LEIDEN
E. J. BRILL
1977

THE SOCIAL REGULATION OF POPULATION DENSITY AND AGE-SEX DISTRIBUTION IN THE TOQUE MONKEY

by

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INTRODUCTION

In this paper, I will consider the role of agonistic and affiliative behaviors in determining the organization of macaque societies. Can social behavior determine not only the density of macaque populations, but also their age and sex distributions?

The data herein are based on 6½ years of observation of a wild population of toque monkeys, *Macaca s. sinica* (Linnaeus 1771) of Sri Lanka. Research began in September 1968 and terminated 3½ years later in January 1972. An additional 2 months of research occurred during March and April of 1975. My assistent Mr S. M. S. FAROOK carried out intermittent observations between early 1972 and March 1975.

The main study site is in a semi-evergreen forest at Polonnaruwa in the dry zone plains (Figure 1). Here a population of nearly 450 animals from 18 troops was investigated. Comparative observations were taken in Anuradhapura, a secondary study site in the same climatic zone.

The toque monkey is confined to the island of Sri Lanka where its

distribution is limited to the forested and watered regions. It is a small and long-tailed macaque and is agile both on and above ground. (GRAND, 1972, 1976). Its nearest relatives are the bonnet macaques, *Macaca radiata*, of southern India.
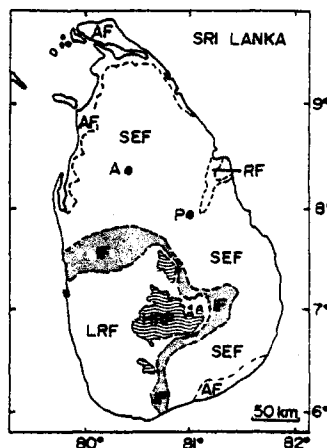

Fig. 1. Map of Sri Lanka indicating location of study sites in relation to forest types. The main study site is in Polonnaruwa (P), a secondary study site is in Anuradhapura (A). The zones of natural vegetation are: AF = arid zone forest; HRF = highland rain forest; IF = intermediate forest; LRF = lowland rain forest; RF = riverine forest; SEF = semi-evergreen forest (modified after FERNANDO, 1968).

Toque monkeys live in troops that average 20.6 (standard error = 2.5) animals excluding first year infants, and 24.7 (s.e. = 3.0) including them at the time of birth. The size of troops ranged from 8 to 43 in Polonnaruwa and the frequency distribution of their size is skewed, the modal class being less than the average (DITTUS, 1974).

METHODS AND AGE CLASSIFICATION

Observations were made with the aid of Leitz Trinovid 7 X 42 binoculars. Data were taken in notebooks in a form as complete as possible in the field itself, thereby minimizing supplementary notes after field hours. For most data, the troop, or a selected individual was followed for the entire 11 to 13 hours of the day, and frequently for several days in succession in order to maintain some long-term continuity.

I distinguished at least 175 individuals from many troops. Identification was made by variations in facial coloration, structure of the toque, or whorl of hair radiating from the crown of the head, color of pelage, size, and sex. Facial features were particularly characteristic for individuals. Differences in the distribution and size of dark or red pigment spots and scars frequently on the ears were most helpful. Photographic records are available for most individuals in the population.

Detailed quantitative observations were initiated after 1½ to 2 years of study, when the main study troops were well habituated. Some animals would even approach me to within less than one meter. With few exceptions animals were not fed or otherwise

interfered with. Two troops of 18 and 36 members, respectively, served as the focal study troops. An additional 5 troops were investigated less regularly and intensively, and an additional 11 troops were observed for certain comparative and ecological information.

For all infants of known birth date, a record of morphological changes for the first year was maintained, including the color and distribution of fur, development of head hair, and degree of skin pigmentation, especially the ears and dorsum of the hands and feet. Where an infant's birth date was unknown, its age was estimated from morphological development. An individual was considered as an infant until one year of age.

The ages of juveniles were estimated less accurately but, since toque monkeys have a narrow birth peak from December to February (DITTUS, in preparation), the one and two year olds especially could be distinguished by size differences. As I followed the development of several juveniles for three years or more, it became evident that growth rates were much less than originally anticipated; therefore, the following juvenile classes were established: juveniles-1, aged 1 to 2 years; juveniles-2, aged 2 to 3½ years; and juveniles-3, aged 3½ to 5 years. The ages of other juveniles were estimated by comparison with those of known ages.

Young females were considered adult with the first pregnancy at 4½ to 5½ years old, or on an average of 5 years old. Males, on the other hand, were not fully adult until 7, possibly 8, years of age, as judged by body size, testes, canine teeth and muscular development. Subadult males from 5 to 7 years of age were as large as, or larger than, adult females, but were smaller and physically less developed than adult males.

Adults were classified according to five broad categories: young, young to middle age, middle age, old, and senile. A host of subtle morphological changes, similar to those criteria one might use in subjectively assessing the ages of humans, formed the basis of this classification.

With increasing age there occurred erosion and tartarization of the teeth, wrinkling of the facial skin, loosening of folds of body skin especially near the eyelids, lips, and cheek pouches. The degree of facial pigmentation often intensified and facial hair became more prominent. In addition, the pelage of old or senile individuals was frequently dull, and some hair loss occurred, especially on the tail. Senile males were also very lethargic. Longevity in the toque monkey was thought to be approximately 30 years (DITTUS, 1974) which is supported by records of captive animals (HILL, 1937; JONES, 1962). Young adult males (7 to 10 year old) were larger than subadult males, or as large as most adult males, but their muscular development was less than in males in their prime (young to middle age class). The numerical age ranges (*e.g.*, Figure 5) attributed to adult age classes were arbitrarily determined by dividing the number of unassigned adult years (25 for females, and 20 for males) by the number of unassigned adult age classes (5 for females, 4 for males). A more detailed and systematic scheme of age class determination among adults was presented in Appendix 1 of DITTUS (1974).

POPULATION DYNAMICS
A. THE AGE AND SEX STRUCTURE OF THE POPULATION

The structure of the population by proportions of age and sex classes, based on 370 animals in Polonnaruwa, is given in Figure 2. The total number of males almost equalled that of females. There were more than twice as many adult females as adult males, but among the juveniles and infants there were more males than females.

The differences in the proportions of the various age and sex classes were consistent between troops (Figures 3 and 4). Comparisons of the proportions

of males to females among the juveniles and infants between troops indicated
that in 14 troops males outnumbered females, one troop had equal proportions,
and 3 troops had one more female than males. According to the Wilcoxon
Matched-Pairs Signed-Ranks Test (SIEGEL, 1956), most troops had signif-

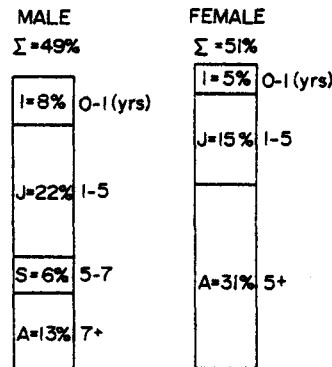Fig. 2. The proportion of age and sex classes in a population of 370 macaques. The
ages appropriate to each age-sex class are given in years. The abbreviations are: I =
infant, J = juvenile, S = subadult male, A = adult.
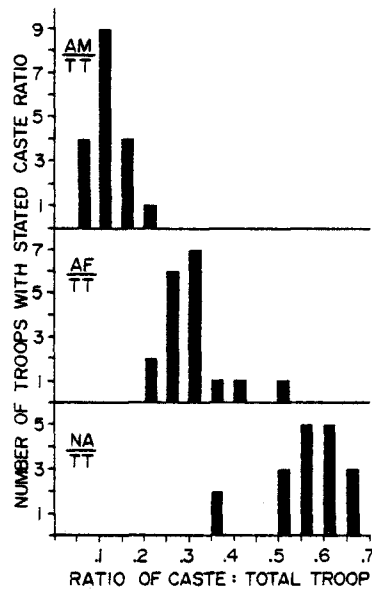
Fig. 3. The number of troops in the Polonnaruwa population showing a particular caste
ratio. The castes are: AF = adult female, AM = adult male, NA = non-adults. TT =
total number of animals in any particular troop.

icantly (p<.005) more male than female infants and juveniles. In 1974 an additional survey was taken of 6 troops located in areas immediately surrounding the main study population in Polonnaruwa. It indicated a ratio of
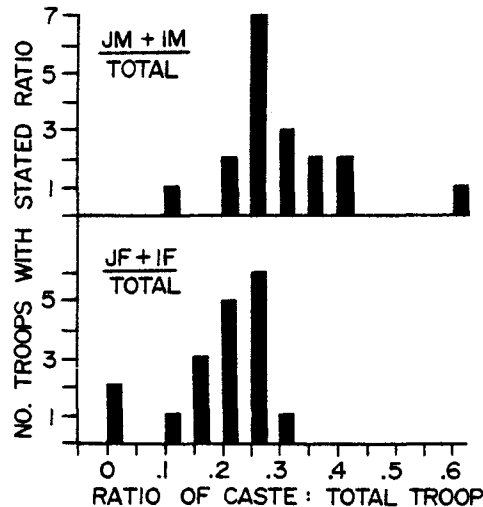
Fig. 4. The number of troops showing a particular caste ratio. The castes are: JM = juvenile male, IM = infant male, JF = juvenile female, IF = infant female.

190 juvenile males per 100 females; 5 troops had more juvenile males than females, one had equal proportions. Thus regardless of the proportion of young (infants plus juveniles) in the troop, young males consistently outnumbered young females. There were no statistically significant correlations between the proportion of any age-sex class and the size of the troop.

A preponderance of females among adults is also reported for *Papio* (DeVore & Hall, 1965; Altmann & Altmann, 1970); *Cercopithecus* (Struhsaker, 1967, 1973); *Macaca mulatta* (Southwick *et al.*, 1965; Lindburg, 1971); *M. radiata* (Simonds, 1965); *Presbytis entellus* (Jay, 1965); *P. senex* (Rudran, 1973); and *Alouatta* (Carpenter, 1934); and others. DeVore & Washburn (1963) and DeVore & Hall (1965) attributed the unequal sex ratio in baboons to sexual differences in the rates of maturation, males requiring several more years than females to attain the adult class.

Age-sex classes for the toque monkeys (Figure 2) were derived from known or estimated ages. A comparison of the proportions of males and females above 5 years of age indicates that adult females (31%) outnumber the combined subadult male and adult male classes (19%). Moreover, the sex ratio at birth (57 males : 54 females) dit not differ significantly from

unity (DITTUS, 1975). The sex ratios among the adults and juveniles therefore reflect differences in the mortality between the sexes with age. These age and sex specific rates of mortality are portrayed in Figure 5, and are based on a life-table in DITTUS (1975).

