



MONOGAMY IN MAMMALS

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ABSTRACT

This review considers the behavioral, ecological, and reproductive characteristics of mammals exhibiting monogamy, i.e., mating exclusivity. From a discussion of the life histories of selected species of monogamous primates, carnivores, rodents and ungulates, several trends emerge. Two forms of monogamy occur, Type I, facultative, and Type II, obligate. The selective pressures leading to these two forms of monogamy may have been different. Facultative monogamy may result when a species exists at very low densities, with males and females being so spaced that only a single member of the opposite sex is available for mating. Obligate monogamy appears to occur when a solitary female cannot rear a litter without aid from conspecifics, but the carrying capacity of the habitat is insufficient to allow more than one female to breed simultaneously within the same home range.

Within both types of monogamy, the following traits are typically seen: (1) adults show little sexual dimorphism either physically or behaviorally; (2) the adult male and female exhibit infrequent socio-sexual interactions except during the early stages of pair bond formation. Additional trends specific to mammals exhibiting obligate monogamy are: (1) the young exhibit delayed sexual maturation in the presence of the parents, and thus only the adult pair breeds; (2) the older juveniles aid in rearing young siblings; and (3) the adult male (father) aids in the rearing of young by any or all of the following: carrying, feeding, defending, and socializing offspring.

INTRODUCTION

AZOOLOGICAL definition of monogamy is the "habit of having only one mate" (Webster's *New World Dictionary*, 1966). In mammals, it is usually implied that the mated pair remain together through several breeding seasons; thus the relationship may cover a considerable portion of the lifespan of the pair. It need not imply a lifetime relationship since, if one member of the pair dies, the remaining mate may develop a bond with a new conspecific individual. In birds, the concept covers both species with long-term relationships and species in which the pair bond is only maintained for a single breeding season, but the male remains with the female after mating and during the rearing of offspring (Lack, 1968).

The concept of monogamy implies exclusivity in mating, i.e., a given male and female will mate only with each other. This requirement, of

course, has yet to be proven to exist for the vast majority of birds and mammals which are said to be monogamous. Only biochemical or long-term behavioral evidence could demonstrate mating exclusivity (see Hendrichs, 1975, for proof of long-term bonding in the dik-dik, *Madoqua kirki*). Thus, monogamy is generally recognized in the field and in captivity by a variety of less stringent characteristics, including (1) the continual close proximity of an adult heterosexual pair both during and outside periods of reproduction, (2) mating preferences, and (3) an absence of adult unrelated conspecifics from the pair's home range, territory, or nest. Overt aggression towards adult conspecifics of the same sex (excluding their own offspring) need not be seen, but might support Point # 3. (4) Breeding by only one adult pair in a family group also supports the probability of monogamy.

Monogamy does not imply anything concerning the frequency of social or sexual interac-

tions between mates. Rothe (1975), in a recent discussion of sexuality in the common marmoset (*Callithrix jacchus*), has suggested that an emotional bond is a requirement for monogamy. The usefulness of this condition as a criterion for monogamy is limited because mating exclusivity has genetic consequences, whereas an emotional bond (or lack of bond) does not. Monogamy also does not imply anything about the degree of paternal investment. However, since pairs often live in proximity, males may be frequently exposed to their own offspring.

Monogamy is a relatively rare phenomenon in mammals (Eisenberg, 1966, in press; Orians, 1969; Alexander, 1974), but is among the more highly evolved forms of social organization in this class of animals, since it often involves a considerable degree of tolerance towards a single conspecific individual over a long period of time and usually outside the context of mating. Whereas more than 90 per cent of all bird species are monogamous (Lack, 1968), the reverse appears to be true for mammals, less than 3 per cent of mammalian species having been reported as monogamous. Table 1 summarizes the mammalian species in which monogamy apparently occurs. Due to the paucity of information on the social behavior of many mammalian species, especially small rodents and bats, this list is obviously incomplete. Moreover, the basis for each decision differs and is stronger for some species than others. Where data are available from both captive and field studies, the decision is more reliable. Even so, some species may have to be removed from the list after further study. In some families of mammals, e.g., the marmosets and tamarins (Callitrichidae) and dogs and foxes (Canidae), monogamy is the most common form of social organization.

Close examination of Table 1 suggests that the size of the typical social grouping observed in the field may differ between species all of which are called monogamous. For example, in the elephant shrews *Rhynchocyon chrysopygus* and *Elephantulus rufescens*, in which males and females exhibit mating exclusivity, adult pairs have completely overlapping territories, but are not often observed together (Rathbun, 1976). They are never reported as occurring in family groups. Field observations of dik-diks, *Madoqua kirki* (Hendrichs and Hendrichs, 1971; Hen-

drihs, 1975), suggest a similar pattern although the parents and young are occasionally seen as a family unit. This pattern of monogamy will hereafter be referred to as Type I Monogamy.

By contrast, the marmosets and tamarins (Callitrichidae), gibbons and siamang (Hylobatidae), beaver (*Castor fiber*), and wolf (*Canis lupus*) are commonly observed as family groups consisting of the adult pair and more than one generation of young. This pattern will be referred to as Type II Monogamy. Differences between these two observed forms of monogamy will emerge in this paper. Some monogamous species cannot be placed easily into either category.

In this review I will summarize the behavioral and morphological characteristics common to mammalian species exhibiting monogamy, and especially the variations in the degree of paternal investment that exist within the monogamous social system and the form and frequency of social and sexual interactions. I will concentrate on only a few reasonably well studied species, since it is difficult to compare data from different studies, some of which were conducted in captivity and others in the field.

One comment should be made at the outset. The intent of this review is to determine whether there is an adaptive syndrome that characterizes the monogamous mammal, on the basis of behavioral, morphological, and ecological characteristics. If such a syndrome exists, it does not mean that each characteristic will be observed in every species exhibiting monogamy. Alternatively, a feature common to monogamous mammals may be found in a species exhibiting another breeding system.

Finally, it should be emphasized that many factors influence the social organization of a species and that, under different ecological conditions, a species may stray from what is considered to be its modal social system in an optimum habitat. Thus, some species considered to be basically monogamous might, under some conditions, exhibit polygamy. Obviously, the reverse condition also holds (see Barash, 1975, for an example).

ECOLOGICAL AND REPRODUCTIVE CORRELATES OF MONOGAMY

Table 2 summarizes the basic features of selected genera of mammals from four orders

in which monogamy has been reported as the most common form of social system. These forms were chosen since (1) they exhibit a variety of life styles (including both Type I and Type II Monogamy), and (2) there is a reasonable literature on their behavior, either in captivity, in the wild, or both.

Eisenberg (1966) has suggested some recurrent patterns found in mammalian species exhibiting monogamy. For example, monogamy is correlated with a low reproductive potential and a long maturation period for young. To some degree, the data in Table 2 confirm the low reproductive potential of monogamous mammals. None of the genera listed raise more than an average of four young per year under natural conditions. However, closely related non-monogamous forms may produce similar numbers of young, e.g., the primates and artiodactyls typically have litters of one or two.

More important, the sexual maturation of young in some monogamous mammals may occur later than in related non-monogamous forms. For example, dwarf mongooses (*Helogale*) and jackals and coyotes (*Canis*) may reach puberty at two years of age or even when older (Asdell, 1964; Rasa, 1973a), whereas other small to medium-sized carnivores, such as the raccoon (*Procyon lotor*) and the mongoose (*Herpestes auro-punctatus*) are sexually mature and breed in the year following birth (Asdell, 1964; Ewer, 1973). The beaver (*Castor fiber*) matures later than any other rodent, i.e., at two years. The acouchi (*Myoprocta pratti*) matures at 9 months, whereas for other non-monogamous and polyestrous caviomorph rodents, sexual maturity occurs at less than 3 months in most cavies (Rood, 1972), at 5 months in the coypu (*Myocastor coypus*) (Newson, 1966), and at 3 to 4 months in the casiragua (*Proechimys guairae*) (Weir, 1973).

The age of puberty in some monogamous species appears to correlate with whether or not the young remain with the parents, i.e., whether they are Type I or II species. In dikdiks (*Madoqua kirki*), which mature at 6 months, the young are weaned and driven off shortly before a subsequent birth (Hendrichs and Hendrichs, 1971), whereas juveniles of the other forms (marmosets, tamarins, gibbons, jackals, dwarf mongooses and beavers) remain with the parents and often aid in the care of the

next litter, and thus create a family unit. Moreover, inhibition of reproduction after the age of sexual maturity is common in juveniles remaining with the adults in the artificial conditions of captivity. This is well documented for the marmosets and tamarins (Epple, 1967; Rothe, 1975) and the dwarf mongoose (Rasa, 1973a). In packs of wolves (*Canis lupus*), which are composed of related individuals (family members), the two dominant parents are often the only animals to breed and rear young (Mech, 1970; Altmann, 1974). This pattern of using juveniles and subadults as parental surrogates has been referred to as a "parental manipulation of progeny" (Alexander, 1974), whereby the older offspring care for subsequent litters of their parents while their own reproduction is inhibited. Such "manipulation" improves the reproductive output of the parent at the expense of that of some of their offspring, at least for a time. There are, of course, benefits to the offspring, mainly in the prolongation of parental protection through the continued association with the family unit and the acquisition of experience in rearing young. Presumably the age at which young do, in fact, leave the family and bear their own young will depend on such ecological factors as the availability of food and a territory. However, it is likely that, under some conditions, the young may remain with the parents throughout their lives and never themselves reproduce. Such "altruistic" individuals will perpetuate their own genes by improving the survivorship of their siblings.

A further look at Table 2 suggests no other clear-cut ecological or reproductive correlations with the existence of a monogamous social system. Monogamous species may be nocturnal, crepuscular, or diurnal in habit. Their feeding habits range from the highest (carnivore) to the lowest (herbivore) trophic level. Their breeding may occur seasonally or at any time in the year, and the condition of the neonate may vary from the altricial dwarf mongoose (Rasa, 1975) to the mobile precocial acouchi (Kleiman, 1972).

EVOLUTION OF MONOGAMY

Since the female mammal has internal gestation and feeds developing offspring with products of her body, she is indispensable for the rearing of young. By contrast, a male partner is essential only for inseminating the female and

TABLE 1

Mammalian species exhibiting monogamy.

The probability that a species exhibits Type I or Type II Monogamy is suggested in parentheses where sufficient data are available to allow such a classification.

MAMMAL	COMMON NAME	BASIS FOR DECISION	REFERENCE
MARSUPIALIA			
Phalangeridae	Honey possum	F2	Troughton 1941; Gewalt & Grzimek, 1972
<i>Tarsipes spencerae</i>			
INSECTIVORA			
Solenodontidae	Solenodon	F3, C1 (II)	Mohr, 1936-38; Eisenberg, 1975
<i>Solenodon paradoxus</i>			
Tenrecidae	Microgale	F2, C1, C2, C4 (I)	Eisenberg & Gould, 1970
<i>Microgale talazaci</i>			
Macroscelididae	Elephant shrew	F1, C1, C2, C4 (I)	Walker, 1975; Rathbun, 1976; Kingdon, 1974a
<i>Elephantulus rufescens</i>			
<i>Rhynchocyon chrysopygus</i>	Golden-rumped elephant shrew	F1, F2, C1, C4 (I)	Grzimek, 1972; Rathbun, 1973 (cited in Kingdon, 1974a), 1976
Soricidae	Etruscan shrew	F3, C1, C2	Fons, 1974
<i>Suncus etruscus</i>			
CHIROPTERA			
Phyllostomatidae	False vampire	F3, C2	Greenhall, 1968; Goodwin & Greenhall, 1961; Bradbury, in press
<i>Vampyrum spectrum</i>			
Nycteridae	Hollow-faced bats	F2, F3	Brosset, 1966; Verschuren, 1957; Bradbury, in press
<i>Nycteris hispidus</i>			
<i>Nycteris arge</i>			
<i>Nycteris nana</i>			
Emballonuridae	Pel's pouched bat Mauritian tomb bat	F3	Brosset, 1966; Verschuren, 1957; Bradbury, in press
<i>Taphozous peli</i>			
<i>Taphozous mauritanus</i>			
Hipposideridae	Old World leaf-nosed bats	F2, F3	Brosset, 1966; Bradbury, in press
<i>Hipposideros brachyotis</i>			
<i>Hipposideros beatus</i>			

Rhinolophidae					
<i>Rhinolophus luctus</i>	Horseshoe bat	F2			Brosset, 1966; Bradbury, in press
Megadermatidae					
<i>Lavia frons</i>	Yellow-winged bat	F2, F3			Wickler & Uhrig, 1969
Vespertilionidae					
<i>Kerivoula</i> sp.	Trumpet-eared bat	F2, F3			Brosset, 1966; Bradbury, in press
PRIMATES					
Indridae					
<i>Indri indri</i>	Indri	F3 (II)			Petter, 1965; Petter & Peyrieras, 1974; Pollock, 1975
Callitrichidae					
<i>Cebuella pygmaea</i>	Pygmy marmoset	F2, F3, C1, C2, C4 (II)			Ramirez, Freese, and Revilla, in press; Christen, 1974
* <i>Callithrix jacchus</i>	Common marmoset	C1, C2, C4 (II)			Epple, 1967; Rothe, 1975
* <i>Saguinus oedipus</i>					
<i>Saguinus geoffroyi</i>	Tamarin	F2, F3, C1, C2, C3, C4 (II)			Moynihan, 1970; Epple, 1970a, 1972, 1975b; Dawson, in press; Neyman, in press; Christen, 1974; Freese, Freese, and Castro, in press; Castro & Soini, in press.
<i>Saguinus mystax</i>					
<i>Saguinus fuscicollis</i>					
<i>Saguinus nigricollis</i>					
<i>Saguinus midas</i>					
<i>Saguinus imperator</i>					
<i>Leontopithecus rosalia</i>	Lion tamarin	F2, F3, C1, C2, C3, C4 (II)			Coimbra-Filho & Mittermeier, 1973; Snyder, 1974, Kleiman, unpubl.
Callimiconidae					
<i>Callimico goeldii</i>	Goeldi's marmoset	C1, C2 (II)			Heltne, et al., 1973; Lorenz, 1972
Cebidae					
<i>Aotus trivirgatus</i>	Night monkey	F2, F3, C1, C2, C3, C4 (II)			Moynihan, 1964
* <i>Callicebus moloch</i>					
<i>Callicebus torquatus</i>	Titi monkey	F2, F3, C1, C2, C3, C4 (II)			Moynihan, 1966; Mason, 1966, 1974a, b; Izawa, 1976
* <i>Pithecia pithecia</i>	Pale-headed saki	F2, F3 (II)			Izawa, 1976
<i>Pithecia monachus</i>	Monk saki	F2, F3 (II)			Napier & Napier, 1967

