some cooperative behavior. Several individuals may work on the same burrow system. Vocalizations which serve to alert the colony of the presence of potential predators may be given by all colony members, thus increasing the potential for appropriate antipredator behavior by any individual within hearing range, etc. Barash relates the differences in social structure among these marmot species to differences in the length of the plant growing seasons. For *M. monax*, the growing season is long and the young of the year appear to be able to obtain sufficient food

to allow them to reach adult size by autumn; thus they can breed in the following year. The yellow-bellied marmot, occurring at higher elevations, has a shorter growing season, takes longer to mature, and does not breed until two years after its birth. The Olympic marmot, restricted to alpine meadows, takes even a year longer to mature.

This brings up an interesting correlation, then: that extended family units very often involve a slow maturation rate, a greater potential longevity for individuals, and a lower reproductive capacity per individual female. This permits some degree of generation overlap and some emergent survivorship benefits deriving to the young generations from such an association with the adults. Thus, in the case of *M. olympus*, the functional reproductive unit is no longer the mother holding her territory for a given breeding season but the whole parental-offspring complex mutually sharing a territory through several breeding seasons.

The Evolution of Reproductive Systems

We must now explore the question of evolutionary history. In order to do this, we have to make some sort of educated guess concerning the ecological and behavioral baseline from which all contemporary mammalian species derive. Since we cannot study the behavior of fossil forms, we must make inferences concerning their behavior based upon their morphology and upon our interpretation of the mode of habitat exploitation that the extinct species showed. Thus, it is essential to study those species alive today which exhibit a conservative morphology, resembling in their brains, sense organs, and bodies the structure of the early mammals. Such conservative species that occupy niches which we believe to be similar to those occupied by mammals at the Cretaceous-Paleocene boundary will serve as a behavioral baseline (see also Jerison, 1973).

If we are to look for evolutionary trends, let us first formulate a working definition of *conservative morphology*, as well as a definition of *conservative niche*, and then examine the trends in the evolution of courtship, copulation, gestation, and parental care. The exact steps in my argument for the definition of a conservative niche are outlined in a previous publication (Eisenberg, 1975); thus, I will only sketch the sequence here. Suffice it to say that the Class Mammalia

embraces a morphological grade with a polyphyletic origin (i.e., the three living orders attained the grade of mammalian morphological organization independently). It is safe to assume that, as these early premammals adapted, they did so in response to a nocturnal, forested niche. They probably climbed reasonably well and relied on chemical and auditory inputs for distance reception. Auditory input was especially important. The eye was probably used for gross differentiation of distant objects. Early on, the mammals evolved homiothermy, and the female became specialized for producing nourishment for the neonate with the evolution of mammary glands.

It seems probable that the trend away from strict oviparity with large-yolked eggs toward the laying of small-yolked eggs together with the development of mammary glands was evolved in a parallel fashion by both the ancestors of the Monotremes and the ancestors of the Pantotheres. The latter were ultimately ancestral in the Marsupialia and the Eutheria. In these latter two taxa, viviparity was evolved. The marsupials have yolky eggs and typically show the formation of a yolk sac placenta or, in the Peramelidae, a temporary chorioallantoic placenta. Intrauterine development is brief. The eutherians evolved the embryonic trophoblast, chorioallantoic placentation, and a longer gestation period. We can discern in both the marsupials and eutherians advanced and conservative characters of reproduction which are parallel or convergent. In both groups we find that the specialized or "advanced" forms show: (1) a reduced number of ova shed at the time of ovulation, (2) a reduced number of young, (3) an increase in the weight of the neonate, and (4) a lengthening of the gestation period (Portman, 1965; Sharman, 1965). Of course, in all the Marsupialia, the neonate is much less developed at birth than is the case in even the most conservative eutherians. It is fair to say that primitively the Eutheria probably produced several rather altricial young which were initially brooded and suckled by the mother in a nest. On the other hand, in the Marsupialia, the conservative forms produced a number of extremely altricial young which by means of their own motility transferred to a teat area for attachment and nourishment. In most of the Marsupialia, the teat area is enclosed in a pouch.

Some eutherians and marsupials today are undoubtedly occupying niches that are similar to those occupied by ancestral forms at the

Paleocene–Eocene boundary. We may speak of these forms as occupying conservative niches and showing a conservative morphology. The following trends are exhibited by such forms. Conservative mammals primarily feed on energy-rich foodstuffs readily digestible, such as invertebrates, small vertebrates, or fruits. Feeding on plant bodies directly, with the capacity to degrade cellulose, aided by microbial symbionts, is a much later evolutionary adaptation. Although morphologically conservative forms may show reduced metabolic rates when compared with more so-called advanced species, they nevertheless show homiothermy even though they may have evolved facultative hypothermia as a means of passing through periods of food scarcity. Because of their food requirements, these conservative species tend to range over a relatively large area to procure their food. Most of these forms are clearly nocturnal, although the eye may not be necessarily reduced in size. Some frontal vision is possible, and their climbing ability is well developed. Audition is extensively employed in the reception of signals from distant objects. Vision is only secondarily useful in resolving objects in space.