B. THE NET REPRODUCTIVE RATE OF THE POPULATION (R_0) IN RELATION TO NATALITY AND MORTALITY

Changes in troop size for 5 troops over 3½ years are shown in Figure 6. Increase in troop size was through births and males immigration; decrease was through death, male emigration and unknown losses. The net reproductive rate of the entire population (18 troops) was R_0 = 1, as indicated by age-specific mortality and natality schedules to the end of 1971 (DITTUS, 1975). That is, the population maintained zero net growth. This was confirmed through tracing the histories of 53 females: the number beginning to reproduce nearly cancelled those ceasing to reproduce through death or other causes (*ibid.*). The average birth rate of 0.688 infants per adult female per year did not vary significantly between 4 birth seasons (*ibid.*), and was sufficiently high to theoretically permit rapid population growth ($R_0 > 1$). The equilibrium was therefore achieved primarily through high rates of mortality (Figure 5). Of all macaques born, 90% of males and 85% of females died prior to adulthood.
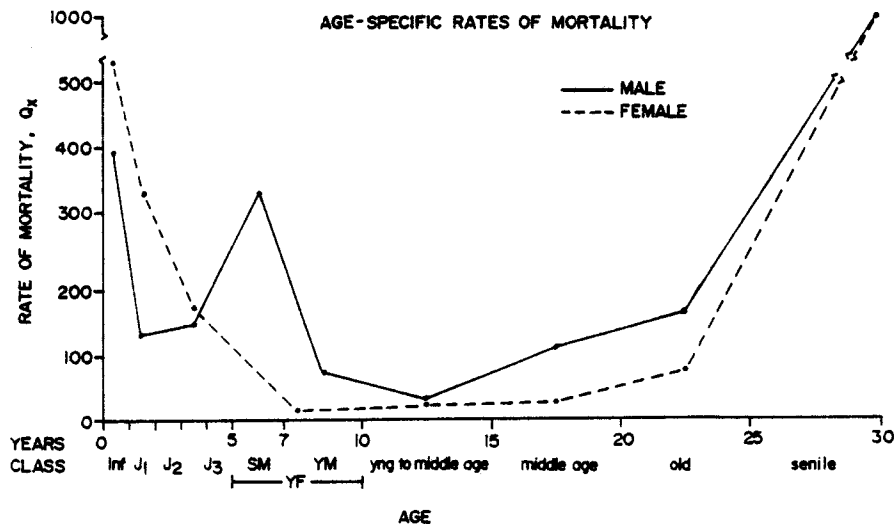
Fig. 5. The age-specific rates of mortality (the number of animals dying (q_x) per 1,000 entering each age class). Age classes were defined in the section "Methods and Age Classification". Young adult females (YF) span the subadult male (SM) and young adult male (YM) age classes.

Although the sample size in Figure 6 is limited, each troop maintained a relatively stable size suggesting that a regulatory mechanism for the maintenance of population equilibrium was operative at the level of the troop.
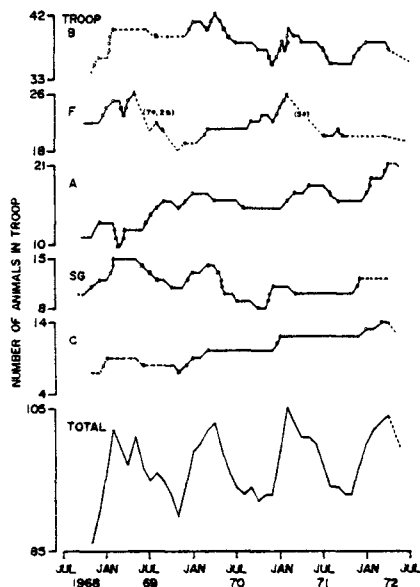
Fig. 6. The fluctuations in troop size. Births are open circles; immigrations are open triangles; deaths are closed circles; emigrations are closed triangles; losses owing to unknown causes are closed squares. Figures in parentheses represent surmised events of uncertain date but within the time span indicated. Dotted lines indicate discontinuous observation.

C. CHANGE IN POPULATION SIZE AND AGE-SEX DISTRIBUTION IN RELATION TO FOOD AVAILABILITY

I. Demographic changes in relation to a decrease in food supply.

Two events led to a general decrease in the food supply for the macaque population after the end of 1971. First, in the years prior to 1972, two large-sized troops, D and M, fed heavily from a rice mill that bordered the study area and that was included in the home ranges of these two troops. Generally, they spent approximately one-half of each day foraging in this area. The rice mill ceased operations in 1972, thereby depriving troops D and M 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 (DITTUS, in prep.).

Secondly, in 1974 the Polonnaruwa area experienced the worst drought in the 44 years for which meteorological records are available. It lasted nearly 11 months, from January through November, contrasting the normal 2 to 4 months of drought between mid May and the end of September. Only 218 mm of rain fell during this period, or one-sixth the 44-year average of 1,300 mm. The phenological activity of plants is geared to the normal pattern of water availability (HLADIK & HLADIK, 1972; MUCKENHIRN, 1972; RUDRAN, 1970). Towards the end of the normal drought most plants lack flowers and fruit, September being the month of least food availability for the macaque (DITTUS, 1974). Although first hand data on food availability in 1974 are lacking, the severe drought condition strongly suggests that, compared to other years, there was a general scarcity of vegetable foods, *i.e.*, plant shoots, mushrooms, flowers, seeds and fruits, which are the mainstay of the macaques' diet (DITTUS, 1974).

The macaque population at Polonnaruwa was recensused in March and April 1975. Each troop that was observed prior to 1972 was again identified in 1975 by the general location of its home range and through recognition of individuals known in 1971. Comparisons in troop size and age-sex composition were made using the Wilcoxon Matched-Pairs Signed-Ranks Test (Table 1). The population decreased significantly ($p < .005$, one-tailed test) by 15.3%. There was no significant numerical decrease among 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%). It is probable that the decrease in food supply caused these demographic changes. STRUHSAKER (1973) reports similar changes in a population of wild *Cercopithecus aethiops* in response to a decreasing food supply.

The relative size of troops did not alter significantly (Table 2), and the weighted mean [1]) decrease per troop was 14.6%. In one troop (C), all females were missing, leaving only an adult male, subadult male and old juvenile male.

II. Demographic changes in relation to a constant and abundant food supply.

Troop "Oval" fed extensively from a municipal garbage dump just outside the study area where food scraps were deposited daily. Hence, in contrast to the

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1) The weighted mean was obtained by calculating the percentage change in troop total for each troop and dividing the sum of these percentage by the number of troops (17).

PLATE I

Fig. 7. A four-year-old juvenile male (left foreground) leaps at a four-year-old juvenile female (left background and facing camera). Two younger juvenile females (to the right) threaten towards the three-year-old juvenile female.

TABLE 1

Comparisons of troop size and age-sex composition in the Polonnaruwa macaque population between 1971 and 1975

	Number of animals		Number of Troops			% change	Wilcoxon T *)	Signifi-cance p
	1971	1975	In-creased	No change	De-creased			
Males:								
Adult	44	48	3	9	5	+ 9.1	9.5	>.05
Subadult	22	23	6	5	6	+ 4.5	33.5	>.05
Old Juv.	56	48	5	3	9	—14.3	38.5	>.05
Young Juv.	51	28	3	3	11	—45.1	12.0	<.005
Total	173	147	4	2	11	—15.0	26.5	<.05
Females:								
Adult	103	94	5	5	7	— 8.7	25.0	>.05
Old Juv.	34	21	4	2	11	—38.2	24.0	<.025
Young Juv.	36	31	5	5	7	—13.9	9.0	<.01
Total	173	146	3	3	11	—15.6	18.0	<.025
Population								
Total	346	293	2	2	13	—15.3	14.0	<.005

*) Data are summarized for the population. 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 2 years old; "old juveniles" are 2 to 5 years old.

TABLE 2

Comparisons of the ranks of troop size between 1971 and 1975

Troop	Troop size		Rank of troop size	
	1971	1975	1971	1975
CF	8	13	1.5	6.5
K	8	7	1.5	4
I	9	6	3	3
SG	10	13	4	6.5
C	12	3	5.5	1
E	12	5	5.5	2
G	13	10	7	5
A	16	15	8	8.5
H	19	15	9	8.5
F	20	17	10	10
Ch	22	22	11	12
IH	24	19	12	11
Bq	28	28	13	14.5
D	31	25	14	13
B	35	28	15	14.5
M	36	32	16	16
22	43	35	17	17

Wilcoxon Matched-Pairs Signed-Ranks Tests: T = 45, N = 13, p>.05.

other troops, troop Oval had a constant and abundant food supply between 1971 and 1975. Therefore troop Oval was omitted from the above analyses. Changes in troop size and composition are shown in Table 3. Troop Oval increased by 60.0% between 1971 and 1975, or at an average annual rate of 12.5%. This rate is comparable to the 16% growth rate reported by KOFORD (1965) for the colony of rhesus macaques, *M. mulatta*, at Cayo Santiago, which is provisioned with food.

Most of the size increase in troop Oval is attributable to an increase among the juveniles and infants, and includes several juvenile females that survived to adulthood.

TABLE 3

Comparisons of troop size and age-sex composition in troop Oval between 1971 and 1975

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

D. THE CAUSES OF MORTALITY

Mortality plays a major role in shaping the age and sex distribution of the population, and in maintaining its net reproductive rate at equilibrium. Mortality is not a random process, but appears to be governed by a very precise mechanism that alters with age, sex, and the population size in relation to the food supply.

Death is rarely observed, but instead may sometimes be inferred by assessing the circumstances surrounding an individual's disappearance. Three possible causes of mortality are: predation, disease and behaviorally induced mortality. Disease was not apparent among the macaques, and predation that resulted in death was observed only 5 times, always involving solitary dogs.

Dogs are the main predators of macaques, as is evident from the numerous

attempts by dogs to catch them, and by the macaque's intense alarm responses to them. The sight of a jackal, *Canis aureus*, also produced alarm and avoidance, even though jackals showed no great interest in the macaques. Of the cats, only the fishing cat, *Felis viverrina*, and the jungle cat, *Felis chaus*, were of sufficient size to be dangerous to the macaques, but there is no information regarding their interaction with the macaques. Leopards, *Panthera pardus*, were absent from the study area, but even in areas of sympatry macaques were not represented among 51 records of leopard predation (MUCKENHIRN & EISENBERG, 1973).

The response to the python, *Python molurus pimbura*, and poisonous snakes, cobra, *Naja n. naja*, and Russell's viper, *Vipera russelli pilchella*, was one of alarm, avoidance and curiosity (nomenclature after DERANIYA-GALA, 1955). Alarm and avoidance was also elicited by the low flight of large raptors. These birds probably prey only on the younger animals and, indeed, these give the most intense responses to raptors. Men occasionally harassed the monkeys but, with one possible exception, did not kill them in the study area.

Although predation and possibly disease contribute to macaque mortality, there is no evidence to suggest that they, by themselves, underlie the observed patterns of mortality. More likely they act in conjunction with more determinate phenomena, perhaps as arise through food-related behavioral-ecological interrelationships. A closer examination of the latter follows.

SOCIOECOLOGICAL ANALYSES

A. THE METHOD OF BEHAVIORAL ANALYSES

Detailed behavioral and ecological information were recorded from two troops whose members I could readily identify (troop A of 18 and troop B of 37 members).

In collecting the data, I followed each individual in the troop for at least one full day and accorded all behavioral interactions, noting the type of behavior, the individuals involved, and the general context in which the behavior occurred. The context was defined by the general activity type, *i.e.*, foraging, resting, traveling, grooming, sleeping, and so forth, as defined below.

Foraging: The active search for and consumption of food.

