

A Study of Social Evolution: The Influence of Environment, Behavior, and Kinship on the Demography of a Population of Toque Monkeys

Principal Investigator: Wolfgang P. J. Dittus, National Zoological Park, Smithsonian Institution, Washington, D. C.

Grant No. 1442: In support of a study of the influence of genealogy in socioecology and social evolution, based on research of a wild population of toque monkeys *Macaca sinica* in Sri Lanka.

Introduction

Recent theoretical advances concerning the evolution of animal societies have brought a closer understanding of how social behaviors might have evolved (e.g., Hamilton, 1964, 1971; Alexander, 1974; West Eberhard, 1975; Wilson, 1975; Dittus, 1979). Notwithstanding, most authors express the need for empirical data from natural populations in order that these theories might be tested and further developed. The most critical need for such data concerns the highly social mammalian species, such as primates, which have long generation times, and which share some fundamental genetic and social attributes with humans.

Testing or developing evolutionary theory among highly social vertebrates requires that the fitness of individuals be measured as well as factors that might influence fitness. My past research has dealt with the influence of behavior and ecology on the survivorship and related vital statistics of individuals in a large population of wild toque monkeys, *Macaca sinica*. This population inhabits the natural semievergreen forest at Polonnaruwa, Sri Lanka. These studies indicated that in macaque society mortality is imposed socially through competition for vital resources and mates. This determines not only the density and net reproductive rate of the population, but also its age and sex class structure (Dittus, 1975, 1977a). Some evidence suggested that socially imposed mortality differs, however, according to kinship relationships, as well. Thus, the variables of environmental change, age, sex, kinship, and behavioral dominance are known or suspected to influence the survivorship of individuals. My long-term goals are to test certain hypotheses concerning the evolution of social behavior by examining the influence of the aforementioned

variables on the survivorship and reproductive success of individual macaques. This requires that the life-histories of a large sample of identified individuals are traced over several years. Over 150 individual macaques had been identified, and the demography of approximately 450 macaques (18 social groups) had been studied at Polonnaruwa between 1968 and 1972.

The immediate objectives during the tenure of the research grant from the National Geographic Society (March 1975 to February 1976) were to reconfirm kinship lineages known up to 1972, and especially to expand the sample size of identified individuals and to recensus the population for demographic information. These data were to serve as a foundation for future research efforts which were to be supported by other research grants.

During the course of the research sponsored by the National Geographic Society, our goals were expanded to include a delineation of the dominance hierarchies among the individuals of all the 18 troops under study. In order to discern differences in the growth rates by such variables as age, sex, and kinship, a large sample of animals also was weighed.

Methods

Identification of Individual Macaques. Individuals are distinguished on the basis of age, sex, fur color, scars, the distribution of red and black spots in the face, and the distribution of black pigment on the ears and lips. Among infants and juveniles, where conspicuous markings are uncommon, the following features are most useful: length, color, and arrangement of the head hair (called the toque); fur color; and distribution of depigmented (white) patches and streaks on the normally light blue skin on the ventral body surfaces. An identification card with a drawing and description of the individual's morphology is made for each individual in the population. One set of cards is used in the field for confirming identifications. A duplicate set is kept in the office.

Population Census. As all individuals in the population are identified, a census involves checking for the presence or absence of each identified animal in each troop. Changes, such as the presence of a new individual either through birth or immigration, are recorded. Each troop is censused once each month. During the birth season the adult females of each troop may be checked two or three times each week in order to pinpoint the date of birth of infants and to sex them very early in case of early mortality.

Establishing Genealogies. Matrilineages are ascertained best by tracing known kinships from birth. Mothers nurse only their own infants. Because of

TABLE 1. Comparisons of the Age and Sex Class Composition of the Macaque Population at Polonnaruwa between 1971 and 1975

To calculate the Wilcoxon statistic, T, data from 1971 were paired with those from 1975 for each of the 17 troops. The one-tailed level of significance was applied. "Young juveniles" are one-half to two years old; "old juveniles" are two to five years old (abridged from Dittus, 1977a).

Macaque population	Number of animals		% change	Wilcoxon T	Significance P
	1971	1975			
Males					
Adult	44	48	+ 9.1	9.5	> 0.05
Subadult	22	23	+ 4.5	33.5	> 0.05
Old Juvenile	56	48	-14.3	38.5	> 0.05
Young Juvenile	51	28	-45.1	12.0	< 0.005
Total	173	147	-15.0	26.5	< 0.05
Females					
Adult	103	94	- 8.7	25.0	> 0.05
Old Juvenile	34	21	-38.2	24.0	< 0.025
Young Juvenile	36	31	-13.9	9.0	< 0.01
Total	173	146	-15.6	18.0	< 0.025
Population Total	346	293	-15.3	14.0	< 0.005

the uncertainty of fatherhood the establishment of patrilineages is impractical.