TABLE I (continued)
Mammalian species exhibiting monogamy

MAMMAL	COMMON NAME	BASIS FOR DECISION	REFERENCE
Cercopithecidae <i>Presbytis potentillani</i>	Mentawai leaf monkey	F2, F3, C1, C2 (II)	Tilson & Tenaza, 1976
Hylobatidae * <i>Hylobates lar</i> <i>Hylobates concolor</i> <i>Hylobates klossi</i> <i>Symphalangus syndactylus</i>	White-handed gibbon Black gibbon Kloss' gibbon Siamang	F2, F3, C1, C2, C3, C4 (II) F2, F3, C1, C2 (II)	Carpenter, 1940; Ellefson, 1974; Tenaza, 1975; Chivers, 1972 Chivers, 1972, 1975
RODENTIA Cricetidae <i>Ondatra zibethicus</i> <i>Peromyscus californicus</i> <i>Peromyscus polionotus</i> <i>Peromyscus maniculatus</i> <i>Peromyscus eremicus</i> <i>Baiomys taylori</i> <i>Onychomys leucogaster</i> <i>Onychomys torridus</i>	Muskrat Deermouse Beach mouse Deermouse Cactus mouse Pygmy mouse Northern grass- hopper mouse Southern grass- hopper mouse African dormouse	F2, F3 F1, F2, F3, C1, C2 C4 (II) C1, C2 F2, F3, C1, C2, C3, C4 (II) F2, F3, C4 (II) F3, C1, C2, C3 (II)	Lowery, 1974; Jackson, 1961 Eisenberg, 1962, 1963, 1968; Blair, 1951; McCabe & Blanchard, 1950; Howard, 1949 Blair, 1941 Horner & Taylor, 1968; Ruffer, 1965; Egoscue, 1960; Pinter, 1970 Hendrichs, 1972; Kingdon, 1974b Stanley, 1971
Gliridae <i>Graphiurus murinus</i>	Hopping mouse	F2, F3, C4 (II)	Hendrichs, 1972; Kingdon, 1974b
Muridae <i>Notomys alexis</i>	Pygmy mouse Striped or zebra mouse	F2	Nel, 1975 Hendrichs, 1972
<i>Mus minutoides</i> <i>Lemniscomys barbarus</i>	Tree rat Dwarf mouse Smoky meadow rat	F2 F2 F2 F2	Hendrichs, 1972 Hendrichs, 1972 Hendrichs, 1972 Hendrichs, 1972

<i>Thallomys paetulus</i>	Acacia rat	F2, F3	Kingdon, 1974b
<i>Mastacomys fuscus</i>	Broad-toothed rat	F1, C1	Calaby & Wimbush, 1964
Castoridae			
<i>Castor fiber</i>	Beaver	F2, F3, C1, C2, C4 (II)	Wilsson, 1968, 1971; Hediger, 1970
Hystricidae			
<i>Hystrix cristata</i>	African porcupine	F3, C1, C2	Shortridge, 1934, Kingdon 1974b; Mohr, 1965
<i>Atherurus africanus</i>		F2, F3, C1	Rahm, 1962; Kingdon, 1974b
Capromyidae			
<i>Capromys melanurus</i>	Hutia	F3, C1, C2, C4 (II)	Bucher, 1937
<i>Plagiodontia aedium</i>		C1, C2, C4	Eisenberg, unpubl.
Caviidae			
<i>Dolichois patagonum</i>	Mara	F3, C1, C2, C3, C4 (II)	Mohr, 1949; Dubost & Genest, 1974; Krieg, 1929
Dasyproctidae			
<i>Myoprocta pratti</i>	Acouchi	F3, C1, C2, C4	Kleiman, 1971, 1972
<i>Dasyprocta punctata</i>	Agouti	F1, C1, C2, C4 (I)	Smythe, 1970
<i>Cuniculus paca</i>	Paca	F1, C1, C2, C4 (I)	Smythe, 1970
Dinomysidae			
<i>Dinomys branickii</i>	Pacarana	F2, C1, C4 (I)	Tate, 1931; Collins & Eisenberg, 1972
Pedidae			
<i>Pedetes affter</i>	Springhaas	F2, F3, C1	Kingdon, 1974b
MYSTICETI			
Balaenidae			
<i>Balaena mysticetus</i>	Bowhead whale	F2, F3	Slijper, 1962
CARNIVORA			
Canidae			
* <i>Canis lupus</i>	Wolf	F2, F3, C1, C2, C3, C4 (II)	Mech, 1970; Golani & Keller, 1975; Ryden, 1974; Van Lawick, 1971; Eisenberg & Lockhart, 1972; Zimen, 1971; Gier, 1975; Van der Merwe, 1953; Hendrichs, 1972
<i>Canis latrans</i>	Coyote		Chesemore, 1975; MacPherson, 1969
<i>Canis aureus</i>	Golden jackal		
<i>Canis mesomelas</i>	Black-backed jackal		
<i>Alopex lagopus</i>	Arctic fox	F2, F3, C1, C2 (II)	

TABLE 1 (continued)
Mammalian species exhibiting monogamy

MAMMAL	COMMON NAME	BASIS FOR DECISION	REFERENCE
<i>Vulpes vulpes</i>	Red fox	F2, F3, C1, C2 (II)	Tembrock, 1957; Storm, 1965; Ables, 1975; Egoscue, 1962; Kilgore, 1969
<i>Vulpes macrotis</i>	Kit fox		
<i>Vulpes velox</i>	Swift fox		
<i>Urocyon cinereoargenteus</i>	Gray fox	F2, F3, C1 (II)	Trapp & Hallberg, 1975
<i>Fennecus zerda</i>	Fennec fox	C1, C2 (II)	Gauthier-Pilters, 1962, 1966; Koenig, 1970
<i>Nyctereutes procyonoides</i>	Raccoon dog	C1, C2, C4 (II)	Seitz, 1955; Kleiman, unpub.
<i>Otocyon megalotis</i>	Bat-eared fox	F2, F3, C1 (II)	Smithers, 1966; Hendrichs, 1972; Kleiman, 1967
<i>Cerdocoyon thous</i>	Crab-eating fox	F2, F3, C1, C2, C4 (II)	Kleiman, unpub.; Cabrera & Yepes, 1960
<i>Dusicyon culpaeus</i>	Culpeo	F2, F3 (II)	Housse, 1949
<i>Dusicyon griseus</i>	Gray fox		
<i>Speothos venaticus</i>	Bush dog	C1, C2, C4 (II)	Jantschke, 1973
<i>Lycan pictus</i>	Cape hunting dog	F2, F3, C1, C2, C4 (II)	Van Lawick 1971; Kühme, 1965
Mustelidae			
<i>Meles meles</i>	Badger	F2, F3, C1, C2 (II)	Neal, 1948; Gucwinska & Gucwinska, 1968; Van Wijngaarden & Van de Peppel, 1964
<i>Lutrogale perspicillata</i>	Indian smooth otter	C1, C2, C4 (II)	Duplaix-Hall, 1971, 1975
<i>Amblonyx cinerea</i>	Asiatic clawless otter	C1, C2, C4 (II)	Lancaster, 1975; Duplaix-Hall, 1971, 1975; Hoogerworf, 1970
Viverridae			
<i>Helogale parvula</i>	Dwarf mongoose	F3, C1, C2, C3, C4 (II)	Rasa, 1973a, 1975
<i>Suricata suricatta</i>	Meercat	F3, C1, C2 (II)	Ewer, 1963, 1973; Wemmer & Fleming, 1975
<i>Fossa fossa</i>	Fanaloka	F2, C1, C2 (II)	Albignac, 1973

<i>Eupleres goudouii</i>	F2, C1, C2 (II)	Albignac, 1973
<i>Gallidia elegans</i>	F2, F3, C1, C2, C4 (II)	Albignac, 1973
<i>Mungotictis decemlineata</i>	F2, F3, C1, C2 C4 (II)	Albignac, 1973
PINNIPEDIA		
Phocidae		
<i>Phoca vitulina largha</i>	F2, F3 (breeds on ice)	Burns & Fay, 1972; Burns et al., 1972
<i>Halichoerus grypus</i>	F2, F3 (only Canadian ice- breeding form)	Hewer, 1974
<i>Lobodon carcinophagus</i>	F2, F3	Stirling, 1975
<i>Cystophora cristata</i>	F2, F3	Olds, 1950; Scheffer, 1958
ARTIODACTYLA		
Bovidae		
<i>Cephalophus maxwelli</i>	F2, F3, C1, C2, C3 (I)	Ralls, 1973, 1974; Aeschlimann, 1963
<i>Sibicapra grimmia</i>	F2, C4	Wilson & Clarke, 1962
<i>Madoqua kirki</i>	(I) F2, F3, C1, C2, C3, C4	Hendrichs & Hendrichs, 1971; Tinley, 1969; Simonetta, 1966
<i>Oreotragus oreotragus</i>	F2, F3, C1, C2 (I)	Cunco, 1965; Hendrichs, 1972; Tinley (cited in Estes, 1974)
<i>Raphicerus campestris</i>	F2, F3, C1, C3 (I)	Hendrichs, 1972; Chalmers, 1963
<i>Redunca arundinum</i>	F1, F2 (I)	Jungius, 1971
<i>Redunca redunca</i>	F2, F3 (I)	Hendrichs, 1972

Key:

Field observations:

- F1 = The members of a pair exhibit complete home range overlap.
- F2 = The members of a pair occur in close proximity.
- F3 = Family groups described.

Captive or close field observations:

- C1 = Heterosexual pair is tolerant and will cohabit at all times.
 - C2 = Heterosexual pair will breed and remain together during rearing phase without fighting.
 - C3 = Mating preference described.
 - C4 = Unisexual aggression is common.
- * All species in a given genus are probably monogamous.

TABLE 2
The natural history of selected mammalian genera exhibiting monogamy

GENUS	TYPE OF STUDIES	HABITAT	MODE OF LIFE	FEEDING HABITS	ACTIVITY RHYTHM	REPRODUCTIVE CYCLE	LITTER SIZE	CONDITION OF YOUNG AT BIRTH*	REFERENCE
Primates									
Marmoset (<i>Callithrix</i>)	C	Tropical rainforest	Arboreal	Frugivore, omnivore	Diurnal	Polyestrus	1-3	2	Epple, 1970a; Rothe, 1975; Hearn, in press
Tamarin (<i>Saguinus</i>) (<i>Leontopithecus</i>)	C,F	"	"	"	"	Seasonally polyestrus	1-3	2	Epple, 1970a; Dawson, in press; Hampton et al., 1966; Neyman, in press; Moynihan, 1970; Kleiman, in press
Gibbon & siamang (<i>Hylabates</i>) (<i>Symphalangus</i>)	C,F	"	"	"	"	Polyestrus	1	2	Carpenter, 1940; Chivers, 1972, 1975; Ellefson, 1974
Carnivores									
Coyote/jackal/wolf (<i>Canis</i>)	C,F	Savanna, mixed forest, scrub	Terrestrial	Carnivore, omnivore	Crepuscular	Seasonally monoestrus	2-6	2	Kleiman, 1968; Kleiman & Eisenberg, 1973; Mech, 1970; Golani & Keller, 1975; Gier, 1975
Dwarf mongoose (<i>Helogale</i>)	C	Mixed savanna	"	Omnivore	Diurnal	Seasonally polyestrus	1-4	1	Rasa, 1972, 1975
Rodents									
Acouchi (<i>Myoprocta</i>)	C	Tropical rainforest	"	Frugivore, granivore	"	"	1-3	3	Kleiman, 1970, 1972
Beaver (<i>Castor</i>)	C,F	Deciduous forest	Terrestrial, aquatic	Herbivore	Nocturnal	Seasonally monoestrus	1-4	3	Wilson, 1968
Artiodactyls									
Dik-dik (<i>Madoqua</i>)	C,F	Mixed forest, savanna	Terrestrial	"	"	Seasonally polyestrus	1	3	Hendrichs, 1975; Hendrichs & Hendrichs, 1971; Timley, 1969; Simonetta, 1966

* The level of precociality is rated on a scale from the most altricial to the most precocial (1-3). C, captive; F, field

thus fertilizing her eggs. Thus, the simplest kind of mammalian social system need only include a short stage of adult male and female interactions that result in a conception, followed by a short period of maternal care and tolerance by the female towards infants and juveniles (Eisenberg, 1966, in press; Trivers, 1972). This is a common form of social system in the Mammalia, and is found throughout the more morphologically conservative orders. Such a system is characterized by the dispersal of adults into exclusive, but possibly overlapping, home ranges, and also by polygyny, in that males may inseminate more than one female in neighboring home ranges.

