

Population Dynamics of the Toque Monkey, Macaca sinica

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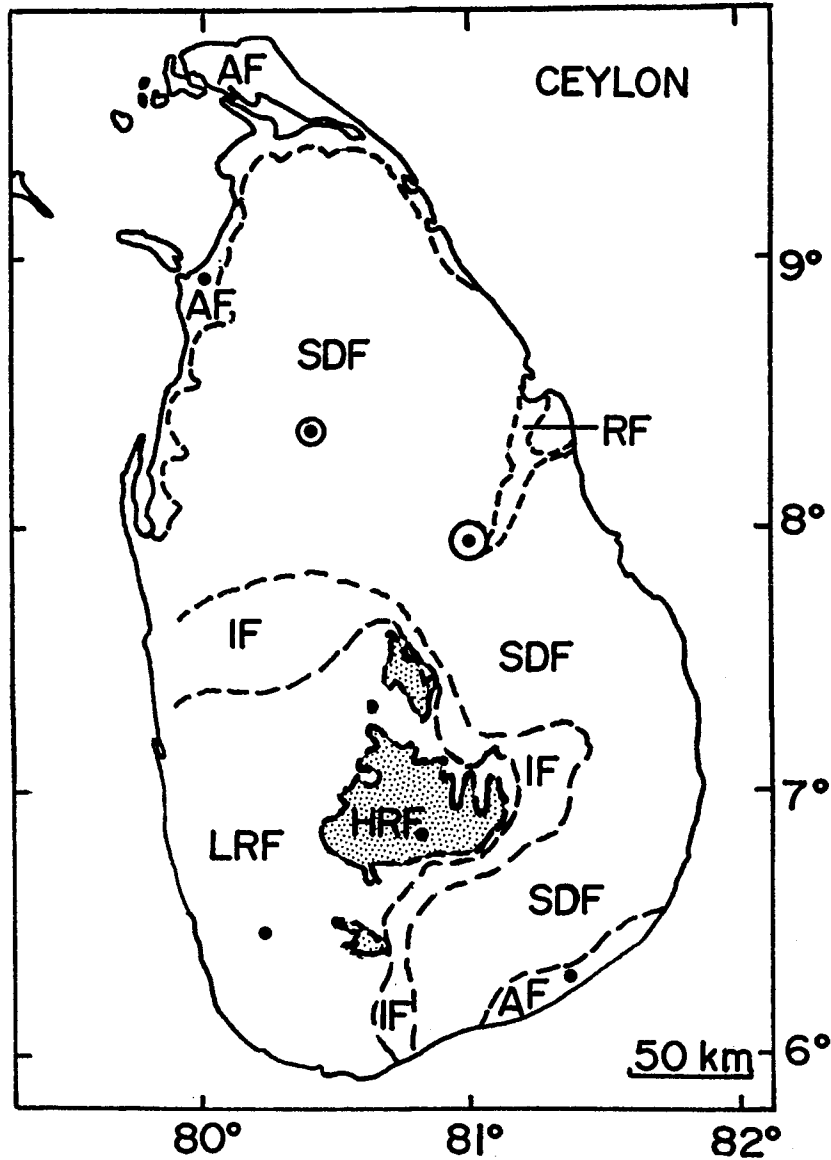
INTRODUCTION

Fundamental to any understanding of the adaptation of animals to their natural environment is the knowledge of their numbers and life and death characteristics. The data on population dynamics to be presented here is based on a three and one-half year field study of the toque macaque, *Macaca sinica* (Linnaeus 1771) of Sri Lanka (Ceylon). Publications dealing with aspects of ecology and behavior are in preparation.

The toque macaque, a member of the family Cercopithecidae, shares the subgenus *Zati* (Reichenbach 1862) with the bonnet macaque, *M. radiata* (Geoffroy 1812), of southern India and possibly *M. assamensis* (McClelland 1839) of northeastern India and Burma (Hill and Bernstein 1969). In its range *M. sinica* is confined to the forested regions of Ceylon, and three subspecies have been recognized; *M. s. sinica* (Linnaeus 1771), *M. s. aurifrons* (Pocock 1931), and *M. s. opisthomelas* (Hill 1942),

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For Plate, see p. vii, between pp. 368-369.



Map 1. Map of the natural vegetation of Ceylon; AF = arid zone forest; HRF = highland rain forest; IF = intermediate forest; LRF = lowland rain forest; RF = riverine forest; SDF = semideciduous forest (after Fernando 1968). Study sites are marked with a dot; Polonnaruwa, the main site, is encircled; Anuradhapura, the secondary site, has a smaller circle

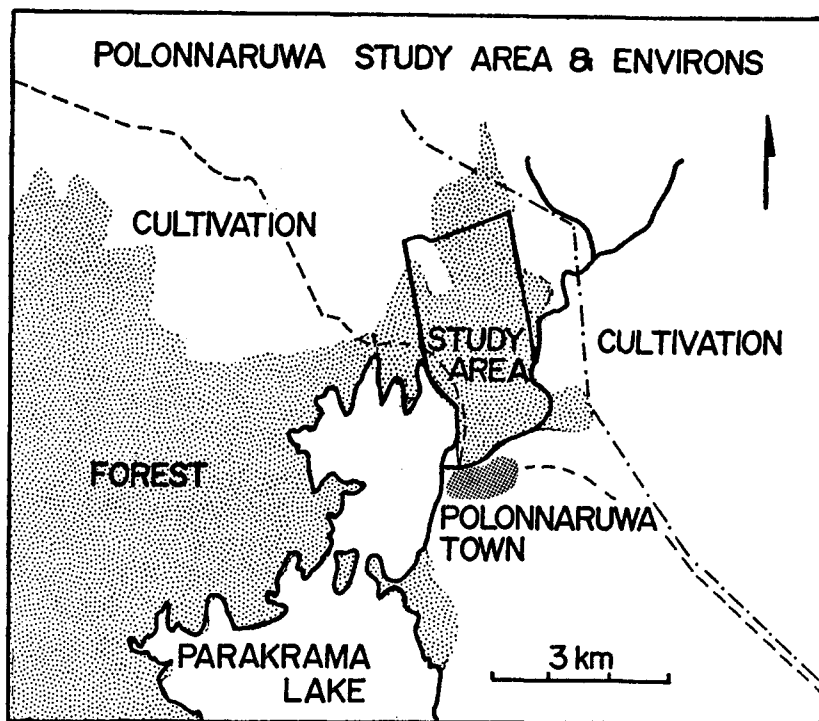
of the low country dry zone, low country wet zone and central hill country, and highlands respectively (Eisenberg and McKay 1970). Other primates in Ceylon are the langurs, *Presbytis entellus* and *P. senex* of the subgenera *Semnopithecus* and *Kasi* respectively, and the prosimian, *Loris tardigradus* (Phillips 1935).

