Demography of *Macaca sylvanus* of Gibraltar

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ABSTRACT. The demographic structure of *Macaca sylvanus* (Gibraltar) is analyzed over a 21 year period in light of human interference on this population. Social behaviour is examined in terms of its influence on the parameters investigated. The findings lead to speculations concerning the nature of homeostatic processes operating in a non-wild group.

INTRODUCTION

Populations are dynamic entities. Longitudinal studies asymptotically permit approximation of a population's spatial-temporal condition. The inter-relationships between behavioural, genetic, ecological, and demographic determinants of population structure become apparent over time. There are few monkey populations in which such a study is possible, and none of these are 'wild' which is understood to mean that condition in which the sympatric human population exerts no more control than any other sympatric animal species, although it may prey on, or alter the ecology. This paper describes basic aspects of the demographic structure of *Macaca sylvanus* of Gibraltar.

The Gibraltar macaques have been previously described elsewhere (MACROBERTS & MACROBERTS, 1966, 1971; MACROBERTS, 1970; BURTON, 1972). Two free-ranging groups at Queen's Gate and Middle Hill constitute the population. The British Army has full responsibility for the animals, and provides approximately one third of their nutritional needs as well as water. Noxious elements are removed, as was the case in 1951 when a green locust tree, thought to be causing enteritis, was ordered to be cut down. Total population size is legislated, with surplus animals culled by the Keeper upon ultimate approval of the Governor, and sent to zoos. Composition of the population is thus left to the Keeper, who bases his judgement on social behaviour and breeding patterns. Health concerns are brought to the attention of an army doctor, and surgery is performed at the Naval Hospital. Rarely, animals that are badly injured or which represent a danger to the human or monkey population are destroyed. The current Keeper, Sergeant ALFRED HOLMES, has had this duty for over a decade, so that policy and procedure have been standardized for the past 15 years.

The data used for this initial study were extracted from that portion of Army records which have consistency in terms of their collection and cover a period of political and social stability for Gibraltar. All data were organized into geneologically oriented units of information, that is the maternal sibship. Each individual within the sibship is characterized by sex, date of birth, place of birth, date of entry, residence, date of loss, cause of loss, and putative ancestry. The data described formed the basis

Table 1. Total demographic loss,* partitioned according to sex as well as age-grades.

	Males			Females			Total	
Age grades	N	%M	%T	N	%F	%T	N	%T
Adults	19	32.76	18.81	16	37.21	15.84	35	34.65
Subadults	12	20.69	11.88	7	16.28	6.93	19	18.81
Juveniles	21	36.21	20.80	10	23.26	9.90	31	30.70
Infant 2	3	5.17	2.97	6	13.95	5.94	9	8.91
Infant 1	3	5.17	2.97	4	9.30	3.96	7	6.93
Total	58	100.00	57.43	43	100.00	42.57	101	100.00

$\chi^2=4, 34$, P is much less than 0, 01. (Note: infant 1 and infant 2 classes are pooled in the χ^2 calculation). *As estimated by combining data on mortality and emigration.

for the reconstruction of the population aggregate (the Queen's Gate and Middle Hill groups) from 1950 to 1970. The age and sex grades used to categorize the Gibraltar macaques follow BURTON's (1972) classification (see Table 1).

RESULTS

POPULATION SIZE

Table 2 numerically depicts the dynamics of the macaque population of Gibraltar at December 31st each year from 1950 to 1970. The census date of December 31st was chosen not only because of its convenience, as army roll calls are kept at 6 month intervals, but because it includes the full birth season and coincides with the decrease in the mating season. The numerical development of the population over the 21 year study period was irregular with periods of growth and decline. Unlike the pattern during the thirties and forties, when it was necessary to import monkeys from North Africa to maintain the "strength" of the primate colony, the pattern under consideration represents a population naturally replacing itself. Population growth was and continues to be restricted by human interference through the removal of those individuals judged to be socially as well as biologically expendable. Growth occurred during the early 1950's and culminated in 1955 when the standing finance company of the Gibraltar Government restricted the number of monkeys to 34. The need for maintenance of a particular size relates to the simple fact of availability of space on a mountainous promontory of land, 3/4 miles wide, 2½ miles long and 7 miles in circumference. Growth of the human population has in an ecological sense driven the animals into refuge areas—space that is undesirable to the more successful competing

Table 2. Demographic characteristics of *Macaca sylvanus* at Gibraltar, based on data extending from December 31st 1950 to 1970.