Presumably, monogamy may evolve when group living, itself, is favored. Several authors have suggested those causative factors which render group living more advantageous for the individual than a solitary existence. These factors include (1) a lower susceptibility to predation, (2) improved acquisition of food, and (3) the localization or limitation of some resource, such as sleeping sites, necessary for survival, reproduction, or both (Eisenberg, 1966; Alexander, 1974). All genera of monogamous mammals under consideration appear to have achieved one or more of these advantages by being social. All of the primates, the dwarf mongoose, the acouchi, the beaver, and the dik-dik have probably benefited from group life by reason of decreased susceptibility to predators. Many of these forms (e.g., marmosets, tamarins, mongooses) have alarm calls to alert conspecific individuals; and in the beaver, tail slapping in response to alarm is well documented (Wilsson, 1971).

The evolution of group life in the canids has probably been most strongly favored by improved food acquisition (Kleiman and Eisenberg, 1973), for it has been shown for several species that hunts involving two or more individuals are more successful than a solitary hunting pattern. Certainly, the dwarf mongoose, marmosets, and tamarins, as opportunistic omnivores, have benefited in this way inasmuch as the pair or the family can share food from an unexpected localized food source when it has been discovered by only one individual in the group, even while foraging and feeding behavior is typically individualistic (see, e.g., the tamarins, Dawson, in press).

The third factor favoring group life, the

localization of a necessary resource, may have been important in the evolution of the beaver's social system, in which somewhat specialized characteristics of a stream or pond will affect the quality of the lodge and dam that can be constructed and maintained.

However, an understanding of why group living may be advantageous in these different mammalian genera does not explain why monogamy should evolve instead of polygyny. Since the female mammal is physiologically capable of providing for her own offspring before and after birth, monogamy should not be favored in mammals (Orians, 1969). This is especially true because a male may reduce his own reproductive potential by copulating with only a single female, unless the population is so thinly distributed that only a single female is available.

Wilson (1975) has presented three biasing ecological conditions which he feels may account for all known cases of monogamy in animals: (1) the territory contains such a scarce and valuable resource that two adults are required to defend it; (2) the physical environment is so difficult that two adults are needed to cope with it; and (3) early breeding is so advantageous that the head start allowed by monogamous pairing is decisive.

For most monogamous mammals, the precise requirements of the species and its interaction with the habitat are too poorly known for us to determine whether they fall into Wilson's categories. For example, several of the genera (e.g., marmosets and tamarins) are dependent for food on scattered but renewable resources of high energy content, a condition which tends to limit population density and group size and to promote territoriality (Eisenberg, in press; Jarman, 1974). However, whether this can be called a "difficult" physical environment remains to be seen. The first condition may apply to beavers, but Wilson's third biasing condition, the advantage of early breeding, certainly would not apply to those monogamous mammals whose puberty may occur later than in related non-monogamous species.

Perhaps another approach would be to consider whether, in fact, the female of a given species can competently rear her young alone, and, if not, why not. Table 3 contains a summary of ratios of litter weight to maternal weight for selected primate species. Among the callitrichids, in which we find monogamy and

TABLE 3

*Neonate (litter): mother weight ratios and care of the young
in selected primate species*

SPECIES	NO. YOUNG	BIRTH WEIGHT (g)	ADULT ♀ WEIGHT (g)	RATIO	CARE OF YOUNG	REFER- ENCES
<i>Tupaia belangeri</i>	2	10	200	0.10	Nest	10
<i>Galago crassicaudatus</i>	2	46.4	1034	0.09	Nest	3, 11
<i>Nycticebus coucang</i>	1	46.7 42.9	1105-1370 658	0.03-0.04 0.07	♀ carries	3, 11 8
<i>Cebuella pygmaea</i>	2	16	145	0.22	♂ carries from day 1	2
<i>Callithrix jacchus</i>	2	25-30 28	220 262	0.23-0.27 0.21	♂ carries from day 1	2 8
<i>Saguinus oedipus</i>	2	35-45	510	0.14-0.18	♂ often carries from day 1	2
<i>Saguinus midas</i>	2	33-45	483	0.14-0.15	♂ carries from day ?	2
<i>Leontopithecus rosalia</i>	2	61.0	745	0.19	♂ carries from day 10-14	6, 7
<i>Callimico goeldii</i>	1	35-45	472	0.07-0.10	♂ carries from day 14	2, 5, 11
<i>Aotus trivirgatus</i>	1	120-150	900-1000	0.12-0.17	♂ carries from day 7-14	12
<i>Saimiri sciureus</i>	1	109	—	0.12-0.16	Other ♀♀ carry from week 5	9, 13
<i>Ateles fusciceps</i>	1	535	8200-9400	0.06-0.07	♀ carries	4, 11
<i>Macaca mulatta</i>	1	330-600	4370-10659	0.03-0.14	♀ carries	11
<i>Hylobates lar</i>	1	400	4110-6800	0.06-0.10	♀ carries	11, 14
<i>Symphalangus syndactylus</i>	1	560	9000-11600	0.05-0.06	♀ carries, ♂ carries from 12th month	1, 11
<i>Gorilla gorilla</i>	1	2040	75000-110000	0.02-0.03	♀ carries	11
<i>Pongo pygmaeus</i>	1	1300-1600	37000	0.04	♀ carries	11

References:

(1) Chivers, 1972, 1975; (2) Christen, 1974; (3) Ehrlich, 1974; (4) Eisenberg, pers. commun.; (5) Heltne et al., 1973; (6) Hoage, in press; (7) Kleiman and Hoage, unpub.; (8) Leutenegger, 1973; (9) Long and Cooper, 1968; (10) Martin, 1968; (11) Napier and Napier, 1967; (12) Renquist, pers. commun.; (13) Rosenblum, 1968; (14) Sasaki, 1964.

well-developed paternal care (see below), these percentages are clearly the highest, mainly because twins are typically born and the marmosets and tamarins are among the smaller primates (the smaller species tend to have a higher ratio, see Leutenegger, 1973). Even within this group, there is a correlation between the relative weight of the neonates and the time post-partum when the father begins to carry the young.

In the pygmy marmoset (*Cebuella pygmaea*) and the common marmoset (*Callithrix jacchus*) with the highest neonate: mother weight ratio, males begin carrying infants immediately after birth (Christen, 1974; Epple, 1967; Rothe, 1973). In the tamarins (*Saguinus* and *Leontopithecus*), the ratio is lower and the time when male carrying begins varies from the first day to three weeks post-partum (Epple, 1967, pers. commun.; Snyder, 1974; Hoage, in press). In the golden lion tamarin (*Leontopithecus rosalia*), the number of young and therefore the weight of the entire litter seems to determine when male transport begins. In two family groups during four rearing episodes, the young were transferred on days 9 and 11 when twins were born and on days 14 and 17 when the litter was a singleton (Hoage, in press).

Goeldi's monkey (*Callimico goeldii*) and the owl monkey (*Aotus trivirgatus*), although not in the Callitrichidae, exhibit paternal care, but the female bears only a single young at a time (Heltne, Turner, and Wolhandler, 1973; Moynihan, 1964). Transfer to the father occurs in the third week in *Callimico* and in the second week in *Aotus* (Renquist, pers. commun.), and the neonate: mother weight ratio is somewhat lower than in marmosets and tamarins.

In the squirrel monkey (*Saimiri sciureus*), the single infant's percentage of the mother's weight is relatively high (12-16%) (Long and Cooper, 1968), yet male participation in paternal care is nil. However, squirrel monkey mothers do turn over their young to "aunts" for short periods, beginning at 5 weeks of age when the young are approximately 30 per cent of the mother's weight (Rosenblum, 1968; Long and Cooper, 1968). These data suggest that, in primates, the mother's ability to carry her young without aid from conspecific individuals is jeopardized when the weight of the litter begins to exceed 20 to 25 per cent of her own weight. Presumably, the difficulties are increased in the

smaller species and in species which are more completely arboreal. One interesting deviation from this trend is the apparent lack of male carrying in white-handed gibbons, *Hylobates lar* (Ellefson, 1974; Carpenter, 1940), although there is extensive male carrying by siamangs, *Symphalangus syndactylus* (Chivers, 1972, 1975). The reasons for this difference are unclear, especially since both genera have similar life histories and selective pressures. Tenaza (pers. commun.) suggests, however, that white-handed gibbons may be more susceptible to predation than siamangs since *H. lar* males spend more time than *S. syndactylus* males acting as "lookouts."

In arboreal or volant mammals, a major problem is obviously whether to carry the young or to keep them in a nest. In terrestrial carnivores, the sheltering of young may not be a problem, whereas the process of weaning may place a tremendous burden on the mother. Not only do the young have to be transferred from milk to meat, but they also have to be taught to hunt. In the case of felids and hyaenids, the solution has been to reduce the number of offspring per litter and to become polyestrous, so that, if one litter does not survive, breeding can occur again when conditions are more favorable (Ewer, 1973; Kleiman and Eisenberg, 1973). Canids, however, are monoestrous and have retained relatively large litters (Ewer, 1973). Thus a considerable burden is placed on the mother during nursing and at the time of weaning. Male participation in feeding both mother and young is the rule (Kleiman and Eisenberg, 1973).

Although the preceding paragraphs do not indicate why monogamy evolved, they suggest that at least Type II Monogamy may be favored (1) whenever more than a single individual (the female) is needed to rear the young or (2) whenever the carrying capacity of the habitat is not great enough to permit another female simultaneously to raise a litter in the same home range; or both. This conclusion suggests that some species may have opted for a greater reproductive burden than a solitary female can handle. The marmosets and tamarins may have up to three young at a time, a large litter for a small primate which carries its young. A third factor favoring Type II Monogamy may involve situations where complex structures (including a large food hoard) are needed for rearing the young, as in beavers (Eisenberg, 1966).

The above discussion applies primarily to monogamous species observed in family groups in the wild — i.e., Type II Monogamy. In Type I species, where family groups are rarely observed together, monogamy may have developed primarily in response to a low population density — i.e., in a thinly distributed population where only a single female may be available to a male for reproduction. Such a situation would arise if food resources were concentrated into rich but widely dispersed patches, as in *Elephantulus rufescens* (Rathbun, 1976).

SEXUAL DIMORPHISM

In species exhibiting long-term pair bonding, there is often a reduction in the degree of sexual dimorphism, both behavioral and morphological. In marmosets and tamarins, gibbons, dwarf mongooses, acouchis, beavers, and dik-diks the female is reported to be as large as, or in some cases, larger than the male (Ralls, 1976). For some groups this situation contrasts strongly with that in related genera showing different breeding systems and also considerable sexual dimorphism, with the males larger. For example, compare gorillas (*Gorilla gorilla*) with gibbons, and most cebids with callitrichids (Napier and Napier, 1967). Among canids, the males are usually larger, but the degree of sexual dimorphism is reduced in comparison with most species of mustelids, felids, and viverrids (Ewer, 1973). In monogamous artiodactyls, monomorphism is common (Hendrichs, 1972).

There may also be an equal distribution of responsibilities with respect to guarding the joint territory. Females may involve themselves in the production of territorial displays as often as males. For example, female tamarins (*Saguinus*) and beavers (*Castor*) scent-mark as frequently or occasionally more frequently than males (Epple, 1970b; Wilsson, 1968). Table 4 contains scent-marking frequencies found in five pairs of lion tamarins (*Leontopithecus*) during a one-month period within the breeding season. It shows individual variations, as well as two cases where the female of the pair scent-marked more than the male (Kleiman, unpub.). Box (1975a) has presented scent-marking frequencies for three family groups of common marmosets (*Callithrix jacchus*). They showed similar variations, both between pairs and over time.

Golden jackal females (*C. aureus*) exhibit high

TABLE 4

Daily frequency (per 30-minute observation period) of anogenital and sternal gland marking in 5 pairs of *L. rosalia* during November 1974

PAIR (♀ × ♂)	♂	♀
33692 × 30571A	.50	2.77
32721B × 33691	4.31	1.54
M00320 × M00276	3.73	9.81
M00277 × M00068	4.65	3.65
M00940 × M00319	4.92	1.38
Average	3.62	3.83

urine-marking levels, although somewhat lower than do males (Golani and Keller, 1975). Golden jackals also exhibit a phenomenon common to many canid species (Kleiman, pers. observ.), but relatively unstudied, namely, sequential urine-marking of the same sites by bonded pairs, either initiated by the male or the female.

Along with a trend towards monomorphism in the frequency of scent marking, there is a tendency for dimorphism to be reduced in the behavior patterns of scent marking, the development of scent glands, or both. For example, it is not generally known that adult females of numerous species within the canid family use a modified leg lift when they urine-mark. Thus the urine-marking movement is somewhat convergent with the typical leg lift of the male. I have personally observed this in the coyote (*C. latrans*), side-striped jackal (*C. adustus*), domestic dog (*C. familiaris*), raccoon dog (*Nyctereutes procyonoides*), Paraguayan fox (*Dusicyon gymnocercus*), crab-eating fox (*Cerdocyon thous*), maned wolf (*Chrysocyon brachyurus*), red fox (*Vulpes vulpes*), and Arctic fox (*Alopex lagopus*) (Kleiman, 1966, unpub.), and it has been described by others for the hunting dog (*Lycan pictus*) (Van Lawick, 1971) and golden jackal (*C. aureus*) (Golani and Keller, 1975). Bush dog females (*Speothos venaticus*) (Kleiman, 1966) use a handstand posture that is undoubtedly derived from the female's modified leg lift.

Several species also have loud vocalizations which may function in the maintenance of territory. In the gibbon and siamang, females usually lead in group calling and use a separate call from that of the male (Ellefson, 1974; Chivers, 1972, 1975), although a duetting format devel-

ops in the pair. Lion tamarin females also initiate group vocalizing although somewhat less often than males (McLanahan and Green, in press). In canids which exhibit group howling, e.g., coyotes, jackals and wolves, the females and the males participate equally.

