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A Demographic Model of Colonization by a Population of St. Kitts Vervets

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Abstract. Two sets of censuses by enumeration (1971, 1981) of an isolated population of vervet monkeys on the island of St. Kitts were used to construct a model of the population history of the group. From a colonizing population, the best-fit model predicts a period of rapid expansion with high birth rates, then continued growth with slowly declining natality to the present population level. Several possible 'futures' for the population are projected.

Introduction

West African vervet monkeys *(Cercopithecus aethiops)* were brought to the Caribbean island of St. Kitts in the late 16th century. By the early 1700's they were widespread, and by the time systematic attempts at censusing were started in the 1960's [Sade and Hildrech, 1965; Poirier, 1972; McGuire, 1974], their numbers were estimated at 1,500–30,000 monkeys on the 176 km^2 volcanic island. There has been much speculation on the state of the vervet populations on St. Kitts and the other Caribbean islands of Nevis and Barbados where they also are well established. In spite of development pressures, and constant hunting and trapping, judgements range from the belief that the populations are generally stable, to the hypothesis that these island colonizers may be subject to 'boom and bust' cycles [Denham, 1982]. In St. Kitts during the study period from 1981 to 1982, local hunters and trappers varied in their opinions as to whether the numbers were steady or increasing. None believed them to be declining.

Enumeration data on a population of vervets living in an easily delimited area on the south end of the island were published for the years 1971–1972 [McGuire, 1974], and the area has remained largely unchanged in terms of vegetation, land use activity and human disturbance, since then. The present study included census by enumeration of the same population after a 10-year interval (1981–1982) and thus gives data directly comparable to the earlier published figures. In addition, the 1971–1972 figures of population composition by age/sex class were used to generate models of population growth by varying birth and mortality rates, and then comparing the predictions of these models to the census figures obtained in 1981–1982. The derivation of the 1971 population from a colonizing group of monkeys was examined in relation to known climatic and land use information from St. Kitts. In this way a simulated history of the study population was constructed and several future projections were made.

Methods

Census by Enumeration: 1971–1972

Data used in the model were published by McGuire [1974]. Some categories had proved problematic in the field and would have been difficult to model. To simplify, we lumped I_1 and I_2 into a single year cohort (infants), and J_1 and J_2 into a single year cohort (juveniles). Thus, our age classification became infants: 0–12 months; juveniles: 13–24 months; subadults: 25–36 months; and adults, 36+ months. These categories proved to be operational in the field, and with captive groups, when the authors compared age/sex classifications. However, although these may be satisfactory 'field' categories, they are not satisfactory measures of reproductive maturity. Adjustments were made when modelling the population to take account of this, and they are explained below. Observation also confirmed the limits of the regional population and the similarity of the groups' ranges after 10 years. Sir Timothy Hill is bounded on two sides by the sea, separated from the next hill by a narrow marshy area and hemmed in on the remaining side by a large real estate development. It has a total area of 0.93 km^2.

Census by Enumeration: 1981–1982

During the period October 1981 to January 1982 the range and movement of the groups in the study population were plotted and counts by age/sex were made whenever possible. By January 1982, stable age/sex class counts were obtained for all 4 groups. It was assumed at that point, that enumeration was complete. From then until May 1982, observation and counts were continued to detect mortality (especially in the infant group), as well as natality, emigration, immigration and predation.

Land Use: 1945–1970, 1971–1981

Information about land use and human activities was obtained from interviews with local farmers, workers, fisherman and other people, including scientists, who had worked in the area during the period under study. Information was collected about major land use changes since the first census in 1971 and during the 25 years prior to the first census. Climatic data were obtained from the records of the National Agriculture Corporation on neighboring sugarcane estates. Some trapping records were supplied by a commercial trapping organization on the island, and individual trappers were interviewed.

The Model

Using the age/sex class population figures from 1971 to 1972, population growth under a variety of natality and mortality schedules was projected up to 1981. The combination of natality and mortality which gave age/sex class and total population membership closest to the observed figures in 1981 was accepted as the best-fit model. All models made the following assumptions.

(1) Age/sex classes up to that of adult are of 1-year intervals; i.e. infant 0–1 years, juvenile 1–2 years, subadult 2–3 years and adult 3+. Studies in captive groups show that vervet females may conceive before 36 months, and generally do so before 48 months [Bramblett et al., 1975]. Studies of captive St. Kitts vervets show that not all females give birth in their 4th year, and that abortions and miscarriages can be high among this age group [Fairbanks and McGuire, in preparation], so only half of the 36- to 48-month cohort was added to the adult female group in the calculation of births. Thus 'b' (birthrate) is calculated as the number of infants born in the population per year, divided by the number of existing adult females plus 1/2 of the recruitment cohort of subadult females. Any tendency for this adjustment to overestimate the number of young adult females of reproductive maturity should be balanced by keeping the interbirth interval at 12 months throughout the model. Captive studies have shown that under good conditions, the interbirth interval of St. Kitts vervets can drop below 12 months. However, there is a definite birth peak on St.

