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POPULATION CHANGES IN RHESUS MONKEYS: CAYO SANTIAGO, 1960-1964

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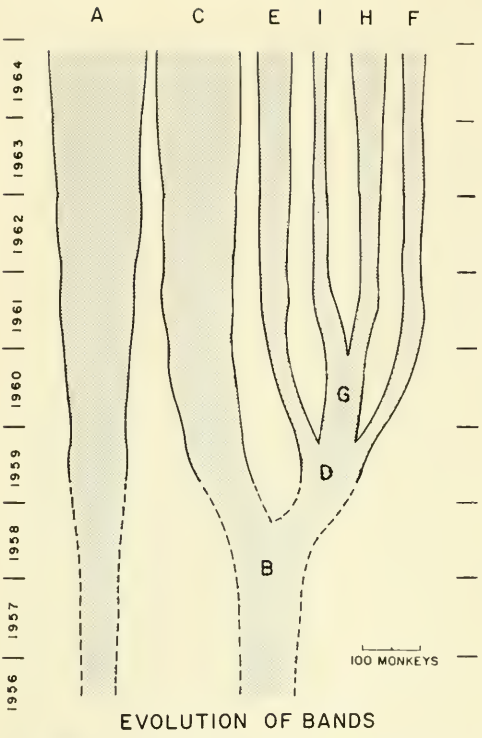
Abstract

A population of introduced rhesus monkeys increased 16% annually during a five year period. Ultimately it consisted of six bands, five of which were formed by subdivision of one of the two original large bands. Divisions occurred during the fall mating season, apparently due to factors other than band size. Of the males at least three years of age about a third changed bands annually. This tendency to shift bore no constant relation to the size or the sex composition of the bands. Nearly all births occurred January to June each year. Mortality rates were greatest in animals less than two years and over six years of age, and in post puberal males. In the adult population the females outnumber males by two to one.

Detailed long term studies of the numerical and social relataions in animal populations are feasible only when the individuals are marked and their movements somewhat restricted. Such a population is the colony of rhesus monkeys *(Macaca mulatta)* on Cayo Santiago, a wooded 40-acre islet situated off the east coast of Puerto Rico. All the animals are descendants of monkeys released here in 1938, and though most of their food has been provided by man, the animals are essentially wild. There were about 350 monkeys in 1940 when Carpenter (1942) studied their sexual behavior. Because of subsequent mortality and occasional heavy removals, there were only about 150 left in 1956 when Altmann (1962) commenced a 2-year study of monkey sociobiology. Largely because he tattooed the majority, I was able to account for every individual by the end of 1959, a year after I commenced work (Koford, 1963); at that time there were 277 monkeys. Since 1959 the population has grown about 16% per year, though this natural increase has been partly offset by the removal of 84 animals, mostly young males.

Band Composition

The current (mid-1964) population comprises 482 monkeys. Four are solitary males and the rest live in six bands of 167, 142, 56, 53, 39, and 21 members. The largest band, *A,* has been an entity since early 1956 or before (Fig. 1). The other five bands, *C, E, F, H,* and *I,* were formed by the subdivision of a single band, *B,* in three stages which occurred about one year apart. Although two bands, *A* and *C,* are now larger than any which split, there have been no divisions in the past 4 years. Contrary to



Fgure 1. Changes in the number and size of bands during the period 1956 to 1964. Capital letters are designations of bands. Horizontal widths indicate numbers of animals. Broken outline indicates early period of incomplete data.

expectation, it was not always the largest band which split. At the time when band *G* divided, in 1960, it was a third smaller than band *A* or *C*. Notably at least two of the divisions occurred in fall, when mating and social tensions were highest.

Reproduction

No monkeys have been added to the colony; numbers have increased only through births. The birth dates of nearly all born from 1960 to 1964 (454) are known within one day. These births occurred from late December to late July, within a span of 210 days. But in any one year a period of 130 days included practically all births (at least 94%). In spite of the increase in numbers born each year from 70 in 1960 to 119 in 1964, there has been no increase in the length of the birth season. In fact, the season with the most births was the shortest, only 126 days (Fig. 2).