Moving: Walking or running not related to foraging, as among canopy branches prior to sleeping.

Travelling: The synchronous and usually rapid movement of the troop as a compact cohesive unit between distant locations in the home range, as between sleeping tree and foraging area.

The other context types are self-explanatory.

In addition to the context of the behavior, notes were taken on the distance between individuals and on the type of foods being consumed. These data were recorded simulta-

neously at one minute intervals. Interindividual distance maps were recorded at five minute intervals.

A threat was defined as any behavior that caused the respondent to alter its spatial position, or behavior, in avoidance. Intensity was not considered, thus threat could range from a mere approach to a full bite with hitting and chasing. When two or more individuals collaborated in threatening another (Figure 7), each collaborator was considered to have given one threat (not one-half or one-third, *etc.*). Similarly, an animal threatening two others gave two threats. Tripartite interactions were treated therefore as two independent dyadic events. This departure from the theoretical "ideal" was adopted because tripartite interactions were relatively rare, and because ignoring them would introduce unwarranted bias to the empirical data.

An analysis of agonistic behavior, regardless of its context, permitted the ordering of all animals in a troop according to a linear hierarchy of dominance (DITTUS, unpublished). Departures from linearity occurred among some juveniles because dominance relations gradually changed over time. Such data are here summarized according to the frequency of threats occurring between age-sex classes. Where the frequency of threats from one caste to another is significantly greater than expected by random (see below), it indicates that all or most individuals in that caste are dominant to those in the other caste.

Behavior and the organization of troop life differed considerably from "normal" during the mating season, therefore these phases will be considered separately.

B. AGONISTIC BEHAVIOR DURING THE NON-MATING SEASON

Table 4 lists the number of threats occurring in various contexts in troop B.

Of all threats, 81.5% involved the sustenance activities of foraging and drinking. Because of the relevance of these activities to the ecology of the macaque, a more complete analysis of agonistic behaviors during only foraging and drinking follows.

TABLE 4

The frequency of threats per activity context in troop B (see text)

Context	Threats given	
	Number	%
Foraging	1442	79.4
Drinking	38	2.1
Moving	74	4.1
Travelling	31	1.7
Playing	20	1.1
Grooming	94	5.2
Resting	94	5.2
Sleeping	22	1.2
Total	1815	

Table 5 lists the frequencies of threats observed (T_o) among age-sex classes of troop B in a foraging context. Some age-sex classes were threatened more than others. To test for the presence of discrimination, theoretical models of the random distribution of threats were established for comparison with the observed frequencies.

TABLE 5

Comparisons of the frequencies of threat vectors observed (To) among age-sex classes, to those expected (Te) from random interactions and the relative abundance of these classes [1])

		Threat objects								Row
		AM	AF	JM	JF	IM	IF	SM	Total	Chi-squares
AM	To	28	83	93	96	11	15	18	344	
	Te	13.3	35.6	40.0	40.0	13.3	4.4	13.3	160	211.60
AF	To	2	88	73	159	20	13	0	355	
	Te	35.6	62.2	80.0	80.0	26.7	8.9	26.7	320	3.83
JM	To	1	52	106	140	35	18	3	355	
	Te	40.0	80.0	80.0	90.0	30.0	10.0	30.0	360	0.07
JF	To	2	73	63	141	34	20	0	333	
	Te	40.0	80.0	90.0	80.0	30.0	10.0	30.0	360	2.03
IM	To	0	0	1	11	21	19	0	52	
	Te	13.3	26.7	30.0	30.0	6.7	3.3	10.0	120	38.53
IF	To	0	1	1	7	4	—	0	13	
	Te	4.4	8.9	10.0	10.0	3.3	0.0	3.3	40	18.23
SM	To	0	2	13	9	1	2	1	28	
	Te	13.3	26.7	30.0	30.0	10.0	3.3	6.7	120	70.53
Total	To	33	299	350	563	126	87	22	1480	
	Te	159.9	320.0	360.0	360.0	120.0	39.9	120.0	1479.9	344.82
Column chi-squares		100.81	1.38	0.28	114.47	0.30	55.23	80.03	352.50	

(Aggressors — left margin label)

I. The model of random threat interactions based on the age-sex class composition of the troop.

The null hypothesis of the first random model assumes that animals threatened one another at random such that the probabilities of threats between castes can be predicted purely from differences in the proportional representation of age-sex classes in the troop. This null hypothesis implies that all animals participated in threatening with equal frequency; that an individual was equally likely to threaten, as to be threatened; and that animals threatened without regard to age, sex, or other attributes of other individuals. That is, special attractions or repulsions between pairs of animals are ignored.

Observation periods were approximately equal between animals. Hence, in

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[1]) The composition of the troop was: adult males (AM) = 4; adult females (AF) = 8; juvenile males (JM) = 9; juvenile females (JF) = 9; infant males (IM) = 3; infant females (IF) = 1; subadult males (SM) = 3.

calculating the expected frequencies (T_e) with which one caste threatens another, only the proportional representation of the age-sex classes, and the direction of threatening were taken into account. A random directional interaction matrix giving the probabilities of threats from one caste to another was established as follows:

If N = total number of individuals in the troop, then the total number of different kinds of pairwise interactions possible is N (N-1). One is lost (N-1) in the matrix because an individual cannot threaten itself.

If i = number of individuals of caste i and j = number of individuals of caste j, then the probability (p) of caste i threatening caste j, or, of caste j threatening caste i is $p_{ij} = p_{ji} = \dfrac{ij}{N(N-1)}$. The probability of threat interactions within caste i only is $p_{ii} = \dfrac{i(i-1)}{N(N-1)}$, similarly $p_{jj} = \dfrac{j(j-1)}{N(N-1)}$.

If Tt = the total number of threats observed, then Te within caste i only is $Te_{ii} = p_{ii} \cdot Tt$, similarly $Te_{jj} = p_{jj} \cdot Tt$; and Te of caste i threatening caste j, or vice versa, is $Te_{ij} = Te_{ji} = p_{ij} \cdot Tt$.

The second row of aech caste cell in Table 5 lists these frequencies of expected threats (Te). The observed frequencies differed significantly from the expected (chi² = 846.928, p<.001).

The marginal row chi-square (RAO, 1973, section 6d.2) is 344.814, indicating that animals of different castes did not threaten at random (p<.001). Similarly, the marginal column chi-square is 353.487 which indicates that they were not random threat objects (p<.001). By inspection of the individual marginal rows and columns totals and their associated chi-square sub-totals, the following may be concluded. From the marginal rows totals: (a) only the adult males threatened more than expected; (b) infants of both sexes and the subadult males threatened less than expected; and (c) the adult females and the juveniles of both sexes threatened more or less as expected by random. From the marginal columns totals: (a) adult males and subadult males were threatened less than expected; (b) juvenile and infant females were threatened more than expected; whereas (c) the males of these ages, and possibly the adult females, were threat objects more or less as expected by random.

The calculation of the above random interaction frequencies (Te) assumes that the probability of an interaction is influenced only by the relative proportions of castes. It is logical, however, that the more frequently animals are closely associated spatially, the greater the chances for an interaction between them. For this reason a second random model was established in accordance with differences in spatial association between age-sex classes.

II. The frequency of nearest-neighbor associations between age-sex classes.

The data in Table 6 are based on estimates of inter-individual distances. Each of the 37 members of troop B was followed for one whole day and its nearest neighbor was charted at five minute intervals. Spatial associations during foraging only are considered; 100 such observations were made for each individual. The observed frequencies (So) represent summaries per age and sex class of the number of times individuals were nearest neighbor to the subject animals. The expected frequencies (Se) were calculated assuming nondirectional random interactions, and according to the relative proportions of the age-sex classes, as follows.

TABLE 6

Frequency of spatial association among age-sex classes

		AM	AF	JM	JF	IM	IF	SM
AM	So	51						
	Se	33			Total of nearest neighbor			
	So/e	1.5			observations = 3700			
AF	So	252	189					
	Se	178	156					
	So/e	1.4	1.2					
JM	So	194	369	287				
	Se	200	400	200				
	So/e	1.0	0.9	1.4				
JF	So	121	395	373	323			
	Se	200	400	450	200			
	So/e	0.6	1.0	0.8	1.6			
IM	So	36	137	160	116	69		
	Se	67	133	150	150	17		
	So/e	0.5	1.0	1.1	0.8	4.1		
IF	So	14	79	32	76	46	*)	
	Se	22	44	50	50	17		
	So/e	0.6	1.8	0.6	1.5	2.8	(>1)	
SM	So	37	73	165	44	8	3	51
	Se	67	133	150	150	50	17	17
	So/e	0.6	0.5	1.1	0.3	0.2	0.2	3.1

*) Troop B had only one infant female. Observations of other troops indicate that infant females cluster in their spatial associations.

The observed number of times (So) animals among age-sex classes were nearest neighbors is compared to the expected frequency (Se) according to a random model. The derivation of the latter is given in the text. Abbreviations and troop composition are as in Table 5.

Let St = total of nearest neighbor observation for the troop, then, for caste i the within caste is $Se_{ii} = p_{ii}St$, and between caste i and j $Se_{ij} = 2.p_{ij}.St$.

The ratio S o/e indicates the degree to which spatial associations between individuals of various castes differed from that expected by random. The frequencies So differed from Se very significantly (chi-square = 721.91, p<.001, with 26 degrees of freedom).

Several facts emerge from these data:

(1) All animals associated with their own age-sex class more than expected.

(2) Male-female associations were strongest among adults and infants, and less than expected among the juveniles.

(3) Infants of both sexes were nearest neighbor to adult males less often than expected. The infant female associated with adult and juvenile females much more than did the infant males, but she associated less than expected with juvenile males, whereas the infant males associated with juvenile males more than expected.

(4) Juveniles of both sexes mingled more or less randomly among the adult females.

(5) Juvenile females associated less than expected with males of all ages, but more than expected amongst themselves and infant females. In contrast, juvenile males associated more or less randomly among males of all ages, and least with the infant female.

(6) Subadult males associated mostly amongst themselves, and much less than expected with all other troop members, reflecting their peripheral position to the troop. Their near random association with juvenile males reflects the peripheral tendencies of older juvenile males.

III. The model of random threat interactions based on nearest-neighbor associations.

A second model of expected threat vectors may now be constructed in light of the differences in spatial associations between castes. The null hypothesis states that animals threatened one another at random such that the probabilities of threats between castes can be predicted from differences in the age-sex class composition of the troop and the degree of spatial association between them.

The empirically derived nearest-neighbor frequencies (So) already account for the age-sex class distribution of the troop. The probabilities of nearest neighbor association were calculated according to a random directional interaction matrix, wherein the probability of intercaste association for caste i is

$p^1_{ii} = So_{ii}/St$, and that between caste i and j is $p^1_{ij} = p^1_{ji} = So_{ij}/2 St$.

The expected frequency of threat vectors (Te¹) is therefore $Te^1 = p^1Tt.a$, where "a" is an index measuring the departure from a direct 1:1 relationship between the frequency of threatening and the frequency of association. The modifying influence of "a" is greatest where the frequency of nearest neighbors is a poor predictor of the probability of an interaction. For example, p¹ ignores the actual distance between individuals which influences the probability of an interaction; also, the critical distance of tolerance may differ between pairs of animals. The real values of "a" must be derived empirically. As a generalization, I have assumed a = 1, in the present analysis.