Besides producing species-specific territorial displays, both the females and males of monogamous mammals may exhibit direct aggression towards conspecific intruders. In many cases, the aggression of each member of the pair is limited primarily to members of their own sex. An aggressive response to same-sexed intruders has been documented for marmosets and tamarins (Epple, 1975b, in press) and for the gibbon and siamang (Chivers, 1972). However, males may play a larger role in intergroup aggressive encounters in these primates (Dawson, in press; Neyman, in press; Chivers, 1975; Ellefson, 1974). Male dwarf mongooses (Rasa, 1973b, 1975) and golden jackals (Golani and Keller, 1975) are also more aggressive than females in intergroup encounters.

In captivity, when large family groups are allowed to develop, aggression within sexes results in the development of two separate dominance hierarchies, with the adult pair acting as the alpha male and female. This has been observed commonly in marmosets and tamarins (Epple, 1975b; Rothe, 1975), wolves (Zimen, 1975), and dwarf mongooses (Rasa, 1972, 1973a, 1975).

Finally, some comment must be made concerning heterosexual aggression. It has been suggested that marmoset, tamarin, acouchi, beaver, and dwarf mongoose females are aggressive towards and dominant over the males (Christen, 1974; Kleiman, 1972; Willson, 1968, 1971; Rasa, 1972, 1975). For example, it is reported that in the beaver, a good pair bond develops when a large female is placed with a smaller male and the male initially submits to the female's threats and attacks (Willson, 1968). In unfamiliar acouchi pairs, it is often the female who is aggressive and who attacks the male during first introductions. Some pairs are incompatible because of the intensity of female hostility (Kleiman, unpub.). In established pairs, female aggression may vary with the reproductive cycle. In two pairs of closely observed white-handed gibbons (*Hylobates lar*), Ellefson (1974) reported that in one pair the female was more dominant with respect to feed-

ing in the late stages of pregnancy and early post-partum period, while at other times dominance between the pair shifted from day to day. Some acouchi and lion tamarin females have also been observed to be extremely aggressive and clearly dominant over their mates shortly after parturition (Kleiman, 1972, unpub.). Thus, the females of monogamous mammals appear to exhibit high levels of both intersexual and intrasexual aggression and dominance, a situation which contrasts with what is typically reported for non-monogamous species.

Supportive data for this difference are difficult to find, since there have been few investigations in which the relative levels of aggression of males and females have been studied (see Ralls, 1976). Moreover, female (and male) aggression and dominance are clearly affected by a number of factors, including the reproductive cycle and social learning (Rowell, 1974). Perhaps the best support for the hypothesis that some females of monogamous species are more aggressive than non-monogamous counterparts in both intersexual and intrasexual contexts arises from the lack of comparative data. It is an accepted characteristic of mammals that adult females are less aggressive than adult males, and that male aggression is strongly influenced by androgenic hormones (e.g., Hart, 1974). Where exceptions exist, as in the case of the golden hamster (*Mesocricetus auratus*), considerable research has been done on the sex difference and its hormonal basis (Payne and Swanson, 1972a,b, 1973; Vandenberg, 1971). It should also be noted that the two most widely recognized exceptions, the hamster and the spotted hyena (*Crocuta crocuta*) (Kruuk, 1972), are not monogamous (see Ralls, 1976, for a more complete discussion of female aggression and dominance).

PATERNAL INVESTMENT

Trivers (1972) has suggested that there should be a strong selective advantage for male participation in parental care, such as guarding and defending offspring, whenever monogamy evolves. If there is mating exclusivity, it is important that a male ensure that his offspring survive to reproductive age. There are, however, several methods by which a male can contribute to the rearing of his offspring, and the males of different species may exhibit any one

of these paternal patterns in varying degrees. An attempt to rate the paternal investment of several monogamous species is presented in Table 5. The behavior patterns are divided into indirect and direct forms of help. Indirect paternal investment includes nest-building and defense of the home range or nest, whereas direct interactions involve both proximity and responsiveness to the young. In Table 5 direct forms of paternal care have been rated higher than indirect forms of aid. Clearly, the final rating for each genus is only an estimate of the paternal investment. An exact measurement would require knowledge of the energy output required for each behavior pattern, as well as its overall contribution to the survival of the young.

The male's territorial defense, which prevents the over-utilization of necessary resources, is practiced by males of all monogamous species. It occurs in polygynous mammals as well. Nest-building by males is uncommon, although male acouchis have occasionally been observed to carry nest material to sites where juvenile nests are located (Kleiman, unpub.). One of the major burdens of the beaver male is to aid in the building of a lodge and in gathering the food hoard to be used during the winter by the entire beaver family (Wilsson, 1968, 1971). In the remainder of the species listed, either the female constructs a nest site alone, or no special structure is necessary for depositing the young. Jackal and coyote females are responsible for the construction of a burrow and appear to make the major decisions about when and where to move the young (Van Lawick, 1971; Ryden, 1974).

Actual guarding of the young by males is difficult to document, but it is well known for dwarf mongooses (Rasa, 1975) and for golden jackals (Van Lawick, 1971), and it occurs in the Callitrichidae, where males typically carry young in alternation with the mother (Epple, 1975a). Neyman (in press) reports that all group members guard infants during intergroup encounters. Some degree of protection is also provided by acouchi males, who visit and rest with the infants and juveniles during the mother's absence (Kleiman, 1972). Observations of captive dik-diks suggest that the male does defend the young, not by showing aggression but by an alarm display which could attract predators to the male himself instead of to the young (Simonetta, 1966).

Grooming and feeding of the young are unequally distributed among monogamous males. Canids possess the most highly evolved feeding rituals, with the father and mother regurgitating partially digested meat to feed the young around the time of weaning (Ewer, 1973; Kleiman and Eisenberg, 1973). There is even a documented case of a litter of Cape hunting dog (*Lycan pictus*) pups reared solely by a group of males when the female had died at about the time of weaning (Estes and Goddard, 1967).

For most of the other species under discussion, feeding usually involves no more than tolerance by the male when the young take food (food-stealing), although the male may actually approach the young while he is carrying food. Rasa (1975) describes all family members of the dwarf mongoose as approaching infants with food while growling, which induces food-stealing by the young. Hoage (unpub.) has observed lion tamarin males presenting food to their offspring. Young gibbons and siamangs feed close to both parents as they develop independence (Ellefson, 1974; Chivers, 1975).

Among the monogamous forms being discussed, the carrying of young is a basic characteristic of marmoset and tamarin males. Epple (1975a) has recently estimated that in *Saguinus fuscicollis*, the male carries the young on an average 52.5 per cent of the time, the mother contributes 32.8 per cent, and other group members the remainder. The siamang male (*Symphalangus syndactylus*) carries and sleeps with young ones between the ages of 1 and 2½ years until the juvenile is coordinated enough to follow the female (Chivers, 1972, 1975).

The last category, that of playing with or teaching the young, is especially difficult to evaluate. It depends upon the degree to which a male interacts socially with his offspring, exclusive of caring for their needs of body care, shelter, and food. Such interactions are reported to occur in several species of monogamous mammals (see Table 5).

In the acouchi, the male may follow and urinate over the offspring, but also may join in with them in play, consisting of running, leaping, and twisting (Kleiman, 1971, 1974). The mother only rarely participates. Marmoset and tamarin males, although they may carry and groom infants, do not consistently involve themselves in play. However, their close contact with the infants during the early stages of rear-

TABLE 5
Paternal investment in selected species of monogamous mammals.
 The frequency of occurrence of a particular type of behavior is rated on a scale 0-5.
 Ratings for direct forms of investment are multiplied by two.

SPECIES	INDIRECT		DIRECT × 2						RATING	REFERENCES
	Defends territory	Builds nest	Defends or guards young	Grooms young	Feeds young	Carries young	Socializes or teaches young			
Primates										
Marmoset (<i>Callithrix</i>)	5	0	10	6	4	10	6	41	Epple, 1967, 1970a; Box, 1975b	
Tamarin (<i>Saguinus</i>) (<i>Leontopithecus</i>)	5	0	10	6	4	10	6	41	Muckenhirn, 1967; Epple, 1975a; Kleiman, unpub.	
Gibbon (<i>Hylobates</i>)	5	0	10	4	4	0	4	27	Ellefson, 1974;	
Siamang (<i>Symphalangus</i>)	5	0	10	6	4	6	8	39	Carpenter, 1940	
Carnivores										
Coyote and jackal (<i>Canis</i>)	5	0	8	4	10	0	6	33	Chivers, 1972, 1975	
Mongoose (<i>Helogale</i>)	5	0	10	6	8	0	4	33	Van Lawick, 1971; Ryden, 1974	
Rodents										
Acouchi (<i>Myoprocta</i>)	5	1	4	2	2	0	4	18	Rasa, 1975 Kleiman, 1971, 1972	
Beaver (<i>Castor</i>)	5	4	8	4	6	0	4 (♂ marks young)	31	Wilsson, 1968	
Artiodactyls										
Dik-dik (<i>Madoqua</i>)	5	0	6	2	0	0	2	15	Hendrichs and Hendrichs, 1971; Simonetta, 1966	

ing and their continued grooming and interacting with juveniles certainly must aid in the socialization process. Similarly, coyote and jackal males become involved in the socialization and learning process of the young during hunting in family groups, as the young are weaned. Siamang males may play the greatest role in socializing infants and juveniles. Males sleep with and groom the young, as well as controlling their activities during the six months to one year period while the male carries the young (Chivers, 1972, 1975).

A scale indicating the relative degree of paternal investment can also be seen in Table 5. It suggests that the marmoset, tamarin, siamang, and beaver males show the most paternal behavior, whereas acouchis and dik-diks exhibit the least paternal care. The greatest degree of paternal investment occurs in those species in which sexual maturity may be delayed and the older offspring remain with the family group (Type II Monogamy).

Some comments should be made concerning the level of paternal investment in mammals exhibiting other social systems, as well as in other additional monogamous species. Paternal care in primates has been reviewed by Mitchell (1969), Mitchell and Brandt (1972), and Jolly (1972). Spencer-Booth (1970) has discussed paternal care patterns in other mammals.

Among the primates, paternal care has been extensively discussed for the Japanese macaque, *Macaca fuscata* (Alexander, 1970; Itani, 1963), the Barbary macaque, *Macaca sylvana* (Deag and Crook, 1971), the Anubis baboon, *Papio anubis* (Ransom and Ransom, 1971), and the Hamadryas baboon, *Papio hamadryas* (Kummer, 1968).

In the Japanese macaque (Itani, 1963), paternal behavior by dominant males is most common during the birth season, when the females reject the juveniles born in the previous year. But it is not a species characteristic in the sense that the dominant males of all troops exhibit it. Itani (1963) reported that of 18 troops, paternal care was common in 3, very rare in 7, and absent in 8 troops. Similarly, in the Barbary macaque only certain males at certain times exhibit grooming and carrying of infants (Deag and Crook, 1971; Burton, 1972), and with both the Barbary macaque and the Hamadryas baboon (Kummer, 1968) it appears as though the infant is often "used" to reduce

the aggression of other troop males. Deag and Crook (1971) proposed the term "agonistic buffering" for such situations, which apparently occur also in the Anubis baboon (Ransom and Ransom, 1971) and the Japanese macaque (Itani, 1963).

In Anubis baboons, adult males interact with an infant (1) where there is an intense pair bond between the male and the infant's mother, (2) where there is a protective relationship between an adult male and a particular infant, and (3) where the mother is low-ranking, in addition to situations involving "agonistic buffering" (Ransom and Ransom, 1971). Yet the relationships are highly specific and individualistic, in that the males do not generalize their paternal care from one infant to all infants. This situation contrasts with the behavior of the New World callitrichids, the owl monkey (*Aotus trivirgatus*) and Goeldi's monkey (*Callimico goeldii*), in which paternal care is pervasive in the rearing of infants.

In other mammals, there are many descriptions of paternal care in just those species which have been described as monogamous (Spencer-Booth, 1970). For example, the canids tend towards monogamy, and the males participate actively in rearing the young. Except for the meercat *Suricata suricatta* (Ewer, 1963), the dwarf mongoose, and the banded mongoose *Mungos mungos* (Rood, 1974), most records of paternal care in other carnivores appear to be anecdotal or describe unusual cases (Spencer-Booth, 1970).

Among four species of the myomorph rodent genus *Peromyscus*, in which monogamy apparently occurs (see Table 1), the males have all been described as exhibiting paternal care (Eisenberg, 1968; Dudley, 1974), whereas in *P. crinitus* and *P. leucopus* such behavior apparently does not occur (Eisenberg, 1968). Of course, in the latter two species, females are intolerant of males after parturition, and the males may rarely achieve contact with the young.

Other examples of myomorph rodents in which monogamy has been described and paternal care is common include pygmy mice, *Baiomys taylori* (Blair, 1941), and grasshopper mice, *Onychomys* sp. (Horner and Taylor, 1968).

There are numerous examples of non-monogamous mammals in which males exhibit care-giving behavior towards infants, at least some of the time (Spencer-Booth, 1970). Ac-

ording to recent sociobiological theory (Wilson, 1975; West Eberhard, 1975), paternal care is expected to evolve wherever the parentage of the infant is known to the males. Thus, primates living in one-male troops, e.g., Hamadryas baboons, should exhibit paternal care more commonly than species living in large multimale troops. This is indeed apparently the case (Mitchell and Brandt, 1972). In other mammals, one can compare the frequency of paternal care in species living in harems or small extended families with that in large polygamous groups. (In polygynous but dispersed species, the male has little opportunity to interact with the young.) For example, in mammals living in large groups of mixed age and sex classes, such as wildebeest (*Connochaetes*) and whiptail wallabies (*Macropus parryi*, Kaufmann, 1974), paternal care has not been described, whereas in harem-forming species, such as horses, males are at least tolerant and often protective toward the young (Tyler, 1972).