From year to year the time of the birth season has varied moderately. For the 5-year period, the range of the initial birth date has been 46 days (December 29 to February 13), and of the median date 34 days (March 2 to April 5), while the final birth date, sometimes more than a month after the others, has ranged 65 days (latest, July 26). The interval from the last birth of one year to the first of the next year has varied from 165 to 224 days. Apparently some of the annual variations in birth season were caused by differences in weather and its influence on the nutritional quality of plan foods, because delay in the start of heavy rains in spring has been accompanied by delay in the onset of mating in summe (Koford, 1965).

In any one year, the distribution of birth was also influenced by the survival of in fants born the previous year, because multi parous females that failed to reproduce, o which lost their infants before the matin season, tended to come into estrus and con ceive earlier than others. In adults the dif ference was probably caused by the fact tha lactation delays the onset of reproductiv cycles (Hartman, 1932). Nevertheless, mor keys conceiving for the first time (normall at 3½ years of age) give birth at about th

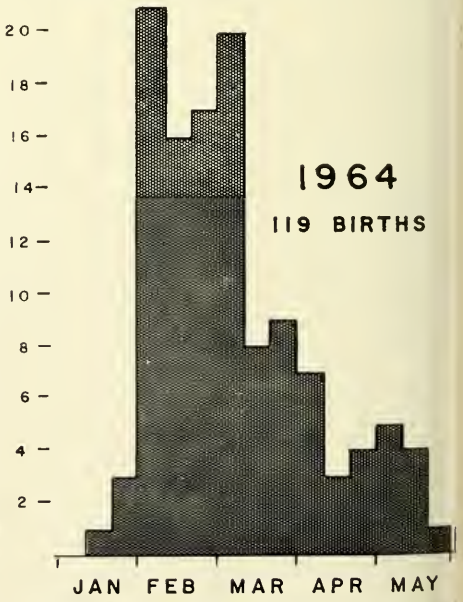


Figure 2. Distribution of all (119) birt dates during 1964. Ordinate is number births per one-third-month period.

same time as lactating adults. For the 5 year period, the peak month of births to non-lactating adults occurred in February, a month earlier than the peak for other females (Fig. 3). Therefore, when reproduction is poor and early infant mortality is high, the following birth season tends to be early. There are exceptions and a few non-lactating adult females breed late (Fig. 4).

The overall birth pattern also differed among the bands (Fig. 4). In 1964, the spread of initial births among the six bands was 28 days, and of the median birth dates, 24 days. That birth season was unusually compact; in other years, the respective spreads have been as much as 67 and 33 days. Even between the two largest bands, in a single year (1960) the initial dates (for 21 and 25 births) differed by 32 days. Considerable variations are to be expected, of course, in view of individual differences in the virility of males, irregularities in the frequency, intensity, and duration of estrus in females, and the complex social interactions within the breeding population during the mating season (Conaway and Koford, 1964).

Population growth is influenced by fertility, which varies from year to year and among bands. Over a period of 5 years the reproductive rate, or ratio of births to the number of mature females, has ranged from 78% (1960) to 86% (1964), with an apparent tendency to increase. For newly mature females, 4 years old, the mean reproductive rate has been the same as for older ones (81% of 89 vs. 82% of 460). On rare occasions (7 in 6 years) a 3-year-old female has given birth. So far, there has been no obvious relation between the size of bands and high reproductive rate; the band with the highest mean rate (93%) was the third largest.

Mortality

Births tended to increase numbers about 25% annually, but deaths partly offset this increment. Considering mortality rate to be the number dying during the year as a percentage of the number alive at the start of the year, the mean mortality rate for the years 1960-1963, excluding infants, was 6.7% (N=1235), with little year to year variation (5.9% of 320 in 1961, to 7.3% of 372 in 1963). Mortality tended to be high in the old and young; for yearlings the mean rate was 9.8% (N=235) and for animals