TABLE 7

Comparisons of the frequencies of threats observed (To) among age-sex classes, to those expected (Te¹) from the frequency of nearest neighbour associations among castes

		AM	AF	JM	JF	IM	IF	SM	Total	Row Chi-squares
				Threat objects						
AM	To	28	83	93	96	11	15	18	344	
	Te¹	20.4	50.4	38.8	24.1	7.3	2.8	7.4	151.2	245.85
	To/e¹	1.4	1.6	2.4	4.0	1.5	5.4	2.4		
AF	To	2	88	73	159	20	13	0	355	
	Te¹	50.4	75.6	73.8	79.0	27.4	15.8	14.7	336.7	0.99
	To/e¹	0.0	1.2	1.0	2.0	0.7	0.8	0.0		
JM	To	1	52	106	140	35	18	3	335	
	Te¹	38.8	73.8	114.8	74.6	32.0	6.4	33.0	373.4	0.91
	To/e¹	0.0	0.7	0.9	1.9	1.1	2.8	0.1		
JF	To	2	73	63	141	34	20	0	333	
	Te¹	24.1	79.0	74.6	129.2	23.2	15.2	8.7	354.0	1.25
	To/e¹	0.1	0.9	0.8	1.1	1.5	1.3	0.0		
IM	To	0	0	1	11	21	19	0	52	
	Te¹	7.3	27.4	32.0	23.2	27.5	9.2	1.6	128.2	45.29
	To/e¹	0.0	0.0	0.0	0.5	0.8	2.1	0.0		
IF	To	0	1	1	7	4	—	0	13	
	Te¹	2.8	15.8	6.4	15.2	9.2		0.6	50.0	27.38
	To/e¹	0.0	0.1	0.2	0.5	0.4		0.0		
SM	To	0	2	13	9	1	2	1	28	
	Te¹	7.4	14.7	33.0	8.7	1.6	0.6	20.4	86.4	39.47
	To/e¹	0.0	0.1	0.4	1.0	0.6	3.3	0.0		
Total	To	33	299	350	563	126	87	22	1480	
	Te¹	151.2	336.7	373.4	354.0	128.2	50.0	86.4	1479.9	361.14
Column chi-square		92.40	4.22	1.47	123.39	0.38	27.38	48.00	236.90	

(Aggressors — row labels at left)

See text for the derivation of Te¹. Abbreviations and troop composition are as in Table 5.

The values of Te^1 (Table 7) then take into account the composition of the troop, and approximate the effects of differences in spatial association between castes.

Despite the weighting of Te^1 vectors, they differed significantly from the observed frequencies (To) (chi-square = 830.883, p<.001). The marginal row and column chi-squares were 361.139 and 296.902 respectively, again indicating that animals did not threaten, nor were they treatened, at random (p<.001), and examination of the rows and columns totals and their associated chi-square subtotals support the conclusions of the same test in Table 5.

The magnitude of the difference between To and Te^1 is expressed as the ratio To/e^1 (Table 7). Those ratios greater than 1.0 are of special interest because they suggest possible discrimination against a caste during foraging.

Figure 8 summarizes these relationships diagramatically. An arrow was drawn between castes only where the ratio of To/e^1 was greater than 1.0.

RATIO
threats received
threats given

AM = 0.1
SM = 0.5
AF = 0.8
JM = 1.1
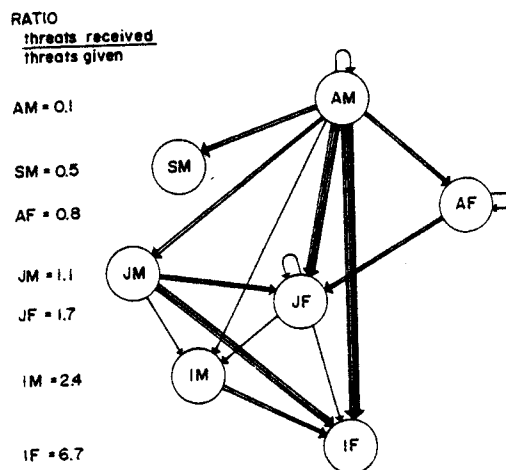JF = 1.7
IM = 2.4
IF = 6.7

Fig. 8. The vectors of threat between age and sex classes (see text). Abbreviations are as in Table 5.

The length of the lines is no reflection of the spatial association between castes, but the thickness of the arrows roughly indicates magnitude of To/e^1. To the left of the diagram are indicated the ratios of threats received to those given. These reflect the hierarchical relationships between the age and sex classes. Adult males have the lowest ratio, then subadult males, adult females, juvenile males, juvenile females, then infant males and females.

It must be emphasized that there are limitations to the scheme as I have outlined it. First, it represents only one of several types of relationships that constitute the society. For example, kinship relationships are completely

obscured, and hierarchical differences within age and sex classes de-emphasized. Second, statements of significance or magnitude refer only to the number of threats transacted. Obviously not all threats had equal social significance.

Keeping these limitations in mind, the following facts can be read from the diagram (Figure 8) and Table 7:

(1) Adult males were threatened more than expected only by other adult males, yet they threatened all other castes more than expected. A greater than expected flow of threats occurred (2) from adult females to each other and to juvenile females, (3) from juvenile males and females to juvenile females and to the infants of both sexes, (4) from infant males towards the infant female, and (5) from all members of the society (except adult females) to the infant female.

In addition, the marginal columns totals in Tables 5 and 7 indicate that juvenile and infant females were threatened much more than the males of these ages. A test wherein the expected frequencies are calculated specific to these castes only, established this difference as significant (Table 8). In

TABLE 8

Comparisons of the total number of threats received by males versus females among juveniles and infants, respectively

| | | Threat objects | | |
		JM	JF	Chi-square
Total threats	received	350	563	
	expected	456.5	456.5	49.692
		IM	IF	
	received	126	87	
	expected	159.8	53.2	28.521

The totals are tested against those expected from the proportional abundance of castes in the troop.
Both chi-square values were significant beyond the .001 level with one degree of freedom.

order to ascertain which castes contributed to this difference, the frequency of threats directed (To) by each caste towards males versus females was compared among juveniles and infants, and tested against those frequencies expected (Te[1]) according to nearest neighbor associations (Table 9). These tests show that the juvenile females were threatened much more than the juvenile males by all members of the society except the infant female and other juvenile females. Similarly, the infant female was threatened much more than the infant males, but only by all the male castes.

TABLE 9

Comparisons between the frequencies of threats (To) directed by various castes towards males versus females, among juveniles and infants

<table>
<tr><th rowspan="2"></th><th rowspan="2"></th><th colspan="2">Threat objects</th><th>Chi-</th><th>Proba-</th><th colspan="2">Threat objects</th><th>Chi-</th><th>Proba-</th></tr>
<tr><th>JM</th><th>JF</th><th>square</th><th>bility</th><th>IM</th><th>IF</th><th>square</th><th>bility</th></tr>
<tr><td>AM</td><td>To</td><td>93</td><td>96</td><td></td><td></td><td>11</td><td>15</td><td></td><td></td></tr>
<tr><td></td><td>Te[1]</td><td>116.4</td><td>72.6</td><td>12.25</td><td><.001</td><td>25.9</td><td>10.1</td><td>10.95</td><td><.001</td></tr>
<tr><td>AF</td><td>To</td><td>73</td><td>159</td><td></td><td></td><td>20</td><td>13</td><td></td><td></td></tr>
<tr><td></td><td>Te[1]</td><td>112.1</td><td>119.9</td><td>26.39</td><td><.001</td><td>20.9</td><td>12.1</td><td>0.11</td><td>>.300</td></tr>
<tr><td>JM</td><td>To</td><td>106</td><td>140</td><td></td><td></td><td>35</td><td>18</td><td></td><td></td></tr>
<tr><td></td><td>Te[1]</td><td>149.1</td><td>96.9</td><td>31.63</td><td><.001</td><td>44.2</td><td>8.8</td><td>11.53</td><td><.001</td></tr>
<tr><td>JF</td><td>To</td><td>63</td><td>141</td><td></td><td></td><td>34</td><td>20</td><td></td><td></td></tr>
<tr><td></td><td>Te[1]</td><td>74.7</td><td>129.3</td><td>2.89</td><td>>.050</td><td>32.6</td><td>21.4</td><td>0.15</td><td>>.200</td></tr>
<tr><td>IM</td><td>To</td><td>1</td><td>11</td><td></td><td></td><td>21</td><td>19</td><td></td><td></td></tr>
<tr><td></td><td>Te[1]</td><td>7.0</td><td>5.0</td><td>12.34</td><td><.001</td><td>30.0</td><td>10.0</td><td>10.80</td><td><.001</td></tr>
</table>

Aggressors (left margin label)

The probabilities associated with all chi-square values were determined with one degree of freedom.

The observed frequencies (To) are tested against those expected (Te[1]) from the frequencies of nearest neighbour associations between the castes and the juvenile or infant males and females. Abbreviations and troop composition are as in Table 5.

Subadult males were so peripheral to the troop (Table 6) that very few threat interactions with the rest of the troop emerged in these analyses. Their very peripheral position was indicative of chronic avoidance of the more central regions of the troop; the slightest threat from a dominant adult male, even over a long distance, caused subadult males to avoid. It appears that repeated "punishment", particularly as older juveniles, had taught them to remain at a distance. Adult male — subadult male interactions were most significant during the mating season and are considered later.

Only one infant female was present in troop B at the time the above data were collected. An identical analysis was done on the smaller troop A that had two infant females and additional observations were taken on several troops. Table 10 illustrates the hierarchical relationship between the age and sex classes of troop A. The conclusions outlined above are supported by these additional data.

In summary, a major point in the above data is that during foraging infant and juvenile females were threatened much more than infant and juvenile males.

C. AFFILIATIVE BEHAVIOR DURING FORAGING

Affiliative behavior can be measured in several ways. Because grooming generally occurred during long resting and grooming sessions, that is, out of the foraging context, I have instead summarized the frequency of hugging

TABLE 10

Comparison of ratios of threats received: threats given during foraging,
between age and sex classes of troop A

Age-sex class	Number of individuals	Threats received/ threats given
Adult Males	2	0.1
Subadult Males	3	0.4
Adult Females	4	0.9
Juvenile Males	3	1.3
Juvenile Females	3	2.4
Infant Males	1	0.0 *)
Infant Females	2	3.7

*) The infant male was a neonate, mostly carried by the mother and foraging very little.