Determination of Dominance Hierarchies. The dominance relations or hierarchies in 18 troops were ascertained on the basis of the behaviors observed among individuals within a troop. Priority of access to food, approach-avoidance interactions and similar behaviors serve as criteria for dominant-surbordinate assessments (Richards, 1974, Farres and Haude, 1976).

Weighing Macaques in the Field. A spring-balanced weighing scale is suspended from a tree support; small known amounts of rice are placed in the weighing pan to entice animals to sit in the pan.

Results

DEMOGRAPHY

The numerical composition of the macaque population by age and sex class is given in Tables 1 and 2. Data from 1975 are compared to those of 1971. The data of Table 1 indicate a significant ($P < 0.005$) 15.3-percent

TABLE 2. Comparisons of Troop Size and Age-Sex Composition in Troop Oval Between 1971 and 1975 (from Dittus, 1977a)

Troop Oval composition	Number of animals	
	1971	1975
Males		
Adult	4	6
Subadult	1	2
Old Juvenile	4	6
Young Juvenile	2	2
Total	11	16
Females		
Adult	8	11
Old Juvenile	1	7
Young Juvenile	4	2
Total	13	20
Troop Total	24	36

decrease in total population size. There was no significant numerical decrease among the adult females or among the adult, subadult, and old juvenile males. But the numbers of young juvenile males, and old and young juvenile females decreased significantly. Overall, the numbers of young juveniles (sexes combined) decreased more (32.2%) than those of old juveniles (23.3%).

These changes were distributed evenly among the troops in the population; the mean decrease per troop was 14.6 percent, and the relative ranks of troop sizes did not alter significantly among these 17 troops (see table 2 in Dittus, 1977a). These changes probably are attributable to increased mortality resulting from a food shortage between 1972 and 1975 (see Discussion).

In contrast to other troops, troop Oval (table 2) had a constant and abundant food supply from a municipal garbage dump between 1971 and 1975. There was no increase in mortality evident among any of the age-sex classes. Rather, the data indicate a 50-percent net increase in troop size, or an annual growth rate of 12.5 percent.

GENEALOGY

The composition of the macaque population in terms of known genealogical relationships by April 1976 is summarized in table 3. Except for lineages traced since 1968, most of the relationships identified by April 1976 were among the infants and young juveniles born in the two birth seasons 1974 to

TABLE 3. Summary of the Kinds and Numbers of Matrilineal Relationships Identified Among All Living Individuals from 18 Troops by April 1976

Some of the data are not mutually exclusive

<i>Kinds of individuals</i>	<i>Number known April 1976</i>	
	<i>Infants and juveniles</i>	<i>Subadults and adults</i>
Total animals living and identified	208	206
Different matrilineages		98
Adult females or mothers		114
Daughters	57	10
Sons	69	4
Grandmothers		5
Grandsons and granddaughters	9	
Sets of 2 or more brothers	13	0
Sets of 2 or more sisters	11	3
Sets of 2 or more brothers-sisters	20	
Sets of distant relatives other than above	10	

1975 and 1975 to 1976. By maintaining life-history records up to the present, more relationships are now identified among the older juveniles and adults (unpublished data).

DIFFERENTIAL SURVIVORSHIP BY SOCIAL RANK AND KINSHIP

The data in Table 4 indicate that high-ranking adult females had greater reproductive success than mid- or low-ranking ones. A female's social rank was determined by her position in the hierarchy or dominance-subordinate relationships (see Methods). Reproductive success is measured by the number of sons and daughters that survive to adulthood. The data also indicate that the kinship of an infant determines its probability of survival to adulthood. Infants of high-ranking mothers survived better than those of mid- or low-ranking ones.

GROWTH RATES OF MALES AND FEMALES

The data in Table 5 indicate that juvenile males grow significantly faster (0.590 kg per year) than their female peers (0.407 kg per year); and adult males weigh considerably more than adult females.

TABLE 4. The Reproductive Success of Adult Females Differing in Social Rank

High-ranking mothers have significantly more daughters ($p < 0.01$) and total offspring ($p < 0.01$) surviving to reproduce than mid- or low-ranking ones, and offspring survivorship is not proportional ($p < 0.03$) to differences in birth rates per maternal rank. [Kolmogorov-Smirnov one sample two-tailed test (Siegel, 1956).] Data are from 9 troops observed for periods of 3 to 9 years (from Dittus, 1979a).