Whether we consider either a eutherian or a marsupial, it is fair to say that the precursors were probably relatively small (50- to 150-gram animals), insectivorous or omnivorous, produced large litters of relatively altricial young and were predisposed for individual foraging patterns and, very probably, a dispersed social organization. For this reason, I choose to consider the contemporary *Marmosa robinsoni*, a marsupial, and other members of the insectivore family, Tenrecidae (*Microgale dobsoni*, *M. talazaci*, and *Hemicentetes semispinosus*), as forms which resemble the early mammals in their foraging patterns and morphology. The living Monotremes (the echidnas and platypus) represent specialized derivatives of an earlier radiation.

This is not to imply that there cannot be specialization within a conservative morphological framework; indeed, many would argue that *H. semispinosus* is highly specialized, which it certainly is. It has specialized for feeding on earthworms with concomitant modifications in its dentition, skull, and forepaws; it has lost its tail, its eye is vastly reduced, and instead of fur it has a spinescent coat and a complicated antipredator defense mechanism. Such specializations offer instructive insight into the limits of specialization within a conservative morphology (Eisenberg & Gould, 1970).

Courtship and Mating

In morphologically conservative species, a given male and female may show overlap in home range and yet show very limited contact except at the time of mating. Parental care generally falls entirely to the female. Nevertheless, the same male and female may mate during consecutive seasons as the result of the proximity of their home ranges and as a result of their own agonistic tendencies toward conspecifics of the same sex. When a male and female establish contact for the purpose of mating, there are preliminary interactions which might be relatively stereotyped in either configuration or sequencing. Such predictable sequences are thought to involve information exchange and may include aspects of chemical, auditory, visual, and tactile input.

Let us then review the trends in mating behavior shown by such morphologically conservative mammals. It will be noted that the production of sound (clicks during the courtship of *Marmosa*, piffs during the courtship of *Tenrec*), olfaction (e.g., nasogenital sniffing and marking), and tactile input (e.g., licking and touching) form prominent aspects of the initial courtship behavior (Eisenberg & Gould, 1970). Visual display is rudimentary at best (see Gould, 1969).

Chemical mediators are strongly implicated in signaling receptivity by the female, and the odors from the male often induce receptivity on the part of the female (for a review see Eisenberg & Kleiman, 1972). The work of Devor and Murphy (1973) and Murphy (1973) on *Mesocricetus auratus* demonstrates that the female produces a substance in her vaginal secretions which actually triggers mounting and copulation on the part of the male. If the olfactory nerves are severed in the male hamster, he will be unable to complete copulation. Thus, in the case of the hamster, odors from the female act on the male almost as classical releasers.

The "priming" effect of odors, sounds, and touch must not be underestimated regardless of whether the female is an induced or spontaneous ovulator. Of course, the distinction between induced and spontaneous ovulation is arbitrary at best. Actually, there appears to be a continuum between, on the one hand, a strict induced ovulator, such as the rabbit, *Oryctolagus*, and, on the other hand, the spontane-

ously ovulating laboratory mouse, *Mus musculus* (Richmond & Conway, 1969).

There have been too few detailed investigations on mammalian courtship to illuminate the effectiveness of various sensory inputs on the induction of receptivity on the part of the female or in the stimulation of the male. It would appear that morphologically conservative eutherian mammals employ chemical signals in the induction of mating, and it would further appear that the females require considerable stimulation to induce ovulation (Eisenberg & Gould, 1970).

One correlation that emerges from an inspection of courtship and copulation of "primitive" mammals is that once intromission has taken place it tends to be long in duration. Morphologically conservative marsupials, as well as eutherians, tend to show a prolonged intromission time (see Table I). Such intromission times seem to correlate with the induction of ovulation and the fact that the female is primed to receive a certain amount of sustained tactile input during copulation. An advancement away from this process of sustained intromission in other lines of mammals seems to have involved: (1) the use of many short intromissions to achieve maximum stimulation of the female, or (2) highly synchronized ovulation induction mechanisms which require a brief copulation with subsequent ovulation on the part of the female, or (3) brief intromission times with maximum stimulation of the female resulting from the evolution of special spines and plates on the penis of the male (see Kleiman, 1974a, for a review of this phenomenon in the caviomorph rodents). Such trends in copulatory behavior have occurred convergently and in parallel fashion across the mammalian orders.

Thus, it would appear that one phylogenetic trend has been to evolve signals which more closely coordinate the timing of copulation and ovulation in the female. The net result may be to reduce actual courtship time in some cases and, in other cases, to reduce the amount of time spent in copulation. Which solution has been selected for, when various species are compared, depends on a great many environmental factors, which are poorly understood.