Parameters	$\bar{X}$	S.D.	C.V.	Min.	Max.	Mode	Median
Population size	33.90	4.06	11.92%	28	45	32 & 33	33
Ratio:							
Males/Females	0.841	0.212	25.21%	0.474	1.143	0.800	0.800
Adult males/Adult females	0.295	0.088	29.83%	0.100	0.500	0.222 & 0.250	0.300
Adult males/Total population size	0.103	0.088	85.44%	0.031	0.156	0.071	0.086
Adult females/Total population size	0.290	0.039	13.45%	0.212	0.367	0.286	0.286

species. In this manner, the nuisance these animals represent, by incursion into dwellings, theft of property, and hygienic problem, as well as outright physical danger, is minimized. Within the next five years, a total of 24 animals were culled from the population. By 1960, the macaque population numbered 28. Growth over the subsequent decade was less pronounced, with periodic fluctuations of decline.

Population Composition

Under British Army policy, the Queen's Gate and Middle Hill groups are modified differentially to meet the requirements of perpetuating the population while ensuring minimal incursion and possible danger to the human population. In addition, to human interference, a number of other mechanisms have been cited as potential modifiers of population composition (see, e.g., Rowell, 1967; Crook, 1972). These include: Random determination of the sex ratio at birth in any limited period, differential rates of sexual maturation in each sex, and age-sex specific differences in mortality and migration patterns. In addition, a factor undoubtedly applying to small populations is random fluctuations arising through the relatively limited number of individuals occupying a particular age-sex grade at any one point in time.

Data on the age and sex composition of the population aggregate is also presented in Table 2. The overall sex ratio for the 21 year study period was 0.841 (or 1 male to 1.89 females), consistent with cercopithecinae generally. The proportion of adult males to adult females (0.295 ± 0.088) is the lowest yet reported for *Macaca*, where estimates range from about 0.500 to 0.950 (see, e.g., Deag & Crook, 1971; Mukherjee & Mukherjee, 1972; Simonds, 1973; Sugiyama, 1971). Of the parameters examined here, the ratio of adult males to all other individuals exhibited the greatest variation over time. The variability exhibited by this parameter is related to the small number of individuals occupying this age grade and the fact that human interference controls the number of males entering adulthood. The age profile of the Gibraltar macaque suggests a demographically young or expanding population, where pre-reproductive individuals typically comprise 60% of the population aggregate. This is further substantiated by the data presented on the reproductive performance of Gibraltar macaques.

Migration

During the period under review no immigration occurred. Emigration took two forms: Removal through human agency and peripheralization through social process. It is consistent with British Army policy that the culling of animals is directed behaviourally at those animals which represent a physical threat (are given to jumping on people, or more apt to bite) or are greater nuisance (are more attracted to hats, jewellery, cameras, etc.) or more inclined to wander into human dwelling areas. Moreover, those monkeys which threaten to seriously affect the others must also be culled. For example, animals that chase mothers with infants, or kill infants, or have a low threshold for fighting and injuring, or even peripheralizing others, are subject to removal. For these reasons, human selection favors more tractable (but not docile) animals, i.e. animals which will readily socialize towards maximum cohesiveness of the group. This means that culling of males at the juvenile and sub-adult grade leaves those who will, for example, permit young and females to feed with them, while they are quick to challenge—but not attack—intrusion from humans (or dogs or birds).

Peripheralization, particularly of juveniles and sub-adults, is a further source of demographic loss occurring through emigration. As they receive less and less positive contact, such animals may eventually not accompany the group in its movements. Lone animals older than 6 months, should have sufficient knowledge of edible foods to survive on their own, barring injury or the unlikely possibility of predation by hawk, eagle, fox, or dog, but documentation on the survivorship of these animals is not secure.