TABLE 11

Frequency of hugging among age and sex classes

		AM	AF	JM	JF	IM	IF	SM
AM	Ho	7						
	He^1	1.8				Total number of hugs		
	Ho/e^1	3.9				observed = 133.		
AF	Ho	4	0					
	He^1	9.0	6.7					
	Ho/e^1	0.4	0.0					
JM	Ho	10	0	9				
	He^1	7.2	13.0	10.1				
	Ho/e^1	1.4	0.0	0.9				
JF	Ho	0	5	1	5			
	He^1	4.3	14.4	13.0	11.5			
	Ho/e^1	0.0	0.3	0.1	0.4			
IM	Ho	17	5	37	4	5		
	He^1	1.2	4.8	5.9	4.3	2.5		
	Ho/e^1	14.2	1.0	6.3	0.9	2.0		
IF	Ho	0	3	0	6	1	—	
	He^1	0.5	2.9	1.1	2.7	1.7		
	Ho/e^1	0.0	1.0	0.0	2.2	0.6		
SM	Ho	6	0	0	0	8	0	0
	He^1	1.4	2.4	5.9	1.6	0.4	0.1	1.9
	Ho/e^1	4.3	0.0	0.0	0.0	20.0	0.0	0.0

The observed frequencies of hugging (Ho) are compared to those expected (He^1) according to a random model. The derivation of the latter is given in the text. Abbreviations and troop composition are as in Table 5.

behavior which occurred sporadically during foraging and moving; I have excluded that which occurred during grooming and sleeping. Hugging refers to the embracing of one individual by another, and was always accompanied by appeasement gestures.

Table 11 lists the observed frequencies of hugging (Ho) between age and sex classes. Directionality is not presented in these data but, with few exceptions, the so-called dominant individuals, as measured by the priority of access to resources (RICHARDS, 1974), initiated the hugging. The expected frequencies (He[1]) were calculated as before and take into account the relative proportions of the age and sex classes and the approximate differences in spatial association between them. The flow diagram (Figure 9) schematically summarizes the information of the ratios Ho/e[1] in Table 11.
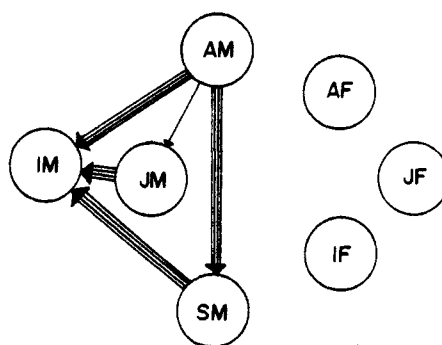
Fig. 9. The vectors of hugging behavior between age and sex classes. Only those vectors greater than random (S o/e[1] = 1.0) are considered. Abbreviations are as in Table 5.

Of 133 hugs observed, 74.4% occurred among males, 14.3% among females, and only 11.3% between the sexes. The context of hugging can differ somewhat between that occurring among adult and subadult males, and that occurring between these older males and juvenile and infant males. The data are presented primarily to show the differences in hugging that older males conferred to very young animals of different sex.

Adult males and juvenile males frequently approached, picked up, and hugged younger males, especially infants (Figure 10). This positive affect was never accorded to young females by males. In fact, when confronted with a choice of infants of different sex, males would pick up and cuddle infant males and ignore or threaten infant females. The lack of hugging of infant and juvenile females, therefore, is not merely a random event as suggested by the data in Table 11, rather it reflects a true partiality by older males, especially the adults, in favor of younger males, but discrimination

against females. Together with the 2 to 3 times greater incidence of threats that the older males directed against young females compared to young males, the complementary discrimination in hugging had the effect of spatially channeling the young females away from males and towards other females, especially other juvenile and infant females. That is, young females apparently learned to avoid older males. Since the older males were also the dominant, or the ones in closest proximity to favored food resources, the young females were, in effect, avoiding these foods. Males in contrast had a greater freedom of association (Table 6) and hence foraging potential.

D. THE ECOLOGICAL SIGNIFICANCE OF SOCIAL BEHAVIOR

Approximately 82% of all threats occurred during foraging (Table 4). A threat during foraging had several effects. It prevented an animal from approaching another engaged in foraging; it caused the respondent to sit still and cease feeding while a dominant fed nearby, but usually it displaced the subordinate from its feeding place and the aggressor fed near or at the same locus from which the subordinate had been displaced. In 36% of all threats during foraging, the aggressor was observed to feed from the very locus from which the subordinate had been threatened. This usurpation of food by dominants from subordinates sometimes was carried to the extreme. Figure 11 illustrates a peripheral adult male, recently fallen in social status, actually emptying and consuming the contents of the cheek pouches of an older juvenile female. This occurred during a period of general food shortage.

What is the effect of this exploitation? A rough index of differences in foraging efficiency with age and sex can be gained from Figure 12. Each point on the abscissa indicates a full day in various months for an entire year. The ordinate indicates the percentage of time that each age and sex class spent in foraging.

Adult males spent the least amount of time in food gathering, then adult females, then juvenile males. The most time in foraging was spent by juvenile females. In certain seasons juvenile females spent twice as much time as the adult males in food finding activity. This differentiation in the activity budget with age and sex was consistent over time and was most marked during general food scarcity when foraging time in all age-sex classes increased. The effect of differences in foraging time is even more pronounced when expressed in terms of time spent per metabolic weight ($kg^{0.75}$) of an animal; that is, in proportion to its metabolic rate, or to its basic energy requirements (KLEIBER, 1975). In fact, some juvenile females spent nearly 5 times more foraging time per unit of energy required than adult males.
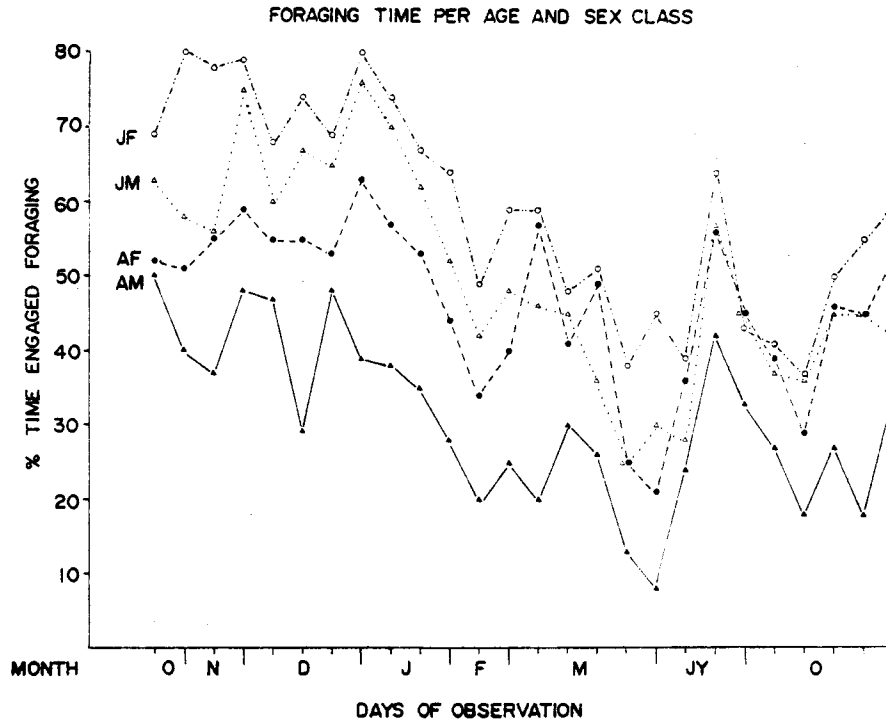
FORAGING TIME PER AGE AND SEX CLASS

Fig. 12. The percent of time various age-sex classes were engaged in foraging at various times of the year. Points along the abscissa refer to one full day of observation during different months of the year (M = March). Abbreviations identifying the curves are as in Table 5.

The low foraging efficiency in the subordinates was further reflected in their lower success in food finding (Table 12). Some subordinate classes were also the younger ones. Therefore, one might suspect that low feeding

TABLE 12

Rates of consumption for the fruits of Ficus amplissima [1]) *per age-sex class*

Age-sex class	Number of animals sampled	Total number of minutes engaged in foraging sampled	Total number of fruits eaten	Feeding rate (fruits per minute)
Adult Male	2	192	2504	13.0
Adult Female	3	225	2648	11.8
Subadult Male	3	399	3283	8.2
Juvenile Male	2	182	1335	7.3
Juvenile Female	2	204	1350	6.6

[1]) Fruits of this species constitute the most common dietary item of *M. sinica* at Polonnaruwa.

PLATE II

Fig. 10. Photograph of an adult male hugging a four-month-old infant male. The adult male had been playing with the infant male.

Fig. 11. Photograph showing an adult male emptying and consuming contents of the cheek pouches of a four-year-old juvenile female. The male had recently fallen in the dominance hierarchy, notice the thin condition of his body.

rates are the result of youthful inexperience, as indicated in some predatory sea birds that employ skilled prey-catching techniques (*e.g.*, ORIANS, 1969; RECHER & RECHER, 1969; DUNN, 1972). However, differences in experience cannot explain differences in feeding rates between male and female macaques of the same age class. In fact, some adult females with low feeding rates were older than the adult males. Although lack of experience may retard feeding rates among infants or very young juveniles, it is doubtful that 2 to 4 year old juveniles have not mastered the relatively simple fruit picking skills to the same degree as adults. Instead, it appears that the low feeding rates are a function of social rank. This is supported by the following facts: (1) Dominant animals consistently fed, to the exclusion of subordinates, in those regions of fruiting trees where fruit was ripest and most abundant. (2) Subordinate animals, in addition to having their foods usurped, generally avoided these "richer" areas where the dominants were feeding, and instead fed at "poorer" areas, or on different foods. This avoidance apparently did not result from a "true" preference for "poorer" areas, because subordinates left the richer areas only with the arrival of dominants, or they shifted to the picked over richer areas after the dominants had gone elsewhere to rest or groom.

There is evidence to suggest that as a consequence of these relationships subordinates were forced to consume a greater proportion of poor quality foods than dominant animals (Table 13). Data in Table 13 are based on full

TABLE 13

A comparison of variations in the composition of the diets between members of different age and sex classes

Age-sex class	Number of animals observed	Percent dry weight of total food intake			
		Fruits and seeds	Leaf shoots and herbs	Grass	Invertebrates
Adult Males	2	47	52	1	0.2
Adult Females	1	24	65	1	11[1]
Juvenile Males	1	26	70	3	1
Juvenile Females	2	13	81	6	0.4

[1] Includes one lizard.
The calorific and protein contents of fruits and seeds in general are greater than those of leaf shoots, herbs and grasses (ALTMAN & DITTMER, 1968).

day observations of known individuals; all food items and their rates of consumption were recorded every minute. Samples of food seen to be taken were collected, weighed and dried. An adult and a juvenile were followed

simultaneously by two observers. Different pairs were followed over 3 days between November 14 and 16, 1970. Range use and food types consumed were comparable during this period. By themselves the data in Table 13 are too sparse to eliminate the possibility that different animals chose foods containing different essential nutrients. However, they do suport the general observation that subordinates fed less on high quality foods than dominants.

There is a significant correlation between rank and physical condition as measured by weight (Table 14). Cause and effect in these data require clarification. If we accept that good physical condition increase fighting ability and

TABLE 14

Test of the correlation between social status in a troop and the average weight for all adult males per social status

Rank of social status	Rank of weight	Number of adult males	Average weight (kg) of males
I	I	13	5.84
2	2	10	5.22
3	3	7	5.09
4	4	6	4.75

Spearman rank correlation coefficient, $r_s = 1.00$, $N = 4$, $p < .05$ one-tailed test (SIEGEL, 1956).

thus maintains high rank, and conversely, that poor physical condition hinders increasing rank, then a male might ensure his physical superiority and rank by actively exercising his priority of access to resources. The latter is a fact. Five males known before and after they had lost social rank, as a result of fighting with other males, were prevented access to resources by the newly dominant males and they chronically avoided conflict with them by remaining peripheral to the troop, that is they avoided favoured feeding areas. In addition, they suffered a conspicuous loss of weight soon after their loss of rank. These data, then, suggest that the lower weight of subordinate males was, at least in part, a result of their inferior social status and imposed low feeding efficiency. Equivalent weights for juveniles of the same sex, and particularly age, and differing in social status are lacking. However, visual size comparisons of juveniles, whose histories have been traced since birth, indicate that high ranking juveniles have faster growth rates than low ranking ones.