Aside from these changes in copulation patterns, the basic interaction during courtship leading up to copulation has remained remarkably conservative. Even in such highly specialized forms as the elephant (*Elephas maximus*), tactile and olfactory inputs are primary

Table I. Some Intromission Times for Selected Mammals

Taxon	Range or average intromission duration	Average number intromissions until ejaculation	Author
Marsupialia			
Didelphidae:			
<i>Didelphis marsupialis</i>	~28 min	1	Reynolds
<i>Marmosa mitis</i>	50 min-5 hr	1	Barnes & Barthold
Dasyuridae:			
<i>Antechinus stuarti</i>	up to 9 hr	1	Collins, Ewer
<i>Sminthopsis crassicaudata</i>	2 hr-11 hr	1	Ewer
Macropodidae:			
<i>Macropus kangaroo</i> ^a	20 min-50 min	1	Sharman, Calaby, & Poole
<i>Megaleia rufa</i> ^a	10 min-25 min	1	Sharman <i>et al.</i>
Peramelidae:			
<i>Perameles nasuta</i> ^a	2-4 sec	Several	Stodart
Insectivora			
Tenrecidae:			
<i>Hemicentetes semispinosus</i>	15-25 min	1	Eisenberg & Gould
<i>Setifer setosus</i>	25-<70 min	1	Eisenberg & Gould
<i>Echinops telfairi</i>	17+ min	1	Eisenberg & Gould
Soricidae:			
<i>Blarina brevicauda</i>	3-5 min		Pearson
<i>Suncus murinus</i> ^a	<15 sec	av. 38	Dryden

^a Presumptive specialization in copulation pattern (see text).

in the initial phases of pairing (Eisenberg, McKay, & Jainudeen, 1971). One further point we should not lose sight of is that the pairing phenomenon between male and female mammals, especially in ones that exhibit a solitary social structure, tends to be somewhat prolonged. It is not simply a brief or casual affair. The male may court actively and remain with the female for a period of 48 hours or more. In the life of a small, short-lived mammal, this is a not inconsiderable interval of time. In such solitary mammals as the tiger (*Panthera tigris*), the male and female may court and mate over a period of several days, and, indeed, considering the low conception

rate, such sexual activity may have to be repeated after 45 days when the female again comes into estrus (Kleiman, 1974b).

Parental Care

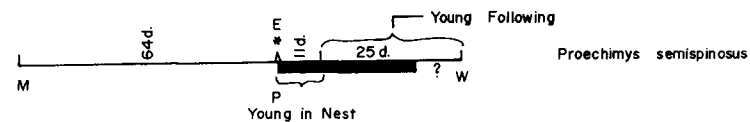
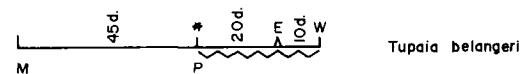
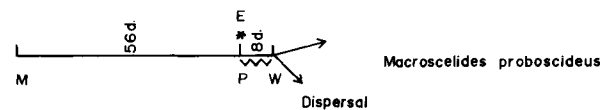
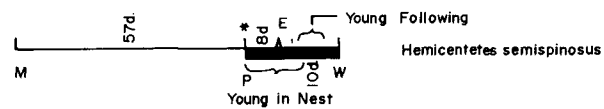
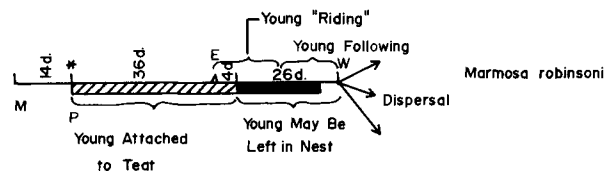
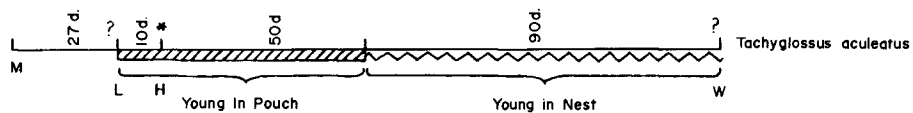
The Basic Maternal Role

The evolution of mammary glands early on set the pattern for reproduction in the Class Mammalia. In a sense, the female is capable of supplying the newborn young with food which is a by-product of her own metabolism. Although certain bird species (Order Columbiformes) have evolved analogous mechanisms, in the main most reptiles and birds do not provide direct by-products from the body as a nutritive source for the hatched young. When parental care is shown in birds, it generally involves either leading the young to food or provisioning the young with foodstuffs collected by the adults. In altricially hatched birds, such provisioning begins at the time of hatching. In birds, very often the feeding involves the participation of both sexes. This is especially true of those bird species in the Order Passeriformes (see Kendeigh, 1952, for review).

The assumption of early neonatal nutrition as the role of the female mammal must have taken place very early in the mammalian evolutionary history, since this is clearly established in the monotremes, marsupials, and eutherians. This initial separation of roles in initial parental care is so profound in the Mammalia that male involvement in parental care during the early development of the neonate is vastly reduced (see Figure 2).