Social rank of mother	Number of mothers	Annual birth rate per rank	Number of offspring surviving to reproduce		
			Daughters	Sons	Total
high	15	0.750	15	4	19
mid	15	0.600	2	2	4
low	14	0.642	4	0	4

TABLE 5. Approximate Difference in the Growth Rates Between Male and Female Juveniles (Aged 0.1 to 5.5 Years), and the Average Weights of Adults of *Macaca sinica* (from Dittus, 1979a)

Item	Male	Female
Number of juveniles weighed	15	8
Rate of growth in kg per year	0.590	0.407
Significance of the difference in juvenile growth rates (t-test)	0.013	
Number of adults weighed	38	37
Average weight of adults in kg	5.35	3.29
Standard deviation of average adult weight	0.70	0.33

Discussion

Most of the data (tables 1, 2, 4, and 5) have been presented and discussed more extensively together with other data in publications dealing with conservation (Dittus, 1977b), population regulation (Dittus, 1977a), and social evolution (Dittus, 1979). The following discussion partially recapitulates the significance of these data.

The demographic changes between 1971 and 1975 (table 1) can be linked to environmental changes for the population of *Macaca sinica* at Polonnaruwa. Two events led to a decrease in the food supply for the macaque population after the end of 1971. First, prior to 1972 two large troops (M and D) fed heavi-

ly from a rice mill that bordered the study area. The rice mill ceased operations in 1972 thereby depriving these two troops of their major food supply. Consequently they expanded their home ranges into those of neighboring troops and competed with them for the more conventional forest foods. Secondly, in 1974 the Polonnaruwa area was subject to the worst drought in the 44 years for which meteorological records are available. Drought lasted for eleven months instead of the usual two to three months; only one-sixth of the normal rainfall was received during these eleven months. Presumably the drought inhibited the normal production of plant shoots, mushrooms, fruits, and seeds which constitute the macaque's normal diet during this period.

The mortality that is assumed to have resulted from these food shortages was highest among the juveniles in general, but especially among the infants and young juveniles, and among the young and old juvenile females.

Troop Oval (table 2) was not subject to these food shortages; it fed extensively from a municipal garbage dump located just outside the study area. In contrast to the other troops it had an abundant supply of food scraps that were deposited almost daily. As a consequence there was no increase in mortality evident among animals of troop Oval. Instead, mortality was lower than under equilibrium conditions ($R_0 = 1$), such that the troop grew in size at a rate of 12.5 percent per annum between 1971 and 1975. This population growth rate is comparable to those of other primate populations that have been provisioned with abundant food by man (see review, Dittus, 1980).

The greater part of a macaque's daily activity involves foraging, or, the search for and consumption of food. About 82 percent of all threats occurring in the society involve competition over food (Dittus, 1977a). Dominant animals exploit subordinate ones by usurping their food, or by preventing them from feeding. Exploitative behaviors vary however, according to the age, sex, and kinship of troop members. In general, dominant animals tolerate juvenile females far less than their male peers during food competition, and young juveniles are exploited more frequently than old ones. Under normal environmental conditions when population growth is at equilibrium ($R_0 = 1$) these behavioral differences result in greater mortality among young versus old juveniles and among female versus male juveniles (ibid.). The food shortages between 1972 and 1975 appear to have accentuated these mortality differences by age and sex. That is, infants and young juveniles and juvenile females died at even greater rates than under stable environmental conditions.

Wild populations of vervet monkeys *Cercopithecus aethiops* (Struhsaker, 1973, 1976; Galat and Galat-Luong, 1977) and of baboons *Papio cynocephalus* (Hausfater, 1975) have similarly diminished in size when their natural food supply was destroyed. The decrease of *C. aethiops* populations was due to

increased mortality, especially among the youngest or most subordinate juveniles (Struhsaker, 1976); and the increased mortality in the diminishing population of *C. aethiops* studied by Galat and Galat-Luong (1977) was attributed to malnutrition.