Partial growth curves for each sex are shown in Figure 13. The ages of animals up to 6 years were known exactly or estimated accurately. Other

ages were estimated to the nearest half-year or year. Animals were weighed in the field at various times in 1971 and in April 1975. Linear regressions of weight on age were calculated for 8 juvenile females between 0.1 and 5 years old, and for 15 males between 0.1 and 5.5 years old, the last being the approximate median age of emigration (see below). For each sex weight correlated positively with age; r = 0.980, p<.001 (t-test) in females, and
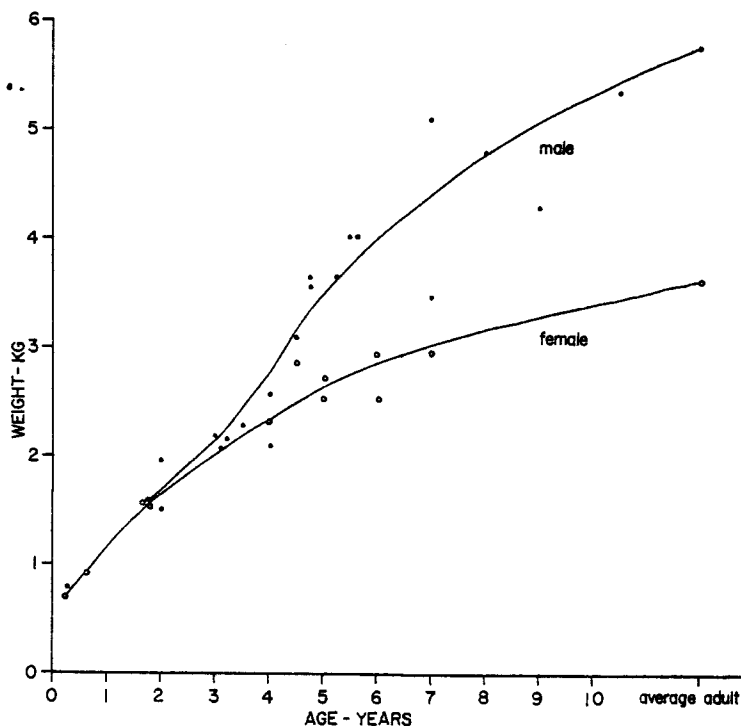

Fig. 13. Approximate growth curves for male and female *M. sinica*. Closed circles represent the weight of individual males; open circles represent those of females. The average weights of adult males and females are also indicated.

r = 0.945, p<.001 in males. The regression coefficients (or growth rates in kg per year) differ significantly (p<.013, t-test) between females (0.407) and males (0.590), with juvenile males growing somewhat faster than juvenile females. Assuming that digestive or assimilative efficiencies do not differ by sex, these data imply that growing young males have greater energy needs than young females.

The significance of these socioecological phenomena in relation to demography will be considered following the next section.

E. AGONISTIC BEHAVIOR DURING THE MATING SEASON

During the mating season, the overall rate of threatening was approximately twice that during the non-breeding season; 5.6 threats per hour of direct observation (N = 60 hours) compared to 2.7 threats per hour (N = 350 hours). Food was generally in plentiful supply during the mating season of July and August (DITTUS, 1974), and most conflict (65.7% of adult male threat behavior) was for access to estrous females.

Although threats were frequently intense during the mating season, only 0.6% resulted in actual body contact, even fewer resulting in injury. Nevertheless, a greater incidence of wounding was evident during the mating season (Figure 14), and many of these wounds were severe.

Adult, subadult and older juvenile males incurred a greater number and more serious wounds than adult females of similar age. This reflects the differences in the nature of threat behavior directed by males between the sexes. Whereas most threats toward estrous females were mild and involved herding them away from competing males, those against males were much more intense. As a consequence, the wounds sustained by females were relatively minor. Males more or less ignored non-estrous females.

The organization of troop life changed somewhat during the mating season, mainly in that estrous females became peripheral to the troop, where they attracted males of their own and neighboring troops. At the peak of estrus, consort pairs split away from the troop, up to 300 meters or more. The consorting pair was usually followed by a group of subadult and older juvenile male "followers" that remained at a "respectable" distance of 10 to 50 meters and that would attempt to approach the estrous female when the consorting adult male was otherwise occupied, as when fighting with another male. Often an older juvenile female in estrus consorted with the largest of the followers. The peripheral tendencies of estrous females meant that a good deal of fighting between males occurred away from the central regions of the troop; that is, most agonistic behavior was confined to the competing adult males, estrous females, and the subadult and older juvenile male followers.

In attempting to assess the significance of vectors of threat behavior among age and sex classes during the mating season, a random model based on the entire troop would yield expected frequencies (T_e) much too low for true comparisons since mating is confined to only a fraction of the troop. That is, the significance of threat behavior would be erroneously overemphasized. In an attempt to balance this, the T_e values for the random model were calculated on a restricted number of animals, those involved in peripheral mating activity at the time of sampling. This included 4 adult

males, 4 estrous adult females, 3 estrous juvenile females, 3 subadult males, 5 juvenile males, and 1 infant (the infant belonged to one of the estrous females).

In Table 15 comparisons are made between the observed and expected frequencies of threat vectors during the mating season. Despite weighting against the significance of a difference, the T_o differed very significantly from the T_e (chi-square $= 2,464.73$, p$<$.001). Adult males threatened all age-sex classes. In contrast to the non-mating season, subadult males were

TABLE 15

Frequency of threat vectors among age-sex classes during the mating season

Threat objects

		AM	SM	JM	AF	JF	I	Total
AM	To	153	48	23	66	33	11	334
	Te	10.7	10.7	17.8	14.2	14.2	3.6	71.2
	To/e	14.3	4.5	1.3	4.6	2.3	3.1	4.7
SM	To	10	2	2	4	0	1	19
	Te	10.7	5.3	13.3	10.7	10.7	2.7	53.4
	To/e	0.9	0.4	0.2	0.4	0.0	0.4	0.4
JM	To	0	0	1	1	4	0	6
	Te	17.8	13.3	17.8	17.8	17.8	4.4	88.9
	To/e	0.0	0.0	0.1	0.1	0.2	0.0	0.1
AF	To	1	0	0	6	3	0	10
	Te	14.2	10.7	17.8	10.7	14.2	3.6	71.2
	To/e	0.1	0.0	0.0	0.6	0.2	0.0	0.1
JF	To	0	0	0	2	2	0	4
	Te	14.2	10.7	17.8	13.2	10.7	3.6	71.2
	To/e	0.0	0.0	0.0	0.1	0.2	0.0	0.1
I	To	0	0	0	0	0	0	0
	Te	3.6	2.7	4.4	3.6	3.6	0.0	17.9
	To/e	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Total	164	50	26	79	42	12	373

(left margin, rotated): Aggressors

The observed frequencies of threats (To) are compared to those expected (Te) according to a random model. Derivation of the latter is explained in the text. Abbreviations are as in Table 5.

threatened considerably during mating season. The lesser incidence of threats directed towards juvenile males reflects the greater distance the latter maintained from the adults. Unlike the subadult males, the juveniles were less prone to attempt to gain access to an estrous female in the proximity of a consorting adult.

The category of "adolescent male" is introduced here to refer to subadult males and older juvenile-3 males. These males often left their home troops

whereas younger males did not. During the breeding season, adolescent males and some low ranking adult males strayed from their own troops and attempted to gain access to estrous females in neighboring troops. These wanderings are probably attributable to a combination of related factors. First, the males were attracted to estrous females in other troops. Second, having no "binding" consort relationship in their own troop, that is, an estrous female to mate with and to guard from competing males, the subordinate adolescents and adults had greater "freedom" of movement away from the home troop. Third, their low status in the home troop was well fixed; adult males readily displaced them and estrous females did not prefer them. Chances for a change within the "establishment" were low. With increasing absenteeism from the home troop, "re-entry" to the troop was progressively more difficult; peers of slightly younger age and lesser status cooperated to prevent their re-association.

Migration was defined (DITTUS, 1975) as the permanent association of an animal with a new troop. The histories of 26 adolescent males, 27 adult males and 56 adult females were traced over 3½ years. Rates of migration were calculated on the basis of these observations. Females never migrated. Rates of migration were highest during the breeding season, and averaged once in 2 to 3½ years per adolescent male and once every 5 to 6 years per adult male (*ibid.*).

DISCUSSION

There is no evidence to indicate that predation or disease alone generated the observed pattern of mortality (Figure 5) in this macaque population. As an individual matures, its social relationships change, particularly its social rank or its priority of access to resources and mates. Because of the importance of food and reproduction to survival, the behaviors that relate to differential access to resources and mates were examined.

A. Mortality in relation to resources.

The observed frequencies of threat behavior between age-sex classes during foraging differed significantly from both of the proposed random models. This indicates that (a) adult males threatened each other and all other age-sex classes more than expected; (b) juveniles and infants were threatened more by adult males than by adult females; (c) subadult males and adult females dominated the juveniles which in turn dominated the infants, and (d) among the juveniles and infants, the males dominated the females. Overall, female juveniles and infants were threatened much more

than the males of these age classes. Subadult males were much threatened by adult males and consequently remained at the periphery of the troop where interactions with the remainder of the society were minimal.

Affiliative behavior during foraging, measured by the frequency of hugging between age-sex classes mirrored the agonistic discrimination in that adult and older juvenile males preferred hugging infant and young males. This gave young males greater freedom to associate with older males that dominated favored feeding areas (Table 6). Hence, relative to young females, young males had greater potential access to food.

Subordinate or threatened individuals were prevented access to food items, or the food items which they had invested time and energy in finding were usurped by the dominant individuals. The net effect of these social relationships was to impose a lower foraging efficiency upon: juveniles relative to adults; infants relative to juveniles; and juvenile and infant females relative to juvenile and infant males, respectively. The vectors of threat and affiliative behaviors during foraging and the resulting socially imposed foraging efficiencies between the age-sex classes named above closely parallel their rates of mortality. This suggests that the pattern of mortality was a direct result of the behaviors observed during foraging. The data, however, do not explain the extreme mortality in adolescent males, or the difference in mortality between adult males and females.

B. M o r t a l i t y i n r e l a t i o n t o m a t i n g a n d m i g r a t i o n .

During the mating season the overall rate of threatening increased twofold. Most conflict was for access to estrous females and involved primarily the adult males, estrous females, and adolescent males that were directly involved in mating. The incidence of wounding increased for these animals during the mating season (Figure 14). Behavioral analyses show that most threats came from adult males. They threatened each other ten times as much, and subadult males twice as much during the mating season than during the non-mating season. Subadult males were threatened less frequently than adult males because they were less likely to be associated with an estrous female, and were easier to supplant than adult males. In addition, adult males recently deposed from high status in the dominance hierarchy, and adolescent males wandered between troops during the mating season. Rates of migration were highest in adolescent males, and coincided with the peak in male mortality during adolescence (Figure 5). Indeed, 72% of adolescent males died or 27% of total male mortality was concentrated in this short phase.