The toque monkey is long tailed and is agile both on and above ground. Its popular name refers to a well formed cap-like whorl of hair (toque) radiating symmetrically outward from the center of its head (Plate 1). It is generally more colorful than its nearest relatives, the pelage varying geographically from dusky brown to golden yellow. The ears and lower lips are black and the face of adult females is usually varying degrees of red. Adult males frequently have black and/or red spots on the face. Facial coloration in both sexes generally becomes more intense with age, and is not strongly associated with the reproductive condition.

The main site for this study was in the semideciduous forests of Polonnaruwa in the north central dry zone. Anuradhapura, a secondary study site, is in the same zone, but is ecologically somewhat more disturbed than Polonnaruwa. Less detailed, comparative information was collected over a wide range from the Wilpattu and Ruhunu National Parks in the northwest and southeast arid zones respectively, the Sinharaje Forest Reserve in the lowland rain forest, Udawattekelle Sanctuary, Kandy, in the midland rain forest, and the Ohiya and Horton Plains region of the highland forests (Map 1).

In both the arid zones, the toque macaque was limited in its distribution to gallery forests and to areas surrounding other sources of permanent water. Troops living within towns, as reported for the rhesus, *M. mulatta* (e.g. Southwick et al. 1965: 111–159), were not found. In general macaques occurred wherever a semblance of natural forest with a permanent source of water was available.

Nearly all of the Polonnaruwa study site lies within a religious and archaeological sanctuary, therefore most of the animals were not seriously harassed and not as shy as they might have been in a "wilder" situation. Botanically, the study site can be considered a peninsula of forest bounded by water and cultivation, and continuous with extensive expanses of forest by only a narrow neck (Map 2). The forest within the study site generally resembled that natural to the area; however, areas surrounding important archaeological sites had been cleared of the shrub layer, and much of the periphery bordered on either abandoned or active cultivation. Cattle grazing occurred in parts of the study site. All species of Ceylon primates occurred there as did most of the native smaller mammals. Only elephants, *Elephas maximus*; sambar deer, *Cervus uni-*



Map 2. The Polonnaruwa Study Area. The irrigation channel (solid line) delimits the southern portion of the study area. The main road and the railway are marked by dashed and dashed and dotted lines respectively

color; wild boar, *Sus scrofa*; bear, *Melursus ursinus*; and leopard, *Panthera pardus*; were absent.

The study site encompassed approximately six square kilometers. Here eighteen troops representing 446 animals were censused. An additional 198 animals from Anuradhapura are considered in this report.

METHODS AND MATERIALS

Observations were made with the aid of Leitz Trinovid 7 x 42 binoculars. Data were initially recorded with a Philips Norelco portable cassette tape recorder, but, owing to its unreliable performance in the field, all data were eventually written by hand. Data were taken in as complete a form as possible in the field itself, thereby precluding supplementary notes after field hours.

Upon arrival in Polonnaruwa, I began to memorize the individual characteristics of animals from many different troops. This was a never-ending process, but by the end of the study, I could readily identify approximately 175 animals, which permitted the maintenance of many long-term individual records. Some individuals from the main study troops could be approached to within two meters or less; animals from less habituated troops usually maintained a ten- to thirty-meter distance from the observer.

In censusing, a troop was followed until all members of a troop had been noted. With a particularly shy or large troop this occasionally involved several days of contact. Individual characteristics of each animal were recorded to reduce the chance of recounts. The best method was to concentrate on each age and sex class separately, making sure that all individuals were accounted for. The final counts are the result of many double checks. Depending on the troop, censusing was conducted by either one observer or myself plus an assistant. For very shy troops, we occasionally used cooked rice to lure animals into the open for better observation.

Age Classification

For all infants of known date of birth, a record of morphological changes with age for the first year was maintained, including the color and distribution of fur, development of head hair, and degree of pigmentation of skin, especially the ears and dorsum of the hands and feet. Rather than ascribing "infant 1" or "infant 2" categories to infants, estimated ages were recorded. For purposes of these data, "infants 1" are those less than six months old, "infants 2" are six months to one year old.

The ages of juveniles were estimated less accurately, but, since toque monkeys have a narrow birth peak from December to February (Dittus, unpublished data), 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 one to two years; juveniles 2, aged two to three and one-half years; and juveniles 3, aged three and one-half to five years. The ages of juveniles were estimated by comparison with those of known ages.

Young females were considered adult with the first pregnancy at four and one-half to five years old. Males, on the other hand, were not fully

adult until seven, possibly eight, years of age, as judged by their morphological maturation. Subadult males from five to seven years of age had the size of an adult female, but were smaller and morphologically less developed than an adult male.

Adults were classified according to five broad categories: young, young to middle aged, middle aged, 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 the following changes 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 with age, 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, and like senile females commonly exhibited signs of illness. The numerical age ranges attributed to adult age classes were arbitrarily determined by dividing the number of adult years by the number of adult age classes.

RESULTS

Longevity

Captive records indicate that macaques may live up to thirty years or more (Jones 1962; Dathe 1971). Some individuals in the field appeared and behaved as though extremely old and I would challenge the assumption that free-ranging primates do not approach the longevity of captive specimens. I have assumed that thirty years is the approximate maximum longevity, but for isolated cases this may still be a slight underestimation.

Fertility

Fertility (m_x) refers to the number of offspring born to a female per unit time. Although it is customary to express fertility or natality on the basis of the entire female cohort, I have given estimates based on only the adult or reproductively mature females. Tables 1 and 2 give estimates of fertility over several seasons for Polonnaruwa and Anuradhapura respectively. The maximum estimates include females judged to be preg-

Table 1. Estimates of fertility (m_x) for Polonnaruwa (N = 154 births)

Year	Number of adult ♀♀	Fertility	
		Maximum	Minimum
68-69	27	.741	.704
69-70	43	.721	.698
70-71	76	.724	.697
71-72	78	.634	.590

Average = .688 infants/adult ♀/year.
Average = .411 infants/♀ of any age/year

Table 2. Estimates of fertility (m_x) for Anuradhapura (N = 38 births)

Year	Number of adult ♀♀	Fertility	
		Maximum	Minimum
69-70	31	.593	.323
70-71	36	.700	.417

Average = .508 infants/adult ♀/year.
Average = .269 infants/♀ of any age/year

nant at the time troops were sampled for newborn infants, whereas the minimum estimates preclude them.