These interrelationships are consistent with hypotheses concerning the evolution of social behavior in the macaque. Briefly, demographic and genealogical data indicate that adult females in a troop are related to one another and to all infants and juveniles. With the exception of fathers, adult males and those adolescent males that immigrated from other troops are least related to the adult females and their young. Thus, kin selection (e.g., see Wilson, 1975) may be operative among related members in the macaque society. Food resources in a population or troop are limiting. Hence, a dominant animal that exploits a subordinate one for limiting resources is enhancing its own fitness at the expense of the subordinate's. If the subordinate is related to the exploiter he may gain in inclusive fitness, however, by an amount that is directly proportional to the number of genes that he shares with the exploiter through descent from a common ancestor. The tradeoff, or ratio of loss to gain of fitness through such exploitative-altruistic behaviors will be partly a function of the degree of relatedness, r , (proportion of identical genes shared) between the actors (Hamilton, 1964).

Parental and kin investment among related troop members can be defined and measured by the frequency of behaviors involving exploitation for limiting resources. Dominant parents invest in their offspring or subordinate relatives by permitting them to share limiting resources in the troop. And, subordinate relatives invest in their dominant kin by being exploited by them for limiting resources. Such investments might be considered as "voluntary" and "imposed altruism," respectively. The altruists gain fitness through the enhanced survivorship that their investment (limiting resources) bestows upon their related beneficiaries. They lose fitness through limiting resources that they relinquish. The gains in inclusive fitness need not necessarily outweigh the loss of fitness in order for altruistic behavior to evolve (see Dittus, 1979).

Parental and kin investment by sex appears to be tailored to sex differences in reproductive strategy.

Adult and adolescent males are wounded and die more frequently as a result of fighting in competition for mates than their female peers. Hence, in order for young male macaques to survive and succeed in their adult reproductive careers they need to acquire larger size and greater fighting ability than their female peers. In order to perpetuate their genes through sons and male relatives, parents and relatives, therefore, invest more in the growth and sur-

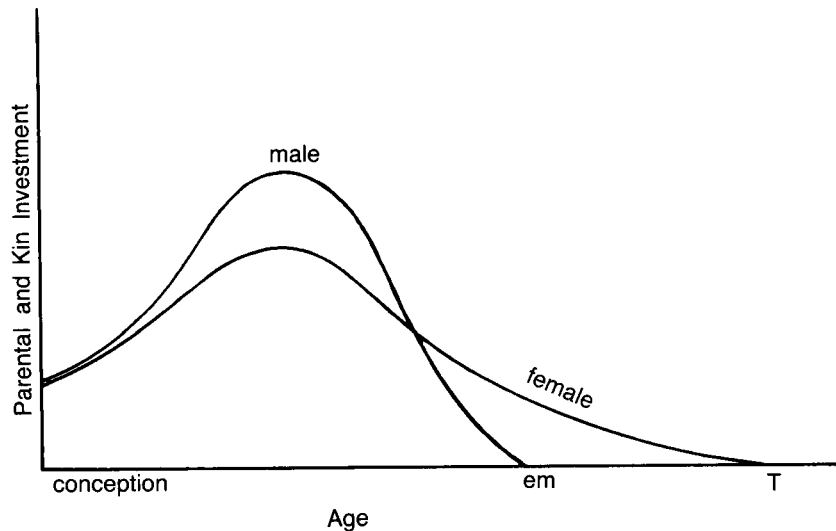


FIG. 1. Schematic representation of the schedule of investment in offspring and other relatives of different sex. Initially, investment in male is greater than in female peers, but it ceases when males emigrate (em) from the natal group at adolescence. On the other hand, investment in females continues into adulthood through the average duration of the female generation (T). Total investment in males and females is equal per generation. (Adapted after Figure 8 in Dittus, 1979).

survivorship of sons (and male kin) than in their daughters (and female kin) during the infant and juvenile phases. The resulting greater growth and survivorship among young males compared to their female peers would tend to improve the young males' chances of survival after they emigrate from their natal troop at adolescence, when they encounter the hazards of competing for resources and mates with males from other troops.

Although males are favored at the expense of females during youth, females are compensated for their altruism because, unlike their male peers, they are not forced to emigrate from their natal troop at adolescence. Instead, they continue to benefit from the tolerance and altruism of their relatives throughout life. Per generation, then, parental and kin investment can be shown to be equal in male and female progeny and kin and the average survivorships of the male and female cohorts are, therefore, equal (Dittus, 1979, see fig. 1).

At times of food shortage when the loss of fitness through food depriva-

tion is inevitable by at least some members of the society, parents and kin should behave in a manner to minimize their loss of fitness. Having invested less in females than in males of the same age and r , such curtailment is more likely to be in females than in males of equal age and r . As a result juvenile females are more likely to die than the males. Similarly, more has been cumulatively invested in older than younger offspring and relatives (of the same sex and r) such that the fitness of parents and relatives is served best if younger rather than older offspring and relatives (of the same sex and r) were to die among juveniles and infants. This would explain the demographic changes observed on the macaque population between 1971 and 1975 in terms of the evolution of social behavior. For a more rigorous consideration of these and similar interrelationships, see Dittus (1979).