Recently Barash (1975) has described variations in the degree of paternal care occurring in the hoary marmot (*Marmota caligata*) on the basis of variations in the social system. Adult males living in isolation from other males and with one female interacted significantly more with their young than males living close to and interacting with each other. In the case of the isolated males, the parentage of offspring was "known," in that other males were not available to compete sexually with the resident. Thus, in at least one case, where ecological circumstances dictated mating exclusivity, paternal care was more developed in the monogamous condition.

SOCIAL AND SEXUAL INTERACTIONS

The next questions that suggest themselves are the following: Can we relate the degree of paternal investment to the strength of the pair bond in monogamous mammals? And which socio-sexual behavior patterns do reflect pair bond strength? Clearly, we expect little serious aggression between pair members, but can we furthermore expect more or less frequent courtship, sexual behavior, and affiliative social interactions?

The energy invested in social and sexual interactions is difficult to assess in mammals because (1) species may interact in quite different ways, and (2) the time and energy devoted to

the performance of different behavior patterns is unequal. I have therefore not tried to develop a "sociality" rating similar to the "paternal investment" rating (see Table 6).

If the members of a pair tend to rest in close proximity, including physical contact, some degree of tolerance is required, although little energy is expended. Resting together is common in most of the monogamous species discussed, especially the marmosets and tamarins, siamang, gibbons, and beavers (Table 6). Acouchis may rest in proximity, but less regularly in direct bodily contact. Dik-diks are reported to rest close together (Simonetta, 1966).

The differences in proximity behavior in two related species, one monogamous, the other polygamous, have been presented by Mason (1974b). In the monogamous titi monkey *Callicebus moloch*, the male and female of a pair rest in contact almost twice as often as a pair of the polygamous squirrel monkey, *Saimiri sciureus*.

Among non-monogamous but social mammals, females rest in contact with each other and with their offspring more often than they do with males. Some examples are the lion *Panthera leo* (Schaller, 1972), the spotted hyena *Crocuta crocuta* (Kruuk, 1972), and many species of Chiroptera (Bradbury, in press).

In some species, allogrooming occupies a considerable portion of the resting time interspersed during activity periods. In marmosets, huddling is common and partners may alternately groom each other (Epple, 1967, 1975b; Rothe, in press; Box, 1975a). Solicitation postures are to be seen, in which there is presentation of the body area to be groomed. Ellefson (1974) and Carpenter (1940) have reported allogrooming in gibbons, Chivers (1972, 1975) in the siamang, and Willson (1968, 1971) in beavers. Kleiman (1971) observed infrequent grooming between mated acouchis. From Van Lawick (1971) and Golani and Keller (1975), it appears that golden jackals do lick and nibble each other's fur, but not with the regularity exhibited by the primates.

Clearly, allogrooming behavior is better developed in monogamous primates than in the other monogamous mammals. However, since most primates commonly allogroom (Sparks, 1967), one must ask whether there are differences in the frequency or direction of grooming behavior in monogamous as contrasted with

TABLE 6

Level of adult male and female social interactions in monogamous species relative to paternal investment
Frequency of occurrence of activity rated from 0 to 5.

GENUS	PATERNAL INVESTMENT RATING	SLEEP TOGETHER	ALLO- GROOM	DIRECT COURTSHIP	REFERENCE
<i>Primates</i>					
Marmoset (<i>Callithrix</i>)	41	5	5	2	Epple, 1967, 1975b; Rothe, in press
Tamarin (<i>Saguinus</i>)	41	5	5	2	Moynihan, 1970; Muckenhirn, 1967; Epple, 1975b; Neyman, in press
Gibbon (<i>Hylobates</i>)	27	5	4	1	Ellefson, 1974; Carpenter, 1940
Siamang (<i>Symphalangus</i>)	39	5	5	1	Chivers, 1972, 1975
<i>Carnivores</i>					
Coyote/jackal (<i>Canis</i>)	33	4	3	2	Golani and Keller, 1975; Van Lawick, 1971
Mongoose (<i>Helogale</i>)	29	5	3	1	Ewer, 1973; Rasa, 1975
<i>Rodents</i>					
Acouchi (<i>Myoprocta</i>)	18	2	2	5	Kleiman, 1971
Beaver (<i>Castor</i>)	31	5	3	?	Wilsson, 1968
<i>Artiodactyls</i>					
Dik-dik (<i>Madoqua</i>)	15	3	2	2	Tinley, 1969; Hendrichs and Hendrichs, 1971; Simonetta, 1966

polygamous primates. In polygamous species the following traits exist: (1) adult females initiate the grooming and groom the adult males more often than the reverse; (2) adult females are mainly involved in grooming interactions with the offspring and with other females, and not with males; and (3) groomers are more often lower in social rank than groomees. (Selected references include a review by Sparks, 1967; Kummer, 1968; Van Lawick-Goodall, 1968; Mori, 1975; Poirier, 1970; and Saayman, 1971.)

In monogamous primates, the males initiate grooming and groom females more often than the reverse situation occurs (lion tamarin, Kleiman, in press; common marmosets, Rothe, in press; Box, 1975a; siamang, Chivers, 1975; gibbons, Ellefson, 1974); and the over-all adult heterosexual grooming frequencies appear to be higher than in non-monogamous primates.

Gibbon and siamang adult pairs groom on the average 15 and 30 minutes per day, respectively (Ellefson, 1974; Chivers, 1975), while adult male-female pairs of chimpanzees, *Pan troglodytes* (totals for all dyads) appear to spend less than 10 minutes per day grooming each other (an extrapolation based on Figs. 35a and b in Van Lawick-Goodall, 1968). Of 134 observations of allogrooming in gorillas, Schaller (1963) saw only one instance of grooming between a black-backed male and an adult female. In comparing titi and squirrel monkeys, Mason (1974b) found that adult titi pairs allogroom significantly more often than squirrel monkey pairs.

The reverse direction of grooming (in which males initiate grooming more often than females) in monogamous primates is related to the reversed dominance status of these species. Ellefson (1974) noted that in one gibbon pair

where dominance relations fluctuated daily, grooming relationships also fluctuated, with the subordinate member of the pair initiating allogrooming bouts. In lion tamarins (Kleiman, in press) and common marmosets (Rothe, in press), fluctuations in relative grooming frequencies occur in relation to the reproductive cycle, which also affects the relative dominance status of each pair member.

Courtship behavior is difficult to define in mammals, since the concept developed from studies of reptiles and birds, and usually suggests rather stereotyped displays exhibited by one individual to the partner prior to copulation. In mammals, male courtship rituals may include following and testing the female (sniffing vaginal or urine odors and attempting to mount), but also such more elaborate rituals as are shown by acouchis, including trembling of the body, tail-wagging, and enurination, with frequent approaches and withdrawals (Kleiman, 1971). In fact, one could include as courtship nearly all social interactions (excluding aggression) that are initiated by one partner, since any time expended interacting socially has some energy cost associated with it (Parker, 1974).

There is considerable diversity with respect to the amount of time spent in courtship (excluding allogrooming) among monogamous mammals. As already mentioned, acouchi males court regularly; between 4 and 6 per cent of observed time was devoted to courtship activities in cohabiting pairs (Kleiman, 1971). In golden jackals, courtship by the male involves following, sniffing, and the assumption of the T-position with increasing frequency, but mainly as the female nears estrus (Golani and Mendelsohn, 1970; Golani and Keller, 1975). More regular interactions not related to the annual cycle of reproduction include greetings (tail-wagging, face-licking) after short separations (Van Lawick, 1971). Neither marmoset, tamarin, gibbon nor siamang males are reported to indulge in frequent courtship, although certain rare displays may be associated with sexual pursuit, e.g., tongue protrusion in tamarins (Epple, 1967; Moynihan, 1970). In long-established breeding pairs of golden lion tamarins, there are relatively few affiliative interactions between cohabiting adult pairs, except for allogrooming (Kleiman, unpub.). Dikdik males also follow and test the female, but again mainly prior to heat (Simonetta, 1966).

A consideration of the three types of male energy expenditure in social interactions suggests that both resting in contact and mutual grooming, each of which requires little energy investment, are the most common forms of interaction. Except for acouchis, in which courtship occurs daily, most monogamous mammals do not interact at a high level of intensity. Rating the behaviors suggests that there is a poor or negative correlation between the level of male parental investment and the intensity of social interactions in the monogamous mammals under comparison.

However, a comparison of monogamous forms with related polygamous species suggests that those behaviors involving little male energy expenditure may, in fact, be more common where monogamy prevails. For example, among the primates living in one-male or age-graded multi-male troops, females probably sleep together with each other and their young more commonly than with males. As already mentioned, among social carnivores, such as the lion and the spotted hyena, females again are in closer contact with each other than with males (Schaller, 1972; Kruuk, 1972).

Differences in social grooming behavior in monogamous and polygamous primate species have already been discussed, and add strength to the suggestion that in non-monogamous but social mammals affiliative interactions are most common within sexes and between mother and young, rather than between sexes (except at the time of estrus). Thus, a basic characteristic of monogamy may be the simple fact that a male and female sleep and groom together. Chivers (1975) has also discussed the remarkable level of synchrony within a siamang family, wherein all family members were engaged in the same activity 73 per cent of the time.

Comparing patterns of sexual behavior is especially difficult because one must take into account (1) whether the sexual behavior is restricted to estrus, (2) how long estrus is, (3) how long copulations last, and (4) how many copulations may occur within a given estrous period. In canids and beavers, which are primarily monoestrous (Kleiman, 1968; Wilsson, 1968), sexual behavior is restricted to a single short period each year. The female must conceive at that time or pass through a complete annual cycle before re-entering the reproductive condition. However, in canids the sexual behavior

is prolonged, and consists of several days of receptivity during which mating may occur 1 to 3 times per day. A single copulation includes a lock which may "tie" the pair together for as much as 30 minutes (Kleiman, 1968; Kleiman and Eisenberg, 1973). The temporal patterning of beaver mating is not known, although copulation has been partly described (Hediger, 1970).

Sexual behavior in other species of monogamous mammals may be even less frequent, in relative terms. Acouchi females are polyestrous, and come into heat approximately every 40 days. Yet, with a gestation of 3½ months and a lactation anestrus of 1½ months, a male may mate only twice a year (Kleiman, 1970). Copulation in acouchis is short, and the male typically does not mate again after a single ejaculation (Kleiman, 1972). Thus, sexual behavior can be said to occur infrequently in acouchis, although courtship is more common.

There are different reports of the frequency of sexual behavior in marmosets and tamarins (Hampton, Hampton, and Landwehr, 1966; Snyder, 1974; Christen, 1974; Moynihan, 1970). Personal observations on the golden lion tamarin suggest that sexual activity in long-established breeding pairs is infrequent and is restricted to a period of estrus lasting 1 to 2 days. Newly formed pairs may exhibit sexual activity more frequently and not during peak estrus. There is a tendency towards a breeding season in the autumn in the Northern Hemisphere, but females may conceive during any month of the year (Kleiman, in press). Table 7 contains data (for the autumn 1974 breeding season) on the average frequency of observed

mounts and sniffs by the male in 5 pairs of lion tamarins which had been cohabiting for different durations of time. Clearly, the number of sexual interactions is highest in newly formed pairs which have not yet had young. Moynihan (1970) had the same impression in respect to Geoffroy's tamarin (*Saguinus oedipus geoffroyi*). Copulations during pregnancy occur in *Saguinus fuscicollis* (Epple, pers. commun.), *L. rosalia* (Kleiman, unpub.) and *Callithrix jacchus* (Hearn, in press), but not frequently. Also, among gibbons and siamangs, sexual behavior is rarely observed (Carpenter, 1940; Ellefson, 1974; Chivers, 1972, 1975).

In none of the monogamous forms does copulation occur outside of the period of physiological estrus, except perhaps in the primates. It may be that captivity produces an artificial increase in primate sexual interactions, since marmosets, tamarins, and gibbons are reported to copulate infrequently in nature (Berkson and Chaicumpa, 1969; Moynihan, 1970). However, it is likely that for most monogamous mammal species sexual behavior occurs infrequently and thus must play a minor role in pair-bond maintenance. While new bonds are being established, both social and sexual interactions may be more frequent. This observation supports Parker's (1974) suggestion that courtship behavior should become reduced once a bond has been established between members of a heterosexual pair.

Because of the lack of data regarding the frequency and intensity of social and sexual interactions in most mammals, it is difficult to compare monogamous species with forms exhibiting polygyny. The one point that can

TABLE 7

*Average number of mounts and male sniffs per month in 5 pairs of L. rosalia between September 1 and November 30, 1974.**

Pairs are arranged according to the duration of cohabitation. (B) indicates that births have occurred.

♀	♂	INTRODUCED	MEAN NO. MOUNTS/MONTH	MEAN NO. SNIFFS/MONTH
33692	30571 (B)	Late 1970	1.0	5.7
32721B	33691 (B)	Late 1970	2.0	16.7
M00320	M00276 (B)	November 1973	4.7	90.3
M00277	M00068	March 1974	17.7	161.3
M00940	M00319	August 1974	21.0	248.0

* This 3-month period comprises a major part of the breeding season.

perhaps be made with some degree of certainty is that there are no more intense socio-sexual interactions in species exhibiting long-term pair-bonding than in polygamous forms.

MONOGAMY IN HUMANS

Humans exhibit both monogamy and polygamy as breeding systems. In most Western societies monogamy is considered the norm, although in practice polygyny is also common. Where monogamy is the cultural norm, it appears as though certain characteristics found in monogamous mammals also occur in humans. There are also characteristics, however, which do not conform to the trends seen in other mammals. Of course, given the variation in human breeding systems, the reliance on culture, and the lack of knowledge concerning how our breeding systems evolved, it is debatable whether one can compare the characteristics found in monogamous mammals with what is seen in monogamous humans. But, perhaps, instead of making direct comparisons, it is worth posing questions that could be examined.