A test for the significance of differences between two independent proportions utilizing a deviate of the unit normal curve (z) (Ferguson 1966) indicated that there was no significant difference ($z = 1.36$, $p = 0.158$) between the highest ($m_x = 0.741$) and lowest ($m_x = 0.590$) fertility estimates in Polonnaruwa for the four seasons sampled. Therefore, the mean value of 0.688 infants/adult female/year is taken as representative and was used in further calculations. The mean fertility value in Anuradhapura ($m_x = 0.508$) was significantly less than that of Polonnaruwa ($z = 2.906$, $p = 0.006$). However, this difference might be attributable to sampling error, since I censused for only one week at the end of the three to four month birth-season in Anuradhapura, and many infants born earlier might have died prior to the sampling period. Moreover, there was no significant difference ($z = 0.841$, $p = 0.280$) between the average maximum fertility estimates for Polonnaruwa ($m_x = 0.705$) and Anuradhapura ($m_x = 0.647$).

In the Polonnaruwa and Anuradhapura populations, there was no correlation between the fertility of females and the size of the troop (N = 26 troops). In the Polonnaruwa population, where more detailed records were maintained, there were differences in the fertility of females of different ages (Table 3), the senile females being significantly lower

Table 3. Age specific fertility rates (m_x)*

Age class	Age in years	Number of adult ♀♀	Number of infants	Number of adult ♀ seasons	Average number of infants born/adult ♀/year
Young	5-10	10	19	27	.704
Young-middle age	10-15	9	21	29	.724
Middle age	15-20	6	13	16	.813
Old	20-25	8	23	26	.885
Senile	25-30	5	4	14	.286

* Adult females were sorted according to 5 age groups each being approximately 5 years in duration. The number of seasons of observation differed between females. An adult-female-season refers to one year of observation of one adult female. Fertility per age group is the sum of infants born to females of the given age group divided by the total of adult female seasons for that age group.

($m_x = 0.286$) than the average ($z = 1.36$; $p = 0.158$). This low fertility results from the incorporation of post-reproductives into the estimates, menopause being defined as two or more successive years without a birth. Approximately 10 percent of the adult female cohort (or 3 percent of the total population) consisted of senile females of which 60 percent were past menopause. Fertility seems to increase with age and remains high right up to menopause. Thereafter the probability of death for a female is extreme; the longest duration of life for a post-reproductive female was three years.

Sex Ratio at Birth

Over four seasons in Polonnaruwa and Anuradhapura, 165 newborn infants were recorded: seventy-six males, sixty-six females, plus twenty-

Table 4. Sex ratio at birth

	Year	Number of infants	
		Males	Females
Polonnaruwa:	1968-1969	2	0
	1969-1970	4	7
	1970-1971	21	14
	1971-1972	22	26
Anuradhapura:	1970-1971	8	7
Total		57	54

Ratio ♀: ♂ = 1.056.

three for which the sex could not be determined. More females than males are undoubtedly included in the undetermined category since the vulva of a female infant was much more difficult to positively identify than was the penis of a male under field conditions.

The data in Table 4 represents the total number of infants of each sex from several troops in four birth seasons. To cancel observational bias, only those counts where the sex of all the infants in the troop had been positively established are considered, thus data from troops where the sex of one or more infants was not determined are not included. The ratio of females to males was 1.056, which does not differ significantly from 1.000 ($z = 0.209$, $p = 0.390$).

Life Table

It is convenient to summarize life and death processes of a population by means of a life table (Deevey 1947: 283–314). This requires a knowledge of the number of animals of different ages that are alive at a given point in time. The life table information presented here is based upon a thorough survey of all troops in the Polonnaruwa study population conducted in October 1971.

It is common to express the number of individuals alive at any age as a fraction of the total number alive. Such fractions are usually put on a "per thousand" basis. That is, one assumes that the data are based on a

Table 5. The number of immature *M. sinica* of different age and sex classes*

	Age class	Age (years)	Males		Females	
			Number observed	$1_x/1,000$	Number observed	$1_x/1,000$
Values per half year	Infant-1	No. born	38	1,000	38	1,000
	Infant-2	$\frac{1}{2}$ -1	30	789	21	553
Average values per annum	Infant	No. born	38	1,000	38	1,000
	Juvenile-1	1-2	23	605	18	474
	Juvenile-2	2-3 $\frac{1}{2}$	30	} 526	18	} 316
	Juvenile-3	3 $\frac{1}{2}$ -5	30		18	
	Subadult ♂	5-7	23		303	
	Adult ♂	7-30	48 (see Table 6)	—	—	—
	Adult ♀	5-30	—	—	111 (see Table 6)	—
Total			192		203	

* The conversion to 1_x per 1,000 of the observed number of infants and juveniles of different ages and sex, as determined from eighteen troops (N = 395) in Polonnaruwa.

cohort of 1,000 animals that theoretically began life together and ran the gamut of death risks together (Quick 1963: 190–228). “ l_x ” is defined as the number of individuals alive at time or age “ x ”, and “ d_x ” as its converse, the number of individuals dead at age “ x .” The rate of mortality “ q_x ” refers to the proportion of animals dying that enter a particular age class. It assumes that each age class begins with a cohort of 1,000 individuals. The mean expectation of life is expressed by the symbol “ e_x ” and refers to the average length of life of a population or cohort, and the average length of life remaining for those individuals that have reached a given age class.

Tables 5 and 6 present the observed data separately for the sexes and its conversion to $l_x/1,000$. The age and sex classification of juveniles and infants was ascertained for all eighteen troops (Table 5). However, the breakdown of adults into different age classes was ascertained with confidence for males in fourteen of the eighteen troops, and for females in eleven of the eighteen troops (Table 6). Comparison of the proportions of adults of each sex to the total number of animals in the respective

Table 6. The number of adult *M. sinica* of different age and sex classes*

Age class	Age (years)	Males		Females	
		Number observed	$l_x/1,000$ per annum	Number observed	$l_x/1,000$ per annum
Young ♂	7–10	10	104	—	—
Young ♀	5–10	—	—	21	152
Young to middle age	10–15	13	81	19	138
Middle age	15–20	11	69	17	123
Old	20–25	5	31	15	109
Senile	25–30	1	6	8	58
Total		40		80	

* The conversion of l_x per 1,000 of the observed number of adults of different ages and sex, as determined from fourteen troops for the males and from eleven troops for the females in Polonnaruwa.

troop totals indicates less than a four percent difference for females and less than 1 percent for males; therefore, the proportions of adults of different ages from Table 6 were extrapolated to all eighteen troops for further derivation of vital statistics (Table 7).