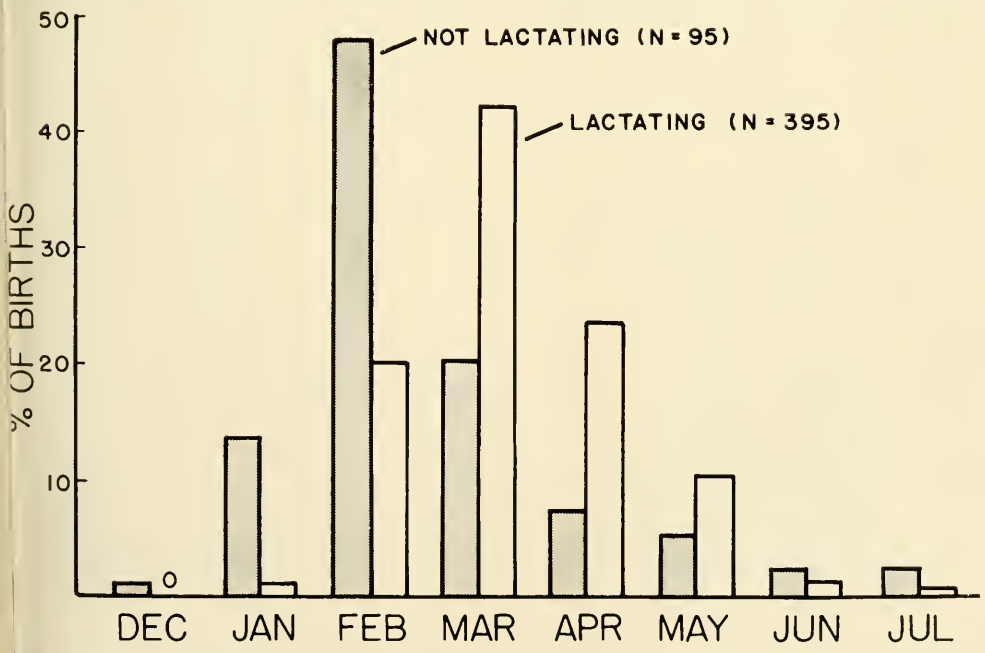


Figure 3. Distribution of births to adults that were not lactating during the mating season (shaded bars, N = 95) and to other females, lactating or primiparous (open bars, N = 359), 1960-1964.

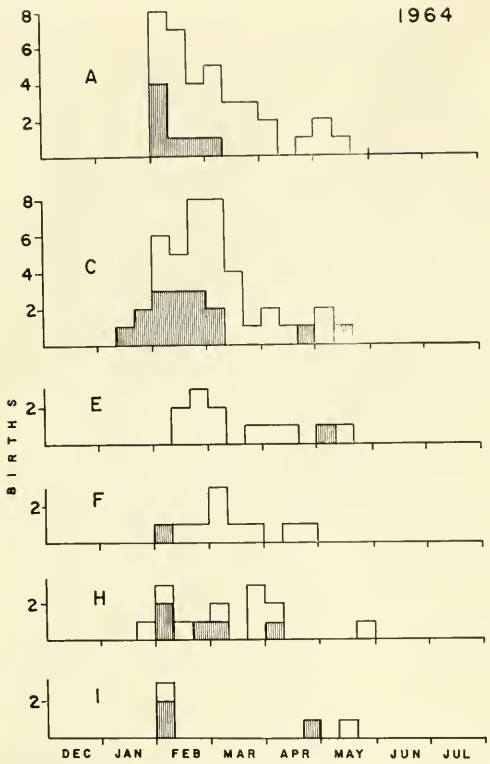


Figure 4. Distribution of birth dates by bands, 1964. Shaded squares indicate births to adults that were not lactating during the preceding mating season. Ordinate as in Fig. 2.

at least 7 years old, 8.4% (N=309), while for those from 2 to 5 years old it was about half as great, only 4.5% (N=575). Over the years the sexes have been born in nearly equal numbers (49% of 518 born were males), and early in life they have died at roughly similar rates. But commencing at four years of age, shortly after puberty males suffered higher mortality than females (Fig. 5). For animals at least 4 years old the comparative rates were 8.8% (N=249) and 5.1% (N=414). This differential mortality largely accounts for the fact that less than half of the mature animals are males. The high mortality of older males is presumably caused by fighting and the debilitating effects of constant strong social tension.