Data on the emigration of those individuals born in and after 1950, partitioned according to sex as well as age-grades, is presented in Table 3. A total of 44 individuals were removed from the population over the 21 year period. Emigration accounted for 43–56% of the total demographic loss recorded for this period. Individuals were subject to removal from the population most frequently during the juvenile period (43.18%) as they represent the greatest potential nuisance. Although there is no statistical difference in the emigration pattern between the sexes, emigration most affected males at the juvenile period. The rationalization for removal of juvenile males is based on the adult requirements for perpetuating the group. Until quite recently, it was assumed that the local groups would not tolerate more than one adult male, with few, historically rare exceptions, most recently at Middle Hill in the late 1960's (and currently at Queen's Gate). The removal of males therefore, was done at an age when their departure would be least significant to the group in terms of role performance. In addition, reducing the number of juvenile males minimizes male disruptiveness at the sub-adult stage as direct observation and the army records indicate that sub-adult males typically wander from the group. Occasionally, they are accompanied by one or more sub-adult or adult females. Wandering of sub-adult males seems unaffected by age or respect of the head male. In the measure that such movements are disruptive to the group and infringe on human domain, at least one of the sub-adult males is removed. Given the decree on population size, and the fecundity and longevity of females, culling occurred slightly more frequently at the adult female period.

MORTALITY

Table 4 presents data on mortality occurring to those born in and after 1950, differentiated on the basis of sex as well as age-grades. Loss through mortality after birth numbered 57 individuals: 31 males (54.55%) and 26 females (45.45%). KOFORD's

Table 3. Emigration of those individuals born in and after 1950, partitioned according to sex as well as age-grades.

	Males			Females			Total	
Age grades	N	%M	%T	N	%F	%T	N	%T
Adults	5	18.52	11.36	7	41.18	15.91	12	27.27
Subadults	9	33.33	20.45	4	23.53	9.09	13	29.55
Juveniles	13	48.15	29.55	6	35.29	13.64	19	43.18
Infants	—	—	—	—	—	—	—	—
Total	27	100.00	61.36	17	100.00	38.64	44	100.00

$\chi^2 = 2.70$, P is less than 0.01.

data (1965) on the rhesus colony of Cayo Santiago suggests a similar trend in the mortality pattern with no significant statistical difference between the sexes. Risk of death was greatest during the adult period (40.35%), moderate during the infant (28.07%) and juvenile (21.06%) periods, and low during the sub-adult period (10.52%). The majority of male deaths occurred during their adult period (45.16%), while female deaths occurred most frequently during their infant (38.46%) and adult (34.62) periods.

Of the 57 deaths recorded, 10 (17.54%) were attributed to natural causes, such a coronary thrombosis and pneumonia; seven (12.28%) to fights; five (8.77%) to human intervention; two (3.51%) to the abandonment of infants by mothers; and 33 (57.90%) to unknown causes. Of this latter category, the majority belong in the class of missing/presumed dead. An animal who has not been seen by the Keeper in Charge for at least three weeks is removed from the records and described as missing/presumed dead. Departures from the group may be attributed to ill health and subsequent death, and in some cases, peripheralization.

Longevity is marked: Adult males frequently reaching 15–17 years and females frequently reaching 13–16. The record age for a female (beyond the study period, however) is 21 years. The present population has one 15-year-old female and one 14-year-old female, both of whom are still breeding. The two males recorded as having died in their 17th year had produced offspring in that year. KOFORD (1965) notes from ALTMANN's data to 1956 that in Cayo Santiago females outlive males. To date this has not generally been the case in Gibraltar.

FERTILITY

During the 1950 to 1970 period, 34 females gave rise to 155 offspring. No precise estimate of male fertility is available, however, the number of adult males during the study period totalled 18. Of these, five, occupied the adulthood grade for three or more years. The number of livebirths varied from year to year, oscillating about a mean of 6.52 and a standard deviation of 2.11. The sex ratio at birth for the Gibraltar macaque over the 21 year study period was 117.5. An examination of the livebirth sex ratio reported for other non-human primates (KOFORD, 1965; VALERIO, 1969; ALTMANN & ALTMANN, 1970; VAN WAGNEN, 1972) revealed a similar tendency with no significant disparity between the sexes at birth. The distribution of births recorded for this period revealed a distinct seasonal aggregation, April to September, consistent with

Table 4. Mortality occurring to those born in and after 1950, partitioned according to sex as well as age-grades.

	Males			Females			Total	
Age grades	N	%M	%T	N	%F	%T	N	%T
Adults	14	45.16	24.56	9	34.62	15.79	23	40.35
Subadults	3	9.68	5.26	3	11.54	5.26	6	10.52
Juvenile	8	25.80	14.04	4	15.38	7.02	12	21.06
Infant 2	3	9.68	5.26	6	23.08	10.53	9	15.79
Infant 1	3	9.68	5.26	4	15.38	7.02	7	12.28
Total	31	100.00	54.38	26	100.00	45.62	57	100.00

$\chi^2 = 3.00$, P is much less than 0.01. (Note: Infant 1 and infant 2 classes are pooled in the χ^2 calculation).