The peak of the birth season is December to February, thus, by the time of the October census, all surviving infants had attained the infant 2 class. To maintain a logical integrity or unity of the population cohort, the few infants 1 born during or just prior to October were not included

Table 7. Life table for a population of 446 *M. s. sinica* in Polonnaruwa

	Age class	Age (years)	Males				Females			
			l_x	d_x	q_x	e_x	l_x	d_x	q_x	e_x
Values per half year	Infant-1	0- $\frac{1}{2}$	1,000	211	211	5.3	1,000	447	447	5.4
	Infant-2	$\frac{1}{2}$ -1	789	184	233	5.6	553	79	143	8.3
Average values per annum	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	2-3 $\frac{1}{2}$	526	74	141	5.0	316	55	174	10.7
	Juvenile-3	3 $\frac{1}{2}$ -5								
	Subadult ♂	5-7								
	Young adult ♂	7-10	104	7.7	74	10.5	—	—	—	—
	Young adult ♀	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	

* Age categories are variable in length according to recognizable classes. Statistics, however, were calculated according to the constant interval of one year, and then averaged per age class.

in the census. Numbers of "infant 1" (thirty-eight infants of each sex) were determined by multiplying the number of adult females in the census (111) by the average fertility rate (0.688) infants/adult female/year. This is equivalent to determining the number of newborn infants recruited into the censused troops during the birth season preceding October.

Because of the high death rates in infants, the first year data are divided into two six-month intervals. For consistency with the rest of the life table, the same data are given again on a yearly basis. In both sexes the observed frequencies for the juvenile 2 and 3 classes were the same; this is probably due to sampling error, that is, some of the smaller juveniles 3 should have been classed as juveniles 2. Thus, one value has been used to represent both classes in Table 7. To calculate l_x and d_x values as per age class, one need only multiply the given yearly averages by the number of years accorded the age class. Note that the average q_x and e_x values for senile animals is 200 and 2.5 respectively, when in fact for the twenty-ninth to thirtieth year these values are as expected: $q_x = 1,000$ and $e_x = 0.5$. The mean life expectancy of the entire cohort is based on the yearly average for the infant class, and for males is 4.5 years, and females 4.8 years.

Figure 1 graphically summarizes the life and death characteristics of males and females at different ages. In both sexes, notice the loss of young animals and the dramatic stabilization, or increase in the proba-

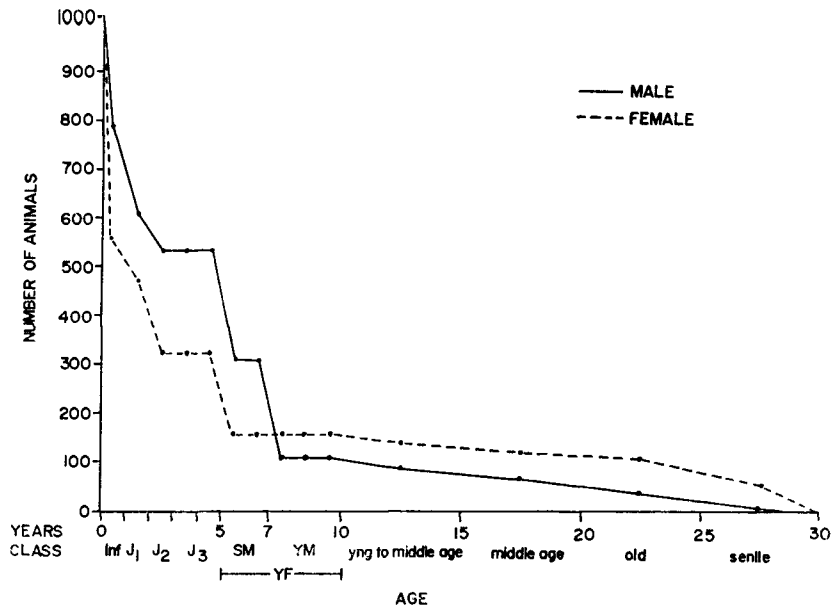


Figure 1. Survival curve. Subadult males (SM) are 5 to 7 years old, young adult males (YM) are 7 to 10 years old, and young adult females (YF) are 5 to 10 years old. "Inf," "J," and "Yng" are infant, juvenile, and young, respectively

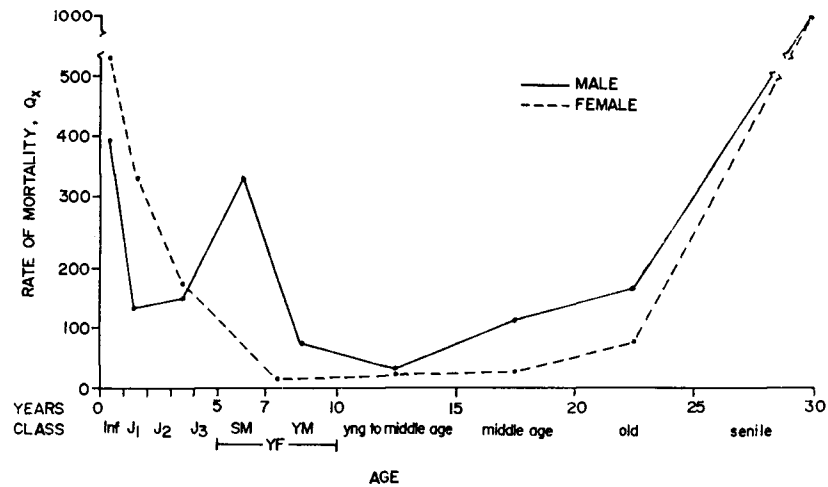


Figure 2. Age-specific rates of mortality. Symbols are as in Figure 1

bility of survival with the attainment of adulthood, which for females is approximately two years earlier than for males. Mortality in infant and juvenile females is higher than in like-aged males, but drops below male mortality as females become adult. Male mortality rates peak during the

Table 8. Approximate life table of a population of 194 *M. s sinica* from Anuradhapura

Age class	Age (years)	Number observed	Males			Females			
			Average per annum			Average per annum			
			l_x	d_x	q_x	Number observed	l_x	d_x	q_x
Infant	0-1	17	1,000	471	471	22	1,000	364	364
Juvenile-1	1-2	9	529	98	185	14	636	395	621
Juvenile-2 and 3	2-5	22	431	55	128	16	241	43	180
Subadult ♂	5-7	9	265	102	384	—	—	—	—
Adult ♂	7-30	24	61	2.7	44	—	—	—	—
Adult ♀	5-30	—	—	—	—	61	111	4.4	40

subadult stage at approximately five to seven years of age and level off again with the attainment of adulthood, but remain higher than the female rates throughout adult life. Senile females are more numerous than senile males, therefore, females are slightly longer lived than are males, as already suggested by the estimates of e_x for the respective cohorts. Figure 2 clearly illustrates the difference in the rates of mortality (q_x) at different ages between the sexes.