Emigration had two negative effects on males. First, they were socially

excluded from the new troop and, with increasing absenteeism, from their own troop. Their access to resources was therefore low, and had its most acute effect during the season of food scarcity in September, towards the end of the breeding season. Many migrating adolescents suffered conspicuous loss of weight following migration. For example, the one adult male weighed before and after migration lost 17% of his original weight. Second, this physical deterioration was exacerbated through wounds from fights with
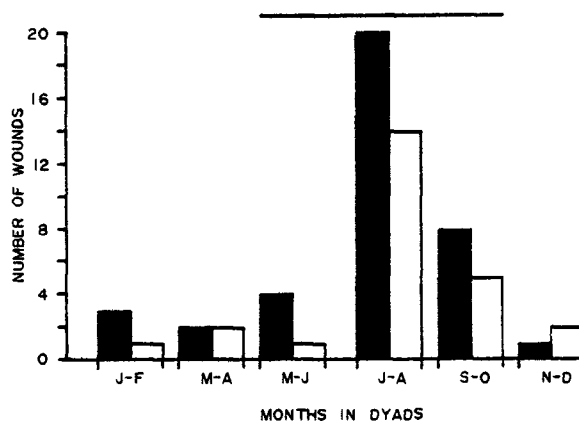
Fig. 14. The number of wounds incurred by adult and subadult males (black bars) and adult and older juvenile females (white bars) at different times of the year. The black line demarcates the breeding season of July to September.

older and larger males for access to estrous females (Figure 14). Some adolescent males appeared in very poor physical condition indeed. Although death through wounding and starvation was never directly observed, the evidence strongly suggests a causal relationship between the rigors of migration and mortality in adolescent males.

Mortality in adult males can be attributed to the same causes as for the adolescent males, but rates of migration were much less for adults and they stood a much greater chance of establishing a high rank in a new troop (DITTUS, in prep.). Once males attained adulthood, their chances of survival were vastly improved but their rates of mortality through adulthood were consistently slightly higher than in adult females.

Despite the advantage in access to food resources that adult males exercise over adult females, the greater survivorship of adult females, relative to adult males, is probably attributable to the fact that adult females do not migrate or sustain the severe wounds that adult males do during the mating season. Competition for estrous females should, however, not be regarded as

the only source of socially imposed mortality for adult males. During both mating and non-mating seasons, subordinate adult males were prevented access to food resources by dominant adult males and sometimes sustained severe wounds from fighting over a choice morsel of food. The most subordinate adult males (in multi-male troops) were often less tolerated during foraging than adult females or juveniles and, like the subadult males, were peripheral to the troop. Regardless of cause and effect, such exclusion undoubtedly contributed to the poor physical condition of these most subordinate adult males and thereby also impaired their ability to compete for estrous females.

C. Secondary causes of mortality.

Competition over food and mates may implicate causes of death other than starvation and wounding through intraspecific fighting. For example, subordinate castes foraged for longer periods of time than dominant castes (Figure 12). When not foraging animals generally rested, groomed or slept in the lower branches of trees where they were protected from exposure to the sun and predators. However, subordinate animals regardless of age or sex were frequently seen peripheral to the troop. Hence, in terms of both space and time, subordinates were exposed to greater risks of predation than dominant animals. Owing to the general food deprivation among subordinates, it is possible that they had a greater risk of poor health and disease than dominant animals.

Competition pervaded the macaque's life in other ways as well. Night time sleeping occurred mostly on the terminal forks of large branches of very tall or emergent trees, and only certain trees were chosen for sleeping (DITTUS, 1974). Much shifting and supplantation occurred before settling for the night. Occasionally subordinate animals slept in locations that were subjectively judged to be unsafe because they were easy to reach from the ground. Similarly, when alarmed by predators, dominant animals often supplanted subordinates in the scramble to ascend to a safe place in a tree.

D. The possibility of population regulation.

In view of the evidence that mortality of subordinates results from competition for food, the decrease in population size, especially among the young subordinate animals when food was scarce in 1974, suggests that this population decrease was attributable to socially imposed mortality in reference to food. Conversely, the greater survivorship of animals where food was abundant implies that food competition is alleviated by food availability. The population of toque monkeys (up to 1972) maintained an equilibrium state

($R_o = 1$) through a precise balance between rates of fertility and mortality. Given the fairly consistent climatic pattern for 44 years prior to 1974, the overall food supply was probably equally consistent during this period.

Together these data imply that social behaviors in reference to access to resources, especially food and estrous females underlie the observed pattern of mortality and thus determine the density and age-sex structure of the society and population. Accordingly, food and related resources constitute a limiting factor for all members of macaque society (albeit differently by age and sex); estrous females constitute an additional limiting resource for adolescent and especially adult males. These topics invite several issues that need clarification.

The upper limit to population growth is set ultimately by the amount of food (DARWIN, 1872; ANDREWARTHA & BIRCH, 1954; ERRINGTON, 1956; WYNNE-EDWARDS, 1962; LACK, 1954). Yet, animals generally do not eliminate their food resources to the point where mass starvation ensues. These apparently contradictory observations have led to the idea that competition over food and consequent starvation is not a proximate factor limiting populations (WYNNE-EDWARDS, 1962, 1970). It is sufficiently clear from my data, however, that food deprivation on a small but chronic scale through the usurpation of food from subordinates is the manner in which dominants stand a greater chance of surviving than subordinates. Instead of sudden mass starvation, there exists a constant erosion of old-aged individuals and subordinate juvenile recruits, with a net result of near zero growth rate for the population, or a net decrease in population size when the food supply decreases.

That the macaques do not deplete their food supply is readily understood in light of the following: (1) the bulk of their diet consists of fruit, that from the plant's "points of view", were specifically designed to be eaten by animals so as to disseminate its propagules; and (2) during critical food shortage, the diet consists of "difficult-to-find" foods, ones where the balance between energetic costs of finding food to that gained is marginal (DITTUS, 1974). The situation is most delicate for the subordinates who not only are the last to partake of foods found, but who upon having spent energy in locating food are often not the ones to gain from this investment; rather, the benefit accrues to the usurping dominant. Hence, long before the hardest to find items are eaten, the most subordinate consumers would be dead.

A central question in the literature (*e.g.*, WATSON & MOSS, 1970) poses whether populations are limited through food shortage or through competition for an unconventional goal, such as status in the dominance hierarchy. In

light of the macaque data, it would seem that animals foremost compete for resources, including mates. It is most efficient to do so with a minimum of energy expenditure, as in physical conflict, such that the outcome of previous encounters between individuals modifies their future behavior and thus molds the dominance hierarchy. Competition for status *per se* (without reference to a contested resource or mate), where it occurs, probably serves to establish or to reinforce a behavioral relationship which confers a biological advantage, that of priority of access to resources. The resources, therefore, constitute the proximate factor which sets the limit to population growth; the hierarchy determines which individuals are to benefit most from these resources. Subordinates survive only if sufficient food is available after the dominants have been satiated.

Since 85% to 90% of young in the Polonnaruwa population die prior to adulthood and the population maintains zero net growth (up to 1972), one might ask why the average rate of fertility is as high as it is. Does high mortality stimulate a compensating rate of fertility or is the high rate of mortality the result of high fertility?

Having established that the pattern of mortality is mediated largely through social behavior in direct reference to food, it seems logical to conclude, as did LACK (1954, 1966) that the rate of mortality is the outcome of the rate of fertility. In reference to data on birds, LACK *(ibid.)* reasoned that the reproductive rate is an individually selected adaptation to produce as many offspring as the birds' capacities and the environment will allow.

Why, however, should a female invest her energies in many offspring, most of which are doomed to die, rather than invest the same energies in fewer offspring, and possibly increase their chances of survival? Accepting that females reproduce at a capacity that is commensurate with nutritional state, the matter of fertility translate into the most efficient temporal partitioning of her energies between successive offspring, so as to maximize her reproductive success (see TRIVERS, 1974: 254). Conceivably then, despite the high risks of mortality facing her offspring, maintaining a high fertility is part of a reproductive strategy to maximize her net reproductive success.

Most behaviors concerning differential access to food resources among age-sex classes occur within the troop. Although troop size fluctuates over time, under relatively normal environmental conditions, troops appear to remain more or less the same size (Figure 6). Even a 15.3% decrease in overall population size in response to food shortage affected most troops equally (weighted mean decrease in troop size 14.6%), and the relative size of troops remained about the same (Table 2). The critical influence of the food base to troop size is further indicated by the fact that the size of home

ranges of different-sized troops correlated positively with the number of
animals per troop, but inversely with the number of critical food items
available per individual during periods of general food scarcity (DITTUS,
1974). These facts suggest that population regulation occurs mainly within
troops in relation to the food supply available in the home range. It does not,
however preclude the possibility that one troop may grow at the expense of
another. Indeed, all females in troop C died, and only 3 males survived the
food shortages following 1972 (Table 2). The elimination of this troop as a
reproductive unit was in part the result of a larger dominant troop expanding
into and supplanting troop C from parts of its home range (DITTUS, in
prep.). Except for immigrant males, animals within a troop are related
(DITTUS, in prep.), and such intertroop competition is a clear example of
inter kinship-group selection (WILSON, 1973). The data also indicate, how-
ever, that such wholesale elimination of troops is relatively rare.

It is proposed that population regulation is the outcome of intertroop
competition that *in part* determines the amount of food available per troop
and thereby contributes to setting the upper limit to troop size. The molding
of the age-sex structure is then determined by socially imposed mortality in
reference to access to food sources within the troop.

E. B e h a v i o r a l   r e g u l a t i o n   o f   s o c i a l   s t r u c t u r e   i n
r e l a t i o n   t o   t h e   f o o d   s u p p l y   a n d   e x t r i n s i c a l l y
i m p o s e d   m o r t a l i t y .

Considering the influence of food scarcity on the age-sex structure, a
significant numerical decrease was found among young and old juvenile
females, but only among the young juvenile males (Table 1). These are
precisely the age-sex classes that one would expect to decrease according to
the observed frequencies of threat during foraging. CROOK (1970) proposed
that adult male representation should decrease in harsh seasonal climates
with low food availability. The conditions that CROOK refers to are, however,
chronic and only characteristic of certain habitats. The prolonged drought
in 1974 at Polonnaruwa was unusual and did not increase mortality among
adult, subadult and most old juvenile males. There are two possible reasons
for this. First, these males, particularly the adults, had priority of access to
whatever resources there were. Second, the most subordinate adult males and
the subadult males are peripheral to the troop where direct competition with
dominant males is minimal and where resources are shared with fewer
animals.

Under a constantly abundant food supply, troop Oval increased in size,
mainly through greater survivorship of young animals (which included

several juvenile females that survived to adulthood) (Table 1). A similar increase in population size has been noted among the provisioned colonies of Japanese macaques *M. fuscata* at Takasukiyama (ITANI *et al.*, 1963, ITANI, 1975) and rhesus macaques *M. mulatta* at Cayo Santiago (KOFORD, 1965). Relative to the survivorship of young in the food limited population of *M. sinica*, the survivorship of juveniles in general and of juvenile females was greater in the food provisioned colonies (DITTUS, 1975).