Table 5. Reproductive performance of *Macaca sylvanus.**

Variables	
Number of females who had at least one livebirth	20
Mean number of liveborn per female	3.70
Variance in progeny number	5.17
Standard deviation	2.27
Mean number of reproductive years**	4.23
Mean number of liveborn per reproductive year	0.87
Mean age of 1st livebirth	4.93
Variance in the age of 1st livebirth	1.17
Standard deviation	1.08

*Based on those females who were born in and after 1950 and had at least on livebirth. **Calculated by subtracting the mean age at arrival of first livebirth from either the date of loss, or as in the case of living females, from December 31st, 1970.

the findings of MACROBERTS and MACROBERTS (1966). Of the 146 livebirths observed, 60 (41.10%) occurred in the month of June.

The nine reported stillbirths constituted 6.16% of observed births. KOFORD (1965) reports a stillbirth rate of 2.7% for *Macaca mulatta* of Cayo Santiago, but estimates "the true proportion of stillbirths (at) probably about 4%." Other estimates of the stillbirth frequency for macaca derive from laboratory populations, where estimates range from 10.5% to 14.31%. (VALERIO, 1969; VAN WAGENEN, 1972).

The only twin birth at Gibraltar for the 1950 to 1970 period was stillborn. This constitutes 1.29% of observed births. VAN WAGENEN (1972) reports a similar twinning frequency for a breeding colony of *Macaca mulatta,* however, the three sets of twins survived to adulthood.

Table 5 presents data on the reproductive performance of those females born in and after 1950 who had at least one livebirth. The data are a mixture of complete and incomplete maternal sibships. Of the 20 females studied, two (57.14%) completed their reproductive period by virtue of death or removal through human agency. Despite the tentative nature of the data, the reproductive parameters listed in Table 5 are suggestive of a rather high fertility rate for the macaque population at Gibraltar. The maternal age at birth of the first liveborn ranged from 3.96 to 7.21 years, with a mean of 4.93 years.

DISCUSSION

Social behaviour operates to permit environmental adaptation according to the relationship: habitat diet group size social organization (etc.), (implicit in, e.g., CROOK & GARTLAN, 1966; EISENBERG, 1972). It is the demographic structure which most readily manifests the interaction between genetic, behavioral and ecological determinants, since group size is the product of resources available and the maintenance of optimal group size is a function of homeostatic mechanisms. Analysis, therefore, of demographic parameters, may provide insight into the fact of naturalistic homeostatic mechanisms. WYNNE-EDWARDS (1965) pioneered the investigation of this phenomenon for wild populations, and recent evidence from human populations suggests a similar phenomenon operating (THOMPSON, 1970; BIRDSELL, 1973). The finding that behaviour varies with the degree of human interference, restriction, provisioning, etc., is expected, but the general assumption has been that non-wild populations, varying from zoo to various forms of free-ranging transplanted (translocated) or captive groups, no longer manifests biological demographic control. There is some evidence however, (BOELKINS & WILSON, 1972) that naturalistic homeostatic mechanisms may also be operating in non-wild populations.

SUMMARY

This paper has described some of the basic demographic features of a non-wild monkey population in which movement is behaviourally restricted, the animals are partially provisioned, and predation is minimized. Analysis of the demographic structure of the Gibraltar macaque over a 21 year period revealed number of significant features:

1. The population aggregate is a demographically young population which is replacing itself naturally.
2. Population size and composition are under human control and differentially modified to meet the requirements of perpetuating the population and at the same time minimizing nuisance to the human population.
3. There was no significant difference between the sexes in the overall mortality or emigration pattern.
4. There was no significant difference between human interference and natural forces with respect to total demographic loss.
5. Longevity for males and females is marked.
6. The stillbirth frequency of 6.16% of observed births is relatively low when compared to those figures obtained for breeding colonies of rhesus macaques.
7. Twinning is a rare event constituting only 1.29% of observed births.
8. Reproductive data on the female macaque, though incomplete, suggests a rather high fertility rate.
9. The mean maternal age at the first livebirth of 4.93 years complements the age grade classification of adult females.

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