A similar census was taken in Anuradhapura. Complete counts were obtained on two troops in March 1970, and five troops in March 1971. An incomplete count of a very large troop of at least fifty-one animals is also included. Two or three troops had the birth peak in the fall, whereas the rest peaked in the spring (Dittus, unpublished data); in one troop there were no infants of one year or less at the time of the census. Further, it was not possible to classify all adults into different age groups. As a result, the life table (Table 8) for Anuradhapura is incomplete and ought to be considered only as a rough approximation.

In general, the Anuradhapura data resemble those of Polonnaruwa, indicating a high rate of mortality during infancy which then decreases to a minimum toward adulthood. There is a slight peak of mortality in the subadult male stage, and a slightly higher rate of mortality in adult males than in adult females.

The rates of mortality between the sexes in the infant stage seemed to differ; in Anuradhapura, infant males suffered a greater mortality than did females during their first year. In the yearling stage, however, female mortality far surpassed that of males and, as in Polonnaruwa, remained somewhat higher in females until approximately five years.

Comparing rates of mortality for the first two years of life, q_x in Polonnaruwa is 474 for males and 684 for females, whereas in Anuradhapura

Table 9. A comparison of proportions of age classes in adults between the populations of Anuradhapura and Polonnaruwa

	Total N	Percent			
		Young and young to middle age	Middle age	Old	Senile
Adult males:					
Anuradhapura	17	53-59	35-41	6	0
Polonnaruwa	40	57	38	12	3
Adult females:					
Anuradhapura	28	61	21-29	4-11	7
Polonnaruwa	80	50	21	19	10

q_x is somewhat higher for both sexes: 569 for males and 759 for females.

Although data on the frequencies of different age classes in adults were insufficient to incorporate into the life table, some indication of the age structure can be gained from the limited sample that was taken. Table 9 compares the percentages of adults of different age classes in Anuradhapura with those of Polonnaruwa. The age classes "young" and "young to middle age" are combined.

Again the age structure of adults in Anuradhapura closely approximates that of Polonnaruwa. However, there was a lower proportion of old and senile animals in Anuradhapura. Assuming a long-term constancy of fertility rates, this might reflect a greater rate of mortality in old age in this population.

Mortality

An important question concerns the causation of the observed mortalities. Death is rarely observed, but instead may or may not be inferred by assessing the circumstances surrounding an individual's disappearance. Although predation is a major factor in mortality, its effects are not random; social and ecological factors potentiate mortality differently among the age and sex classes. This is a complex situation and will be dealt with in detail in future publications.

All five observations of death through predation involved dogs. Dogs are the main predators not only of the macaques, but also of the grey langurs, *P. entellus*, as is evident from the numerous attempts by dogs to catch both species, and by these monkeys' intense alarm responses to dogs. The sight of a jackal, *Canis aureus*, also produced alarm and avoidance, even though jackals appeared to show no great interest in the ma-

caques. 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 macaques. Leopards were absent from the study site.

The response to the python, *Python molurus pimbura*, and the poisonous snakes, cobra, *Naja n. naja*, and Russell's viper, *Vipera russelli pilchella*, was one of alarm, avoidance, and curiosity (nomenclature according to Deraniyagala 1955: 1–121). Nonpoisonous snakes did not elicit these responses.

Alarm and avoidance reactions were elicited by the low flight of most large eagles or hawks, particularly the sea eagle, *Haliaeetus leucogaster*; serpent eagle, *Spilornis cheela spilogaster*; tank eagle, *Ichthyophaga ichthyaetus plumeiceps*; hawk eagle, *Spizaetus cirrhatus ceylonensis*; Brahminy kite, *Haliastur indus indus*; the fish owl, *Ketupa zeylonensis zeylonensis*; and the forest eagle-owl, *Bubo nipalensis blighi* (nomenclature according to Henry 1971). These birds probably prey only on the younger animals and, indeed, these give the most intense responses to raptors. A forest eagle-owl was observed carrying away a captive infant purple-faced langur, *P. senex*, that had been sleeping by itself. Men occasionally harassed the monkeys, but, with one possible exception, did not kill them in the study area.

Migrations

With the exception of one equivocal observation, females were never observed to migrate. In males, migration was confirmed in adults, subadults, and older juveniles 3, but rarely in younger juveniles, and never in infants.

Migrations were of two kinds: (1) Temporary excursions from the troop lasting from a fraction of a day to several days while attempting to consort with estrous females of other troops. These males always returned to the home troop, and, during long absences, visited for short intervals. (2) Occasionally, some males did not return, but became permanent members of another troop. The data presented here refer only to permanent migrations.

Solitary males, in the sense that they were completely independent of a troop, were never found. Whenever single males were encountered and followed, they returned to a troop within a few hours at most. One all-male subgroup was peripheral to the largest troop in the study area (forty-three members including the subgroup). Its composition varied,

especially in the membership of its younger juveniles, but, essentially it consisted of two adult males, one subadult, and six to seven juveniles. The youngest juveniles, three juveniles 2 and one juvenile 1, were born in the main troop and were non-permanent members of the peripheral subgroup. One juvenile 2 from a neighboring troop was also a temporary resident.

Records concerning migrations were maintained on twenty-six subadult and juvenile 3 males (Table 10), and twenty-seven adult males (Table 11).

Table 10. Histories of twenty-six adolescent males, with reference to their migrations

7	Known to have migrated permanently. Later three of these disappeared.
1*	Emigrated temporarily and subsequently disappeared.
4*	Became permanent members of an all-male subgroup peripheral to their maternal troop. Later two of these disappeared.
4	Remained resident members of the same troop for the duration of the period of observation. All of these were relatively young.
10	Disappeared under unknown circumstances.

* See text.

Table 11. Histories of twenty-seven adult males, with reference to their migrations

10	Remained resident members of the same troop throughout the period of observation.
8	Are known to have migrated.
9	Disappeared under equivocal circumstances.