In Western society, the developing pair bond is characterized by more intense affiliative and sexual interactions than the bond which has existed for a long period (Morris, 1969). This appears to be true for monogamous mammals as well. The responsibilities of caring for offspring probably consume considerable energy that was devoted to sociosexual interactions during pair-bond formation.

Interestingly, in Western society, great emphasis is currently placed on maintaining high levels of sexual interactions in married couples after they have started reproducing and are rearing young. Frequent sexual behavior is thought to contribute to the maintenance of a strong bond in humans; clearly this is not the case in many species of monogamous mammals where contact and affiliative behaviors, such as resting together and grooming, are more common than sexual behavior. An interesting question to investigate might then be whether humans with lifetime stable bonds are characterized by as frequent sexual interactions as humans exhibiting serial monogamy or polygamy.

Comparisons of Western cultural norms with those of polygamous societies suggest that paternal investment is greater where monogamy

prevails. Within Western society, juveniles also exhibit a longer delay in sociosexual maturation, although this may be due to economic and technological factors. Juveniles aid in child-rearing in all human societies. With respect to child-rearing patterns and development, therefore, monogamous humans do apparently show some characteristics similar to monogamous mammals. A problem to examine would be the relationship between a society's reproductive strategy and the relative contributions of boys and girls in infant care.

Within Western society, however, where monogamy is considered to be the dominant reproductive system, there are some behavioral characteristics which are at variance with what is seen in monogamous mammals. Firstly, sexual dimorphism in roles and behavior is common in advanced societies, such as our own. The female's role is to rear the children, while the male "works" for food and shelter. Thus, paternal investment (although greater than in polygamous societies) is often indirect and may not involve continuous responsiveness to the needs of the young. Moreover, the legal, legislative, and executive branches of governments, as well as religious establishments, have generally supported this sexual dimorphism. Since both politics and religion are dominated by men in Western society, the result is an apparently monogamous system, with behavioral correlates, however, that are more appropriate to polygyny. In fact, polygyny commonly occurs.

The question that must be addressed is whether (and to what degree) humans must be biologically consistent within a breeding system that is apparently culturally determined. For example, two of the current demands of the women's liberation movement in the West, namely, (1) a reduction in the sexual dimorphism of behavior through equal wages and job opportunities, and (2) a higher paternal investment in child-rearing, are biologically more compatible with monogamy. If our society should actually achieve these aims, does this mean it will move toward stricter monogamy (at least during child-rearing years), and should this move be encouraged since monomorphism and high levels of paternal investment are basic characteristics of monogamous mammals? Moreover, women of reproductive age (with and without children) are also demanding greater sexual freedom. Biologically, this is in-

compatible with an expectation of greater child-rearing investment by males since it is inconsistent for a male to invest heavily in children who might be fathered by another male (unless, of course, the male and female are closely related genetically — West Eberhard, 1975).

It might be worthwhile to examine whether certain stresses in heterosexual relationships arise because of such inconsistencies between biology and culture. On the one hand, we have Western society, in which monogamy is the political and religious norm, yet many characteristics of the society are common to polygamy. On the other hand, we have demands by some Western women that we adopt certain behaviors that are more consistent with monogamy while perhaps adopting polygamy as the breeding system. The effects of such inconsistencies should be investigated and might be measured by comparing the reproductive success of adults whose roles and behavior were or were not compatible with their chosen breeding system as determined by the transmission of genes to subsequent generations. Thus, we could look at the number of children and grandchildren born to persons with differing life styles. Whether persons who choose not to reproduce at all through the use of contraceptives exhibit particular characteristics should also be pursued, although the effects of this revolutionary change might not yet be evident. Such a phenomenon — i.e., choosing not to reproduce — does not occur in mammals, although non-breeding adults do exist and often act as parental surrogates within family groups that are related to them.

SUMMARY AND CONCLUSIONS

Monogamy is rare in mammals, but is seen in a variety of species exhibiting different life styles. However, some characteristic patterns emerge when these species are compared:

(1) For most species, sexual dimorphism in size and dimorphism in territorial behavior is reduced in monogamous species in comparison with related forms. In monogamous species, there is also a reduction in role differentiation in many aspects of behavior (Type I and II Monogamy).

(2) Paternal investment is high when the adult pair retains older juveniles in the family (Type II Monogamy).

(3) Juveniles exhibit delayed sexual maturation when they remain with the family group (Type II Monogamy).

(4) Juveniles, when retained, contribute substantially to the rearing of younger siblings (Type II Monogamy).

(5) When there is a well-established bond between the members of the adult pair, little energy is expended in either sexual or intense social interactions. Newly formed pairs interact more frequently. (Type I and II Monogamy).

One remaining problem concerns the difference in the strength of the bond in monogamous mammals that exhibit a high paternal investment (Type II) in contrast to species in which the male contributes less to rearing the young (Type I). According to Trivers (1972), monogamy with a strong bond and a high paternal investment should be correlated. However, there are some forms, such as the acouchi and dik-dik, in which a considerable direct paternal investment has not been found. This difference however, may simply relate to the possible differences in the selective pressures which led to monogamy. If the evolution of Type I Monogamy was due primarily to over-dispersion of adults, one would expect neither a strong bond nor a heavy paternal investment. This may also explain differences in the degree of flexibility within this social system. For marmosets and tamarins, there appears to be little latitude in behavior, in that more than a single female will not breed within a group situation (Rothe, 1975). Among acouchis, however, such inflexibility does not appear always to be the rule (Kleiman, unpub.). Again, a lack of paternal investment and some flexibility in the social system seem to be more common in Type I species, where monogamy occurs more as a result of necessary resources being thinly and patchily distributed. By contrast the need for a female to have help in rearing offspring characterizes Type II species. These two forms of monogamy are therefore separable in terms of their evolution and the observed behavior; it is thus proposed that they be referred to as *facultative* (Type I), and *obligate* (Type II) Monogamy.

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LIST OF LITERATURE

- ABLES, E. D. 1975. Ecology of the red fox in America. In M. W. Fox (ed.), *The Wild Canids*, pp. 216-236. Van Nostrand Reinhold, New York.
- AESCHLIMANN, A. 1963. Observations sur *Phylantomba maxwelli* (Hamilton-Smith), une Antilope de la Forêt éburnée. *Acta Tropica*, 20: 341-368.
- ALBIGNAC, R. 1973. *Mammifères carnivores. Faune de Madagascar*. CNRS, Paris.
- ALEXANDER, B. K. 1970. Parental behavior of adult male Japanese monkeys. *Behaviour*, 36: 270-285.
- ALEXANDER, R. D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.*, 5: 325-383.
- ALTMANN, D. 1974. Beziehungen zwischen sozialer Rangordnung und Jungenaufzucht bei *Canis lupus* L. *Zool. Garten N. F. Jena*, 44: 235-236.
- ASDELL, S. A. 1964. *Patterns of Mammalian Reproduction*. Cornell University Press, Ithaca.
- BARASH, D. A. 1975. Ecology of paternal behavior in the hoary marmot (*Marmota caligata*): An evolutionary interpretation. *J. Mammal.*, 56: 613-619.
- BERKSON, G., and V. CHAICUMPA. 1969. Breeding gibbons (*Hylobates lar entelloides*) in the laboratory. *Lab. Anim. Care*, 19: 808-811.
- BLAIR, W. F. 1941. Observations on the life history of *Baiomys taylori subater*. *J. Mammal.*, 22: 378-383.
- . 1951. Population structure, social behavior and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus leucocephalus*). *Contrib. Lab. Vert. Biol. Univ. Mich.*, 48: 1-47.
- BOX, H. O. 1975a. Quantitative studies of behaviour within captive groups of marmoset monkeys (*Callithrix jacchus*). *Primates*, 16: 155-174.
- . 1975b. A social development study of young monkeys (*Callithrix jacchus*) within a captive family group. *Primates*, 16: 419-436.
- BRADBURY, J. (In press.) Social organization and communication. In W. Wimsatt (ed.), *Biology of Bats*, Vol. 3. Academic Press, New York.
- BROSSET, A. 1966. *La Biologie des Chiroptères*. Masson, Paris.
- BUCHER, G. C. 1937. Notes on life history and habits of *Capromys*. *Mem. Soc. Cubana Hist. Nat.*, 11: 93-107.
- BURNS, J. J., and F. H. FAY. 1973. Comparative biology of Bering Sea harbor seal populations. In *Science in Alaska*, p. 28. Proc. 23rd Alaskan Science Conf., Aug. 1972, Fairbanks, Alaska.
- BURNS, J. J., G. C. RAY, F. H. FAY, and P. D. SHAUGHNESSY. 1972. Adoption of a strange pup by the ice-inhabiting harbor seal, *Phoca vitulina largha*. *J. Mammal.*, 53: 594-598.
- BURTON, F. D. 1972. The integration of biology and behavior in the socialization of *Macaca sylvana* of Gibraltar. In F. E. Poirier (ed.), *Primate Socialization*, pp. 29-62. Random House, New York.
- CABRERA, A., and J. YEPES. 1960. *Mamíferos Sudamericanos*. 2nd ed. Carlos C. Wiedner, Buenos Aires.
- CALABY, J. H., and D. J. WIMBUSH. 1964. Observations on the broad-toothed rat, *Mastacomys fuscus* Thomas. *CSIRO Wildlife Research*, 9(2): 123-133.
- CARPENTER, C. R. 1940. A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comp. Psychol. Monogr.*, 16: 1-212.
- CASTRO, R., and P. SOINI. (In press.) Field studies on *Saguinus mystax* and other callitrichids in Amazonian Peru. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- CHALMERS, G. 1963. Breeding data — steinbok (*Raphicenus campestris* Thunberg). *E. Afr. Wildl. J.*, 1: 121-122.
- CHESEMORE, D. L. 1975. Ecology of the Arctic fox (*Alopex lagopus*) in North America: A review. In M. W. Fox (ed.), *The Wild Canids*, pp. 143-163. Van Nostrand Reinhold, New York.
- CHIVERS, D. J. 1972. The siamang and the gibbon in the Malay Peninsula. *Gibbon and Siamang*, 1: 103-135.
- . 1975. The siamang in Malaya: A field study of a primate in tropical rain forest. *Contrib. Primat.*, 4: 1-335.
- CHRISTEN, A. 1974. Fortpflanzungsbiologie und Verhalten bei *Cebuella pygmaea* and *Tamarin tamarin*. *Z. für Tierpsychol. Beiheft*, 14: 1-78.
- COIMBRA-FILHO, A. F., and R. A. MITTERMEIER. 1973. Distribution and ecology of the genus *Leontopithecus* Lesson, 1840, in Brazil. *Primates*, 14: 47-66.
- COLLINS, L. R., and J. F. EISENBERG. 1972. Notes on the behaviour and breeding of pacaranas, *Di-nomys branickii*, in captivity. *Internat. Zoo Yearb.*, 12: 108-114.
- CUNEO, F. 1965. Observations on the breeding of the klipspringer antelope, *Oreotragus oreotragus*, and