Theoretical Population

The actual composition of the island population is somewhat artificial because some are removed and a few die of handling injuries. Trends in potential numbers and composition can be judged, nevertheless, by using the rates derived for the unaffected animals, as in Fig. 6. This diagram is based on the assumptions that: (1) initially there were 100 monkeys, 55 of them immatures (1 to 3 years old) in a 1:1 sex ratio, and 45 matures; (2) of the matures, 60% (27) were females, of which 85% gave birth a

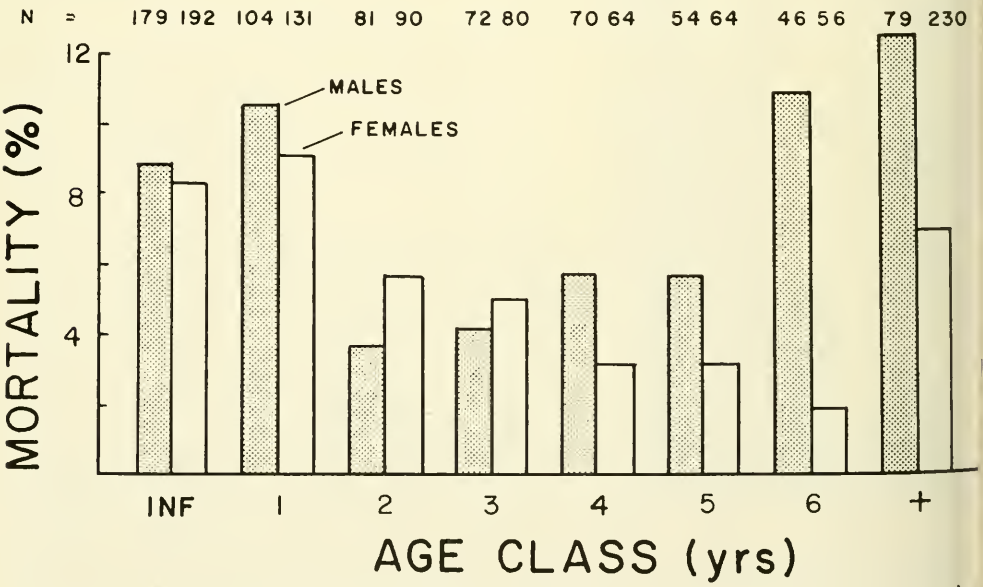


Figure 5. Mean mortality rates by sex and age class, 1960-1963. For infants, the period involved is from birth to the end of the calendar year, not a full year.

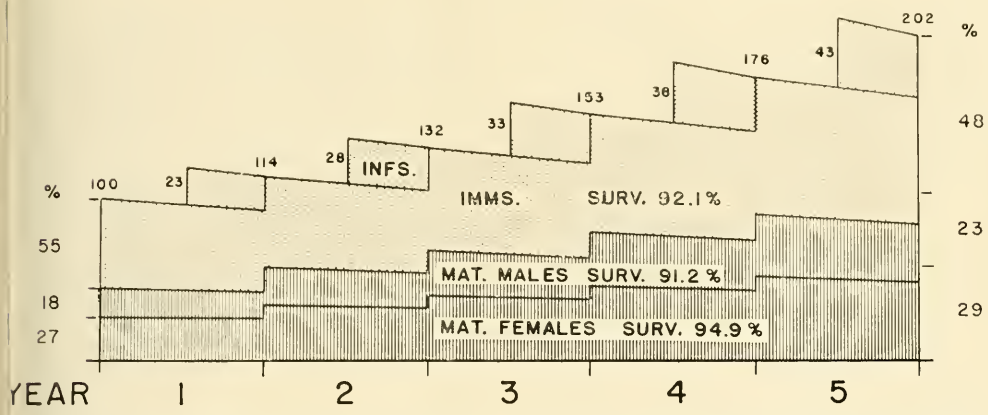


Figure 6. Theoretical growth and composition of a monkey population with reproductive rate of 85% and mean survival rates as computed for the Cayo Santiago population 1960-1963. Numbers above figure indicate population at start of each year and numbers of infants born at midyear.