For the subadult and juvenile 3 males, referred to as adolescent males, an exact estimate of the rates of migration from the data in Table 10 is not possible, but the range might be indicated. The number of days adolescent males were under observation varied between individuals, but totalled 8831 adolescent-male-days of observation. The acquisition of permanent membership in a new troop was ascertained for seven adolescent males (Table 10). With a minimum of seven migrations in 8831 adolescent-male-days, we obtained 0.00079 migrations per adolescent-male-day, or, each adolescent male migrated once on the average of every 3.47 years. In Table 10 I have marked with an asterisk five males whose migratory status is equivocal; if these might be considered as true migrants, then with a total of twelve migrations the rate of migration would be once every 2.01 years.

Ten adolescent males disappeared without trace, and an additional six disappeared subsequent to one migration, or from the all-male subgroup.

The eventual fate of death is probable for most of these sixteen males; a supposition based first on the high probability of death in this age group ($q_{4-7} = 722$), and second on the fact that the Polonnaruwa study site is almost a closed "island" bounded by water and cultivation (Map 2), making it unlikely that any but the exceptional male could successfully emigrate from the study area.

Since death and migration are not mutually exclusive, migration, or an attempt at migration, possibly to the northernmost parts of the study area which were not intensively investigated, should not be ruled out for at least a few of the sixteen males with unknown final destinies. Clearly, the actual rate of migration is above the minimum indicated.

Of the eight adult male migrants in Table 11, six migrated once, two migrated twice, giving a total of ten migrations; five animals immigrated from unknown origins, and five migrated between known troops.

Of the nine that disappeared four were very old and probably died of senility and illness, three of these were obviously becoming progressively weaker through physical impairment. A fifth animal was captured and probably killed by a cultivator.

The disappearance of three males coincided with the establishment of new dominant males, which in two cases were immigrants. One of the disappearing males was multiply wounded during battles for dominance. The circumstances suggest that these three males were evicted from their troops; their fate may or may not have been death. The troop of the ninth male habitually "stole" from a rice mill; he may have been killed.

These data indicate a minimum of ten and a maximum of fourteen migrations if the possibility of emigration is admitted for the last four males with unknown fates.

For adult males the total number of adult-male-days of observation was 21,436. A minimum of ten migrations yields a rate of 0.00047 migrations per adult-male-day, or, each adult male migrated on the average of once every 5.83 years. The maximum of fourteen migrations gives a rate of 0.00065 migrations per adult-male-day, or, each adult male migrated once every 4.21 years. A male that lives to a ripe old age would be expected to change troop membership on the average of five to six times in his lifetime.

All ten emigrations were known to have been by subordinate males who had recently dropped in the dominance hierarchy. Eight of the immigrants were known to have been attracted to the troop by estrous females. The ensuing competition with resident males caused a hierarchical reorganization with subsequent emigration by the resident losers in two cases.

Net Reproductive Rate, R_0

It is of interest to know whether a population of animals is increasing its numbers ($R_0 > 1$), decreasing ($R_0 < 1$), or at equilibrium ($R_0 = 1$). The net reproductive rate, or recruitment rate, is commonly defined as the average number of female infants produced by a female in her lifetime. There are several ways of estimating R_0 from my data.

First, how many female infants born per breeding female live to breeding age? The mean life expectancy of a female having reached breeding age is 16.58 years (Table 7). With a sex ratio at birth of 1 : 1 (Table 4), the birth rate for infant females is $\frac{1}{2} \times 0.688$ per adult female per year. Therefore, the average number of female infants born per adult female in a lifetime is $16.58 \times \frac{1}{2} \times 0.688 = 5.70$. The probability of an infant female dying prior to reaching breeding age is the sum of the d_x values up to four and one-half years of age, or 822 per 1000 (Table 7). That is, of 5.70 female infants born, 82.2 percent die, or 4.69. R_0 , the number of infant females born per adult female that live to breeding age is 5.70 minus $4.69 = 1.01$.

Employing the usual formula for R_0 , the sum of the products $l_x m_x$ for each age class "x," then $R_0 = 0.9976$.

A third estimate of the recruitment rate, also called replacement rate, comes from directly observing the number of juvenile females that begin breeding and subtracting the number of adult females that cease breeding. Records were maintained on fifty-three adult females (from eight troops) resulting in 48,104 female-days of observation over three and one-half years.

During this time, nine juvenile females had their first birth, giving 0.069 female recruits per female year. Four adult females died, three senile females reached menopause, and one pathological female with a malformed pelvis, crippled hind leg, injured jaw, and a generally weak condition was never noted to give birth. Another female missing her left arm gave birth three times but her infants died at an early age suggesting that she was not fully competent in maternal care. She had noticeable difficulty in lending arm support to her infant during arboreal travel.

This amounts to eight, possibly nine, females, or a rate of 0.062 to 0.069 females being lost to the breeding population per adult female year, which nearly or exactly cancels those entering the breeding state (0.069 per female year). Although this estimate might incorporate elements of chance or interpretation, it does reiterate that the net reproductive rate, R_0 , for the Polonnaruwa study population is at or very near equilibrium.

The Number and Biomass of Macaques per Unit Area

The home ranges of fifteen troops were ascertained on the basis of a minimum of 100 hours, and a maximum of several thousand hours of observation per troop. The home ranges of these troops were continuous with one another, and those of immediately adjacent troops overlapped considerably. Together they formed what might be considered a small deme that was surrounded mostly by water and cultivation. The home ranges of three troops, however, overlapped only partially with troops considered in this estimate. To adjust for this, only that fraction of the number of animals in the three troops that was proportional to the amount of home range overlap with the rest of the deme was incorporated in the density estimate, which is: 295 individuals inhabiting 296 hectares, or one individual per hectare.

To obtain biomass estimates, animals were weighed in the field, using a spring weighing scale suspended from a tree support. Animals were enticed to sit in a pan which contained known amounts of food. Because of the persistent domination of the food pan by high ranking animals and the apprehension some animals had of the apparatus, it usually took a day or more to weigh ten animals. Table 12 summarizes the weights of animals of different age and sex.

Table 12. Weights of macaques of different age and sex

Age class	Average weight (kilogram)	Number of animals weighed (N = 76)
Infant-1 (18 days old)	0.44*	1
Infant-2 (0.6 yrs. old)	0.91	1
Juvenile-1	1.35	5
Juvenile-2	2.00	9
Juvenile-3	3.00	11
Subadult ♂	4.10	9
Adult ♂	5.72	16
Adult ♀	3.59	24

* This estimate is based on the weight of a male infant, *Macaca nemestrina*, at the age of 18 days, born in the National Zoological Park, Washington, D.C.