- the behaviour of their young born at the Naples Zoo. *Internat. Zoo Yearb.*, 5: 45-48.
- DAWSON, G. A. (In press.) Composition and stability of social groups of the tamarin, *Saguinus oedipus geoffroyi*, in Panama. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- DEAG, J. M., and J. H. CROOK. 1971. Social behaviour and "agonistic buffering" in the wild Barbary macaque, *Macaca sylvana* L. *Folia Primatol.*, 15: 183-200.
- DUBOST, G., and H. GENEST. 1974. Le comportement social d'une colonie de Maras *Dolichotis patagonum* Z. dans le Parc de Branféré. *Z. Tierpsychol.*, 35: 225-302.
- DUDLEY, D. 1974. Paternal behavior in the California mouse, *Peromyscus californicus*. *Behav. Biol.*, 11: 247-252.
- DUPLAIX-HALL, N. 1971. A comparative study of agonistic behaviour of otters in captivity. Talk presented at XII International Ethological Conference, Sept. 1971, Edinburgh, Scotland.
- . 1975. River otters in captivity: A review. In R. W. Martin (ed.), *Breeding Endangered Species in Captivity*, pp. 315-327. Academic Press, N. Y.
- EGOSCUE, H. J. 1960. Laboratory and field studies of the northern grasshopper mouse. *J. Mammal.*, 41: 99-110.
- . 1962. Ecology and life history of the kit fox in Tooele County, Utah. *Ecology*, 43: 481-497.
- EHRlich, A. 1974. Infant development in two prosimian species: greater galago and slow loris. *Develop. Psychobiol.*, 7: 439-454.
- EISENBERG, J. F. 1962. Studies on the behavior of *Peromyscus maniculatus gambelii* and *Peromyscus californicus parasiticus*. *Behaviour*, 19: 177-207.
- . 1963. The intraspecific social behavior of some cricetine rodents of the genus *Peromyscus*. *Amer. Müll. Nat.*, 69: 240-246.
- . 1966. *The Social Organizations of Mammals*. Handbuch der Zoologie, VIII (10/7), Lieferung 39, De Gruyter, Berlin.
- . 1968. Behavior patterns, In J. A. King (ed.), *Biology of Peromyscus (Rodentia)*, pp. 451-495. Special Publ. No. 2, Amer. Soc. Mammalogists, Stillwater, Oklahoma.
- . 1975. Tenrecs and solenodons in captivity. *Internat. Zoo Yearb.*, 15: 6-12.
- . (In press.) The evolution of the reproductive unit in the class Mammalia. In J. Rosenblatt and B. Komisaruk (eds.), *Lehrman Memorial Symposium, No. 1*.
- EISENBERG, J. F., and E. GOULD. 1970. The tenrecs: A study in mammalian behavior and evolution. *Smithson. Contr. Zool.*, 27: 1-137.
- EISENBERG, J. F., and M. LOCKHART. 1972. An ecological reconnaissance of Wilpattu National Park, Ceylon. *Smithson. Contr. Zool.*, 101: 1-118.
- ELLEFSON, J. O. 1974. A natural history of white-handed gibbons in the Malayan Peninsula. In D. M. Rumbaugh (ed.), *Gibbon and Siangang, Vol. 3*, pp. 1-136. S. Karger, New York.
- EPPLÉ, G. 1967. Vergleichende Untersuchungen über Sexual- und Sozialverhalten der Krallenaffen (Hapalidae). *Folia Primatol.*, 7: 37-65.
- . 1970a. Maintenance, breeding, and development of marmoset monkeys (Callitrichidae) in captivity. *Folia Primatol.*, 12: 56-76.
- . 1970b. Quantitative studies on scent marking in the marmoset (*Callithrix jacchus*). *Folia Primatol.*, 13: 48-62.
- . 1972. Social behavior of laboratory groups of *Saguinus fuscicollis*. In D. D. Bridgwater (ed.), *Saving the Lion Marmoset*, pp. 50-58. Wild Animal Propagation Trust, Wheeling, West Virginia.
- . 1975a. Parental behavior in *Saguinus fuscicollis* ssp. (Callitrichidae). *Folia Primatol.*, 24: 221-238.
- . 1975b. The behavior of marmoset monkeys (Callitrichidae). In L. A. Rosenblum (ed.), *Primate Behavior, Vol. 4*, pp. 195-239. Academic Press, New York.
- . (In press.) Notes on the establishment and maintenance of the pair bond in *Saguinus fuscicollis*. In D. G. Kleiman, (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- ESTES, R. D. 1974. Social organization of the African Bovidae. In V. Geist and F. Walther (eds.), *The Behaviour of Ungulates and Its Relation to Management, Vol. 1*, pp. 166-205. IUCN Publ. No. 24, Morges, Switzerland.
- ESTES, R. D., and J. GODDARD. 1967. Prey selection and hunting behavior of the African wild dog. *J. Wildl. Manage.*, 31: 52-70.
- EWER, R. F. 1963. The behaviour of the meercat, *Suricata suricatta* (Schreber). *Z. Tierpsychol.*, 20: 570-607.
- . 1973. *The Carnivores*. Cornell University Press, Ithaca.
- FONS, R. 1974. Le repertoire comportemental de la pachyure étrusque, *Suncus etruscus* (Savi, 1822). *La Terre et la Vie*, 1: 131-157.
- FREESE, C. H., M. FREESE, and N. CASTRO R. (In press.) The status of callitrichids in Peru. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- GAUTHIER-PILTERS, H. 1962. Beobachtungen an Feneks. *Z. Tierpsychol.*, 19: 440-464.
- . 1966. Einige Beobachtungen über das Spielverhalten beim Fenek. *Z. Säugetierk.*, 31: 337-350.
- GEWALT, W., and GRZIMEK, B. 1972. Phalangers. In W. Fiedler, W. Gewalt, B. Grzimek, D. Heinemann, K. Herter and E. Thenius (eds.), *Grzimek's Animal Life Encyclopedia, Vol. 10, Mam-*

- mals I*, pp. 110-128. Van Nostrand Reinhold Co., New York.
- GIER, H. T. 1975. Ecology and social behavior of the coyote. In M. W. Fox (ed.), *The Wild Canids*, pp. 247-262. Van Nostrand Reinhold Co., New York.
- GOLANI, I., and A. KELLER. 1975. A longitudinal field study of the behavior of a pair of golden jackals. In M. W. Fox (ed.), *The Wild Canids*, pp. 303-335. Van Nostrand Reinhold, New York.
- GOLANI, I., and H. MENDELSSOHN. 1970. Sequences of precopulatory behaviour of the jackal (*Canis aureus* L.). *Behaviour*, 38: 169-192.
- GOODWIN, G. G., and A. M. GREENHALL. 1961. A review of the bats of Trinidad and Tobago. *Bull. Am. Mus. Nat. Hist.*, 122: 195-301.
- GREENHALL, A. M. 1968. Notes on the behavior of the false vampire bat. *J. Mammal.*, 49: 337-340.
- GUCWINSKA, H., and A. GUCWINSKA. 1968. A note on the development and growth of European badgers, *Meles meles*, born at Wroclaw Zoo. *Internat. Zoo Yearb.*, 8: 133.
- HAMPTON, J. K., S. H. HAMPTON, and B. T. LANDWEHR. 1966. Observations on a successful breeding colony of the marmoset, *Oedipomidas oedipus*. *Folia Primatol.*, 4: 265-287.
- HART, B. 1974. Gonadal androgen and sociosexual behavior of male mammals: A comparative analysis. *Psychol. Bull.*, 81: 383-400.
- HEARN, J. P. (In press.) The endocrinology of reproduction in the common marmoset, *Callithrix jacchus*. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- HEDIGER, H. 1970. Zum Fortpflanzungsverhalten des Kanadischen Bibers (*Castor fiber canadensis*). *Forma et Functio*, 2: 336-351.
- HELTNE, P. G., D. C. TURNER, and J. WOLHANDLER. 1973. Maternal and paternal periods in the development of infant *Callimico goeldii*. *Am. J. Phys. Anthropol.*, 38: 555-560.
- HENDRICH, H. 1972. Beobachtungen und Untersuchungen zur Ökologie und Ethologie, insbesondere zur sozialen Organisation, ostafrikanischer Säugetiere. *Z. Tierpsychol.*, 30: 146-189.
- . 1975. Changes in a population of Dikdik, *Madoqua (Rhynchotragus) kirki* (Günther 1880). *Z. Tierpsychol.*, 38: 55-69.
- HENDRICH, H., and U. HENDRICH. 1971. *Dikdik und elefanten Ökologie und Soziologie zweier afrikanischer Huftiere*. R. Piper & Co., Munich.
- HEWER, H. R. 1974. *British Seals*. Collins, London.
- HOAGE, R. J. (In press.) Parental care in *Leontopithecus rosalia rosalia*: Carrying behavior. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- HOOPER, A. 1970. *Ujung Kulon: The Land of the Last Javan Rhinoceros*. E. J. Brill, Leiden.
- HORNER, B. E., and J. M. TAYLOR. 1968. Growth and reproductive behavior in the southern grasshopper mouse. *J. Mammal.*, 49: 644-660.
- HOUSSE, R. P. R. 1949. Los Zorros de Chile o chacales americanos. *Rev. Univ. Chile, Anales Acad. Chilena Cient. Nat. Santiago*, 34: 33-56.
- HOWARD, W. E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of prairie deer mice on the George Reserve, southern Michigan. *Contrib. Lab. Vert. Biol. Univ. Mich.*, 43: 1-50.
- ITANI, J. 1963. Paternal care in the wild Japanese monkey, *Macaca fuscata*. In C. H. Southwick (ed.), *Primate Social Behavior*, pp. 91-97. Van Nostrand Co., Princeton.
- IZAWA, K. 1976. Group sizes and their compositions of monkeys in the Upper Amazon Basin. *Primates*, 17: 367-399.
- JACKSON, H. H. T. 1961. *Mammals of Wisconsin*. University of Wisconsin Press, Madison.
- JANTSCHKE, F. 1973. On the breeding and rearing of bush dogs, *Speothos venaticus*, at Frankfurt Zoo. *Internat. Zoo Yearb.*, 13: 141-143.
- JARMAN, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour*, 48: 215-267.
- JOLLY, A. 1972. *The Evolution of Primate Behavior*. Macmillan Co., New York.
- JUNGIUS, H. 1971. *The Biology and Behaviour of the Reedbuck (Redunca arundinum Boddart 1785) in the Kruger National Park*. Mammalia Depicta, Paul Parey, Hamburg.
- KAUFMANN, J. H. 1974. Social ethology of the whiptail wallaby, *Macropus parryi*, in northeastern New South Wales. *Anim. Behav.*, 22: 281-369.
- KILGORE, D., JR. 1969. An ecological study of the swift fox (*Vulpes velox*) in the Oklahoma panhandle. *Am. Midl. Nat.*, 81: 512-534.
- KINGDON, J. 1974a. *East African Mammals, Vol. II, Part A (Insectivores and Bats)*. Academic Press, New York.
- . 1974b. *East African Mammals, Vol. II, Part B (Hares and Rodents)*. Academic Press, New York.
- KLEIMAN, D. G. 1966. Scent marking in the Canidae. *Symp. Zool. Soc. Lond.*, 18: 167-177.
- . 1967. Some aspects of social behavior in the Canidae. *Am. Zool.*, 7: 365-372.
- . 1968. Reproduction in the Canidae. *Internat. Zoo Yearb.*, 8: 3-8.
- . 1970. Reproduction in the female green acouchi, *Myoprocta pratti*. *J. Reprod. Fert.*, 23: 55-65.
- . 1971. The courtship and copulatory behavior of the green acouchi, *Myoprocta pratti*. *Z. Tierpsychol.*, 29: 259-278.
- . 1972. Maternal behaviour of the green

- acouchi, *Myoprocta pratti*, a South American caviomorph rodent. *Behaviour*, 43: 48-84.
- . 1974. Patterns of behaviour in hystricomorph rodents. *Symp. Zool. Soc. Lond.*, 34: 171-209.
- . (In press.) Characteristics of reproduction and sociosexual interactions in pairs of lion tamarins (*Leontopithecus rosalia*) during the reproductive cycle. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- KLEIMAN, D. G., and J. F. EISENBERG. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Behav.*, 21: 637-659.
- KOENIG, L. 1970. Zur Fortpflanzung und Jugendentwicklung des Wüstenfuchses (*Fennecus zerda* Zimm. 1780).
- KRIEG, H. 1929. Biologische reisestudien in Südamerika, XV. Zur Ökologie der Grossen Nager des Gran Chaco und seiner Grenzgebiete. *Z. Morphol. und Ökol. Tiere*, 15: 755-786.
- KRUUK, H. 1972. *The Spotted Hyena: A Study of Predation and Social Behavior*. University of Chicago Press, Chicago, Illinois.
- KÜHME, W. 1965. Freilandstudien zur Soziologie des Hyänenhundes (*Lycan pictus lupinus* Thomas 1902). *Z. Tierpsychol.*, 22: 495-541.
- KUMMER, H. 1968. *Social Organization of the Hamadryas Baboons*. University of Chicago Press, Chicago.
- LACK, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen & Co., London.
- LANCASTER, W. E. 1975. Exhibiting and breeding the Asian small-clawed otter, *Amblonyx cinerea*, at Adelaide Zoo. *Internat. Zoo Yearb.*, 15: 63-65.
- LEUTENEGGER, W. 1973. Maternal-fetal weight relationships in Primates. *Folia Primatol.*, 20: 280-293.
- LONG, J. O., and R. W. COOPER. 1968. Physical growth and dental eruption in captive-bred squirrel monkeys, *Samiri sciureus* (Leticia, Colombia), In L. A. Rosenblum and R. W. Cooper (eds.), *The Squirrel Monkey*, pp. 193-205. Academic Press, New York.
- LORENZ, R. 1972. Management and reproduction of the Goeldi's monkey, *Callimico goeldii* (Thomas 1904) Callimiconidae, Primates. In D. D. Bridgwater (ed.), *Saving the Lion Marmoset*, pp. 92-109. Wild Animal Propagation Trust, Wheeling West Virginia.
- LOWERY, G. H., JR. 1974. *The Mammals of Louisiana and Its Adjacent Waters*. Louisiana State University Press, Baton Rouge.
- MACPHERSON, A. H. 1969. The dynamics of Canadian Arctic fox populations. *Rept. Ser. Canadian Wildl. Serv.*, 8: 1-52.
- MARTIN, R. D. 1968. Reproduction and ontogeny in tree shrews (*Tupaia belangeri*), with reference to their general behaviour and taxonomic relationships. *Z. Tierpsychol.*, 25: 409-495; 505-532.
- MASON, W. A. 1966. Social organization of the South American monkey, *Callicebus moloch*: A preliminary report. *Tulane Stud. Zool.*, 13: 23-28.
- . 1974a. Differential grouping patterns in two species of South American monkey. In N. F. White (ed.), *Ethology and Psychiatry*, pp. 153-170. Univ. Toronto Press, Toronto.
- . 1974b. Comparative studies of social behavior in *Callicebus* and *Samiri*: Behavior of male-female pairs. *Folia Primatol.*, 22: 1-8.
- MCCABE, T. T., and B. D. BLANCHARD. 1950. *Three Species of Peromyscus*. Rood Associates, Santa Barbara.
- MCLANAHAN, E. B., and K. M. GREEN. (In press.) The vocal repertoire and an analysis of the contexts of vocalization in *Leontopithecus rosalia*. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D.C.
- MECH, L. D. 1970. *The Wolf: Ecology and Social Behavior of an Endangered Species*. Natural History Press, New York.
- MITCHELL, G. P. 1969. Paternalistic behavior in primates. *Psychol. Bull.*, 71: 399-417.
- MITCHELL, G. P., and E. M. BRANDT. 1972. Paternal behavior in Primates. In F. E. Poirier (ed.), *Primate Socialization*, pp. 173-206. Random House, New York.
- MOHR, E. 1936-1938. Biologische Beobachtungen an *Solenodon paradoxus* in Gefangenschaft (Parts I-IV). *Zool. Anzeiger*, 113: 177-188 (1936); 116: 65-76, 117: 233-241 (1937); 122: 132-143 (1938).
- . 1949. Einiges vom Grossen und vom Kleinen Mara (*Dolichotis patagonum* Zimm. und *salinicola* Burm.). *Zool. Gart.*, 16: 111-133.
- . 1965. *Altweltliche Stachelschweine*. Die Neue Brehm-Bücherei., A. Ziemsen Verlag, Wittenberg Lutherstadt.
- MORI, A. 1975. Signals found in the grooming interactions of wild Japanese monkeys of the Koshima troop. *Primates*, 16: 107-140.
- MORRIS, D. 1969. *The Human Zoo*. McGraw-Hill Book Company, New York.
- MOYNIHAN, M. 1964. Some behaviour patterns of platyrrhine monkeys. I. The night monkey (*Aotus trivirgatus*). *Smithson. Misc. Coll.*, 146(5): 1-84.
- . 1966. Communication in the Titi monkey, *Callicebus*. *J. Zool. Lond.*, 150: 77-127.
- . 1970. Some behavior patterns of platyrrhine monkeys. II. *Saguinus geoffroyi* and some other tamarins. *Smithson. Contrib. Zool.*, 28: 1-77.
- MUCKENHIRN, N. A. 1967. The behavior and vocal repertoire of *Saguinus oedipus* (Hershkovitz, 1966) (Callitrichidae, Primates). M. Sc. Thesis, University of Maryland, College Park.
- NAPIER, J. R., and P. H. NAPIER. 1967. *A Handbook of Living Primates*. Academic Press, New York.
- NEAL, E. 1948. *The Badger*. Pelican Books; Penguin Books Ltd., Middlesex.