Consider the monotremes: *Tachyglossus aculeatus*, the echidna, takes approximately 177 days to raise the young from conception to semi-independence. After mating with the male, the female takes approximately 27 days to develop the egg within the oviduct. The egg is laid, apparently with the female curled in such a way as to bring the cloaca opposite her pouch. The egg is deposited in the pouch where it undergoes an incubation period of approximately 10 days duration. During this time the female moves little and remains in her burrow. Upon hatching, the young seeks nourishment from the mammary gland orifices, which open into the pouch. The pouch phase of the young lasts approximately 50 days, whereupon its spines begin to develop. At this time, the young is left in the nest while the mother

20d.






begins to forage more frequently alone, returning to the nest to suckle the young during a period of some 90 days, until the young reaches independence. A single young is generally raised (Griffiths, 1968).

The duckbilled platypus, *Ornithorhynchus anatinus*, takes approximately 144 days to rear from one to two young. After mating and fertilization, the female retires to her own burrow system and seals herself in. The egg develops in the oviduct for some 15 days and is laid in a nest. The mother incubates the egg continuously for some 10 days, whereupon it hatches. The young is brooded and nursed in the nest for approximately 120 days, the mother only making excursions to the outside to feed herself (Fleay, 1944).

Turning to the Marsupialia, we may take *Marmosa robinsoni* as a typical developmental cycle. This small animal, seldom exceeding 35 grams adult weight, takes 80 days to raise a litter of around 10 young. After mating, the sexes separate, with the female becoming quite antagonistic toward the male, and the young develop with the aid of a yolk-sac placenta in her uterus for some 14 days. At parturition, the young crawl unaided to the teat area of the mother. In this particular species of opossum, there is no pouch. The young attach to the teat and remain attached for some 30 days, after which the eyes open. Between the 30th and 40th day of age, the young will begin to detach from the teat and at times are transported on the mother's back. The mother forages actively even with pouch young, but, from about 40 days on, the young are left in the nest while the mother forages alone, returning to suckle them. This nest phase for the young lasts approximately 25 days, whereupon they begin to disperse from the nest and initiate an independent life (Eisenberg & Maliniak, 1967; Collins, 1973).

The eutherian tenrec, *H. semispinosus*, takes about 75 days to rear six young to weaning. As with the eutherians, the intrauterine phase is prolonged; 57 days after mating, parturition takes place in a



Figure 2. Time sequences of maternal care activities for selected mammals.  = pouch phase;  = absentee maternal care phase;  = nest phase with maternal brooding; M = mating; H = hatching; L = laying; P = partus; * = beginning of lactation; W = end of weaning period; E = eye opening; d = days. Convergences and parallelisms are indicated when marsupials, monotremes, and eutherians are compared. (See text from Eisenberg, 1975.)

nest. The young are brooded and suckled by the female in her individual nest site for some 14 days, whereupon the young initiate a following response and are guided in their initial foraging by means of signals produced by specialized quills on the female's back, termed *stridulating quills* (Eisenberg & Gould, 1970). The young are weaned, perhaps 22 days postpartum. During the time from 14 to 22 days, the young are acquainted with the area in the vicinity of the female's nest site and are able to orientate themselves to the environment through the initial following response shown with respect to the mother (Eisenberg & Gould, 1970).

The remaining eutherian patterns that I wish to discuss are all characterized by this extended intrauterine phase of development. I would like to point out two variations in the maternal care patterns. One involves the so-called absentee parental care pattern (see Martin, 1968), where the young are born in a special nest site which is visited periodically by the mother for lactation. This system has evolved in a convergent and parallel fashion several times in the eutherian mammals. The elephant shrew, *Macroscelides probosideus*, bears from one to two precocial young in a secluded nest site after a 56-day gestation period. The young are born fully haired with the eyes open. The lactation phase comprises only 11 to 12 days, with the female returning to the nest site to nurse the young and then departing for 24 to 48 hours (Sauer & Sauer, 1972).

The cursorial caviomorph rodent genus, *Dasyprocta*, exhibits a similar life cycle. After a 115-day gestation period, the young, (one to two), are born with the eyes open, generally in a secluded spot, whereupon the female guides the young to a burrow and induces it to enter. The young itself may enlarge the burrow and remains there only to emerge upon the mother's visits for nursing. This hiding-nursing phase may persist for nearly 20 days until the young is strong enough to follow the mother in a manner reminiscent of parental care patterns in many Artiodactylans (Lent, 1974; Smythe, 1970; Kleiman, 1972).

Lest one think that the absentee parental care system is always found in conjunction with precocial young, I should cite the related caviomorph rodent, *Proechimys semispinosus*, which has a litter of one to five young, born with eyes open and fully furred, after a 64-day gestation period. The young are born in a nest within a burrow and are suckled in the burrow for some 38 days prior to weaning.