To calculate the biomass of the study population, weight differences with age and sex were taken into account (Table 13). Further adjustment was made in accordance with the proportion of the three bordering troops that shared only part of their home range with the other twelve troops. These calculations yield 869 kilograms of macaque inhabiting 296 hectares, or three kilograms per hectare. Considering that part of an ani-

Table 13. Total weights of animals wholly and partially inhabiting 296 hectares

	AF	AM	SM	J ₃	J ₂	J ₁	I	Adjustment for partial residency	Total weight (kilogram)
<i>Troops 1-12</i>									
Number of animals	73	31	18	36	28	31	37		
Weight-kilogram	262	177	74	108	56	42	37	none	756
<i>Troop Oval</i>									
Number of animals	8	4	1	2	3	2	3		
Weight-kilogram	29	23	4	6	8	3	3	76 kg × 0.8	61
<i>Troop Bout</i>									
Number of animals	8	3	1	3	6	4	3		
Weight-kilogram	29	17	4	9	12	5	3	79 kg × 0.5	40
<i>Troop G</i>									
Number of animals	4	1	1	2	3	2	0		
Weight-kilogram	14	6	4	6	6	3	0	39 kg × 0.3	12
Total weight									869

AF = adult female, AM = adult male, SM = subadult male, J = juvenile, I = infant.

mal's weight represents dead contents of the alimentary tract, the estimate might be over by a very small fraction.

DISCUSSION

The population of toque macaques in Polonnaruwa is the first example of a primate population, to my knowledge, where the net reproductive rate, R_0 , has been found to be near equilibrium. Information from two other populations for which extensive data are available, the Takasakiyama colony of Japanese macaques, *M. fuscata* (Itani et al. 1963: 1-42; Carpenter and Nishimura 1969: 16-30), and the Cayo Santiago colony of rhesus, *M. mulatta* (Koford 1965: 160-174), indicates that both of these colonies, which are artificially provisioned with food, have increased their numbers three and one-half times over ten years and seven fold over twelve years respectively.

For the sake of comparison with *M. sinica*, I have taken the data on *M. mulatta* from Koford (1965: 160-174) and that on *M. fuscata* from Itani et al. (1963: 1-42) and Carpenter and Nishimura (1969: 16-30) and have calculated the proportion dying at different ages, d_x per 1,000, separately for the male and female cohorts. Because of inter-observer differences, fine distinctions between ages were not possible, and the

values given here are approximations within broad age categories. The main point of interest is that the rates of mortality for infants and juveniles in both of the provisioned colonies were less than those for the wild population of *M. sinica*. The value of $d_x/1,000$ for males between birth and seven years old was 825 for *M. mulatta*, 765 for *M. fuscata*, and 895 for *M. sinica*. Similarly for females between birth and the end of the fourth year of life, mortality was 737 in *M. mulatta*, 680 for *M. fuscata*, and 849 for *M. sinica*.

The discrepancy is greatest between females, that is, more females reach breeding age in the provisioned colonies than in the wild population of toque macaques. This is reflected directly in the proportions of immatures to adults in these populations. Immature females account for 57.4 percent of the female cohort in *M. fuscata*, but only 45.5 percent in *M. sinica*, whereas immature males account for 79.9 percent of the male cohort in *M. fuscata* and 75.2 percent in *M. sinica*. I was not able to extract equivalent information from Koford's data. In a population that is increasing its numbers a greater proportion of immatures to adults would be expected.

An examination of the rates of fertility shows that *M. sinica*, a population at equilibrium, has the lowest value, $m_x = 0.688$ infants per female per year, when compared with the growing populations of *M. fuscata*, $m_x = 0.723$ infants per female per year (calculated from the data of Itani et al. 1963), and $m_x = 0.850$ infants per female per year in the rhesus of Cayo Santiago (Koford 1965: 160–174).

These data suggest that the equilibrium in the population of *M. sinica* in Polonnaruwa is achieved through lowered fertility and increased mortality in the infant and juvenile classes, especially in females.

Figure 2 illustrates that in Polonnaruwa mortality in males reaches a peak (neglecting infants and senile males) at six years of age. This coincides with a peak of migration rates, between four and seven years old approximately. Migrations occur almost exclusively in the breeding season, when competition between males for estrous females is greatest and when wounding from intra-specific fighting is most common. As mentioned, emigrating adult males are those that have recently attained low status. Unless an immigrating adult establishes himself as a dominant in the host troop, he, with the adolescent immigrants, is relegated to a spatially peripheral position and low status access to resources (Dittus, unpublished data. Of the six instances where the physical condition of peripheral immigrants was known before and after migration, all were conspicuously thinner as well as being wounded (three had large or many wounds) following migration. Although death through wounding

or starvation was never directly observed, the evidence strongly suggests a causal relationship between the rigors of migration and mortality.

The pattern of mortality in males of *M. sinica*, *M. mulatta*, and *M. fuscata* appears to be similar. Mortality begins to surpass that of females between the fourth and fifth year, and reaches a peak at six years in *M. sinica* and *M. mulatta* and then attenuates with the advent of adulthood. In *M. fuscata* a similar peak is attained but at a slightly older age, eight to nine years and drops to a low only at about fifteen years old. As in *M. sinica*, these peaks of mortality coincide approximately with a peak in migration rates in *M. mulatta* and *M. fuscata*. Koford's data (1965: 160–174; 1966: 1–7) indicate that for the rhesus of Cayo Santiago in the years 1960 to 1963 the peak age at migration was six to seven years old in males, yet the rate for three to five year olds was also quite high, and Boelkins' and Wilson's (1972) data, which were collected from the same colony between 1965 and 1967, indicate the peak to be in the three to five year range. Ages of "solitarization" in *M. fuscata* of the Koshima and Ohirayama troops occur between the sixth and the twelfth year of life (Kawai and Yoshida 1968), which correlates closely with the peak of death in males of this species in Takasakiyama. Any significance to this coincidence assumes, of course, that the peaks of mortality and migration occur at the same age between these Japanese colonies. In the rhesus of Cayo Santiago, an increase in wounding and mortality from fighting during the breeding season has been established by Vandenberg and Vessey (1968: 71–79) and Wilson and Boelkins (1970: 719–724) respectively, although no direct link between mortality and migration has been established.