If the food sources available to a troop are limiting, one might expect the effects of competition to be alleviated through the death of other troop members. Like socially imposed mortality, that which occurs through predation or some other extrinsic means, alters the age-sex composition of the troop and thereby the vectors of threat that occur between them. Several of the interrelationships presented above may be summarized in the flow chart of Figure 15.
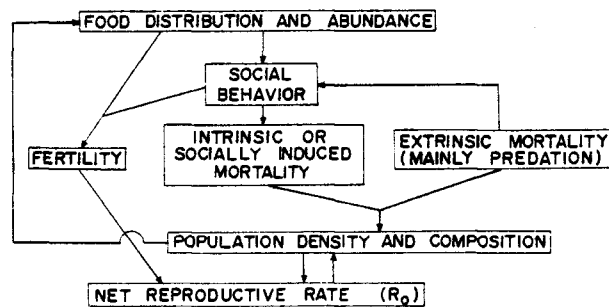

Fig. 15. Flow chart indicating the interrelationships between behavioral, ecological and demographic factors.

Based on the data concerning wild *M. sinica*, I propose the following hypothesis. The effects of social behavior (mainly aggressive and affiliative behaviors) and possibly its nature, change in accordance with the age and sex distribution of the society, its density, and available resources. Social behavior determines, through socially imposed mortality, the age and sex distribution and density of the society (and hence the population) in such a way as to maximize the reproductive success of some of its members, and results in bringing the society (and population) towards an equilibrium state ($R_o = 1$) with the resources and extrinsically imposed mortality.

The evolution of the behaviors which impose mortality and regulate the density and composition of macaque society is discussed elsewhere (DITTUS, in prep.).

SUMMARY

The relationships between behavioral, ecologicaland demographic data are examined for a wild population of nearly 450 toque monkeys, *Macaca sinica*, of Sri Lanka, based on 3½ years of continuous, plus 3 years of intermittent study.

Under relatively stable ecological conditions troops fluctuated in size within limits, and the net growth of the population was zero ($R_o = 1$). Decrease in food supply caused a net decrease in population size. An abundant food supply stimulated population growth. A lifetable indicated that mortality differed markedly according to age and sex, and that this pattern was not attributable to predation or disease alone.

Behavioral analysis revealed that 81.5% of all threats occurred during foraging. Threatened individuals were prevented from feeding, and their foods were usurped directly in 36% of all threat interactions.

The observed frequency of threats between age-sex classes during foraging differed significantly from two progressively stronger null hypotheses. These hypotheses took into account, respectively, the age-sex distribution of the society, and the frequencies of nearest neighbor associations between animals of different age and sex. The agonistic discrimination between animals of different age and sex was mirrored by a similar affiliative discrimination. Some conclusions of this analysis were that adults dominated the juveniles which in turn dominated the infants, and among juveniles and infants males dominated their female peers. Adults likewise discriminated against the young females.

The behavioral relationships during foraging influenced the foraging efficiency of animals, which was measured by the amount of time spent in foraging, feeding rates, and the quality of foods that were consumed. By these measures adult males fared best, then adult females, then juvenile males, and juvenile females fared worst.

I proposed that as a consequence of these behaviorally imposed feeding efficiencies, young animals died at greater rates than adults, and infant and juvenile females died at greater rates than their male peers; behaviorally mediated access to other resources is likely to influence mortality in a similar manner.

During the mating season, threatening and wounding increased markedly among adult and subadult males that competed for mates and that migrated. The peak of migration rates in males occurred during the subadult phase and coincided with the peak of mortality in males. This suggested that the rigors of migration (low priority of access to resources and frequent wounding) underlie the observed mortality. Mortality in adult males was (1) less than in subadult males which migrated more frequently, and (2) greater than in adult females which do not migrate.

Competition between troops, in part, determines the amount of food available per troop, and thereby contributes to setting the upper limit to troop size. The molding of the age-sex structure is then determined by social processess within a troop.

I hypothesized that the effects of social behavior (mainly aggressive and affiliative behaviors) and possibly its nature, change in accordance with the age and sex distribution of the society, its density, and available resources. Social behavior determines, through socially imposed mortality, the age and sex distribution and density of the society (and hence the population) in such a way as to maximize the reproductive success of some of its members, and results in bringing the society (and population) towards an equilibrium state ($R_o = 1$) with the resources and non-socially imposed mortality.

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ZUSAMMENFASSUNG

Die Beziehungen zwischen Daten betreffend Verhalten, Ökologie, und Demographie des Hutaffen, *Macaca sinica* werden untersucht. Diese Daten sind das Ergebnis von Beobachtungen an einer Population von etwa 450 frei-lebenden Individuen in Sri Lanka, gesammelt über einen Zeitraum von 3½ Jahren, und ergänzt durch Stichproben über 3 weitere Jahre.

Unter relativ stabilen ökologischen Bedingungen schwankte die Trupp-Grösse innerhalb enger Grenzen, und das Netto-Wachstum der Population war null ($R_0 = 1$). Verringerung des Nahrungsangebotes bewirkte einen Rückgang der Population, der hauptsächlich durch die erhöhte Mortalität der Jungtiere, besonders der Weibchen, verursacht war. Reiches Nahrungsangebot förderte das Wachstum der Population. Die Mortalität

war im Allgemeinen nach Alter und Geschlecht deutlich verschieden; diese Unterschiede konnten nicht ausschliesslich auf Raubfeinde oder Krankheit zurückgeführt werden.

Die Verhaltensanalyse ergab, dass 81.5% aller Drohungen während des Fressens oder Trinkens auftraten. Die bedrohten Individuen wurden am Fressen verhindert, und in 36% aller Auseinandersetzungen wurde ihnen das Futter weggenommen.

Zwei Null-Hypothesen von unterschiedlicher Stärke wurden aufgestellt, unter Berücksichtigung der Alters- und Geschlechtsverteilung der Gesellschaft, und der Häufigkeit der Nachbarschaft zwischen Tieren verschiedener Alters- und Geschlechtsklassen. Die beobachteten Daten wichen aber signifikant von den Voraussagen beider Hypothesen ab: sie weisen darauf hin dass eine agonistische Diskrimination zwischen Tieren verschiedenen Alters und Geschlechts stattfindet. Kontaktverhalten war ein Spiegelbild der agonistischen Diskrimination. Einige Schlüsse dieser Analyse waren, dass Erwachsene die Jungtiere dominierten welche ihrerseits die Säuglinge dominierten, und dass Jungtiere und Säuglinge männlichen Geschlechtes ihre weiblichen Altersgenossen dominierten. Erwachsene, in ähnlicher Weise, bedrohten weibliche Jungtiere und Säuglinge öfters als männliche, so dass, im Ganzen gesehen, weibliche Jungtiere und Säuglinge öfters bedroht wurden als ihre männlichen Altersgenossen.

Diese Ergebnisse, gemeinsam mit ökologischen Daten, weisen darauf hin dass der Wettbewerb um Nahrung zwischen Tieren verschiedenen Geschlechts und Alters deren Leistungsfähigkeit bei der Nahrungssuche beeinflusst. Die Leistungsfähigkeit bei der Nahrungssuche wurde gemessen als Funktion von Zeitaufwand, Fressgeschwindigkeit, und der Qualität des verzehrten Futters. Nach diesem Masstab waren die erwachsenen Männchen am besten gestellt, und dann folgten in absteigender Ordnung die erwachsenen Weibchen, die männlichen Jungtiere, und als Letzte die weiblichen Jungtiere.

Ich schlage vor, dass die erhöhte Mortalität der weiblichen Jungtiere und Säuglinge, verglichen mit derjenigen ihre männlichen Altersgenossen, durch die, auf dem Verhalten beruhende, unterschiedliche Leistungsfähigkeit der Nahrungssuche verursacht wird, wiewohl verhaltensbedingter Zugang zu anderen Gütern die Mortalität in ähnlicher Weise beeinflussen kann.

Während der Paarungszeit steigen Häufigkeit des Drohens und Verwundungen deutlich an, und zwar hauptsächlich bei männlichen Erwachsenen und Subadulten, welche um Partner werben und während der Paarungszeit wandern. Der Gipfel der Wanderungsrate tritt während der subadulten Phase auf, während der auch die Mortalität der Männchen ihren höchsten Wert erreicht. Dies lässt vermuten, dass die Härten der Wanderschaft (verminderten Zugang zu Gütern, und häufige Verwundung) die Ursache der beobachteten Mortalität sind. Die Mortalität erwachsener Männchen war (1) geringer als die von subadulten Männchen, welche oft wandern, und (2) grösser als die von erwachsenen Weibchen, welche nicht wandern.

Einige sozio-ökologischen Phänomene, welche für die Theorie der Regelung der Bevölkerungsgrösse von grundlegender Bedeutung sind, werden erwogen und in Hinblick auf die Ergebnisse dieser Untersuchung besprochen.

Der Wettbewerb zwischen Trupps bestimmt, zu einem gewissen Teil, die Grösse des Lebensraumes und bewirkt daher eine Begrenzung der Trupp-Grösse.

Auf Grund unserer Daten wurde die folgende Hypothese aufgestellt. Die Wirkung des Sozialverhaltens (hauptsächlich agonistisches und geselliges Verhalten) und möglicherweise seine Natur selbst, ändert sich je nach der Alters- und Geschlechts-Zusammensetzung der Sozietät, ihrer Bevölkerungsdichte, und vorhandenen Nahrung. Das Sozialverhalten bestimmt anderseits durch sozial bedingte Mortalität die Alters- und Geschlechts-Zusammensetzung und Bevölkerungsdichte der Sozietät (und daher der Population) in einer Weise, die den Vermehrungserfolg mancher ihrer Mitglieder maximaliziert und daher die Sozietät (und Population) auf ein Gleichgewicht ($R_0 = 1$) mit der vorhandenen Nahrung und der von aussen hervorgerufenen Mortalität einstellt.

APPENDIX 1

Life table for a population of 446 *M. s. sinica* in Polonnaruwa. The tabulated values are averages per annum within each age class (modified from DITTUS, 1975)

Age class	Age (years)	Males l_x	d_x	q_x	e_x	Females l_x	d_x	q_x	e_x
Infant	0-1	1,000	395	395	4.5	1,000	526	526	4.8
Juvenile-1	1-2	605	79	131	6.2	474	158	333	8.6
Juvenile-2	2-3½	526	74	141	5.0	316	55	174	10.7
Juvenile-3	3½-5								
Subadult male	5-7	303	99.5	328	5.1	—	—	—	—
Young adult male	7-10	104	7.7	74	10.5	—	—	—	—
Young adult female	5-10	—	—	—	—	152	2.8	18	16.6
Young to middle age	10-15	81	2.4	30	9.0	138	3.0	22	13.0
Middle age	15-20	69	7.6	110	5.2	123	2.8	23	9.3
Old	20-25	31	5.0	161	3.5	109	10.2	94	5.2
Senile	25-30	6	1.2	200	2.5	58	11.6	200	2.5