midyear. The mean survival rates (100% minus mortality rate) derived from data for the period 1960-1963 were 92.1% for infants and immatures pooled, 91.2% for mature males, and 94.9% for mature females. Under these conditions, births would increase numbers about 25% at midyear, but mortality reduces the annual population growth to about 16%. Further, over a period of 5 years the proportion of immatures decreases somewhat, the proportion of females in the mature population decreases slightly, and total numbers approximately double. Assuming that year 1 in Fig. 6 represents 1960, which started with 277 animals, by the end of 1964 there would be 560. This figure is about 85 more than the actual number living on the island, and approximates the number removed.

Interchange Among Bands

Population composition is affected not only by reproduction and mortality, but also by the joining and departure of animals. For the whole colony the only such movements have been artificial removals. Among the bands, however, there has been much interchange of animals. Considering only changes persisting at least one month, during the period 1960-1963 there were 151 interchanges among bands or between band and solitary status, 91% of them by males. Infants and yearlings never, and 2-year-olds rarely (3 instances), changed bands unless their mothers did. But of all males at least 3 years old, a mean of 34% (N=301) departed from their initial band each year (Fig. 7). These shifts involved 78 males, about a fourth of which shifted in more than one year. A similar proportion shifted more than once in a single year, and two animals spent a month or more in four different bands over a period of three or four years. Males changed bands in all months, but most frequently during the mating season (Fig. 8). Of 126 male departures from bands, only 14 (11%) occurred from March to June, where 83 (66%) occurred from

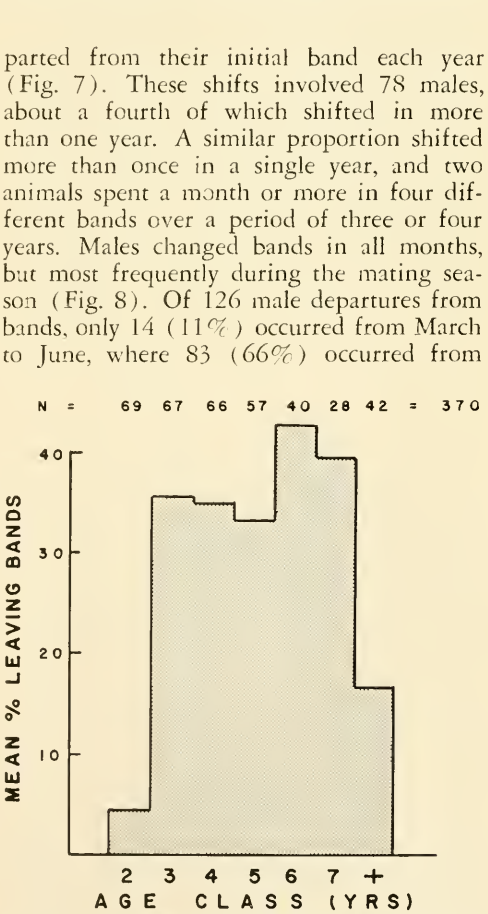


Figure 7. Mean proportion of each male age class departing from bands each year, 1960-1963. N is pooled number of males in each class at the start of the year.

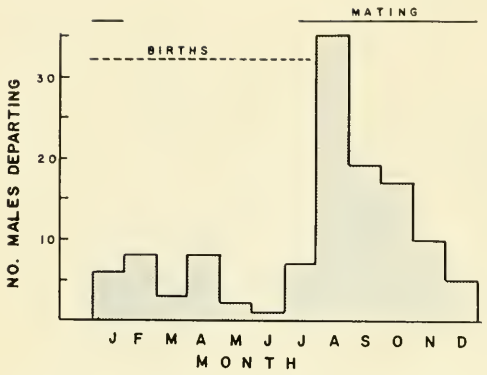


Figure 8. Month of male departures (126) from bands, 1960-1963. Males becoming solitary are included.

August to November. The restlessness of males during the mating season was also indicated by frequent fighting.