- NEL, J. A. J. 1975. Aspects of the social ethology of some Kalahari rodents. *Z. Tierpsychol.*, 37: 322-331.
- NEWSON, R. M. 1966. Reproduction in the feral coypu (*Myocastor coypus*). *Symp. Zool. Soc. Lond.*, 15: 323-334.
- NEYMAN, P. F. (In press.) Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Sagunus oedipus*) and the conservation status of the species. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- OLDS, J. M. 1950. Notes on the hood seal, *Cystophora cristata*. *J. Mammal.*, 31: 450-452.
- ORIAN, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.*, 103: 589-603.
- PARKER, G. A. 1974. Courtship persistence and female-guarding as male time investment strategies. *Behaviour*, 48: 157-184.
- PAYNE, A. P., and H. H. SWANSON. 1972a. Effect of sex hormones on the agonistic behavior of the male golden hamster (*Mesocricetus auratus* Waterhouse). *Physiol. Behav.*, 8: 687-692.
- . 1972b. The effect of sex hormones on the aggressive behaviour of the female golden hamster (*Mesocricetus auratus* Waterhouse). *Anim. Behav.*, 20: 782-787.
- . 1973. The effects of neonatal androgen administration on the aggression and related behaviour of male golden hamsters during interactions with females. *J. Endocrinol.*, 58: 627-636.
- PETTER, J.-J. 1965. The lemurs of Madagascar. In I. DeVore (ed.), *Primate Behavior*, pp. 292-321. Holt Rinehardt and Winston, New York.
- PETTER, J.-J., and A. PEYRIERAS. 1974. A study of population density and home range of *Indri indri* in Madagascar. In R. D. Martin, G. A. Doyle, and A. C. Walker (eds.), *Prosimian Biology*, pp. 39-48. Duckworth, London.
- PINTER, A. J. 1970. Reproduction and growth for two species of grasshopper mice (*Onychomys*) in the laboratory. *J. Mammal.*, 51: 236-243.
- POIRIER, F. E. 1970. The Nilgiri langur (*Presbytis johnii*) of South India. In L. A. Rosenblum (ed.), *Primate Behavior Vol. I*, pp. 251-383. Academic Press, New York.
- POLLOCK, J. I. 1975. Field observations on *Indri indri*: A preliminary report. In I. Tattersall and R. W. Sussman (eds.), *Lemur Biology*, pp. 287-311. Plenum Press, New York.
- RAHM, U. 1962. Biologie und Verbreitung des Afrikanischen Quastenstachlers *Atherurus africanus* Gray. *Rev. Suisse Zool.*, 69: 344-359.
- RALLS, K. 1973. *Cephalophus maxwellii*. *Mammalian Species*, No. 31: 1-4.
- . 1974. Scent marking in captive Maxwell's duikers. In V. Geist and F. Walther (eds.), *The Behaviour of Ungulates and Its Relation to Management, Vol. I*, pp. 114-123. IUCN Publ. # 24, Morges, Switzerland.
- . 1976. Mammals in which females are larger than males. *Q. Rev. Biol.*, 51: 245-276.
- RAMIREZ, M. F., C. H. FREESE, and J. REVILLA. (In press.) Feeding ecology of the pygmy marmoset, *Cebuella pygmaea*, in northeastern Peru. In D. G. Kleiman (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Press, Washington, D. C.
- RANSOM, T. W., and B. S. RANSOM. 1971. Adult male-infant relations among baboons (*Papio anubis*). *Folia Primatol.*, 16: 179-195.
- RASA, O. A. E. 1972. Aspects of social organization in captive dwarf mongooses. *J. Mammal.*, 53: 181-185.
- . 1973a. Intra-familial sexual repression in the dwarf mongoose, *Helogale parvula*. *Naturwissenschaften*, 6: 303-304.
- . 1973b. Marking behaviour and its social significance in the African dwarf mongoose, *Helogale undulata rufula*. *Z. Tierpsychol.*, 32: 293-318.
- . 1975. Mongoose sociology and behaviour as they relate to zoo exhibition. *Internat. Zoo Yearb.*, 15: 65-73.
- RATHBUN, G. 1976. The ecology and social structure of the elephant-shrews, *Rhynchocyon chrysopygus* Gunter and *Elephantulus rufescens* Peters. Ph.D. Thesis, University of Nairobi, Nairobi.
- ROOD, J. P. 1972. Ecological and behavioural comparisons of three genera of Argentine cavies. *Anim. Behav. Monogr.*, 5: 1-83.
- . 1974. Banded mongoose males guard young. *Nature*, 248: 176.
- ROSENBLUM, L. A. 1968. Mother-infant relations and early behavioral development in the squirrel monkey. In L. A. Rosenblum and R. W. Cooper (eds.), *The Squirrel Monkey*, pp. 207-234. Academic Press, New York.
- ROTHER, H. 1973. Beobachtungen zur Geburt beim Weissbüscheläffchen (*Callithrix jacchus* Erxleben, 1777). *Folia Primatol.*, 19: 257-285.
- . 1975. Some aspects of sexuality and reproduction in groups of captive marmosets (*Callithrix jacchus*). *Z. Tierpsychol.*, 37: 255-273.
- . (In press.) Allogrooming by adult *Callithrix jacchus* in relation to post partum oestrus. *J. Human Evol.*
- ROWELL, T. E. 1974. The concept of social dominance. *Behav. Biol.*, 11: 131-154.
- RUFFER, D. G. 1965. Sexual behaviour of the northern grasshopper mouse (*Onychomys leucogaster*). *Anim. Behav.*, 13: 447-452.
- RYDEN, H. 1974. The "lone" coyote likes family life. *Nat. Geogr. Mag.*, 146(2): 279-294.
- SAAYMAN, G. S. 1971. Grooming behaviour in a troop of free-ranging Chacma baboons (*Papio ursinus*). *Folia Primatol.*, 16: 161-178.

- SASAKI, T. 1964. Hand-rearing a baby gibbon (*Hylobates lar*). *Internat. Zoo Yearb.*, 4: 289-290.
- SCHALLER, G. B. 1963. *The Mountain Gorilla*. University of Chicago Press, Chicago.
- . 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press, Chicago.
- SCHEFFER, V. B. 1958: *Seals, Sea Lions and Walrus: A Review of the Pinnipedia*. Stanford University Press, Stanford.
- SEITZ, A. 1955. Untersuchungen über angeborene Verhaltensweisen bei Caniden. *Z. Tierpsychol.*, 12: 463-489.
- SHORTTRIDGE, G. C. 1934. *The Mammals of South West Africa*. William Heinemann, Ltd., London.
- SIMONETTA, A. M. 1966. Osservazioni etologiche ed ecologiche sui dik-dik (*Madoqua*; Mammalia, Bovidae) in Somalia. *Monit. Zool. Ital.*, 74: 1-33.
- SLIJPER, E. J. 1962. *Whales*. Hutchinson and Company, London.
- SMITHERS, R. H. N. 1966. *The Mammals of Rhodesia, Zambia and Malawi*. Collins, London.
- SMYTHE, N. 1970. Ecology and behavior of the agouti (*Dasyprocta punctata*) and related species on Barro Colorado Island, Panama. Ph. D. Thesis, University of Maryland, College Park.
- SNYDER, P. A. 1974. Behavior of *Leontopithecus rosalia* (golden lion marmoset) and related species: A review. *J. Human Evol.*, 3: 109-122.
- SPARKS, J. 1967. Allogrooming in Primates: A review. In D. Morris (ed.), *Primate Ethology*, pp. 146-175. Aldine Publishing Co., Chicago.
- SPENCER-BOOTH, Y. 1970. The relationship between mammalian young and conspecifics other than mothers and peers: A review. In D. S. Lehrman, R. A. Hinde, and E. Shaw (eds.), *Advances in the Study of Behavior*, Vol. 3, pp. 120-194. Academic Press, New York.
- STANLEY, M. 1971. An ethogram of the hopping mouse, *Notomys alexis*. *Z. Tierpsychol.*, 29: 225-258.
- STIRLING, I. 1975. Factors affecting the evolution of social behaviour in the Pinnipedia. *Rapp. P.-V. Réun. Cons. int. Explor. Mer*, 169: 205-212.
- STORM, G. L. 1965. Movements and activities of foxes as determined by radiotracking. *J. Wildl. Manage.*, 29: 1-13.
- TATE, G. H. H. 1931. Random observations on habits of South American mammals. *J. Mammal.*, 12: 248-256.
- TEMBROCK, G. 1957. Zur Ethologie des Rotfuchses (*Vulpes vulpes* L.) unter besondere Berücksichtigung der Fortpflanzung. *Zool. Gart. Leipzig*, 23: 289-532.
- TENAZA, R. R. 1975. Territory and monogamy among Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Folia Primatol.*, 24: 60-80.
- TILSON, R. L., and R. R. TENAZA. 1976. Monogamy and duetting in an Old World Monkey, *Presbytis potenziani*. *Nature*, 263: 320-321.
- TINLEY, K. L. 1969. Dikdik, *Madoqua kirki* in South West Africa: Notes on distribution, ecology and behaviour. *Madoqua*, 1: 7-33.
- TRAPP, G., and HALLBERG, D. L. 1975. Ecology of the gray fox (*Urocyon cinereoargenteus*): A review. In M. W. Fox (ed.), *The Wild Canids*, pp. 164-178. Van Nostrand Reinhold Co., New York.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. In B. Campbell (ed.), *Sexual Selection and the Descent of Man, 1871-1971*, pp. 136-179. Aldine Publishing Co., Chicago.
- TROUGHTON, E. 1941. *Furred Animals of Australia*. Angus and Robertson, Sydney.
- TYLER, S. J. 1972. The behaviour and social organization of the New Forest Ponies. *Anim. Behav. Monogr.*, 5: 87-196.
- VANDENBERGH, J. G. 1971. The effects of gonadal hormones on the aggressive behaviour of adult golden hamsters (*Mesocricetus auratus*). *Anim. Behav.*, 19: 589-594.
- VAN DER MERWE, N. J. 1953. The jackal. *Fauna Flora* (Transvaal), 4: 4-80.
- VAN LAWICK, H. 1971. Golden jackals. In H. and J. Van Lawick-Goodall (eds.), *Innocent Killers*, pp. 105-149. Houghton Mifflin Co., Boston.
- VAN LAWICK-GOODALL, J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.*, 1: 165-311.
- VAN WIJNGAARDEN, J., and VAN DE PEPPEL, J. 1964. The badger, *Meles meles* (L.), in the Netherlands. *Lutra*, 6: 3-60.
- VERSCHUREN, J. 1957. Ecologie, biologie, et systématique des Chiroptères. *Explor. Parc Nat. Garamba: Miss. de Saeger Inst. Parcs Nation. Congo Belge, Bruxelles*, # 7.
- WALKER, E. P. 1975. *Mammals of the World, Vol. 1*; 3rd ed. Johns Hopkins Press, Baltimore.
- WEBSTER'S NEW WORLD DICTIONARY OF THE AMERICAN LANGUAGE. 1966. World Publishing Co., New York.
- WEIR, B. J. 1973. Another hystricomorph rodent: Keeping casiragua (*Proechimys guairae*) in captivity. *Lab. Anim.*, 7: 125-134.
- WEMMER, C., and FLEMING, M. J. 1975. Management of meercats, *Suricata suricatta*, in captivity. *Internat. Zoo Yearb.*, 15: 73-77.
- WEST EBERHARD, M. J. 1975. The evolution of social behavior by kin selection. *Q. Rev. Biol.*, 50: 1-33.
- WICKLER, W., and UHRIG, D. 1969. Verhalten und ökologische Nische der Gelbflügel fledermaus, *Lavia frons* (Geoffroy) (Chiroptera, Megadermatidae). *Z. Tierpsychol.*, 26: 726-736.
- WILSON, E. O. 1975. *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge.
- WILSON, V. J., and CLARKE, J. E. 1962. Observations on the common duiker, *Sylvicapra grimmia* Linn., based on material collected from a tsetse control game elimination scheme. *Proc. Zool. Soc. Lond.*, 138: 487-497.

- WILSSON, L. 1968. *My Beaver Colony*. Doubleday and Co., Garden City.
- . 1971. Observations and experiments on the ethology of the European beaver (*Castor fiber* L.) *Viltrevy*, 8(3): 115-266.
- ZIMEN, E. 1971. *Wölfe und Königspudel*. R. Piper and Co., Verlag, München.
- . 1975. Social dynamics of the wolf pack. In M. W. Fox (ed.), *The Wild Canids*, pp. 336-362. Van Nostrand Reinhold Co., New York.