The data in table 4 confirm the importance of dominance rank and kinship to survivorship. The offspring of high-ranking adult females stand a greater chance of surviving to reproduce than those of lesser-ranking females.

The influence of kinship on the behavioral determination of survivorship and reproductive success is currently being further investigated. The growing number of kinship relationships being identified (table 3) and the life-history data being accumulated are fundamental to the research concerning the evolution of social organization and behavior in *Macaca sinica*.

Summary

A wild population of about 450 toque monkeys *Macaca sinica* of Sri Lanka was reinvestigated between March 1975 and February 1976 for demographic, genealogical, and behavioral information. The population size decreased by 15.3 percent from previous years (1971). This was attributed to increased mortality among the juveniles in general, but especially among the infants and youngest juveniles, and among female juveniles. The mortality resulted from a diminished food supply for the macaque population between 1972 and 1975. Records concerning genealogical relationships and life-history data were updated from previous years and were expanded to include all individuals in the 18 social groups being studied. Dominance relations among troop members in all troops were also established.

Long-term records indicate that adult females of high social rank have greater reproductive success than low-ranking ones in terms of the number of offspring that survive to an age when they can reproduce.

The new data have contributed to our understanding of the evolution of social behavior. These theoretical considerations have been published elsewhere and are outlined only briefly in this report.

Acknowledgments

I am grateful to the National Geographic Society for the grant which supported this research on social evolution of a population of toque monkeys. I also thank Mr. S.M.S. Farook for valuable field assistance.

REFERENCES

- ALEXANDER, RICHARD D.
1974. The evolution of social behavior. . Ann. Rev. Ecol. Syst., vol. 5, pp. 325-383.
- DITTUS, WOLFGANG, P. J.
1975. Population dynamics of the toque monkey, *Macaca sinica*. Pp. 125-152 in "Socioecology and Psychology of Primates," R. H. Tuttle, ed. Mouton Publishers, The Hague.
1977a. The social regulation of population density and age-sex distribution on the toque monkey. Behaviour, vol. 63, pp. 281-322, illus.
1979. The evolution of behaviors regulating density and age-specific sex ratios in a primate population. Behaviour, vol. 69, pp. 265-302.
1980. The social regulation of primate populations: A synthesis. Pp. 263-286 in "The Macaques: Studies in Ecology, Behavior, and Evolution," D. G. Lindburg, ed. Van Nostrand Reinhold, New York. (In press.)
- FARRES, ALBERT, G., and HAUDE, RICHARD H.
1976. Dominance testing in rhesus monkeys: Comparisons of competitive food getting, competitive avoidance, and competitive drinking procedures. Psychol. Rep., vol. 38, pp. 127-134.
- GALAT, GERARD, and GALAT-LUONG, ANH
1977. Demographie et regime alimentaire d'une troupe de *Cercopithecus aethiops sabaus* en habitat marginal au Nord Senegal. La Terre et la Vie, vol. 31, pp. 557-577.
- HAUSFATER, GLEN
1975. Dominance and reproduction in baboons (*Papio cynocephalus*). Contrib. Primatol., vol. 7, pp. 1-150.
- HAMILTON, WILLIAM D.
1964. The genetical evolution of social behaviour. Journ. Theoret. Biol., vol. 7, pp. 1-51.
1971. Selection of selfish and altruistic behavior in some extreme models. Pp. 57-91 in "Man and Beast: Comparative Social Behavior," J. F. Eisenberg and W. S. Dillon, eds. Smithsonian Institution Press, Washington, D. C.
- RICHARDS, SANDY M.
1974. The concept of dominance and methods of assessment. Anim. Behav., vol. 22, pp. 914-930.
- SIEGAL, SYDNEY
1956. Non-parametric statistics, 312 pp. McGraw Hill, New York.

STRUHSAKER, THOMAS T.

1973. A recensus of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. *Ecology*, vol., 54, pp. 930-932.

1976. A further decline in numbers of Amboseli vervet monkeys. *Biotropica*, vol., 8, pp. 211-214.

WEST EBERHARD, MARY JANE

1975. The evolution of social behavior by kin selection. *Quart. Rev. Biol.*, vol. 50, pp. 1-33.

WILSON, EDWARD O.

1975. *Sociobiology*, 697 pp. Harvard University Press, Cambridge.

WOLFGANG P. J. DITTUS