The interchange of males among bands was complex, even in single years (Fig. 9). Size, sex ratio, or identity of bands did not affect interchanges; the frequency of departures seemed to depend on social tensions among certain individuals, and in part on the readiness of other bands to accept the

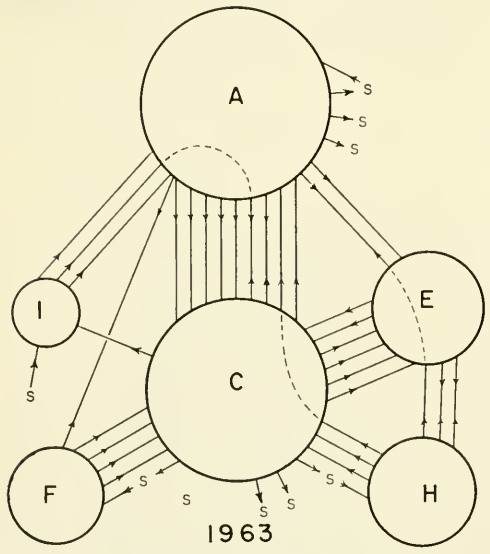


Figure 9. Movements of 49 males among bands, or between band and solitary status (S), during 1963. Only changes persisting at least one month are shown. Areas of circles are proportional to the number of sexually mature animals (at least 3 years old) in each band at midyear. One male remained solitary throughout the year.

aliens. Over the four-year period, the number of males departing from each band constituted from 10% (band *A*, N=263) to 21% (band *H*, N=72) of the sexually mature animals (both sexes, at least 3 years old), except for the smallest band in which the loss was 42% (band *I*, N=46). As to losses versus gains, these were about equa in the four largest bands (*A*, *C*, *E*, and *F*, but losses were about twice gains in the two smallest bands (*H*, *I*). Lastly, in terms of the sexually mature population of the island the proportion leaving bands each year ha varied from 10% to 15%, with no regula increase in spite of a 45% increase in numbers.

Of the male departures from bands, 17% (N=126) were to solitary status, and o the 18 monkeys involved, all save two adult were 4 to 7 years old. Apparently the tend ency of a young male to depart from hi band is inhibited by the presence of hi mother, for of the 2- and 3-year-old male having a mother in the same band only 13% (N=111) departed, whereas for orphans o the same age, 42% (N=24) departed. Fo older males, the presence of the mother ha no apparent influence on the rate of de parture.

Females did not become solitary, eve temporarily, and less than 3% of the female changed bands. Evidently the social force causing females to shift bands are differen from those affecting males, because mo (10 to 14) changes occurred in the birt season, from January to May, rather than i the mating season. These movements in volved eight females, at least 3 years old none of which became a member of mor than two bands. Three females change bands about one month before giving birth and five were accompanied by infants.

Summary

Over a period of five years the number o free-ranging monkeys in a provisioned islan population increased 16% annually, and i mid-1964 there were 482 animals in si bands. Five of these formed by subdivisio of a single large band, whereas a secon large band did not divide. Divisions o curred during the fall mating season an apparently depended on social factors othe than band size. Nearly all births occurre from January to June, and in spite of a 70% increase in numbers born the length of th

birth season did not increase. Among years the initial birth dates varied 46 days and the median dates 34 days. These variations were presumably caused by annual differences in weather and vegetation, and in the proportion of non-lactating parous females, which tended to breed early. Social factors also probably influenced the time of mating, for the spread of birth dates among bands in some single years was as great as for the entire population in different years. The ratio of births to the number of mature females ranged from 78% to 86%, with an apparent tendency to increase.

Excluding infants, mortality reduced numbers at a mean rate of 6.7%. Animals less than 2 years and over 6 years of age suffered the highest mortality. Commencing about puberty, females survived better than males, so that in the adult population females outnumber males more than two to one. Of the monkeys at least three years old, each year about a third of the males changed bands, principally in the mating season. This tendency to shift bore no constant relation to either the size nor the sex composition of the band, but among immatures orphans shifted more readily than other males.

These data suggest that under natural conditions it is chiefly the adolescent and adult males which tend to disperse and distribute genetic material among all bands in a region. Verification of the theoretical implications of these and other characteristics of the island colony will require similar information for wild populations of rhesus and other primates.

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