The young generally do not follow the mother on her nocturnal excursions from the nest until approximately 12 days postpartum. In this case, however, the mother always returns to the same nest site to brood and suckle her litter (Maliniak & Eisenberg, 1971).

Even in highly specialized, recently evolved taxa, the primary female parental role may remain. In the leopard (*Panthera pardus*), the female may carry out all of the primary parental care functions. It would seem that the role of the male, whose home range overlaps that of the female, is in part involved with keeping the area free from other males; the presence of such other males on a long-term basis could considerably reduce the carrying capacity of the area. Thus, the female and her progeny derive indirect benefits through the activities of the male (Muckenhirn & Eisenberg, 1973; Eisenberg & Lockhart, 1972). Furthermore, in species such as the larger cats, the young may remain with the mother for over two years and learn to hunt. The youngsters will simply not be able to survive if they are separated from the mother at too early an age. Thus, a social grouping of two to three individuals is not uncommon in the leopard, but it is a mother family.

The Role of the Male

In all of the preceding examples, we see variations on a common theme, i.e., the initial phases of rearing fall in the main to the female. In spite of this seeming lack of participation, one of the primary roles of the male is to maintain the home range of the female free of males which could compete for resources. As Lockie (1966) has outlined for the Mustelidae, a given female's home range is encompassed by a male's range. In fact, he may even mate with her on subsequent breeding seasons, and, although he does not participate directly in parental care, he certainly reduces competition for prey by keeping the area free from other males.

Brown (1966) comments on similar behavior in small rodents of the genera *Apodemus* and *Clethrionomys*. The home range of an adult male may encompass the home ranges of one or more females. In addition, a dominant adult male has a relatively large home range compared to other subordinate adult males which may partially inhabit the same living space. It appears then that a dominant adult male will tolerate subordinate adult males within his home range but that these

males' movements are inhibited such that they do not forage over an area as widely as would be the case if the dominant adult male were not present. Myton (1974) refers to this as a form of "family clustering" and finds the same sort of behavior in the North American rodent genus, *Peromyscus*.

On the other hand, although early nutritive care in the Mammalia invariably falls to the female, the male may be involved in the rearing of the young at a somewhat later stage. Species of the primate family Callithricidae exhibit profound parental care on the part of the male, since the male generally carries the young during their dependent phase or a major portion of it, transferring them to the female for lactation (Epple, 1967). Furthermore, in the family Canidae of the Carnivora, provisioning of the female by the male and subsequent provisioning of the offspring often involve the adult male or the young of the previous year (Kleiman & Eisenberg, 1973).

In the cape hunting dog (*Lycaon pictus*) and the wolf (*Canis lupus*), males actively provision the female, and the integrity of the pack results from two factors: (1) the tendency for only one pair to reproduce within the pack and (2) the slow maturation of the progeny of the founding adults. These half- to three-quarters-grown animals can provide additional foraging ability in provisioning the founding female and her subsequent progeny (Kleiman & Eisenberg, 1973). Furthermore, such a pack of related individuals can hunt more efficiently and, indeed, show significant cooperation during the hunt for small game, resulting in greater efficiency in prey capture (see Schaller & Lowther, 1969; Mech, 1970). These examples are exceptions rather than the rule, so that when the Class Mammalia is surveyed as a whole, primary parental investment appears to fall to the female.

The overall consequence of this differential investment of energy may be related to the theories of Trivers (1972). As he rightly points out, the parental investment of the female mammal is so heavily involved with her own offspring that male replication of genotype is often not involved with the particular defense of a given female, but rather his reproductive success is a function of how many females he can effectively inseminate. Thus, polygynous systems, in their many forms of expression, are more often the rule in the Class Mammalia than is the case in the Class Aves (see Orians, 1969). The consequences of polygynous mating systems have been reviewed many

times. It should be pointed out, however, that ritual competition among males for access to several breeding females places a high selective advantage upon males with great size: larger horns, teeth, etc. The competition of males imposes a form of social selection often leading to pronounced sexual dimorphism within species. The problem is ably placed in perspective by Crook (1972).

The Derivation of Complex Social Structures

If the social structures exhibited by a species are viewed as adaptive expressions of behavioral phenotypes (Eisenberg, 1966; Crook & Gartlan, 1966; Crook, 1964), then the reproductive unit as a subset of the species' social system is no less the product of natural selection. Mating systems of the Cervidae and Bovidae have been treated from the standpoint of general adaptations to existing environmental conditions (Eisenberg & Lockhart, 1972, pp. 81 to 90; Jarman, 1974), as well as from the perspective of evolutionary history (Geist, 1971, 1966). Of course, such integrative efforts attempt to determine the "averages" of a species' behavior—they seek to define a behavioral "mode" (Leyhausen, 1965b). It is necessary to keep in mind that the methods of sexual attraction and mating as well as parental care are subject to some interindividual variation, and, at best, a "species typical" form of behavior is an abstraction.