In Polonnaruwa every older juvenile 3 or subadult male migrates once in two to three and one-half years or less. This means in effect, that all males leave their maternal troops during adolescence. Further, although the rate of migration for adult males is less than for the adolescent males, the data strongly indicate that adult males do not remain with the same troop throughout their lives. Unless one postulates the return of males to their maternal troops when adult, emigration by itself would seem to provide an effective barrier to sibling or mother-son matings, or at least render such matings extremely unlikely.

If the rates of migration in *M. sinica* hold for other congenetics, then the contradictions between the reports of Sade (1968: 18–38; 1972: 378–398) and Missakian (1973b: 621–624) regarding factors preventing or inducing inbreeding are understandable since migration for rhesus on the sixteen hectare islet of Cayo Santiago is extremely limited. Patterns atypical of the wild situation may emerge as a consequence. The value of

long term studies of a species in its natural habitat is underscored.

The density of *M. sinica* in the Polonnaruwa habitat was one macaque per hectare. No estimate of density for *M. fuscata* at Takasakiyama is given, but, from a scale and map provided by Mizuhara (1963), the combined home ranges of the troops in 1952 is approximately 1.75 square kilometers, which with 220 animals at the onset of provisioning (Itani et al. 1963: 1–42) converts to 1.3 macaques per hectare. The density of rhesus in their natural habitats in India ranges from 0.2 to 0.5 macaques per hectare in forests, and up to 8.8 per hectare in towns (after Neville 1968: 111–123; Southwick 1961: 698–710). Clearly, the densities of these species in their natural habitats are of the same order of magnitude. The high density of 8.8 rhesus per hectare in a town, Neville (1968) attributes to the nature of the food sources. Artificial provisioning of food has “exploded” the Takasakiyama colony to 4.5 per hectare by 1962 and especially the rhesus of Cayo Santiago to twenty-five per hectare by 1962 (after Koford 1965: 160–174) and forty-four per hectare by 1968 (after Missakian’s 1973b report of 700 rhesus by 1968). Taking the average weight of a rhesus macaque to be 7.9 kilograms (after Napier and Napier 1967), the carrying capacity of Cayo Santiago is over 110 times greater than that of Polonnaruwa. Hence, a tolerance for densities far above those found in the wild is indicated at least in the rhesus, in the presence of a superabundance of food. Interestingly, Boelkins and Wilson (1972: 125–140) noted a decline of fertility and an increase in adult male mortality at the extreme densities between 1964 and 1967. A high tolerance for the proximity of individuals seems almost self-evident in a group-living species. Within the range of densities found in forest habitats, it is unlikely, therefore, that density *per se* is a factor limiting population growth.

The Polonnaruwa area is subject to a dry and wet season annually. Hladik and Hladik (1972: 149–215) have profiled the corresponding seasonal availability of various woody plant foods for the three large primates in Polonnaruwa, and Rudran (1973: 41–60) with similar information has related this to the seasons of birth and mating in *P. senex*.

Refuges and sleeping trees are always abundant for *M. sinica*, but a season of food scarcity is prevalent (Dittus, unpublished data). At this time animals spend almost all their daylight hours in search for food, which is generally of low nutritional value (Dittus, unpublished data). The animals of several troops in sub-optimum habitat are of lesser weight and generally exhibit a poorer physical condition than normal (Dittus, unpublished data). These facts, together with a low density of less than 0.3 macaques per square kilometer in the arid zone forest of

the Wilpattu National Park (Eisenberg et al. 1972: 863–874) suggest that the availability of food, at least in part, determines the carrying capacity of the forest and the level of equilibrium of the population. The two folivorous species of langur, *P. entellus* and *P. senex*, both maintain densities far greater than the frugivorous-omnivorous macaque with whom they share the Polonnaruwa habitat (Eisenberg et al. 1972: 863–874).

Compared to Polonnaruwa, the habitat in Anuradhapura was generally much less benign. The shrub layer has been cleared almost completely in most areas and the density of trees was less, thereby depriving animals of refuges and sources of food. This unfavorable situation also brought them into closer conflict with garden owners and dogs. Animals in the two largest troops (fifty-one and thirty-three members) were noticeably undernourished, and most troops had one or more individuals with signs of human harassment including cut tails, broken bones, missing hands (amputated as “punishment” for thievery) or wire collars. In light of this, it may be significant, that the most vulnerable age classes, the very young and the old, constituted a lesser proportion in the Anuradhapura population than in Polonnaruwa. That is, increased harshness of the environment and predation had the effect of accentuating the peaks of the age-specific rates of mortality very early and late in life and left unaffected the overall pattern of mortality. This conclusion assumes that rates of fertility in Anuradhapura had been more or less constant over several generations.

SUMMARY AND CONCLUSIONS

In the population of toque macaques in Polonnaruwa, mortality rates differed with respect to age and sex, and the highest probability of survival was found in animals as they attained effective breeding age. For young adult females the probable average number of years of life remaining (e_x) was 16.6, and for young adult males it was 10.5 years. Prior to these ages the risk of death for both sexes was extreme. In females nearly 85 percent ($d_{0-5} = 849$) of all deaths occurred prior to adulthood, and in males nearly 90 percent ($d_{0-7} = 895$) of all deaths occurred prior to seven years. The peak in female mortality was during the first few weeks of life, whereas in males risks of death were greatest for adolescents, approximately 72 percent ($q_{4-7} = 722$) of which died between the age of four and seven years. That is, 27 percent ($d_{4-7} = 273$) of total male mortality is concentrated in this short phase. This high mortality in adolescent males is associated with their expulsion from

their maternal troops, or attraction to another troop, predominantly during the mating season. Progressive debilitation through food deprivation which was attributable to low status in the host troop, and exacerbated through injury from competitive fights with other males for estrous females, is thought to be a principal cause of death. The high rates of mortality early in life had the effect of greatly reducing the overall or mean life expectancy of the male and female cohorts to 4.5 and 4.8 years respectively.

A comparison with the Anuradhapura population, where there was more predation pressure and access to food sources was less favorable, indicates that the peaks of mortality early and late in life are accentuated, rather than the overall pattern of mortality.

The density of macaques in Polonnaruwa is one animal per hectare, or up to forty-four times less than the provisioned colony of rhesus on Cayo Santiago, yet the net reproductive rate of *M. sinica* at Polonnaruwa is near one. Ecological data (Dittus, unpublished data) suggest that the macaques in Polonnaruwa are saturating their habitat, but density *per se* is not regarded as a major factor maintaining the equilibrium. Rather, it is proposed that the age and sex composition of the population and its net reproductive rate is attuned to the availability of food, and is regulated through socioecological mechanisms. The nature of the latter will be explored in future publications.

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