Given the species-typical variations of parental care displayed by females whose primary responsibility is the initial rearing of young, we may note in comparing the various evolutionary lines of mammals that the formation of more complicated social configurations has occurred independently many times. If we leave aside migrating herds and roosting colonies of bats, where mother-infant bonds are usually strong but where, otherwise, individual recognition does not seem to be important, and consider only those social structures where individual recognition is important and where the structure itself exhibits a high degree of cohesion, then we find that, over a wide range of mammalian orders, similar forms of social structure have been evolved in a parallel and/or convergent fashion. What specifically have evolved are the behavioral regulatory mechanisms and modes of communication which permit the control of individuals within a social context without pathological repercussion.

As pointed out in an earlier paper (Eisenberg, 1967), species of mammals which are adapted for a more or less solitary existence may in fact be conditioned to live in groups, but, when this is done, reproductive failure generally results (Eisenberg, 1969). Thus a truly social species is one that has the necessary communicatory mechanisms and modes of interaction which permit tolerance with conspecifics without loss of the potential to reproduce. In short, the social structure so formed is in fact a device for replication of itself, and indeed, in an evolutionary sense, the structure has been favored because it favors the reproduction of the species.

The reproductive unit in the Mammalia becomes more complex in terms of the numbers of interacting individuals, if either one or both of the following steps occur: (1) involvement of the male in parental care and (2) retention of some or all current young with the female through a second rearing phase. If (2) occurs, then often the more mature young assist in some manner in the rearing and socialization of the next age class. In order for such systems to develop, the potential for the expression of interindividual aggression must be controlled. Competition among females must be reduced, as well as competition among males. The latter is apparently accomplished less easily since the very fact that primary parental investment lies with the females means that any given male can increase his fitness by mating with as many females as possible (see Trivers, 1972). Such a mating system, however, inevitably leads to competition among males. Thus it should not be surprising that male-male competition is common and has often led in an evolutionary sense to the formation of ritualized mechanisms (e.g., leks, harems, etc.) for competition among males for access to breeding females (Buechner, 1961; Bartholomew & Hoel, 1953; Koford, 1957; Leuthold, 1966; Geist, 1971).

Why have such different reproducing systems evolved? Clearly, the answer must lie in the overall adaptation of the species for the exploitation of its habitat. As Crook (1970) has pointed out, a multiplicity of influences shapes the form of a species' social organization. The distribution of foodstuffs in space, whether clumped and scattered or broadly distributed, sets the stage for, on the one hand, discrete defense of an area utilized and, on the other hand, virtually no defense of a foraging area. As Jarman (1974) has so elegantly shown, the form of an ungulate social organization is very much a function of its overall adaptation to the environment. Its mode of

foraging determines the effective size of the group. The permissibility of area defense by a nonmobile species results in a territorial distribution. Pairing is common among small sedentary browsing ungulates where a male and female defend an area in common and rear their progeny. Larger mobile grazing ungulates show a consistent trend toward the formation of herds.

The form of the antipredator behavior, whether it is built around concealment or individual responses, on the one hand, or, on the other hand, group mobbing effects, profoundly affects the selective advantage for differing forms of social organization (Eisenberg & Lockhart, 1972). Rather than review all the criteria, I refer the reader to Crook's excellent summary (Crook, 1970).

Bearing in mind that the evolution of extended periods of reproductive activity with concomitant longer life and slower maturation rates has often led to the formation of multigenerational social groupings, let us look at some case studies concerning selective advantages that favor evolution of higher social units in the Class Mammalia.

The Matriarchy

One of the more common forms of social organization repeatedly evolved within the Class Mammalia consists of a matriarchy. Essentially, a female and a series of daughters or sisters, age graded, participate mutually in the rearing of their collective progeny. The elephant serves as a typical example.

In a species such as *E. maximus*, the Asiatic elephant, the male participates very little in the initial phases of rearing the young. The most cohesive social structure is the basic matriarchy, a series of related females, raising their calves in common. In the Asiatic elephant, McKay (1973) has shown that the home ranges of these matriarchal herds tend to be distinct and show little overlap. Adult male home ranges overlap considerably with the females'. The males, however, have some input in the parental care system in that they allow younger males, when driven out from the matriarchal herd, to attach themselves to them and thus learn foraging habits, watering places, etc., through association with the adult males. The cow herd itself remains as a very effective antipredator device. Since the young calf would be an easy prey for large predators, the cows through cooperative rearing of the young can provide maximum protection to

the young animals during the first four years of their lives (McKay, 1973).

An incipient form of such a social structure may be shown by the tenrec, *H. semispinosus*. The tenrec configuration generally involves the communal use by several females of a burrow system, but they forage independently. The elephant system actually involves a functional subdivision of the herd into groups of females with young of a similar age class. The female elephants in part act as a defensive unit for the young, and the elephant social structure is necessary for the rearing of young. The tenrec female *Hemicentetes* may in fact rear her young alone, but it is highly dubious that an elephant female would be capable of the same act. It would appear that different selective pressures have promoted similar social configurations, when these two distantly related species are compared. The elephant matriarchy shows cohesion as it moves about and feeds together. In the tenrec, however, collective nesting appears to occur only under conditions where the foraging area for evening feeding is sufficiently large to support a great many tenrecs, while only an extensive burrow system is used in common by several females. If the burrow of the tenrecs is inadvertently broken open by a predator, individual defensive reactions by several females may prove more of an antipredator deterrent than those by a single adult female. Whether this is of any selective advantage in promoting sociality in *H. semispinosus* is at this point speculative. It would appear, however, that the capacity to use restricted burrow sites for communal rearing has some adaptive advantage (Eisenberg & Gould, 1970).

A Matriarchy with Male Attachment

In a similar fashion, lion (*Panthera leo*) prides have evolved essentially because of the mutual advantage accruing to females who hunt communally, since their hunting success is higher when several females hunt together than when one hunts alone (Schaller, 1972). Although each female individually rears her cubs until they are of an age to follow, during the later phases of rearing females hunt together and no doubt increase the chances of cub survivorship by communal feeding at the kill. It would appear that the male lion's primary role in lion society is to keep the area clear of strange males, thus maintaining a higher carrying capacity for the reproductive females and

reducing the amount of interference to the females and cubs from strange males.

Packs as Extended Families

In the case of group-living canids, such as *Canis lupus*, *Lycan pictus*, and *C. aureus*, we have an extended family based on a single reproductive pair and their progeny of the previous breeding season. In the case of the wolf pack, delayed sexual maturation on the part of young males may maintain them in the group for two or three years. In the case of the jackal, with the onset of sexual maturity the young males and often young females disperse immediately. Thus, the jackal maintains what appears to be a pair configuration or pair with young, while the wolf may show a larger grouping. Nevertheless, the basic structure is quite similar. In these group-living canids, participation in hunting permits them to obtain larger prey than would necessarily be the case if they hunted alone. The male actively provisions the female and her cubs, and provisioning is a group effort, with parents and subadults provisioning younger animals. In all cases, however, there is generally only one reproducing pair of animals, the founding father and mother, within the so-called pack (see Kleiman & Eisenberg, 1973).

The Influence of Phylogeny

Some mammalian taxa exhibit rather uniform trends in the expression of their social organization, which may in fact be related to a single overriding environmental parameter, interplaying with the unique phylogenetic background of the family in question. If we compare two families of desert rodents, the Dipodidae (jerboas), on the one hand, and the Heteromyidae (kangaroo rats and pocket mice), on the other, this point can be made clear. The kangaroo rats evolved in the deserts of North America convergent to the evolution of the jerboas in Central Asia and North Africa. The dipodids have apparently had the longer evolutionary history and in many respects are more specialized. The two families show in common the following attributes: bipedal locomotion, highly developed techniques for gathering seeds from sand, similar forms of burrow construction; but they differ profoundly in that most of the dipodids accumulate large fat

reservoirs and hibernate during the winter, whereas the kangaroo rats do not accumulate fat reservoirs, do not hibernate, and instead cache vast quantities of seeds in individually defended burrow systems. The seed-caching habit and the high development of potential to express aggressive behavior results in individual occupancy of burrows for all adult kangaroo rats (Eisenberg, 1963).

On the other hand, in the family Dipodidae, greater degrees of social tolerance may be shown. Apparently selection has not favored mechanisms to ensure complete burrow defense, probably as a response to relaxed selective pressure for defense of a cache. Thus, a family such as the North American Heteromyidae may show an enduring trend toward a solitary dispersed social system, whereas the convergently evolved Dipodidae show more variations on the theme, presumably because their overwintering system is not based upon a seed-caching pattern (Eisenberg, 1967).

To summarize then, the social structures manifested by a given species are the product of selective pressures, which vary from one species to the other as a function of the particular ecological niche they exploit. Given the basic mammalian reproductive unit, in the course of adaptation the mammals have evolved alternative expressions based upon either (1) extending the group by retaining females within it, creating a matriarchy, or (2) incorporating the male in some form of parental care, thus constituting a nuclear family, or (3) a combination of both. The step beyond this is to incorporate several males and several females into an extended rearing group, and this has been accomplished within primates, cetaceans, and some ungulates (Eisenberg, 1966). Even so, there is almost invariably a hierarchy among the males and females with differential reproductive success depending upon one's position in the hierarchy. Generally in such social configurations more dominant males have a greater reproductive success. To some extent the trend is masked in the female hierarchy.

The Multimale System

In spite of the apparent differences in such multimale and multifemale social groupings, they are in fact variations on the same theme of extended nuclear families, and almost invariably the affiliation mechanisms among the members result from a developmental

history within the same kin group. I think as a rule of the thumb it is fair to say that the female band or female component of such social configurations shows the greatest stability and that young males tend to move between groups, thus introducing outbreeding and reducing the potential for extensive inbreeding.

The manner in which young males can transfer from one social group to the next is variable. In primates, such as the langurs of the genus *Presbytis*, the takeover is often violent with loss of young and serious wounding through male fighting (Rudran, 1973). [A similar phenomenon has been noted for the lion (*Panthera leo*) (B. Bertram, personal communication).] In species of primates such as the Ceylon macaque, *Macaca sinica*, the takeover may be gradual and may in-

Table II. Glossary of Common Names

<i>Antechinus stuarti</i> , Stuart's marsupial mouse	<i>Marmota olympus</i> , Olympic marmot
<i>Apodemus</i> , Old World wood mouse	<i>Megaleia rufa</i> , red kangaroo
<i>Blarina brevicauda</i> , short-tailed shrew	<i>Mesocricetus auratus</i> , golden hamster
<i>Canis aureus</i> , golden jackal	<i>Microgale dobsoni</i> , Dobson's long-tailed tenrec
<i>Canis lupus</i> , wolf	<i>Microgale talazaci</i> , long-tailed tenrec
<i>Clethrionomys</i> , red back vole	<i>Mus musculus</i> , house mouse
<i>Cynomys ludovicianus</i> , black-tailed prairie dog	<i>Ornithorynchus anatinus</i> , platypus
<i>Dasyprocta</i> , agouti	<i>Oryctolagus</i> , rabbit
<i>Didelphis marsupialis</i> , Virginia opossum	<i>Panthera leo</i> , lion
<i>Echinops telfairi</i> , lesser hedgehog tenrec	<i>Panthera pardus</i> , leopard
<i>Elephas maximus</i> , Asiatic elephant	<i>Panthera tigris</i> , tiger
<i>Hemicentetes semispinosus</i> , streaked tenrec	<i>Peromyscus</i> , deer mouse
<i>Lycaon pictus</i> , African hunting dog	<i>Presbytis</i> , langur monkey
<i>Macaca sinica</i> , toque macaque	<i>Proechimys semispinosus</i> , spiny rat
<i>Macropus gigantea</i> , grey kangaroo	<i>Setifer setosus</i> , giant hedgehog tenrec
<i>Macroscelides proboscideus</i> , elephant shrew	<i>Sminthopsis crassicaudata</i> , fat-tailed marsupial mouse
<i>Marmosa mitis</i> , masked mouse opossum	<i>Suncus murinus</i> , musk shrew
<i>Marmosa robinsoni</i> , mouse opossum	<i>Tachyglossus aculeatus</i> , echidna
<i>Marmota</i> , woodchucks and marmots	<i>Tamiasciurus</i> , North American red squirrels
<i>Marmota flaviventris</i> , yellow-bellied marmot	<i>Tenrec</i> , common tenrec
<i>Marmota monax</i> , woodchuck	

volve mutual support among males seeking to attach themselves to a new troop with reduced antagonism (Dittus, 1974).

This brings us then to the question of the genesis of multimale units, that is, social structures where several males are combined with several females into a cohesive foraging unit or, if it subdivides, then a unit where great mutual tolerance is shown when the subdivisions come together. Although multimale social groupings are found in several mammalian orders, the question is most controversial in the order Primates. In an earlier publication (Eisenberg *et al.*, 1972), it was suggested that, although this form of social structure appears to have evolved convergently several times within the primates, many of such multimale societies that have been described are more apparent than real. It was suggested that the multimale condition in some species may in fact be viewed as an age-graded male system with a dominant founding male in reality doing most of the breeding. His nearly grown sons by their presence may contribute to successful antipredator defense or competitive defense against conspecific troops but, in fact, be dominated and graded according to their age. Ultimately, emigration by nearly adult or adult males would result in the formation of new troops either by stealing females or by taking over established troops while displacing the resident adult and his cohorts. Some credence for his view is to be derived from the research on monkeys of the genus *Presbytis*. As outlined by Rudran (1973), the structure of langur troops may in fact reflect differential responses to density, and the male takeover so dramatically demonstrated in these species may occur with a frequency that parallels the density of the troops themselves. While I do not mean to imply that the genesis of *Presbytis* groupings is typical for all primates which exhibit multimale or age-graded male systems, I do want to suggest that trends toward polygyny and exclusive access to females during the time of ovulation by a single male may be more widespread than is supposed.

Future Problems

Although we have talked a great deal about discrete social systems as mechanisms for self-replication, it should be pointed out that in natural populations these reproductive systems are functionally organized within an ecosystem to constitute a deme. The deme is a

temporarily reproductively isolated collection of individuals which may produce young of at least two behavioral phenotypes, young which will be integrated as replacements in the founding area and young that emigrate to found new groups in new areas. This, in fact, is the real unit of reproduction as so ably pointed out by Anderson (1970). While I do not want to make excursions into population genetics at this point, I only wish to indicate that the discrete social structures which we have been talking about are components of a larger integrated system for self-replication, which we have only begun to think about, let alone describe and classify.

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