Kitts, and b values of greater than 1 were not employed. Vervet males can sire offspring at 36 months, but generally remain behaviorally subadult until much later.

(2) Sex ratio at birth is considered to be 1:1. The models proved sensitive to small changes in all variables, and even small systematic changes in sex ratio and infant mortality produced rapid and inaccurate age/sex memberships in a 10-year run (fig. 1, 2).

(3) Real estate development during the past 20 years has cut off the population on Sir Timothy Hill from all but one neighboring vervet group. Thus, immigration/emigration would appear to be very restricted. No immigration/emigration was observed during the 1971–1972 studies, which included intense observation of the neighboring groups, nor was any seen during the present study in 1981–1982. The large number of adult males in the Sir Timothy Hill population may reflect a lack of emigration 'corridors': adult males often seemed to frequent the 'cutoff' edge of their home range, which had perhaps formerly been their direction of emigration. Finally, one of the Sir Timothy Hill groups occasionally met and mingled with the population on the neighboring hill without any exchange of animals being observed [Chapman, 1983]. As a consequence, for the purpose of the model, the population is considered closed. However, higher mortality rates for subadult and adult males, were required by the best-fit model, and such higher male loss rate could be considered to represent mortality and/or emigration.

(4) In the 1971–1972 count, all females gave birth. In 1981, only 45% of females had infants at the time stable counts were obtained. Sets of curves can be generated corresponding to two underlying patterns that differ in a very important manner. The first is a pattern of a generally constant birthrate, that is, with irregular yearly fluctuations more or less around an 'average' value. In this pattern, the b = 1.0 value of 1971 and the b = 0.45 value of 1981 would represent fluctuations around an average fertility of b = 0.75. In other words there is no trend for birthrate or interbirth interval to change systematically. The second pattern shows changes in average birthrate, either suddenly (e.g. as a population 'crashes'), or slowly, with steadily increasing or decreasing average natality. Examples of all of these patterns have been reported in population studies or predicted from demographic theory. Models were constructed in which birthrate varied, 'regularly' or 'irregularly', with constant and variable mortality rates.

(5) No mortality was recorded during the 1971–1972 study, nor in the 1981–1982 study once stable numbers had been established. Observations during the summer and fall of 1982 indicated some infant mortality of unknown causes, and some mortality from 'unusual' events (taking of an infant for a pet; releasing hunting dogs on the hill by mistake [Chapman, 1983]). It seems likely that there is, and has been, some loss due to trapping or hunting by humans or dogs, but these losses are quite low. Constant and variable mortality rates were entered into the model, as well as 'catastrophic' events (e.g. loss of a complete age/sex class).

Results

Census by Enumeration

McGuire [1974] described 2 groups of vervets living on Sir Timothy Hill in 1970. These groups split in 1971, forming 3 relatively similar sized groups and 1 very small group. The total number of monkeys living on the hill in 1971–72 was 50. In 1981–82 there were still 4 groups on the hill; 3 of relatively similar size and 1 very small. The total population was 181. Although the ranges of the 4 groups were similar to those described by McGuire for 1971–1972, we believe that it would not be justified to treat them as the 'same' groups; so we have chosen for our unit of comparison the regional population of Sir Timothy Hill; that is, the combined numbers in the groups. The first 2 columns of table I show the total population by age/sex class at the 2 census times.

Models of Population Change 1971–1981

The need to 'fit' total population growth to two known distributions by age/sex categories proved very sensitive to minor changes in natality and mortality rates. All models which were structured to include considerable variation in natality or mortality

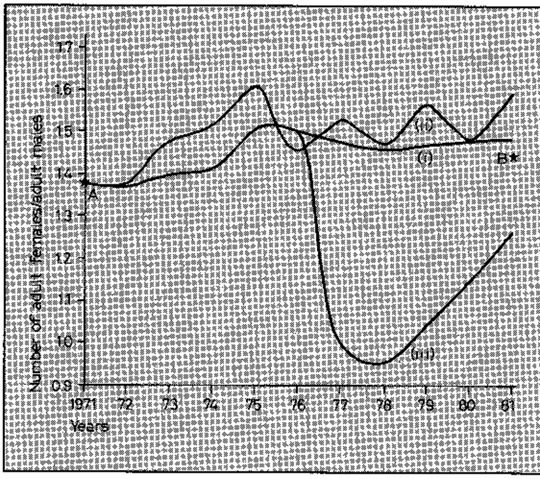

Fig. 1. Models showing relation of birth ratio to adult sex ratio. *A = Adult sex ratio, 1971 census; *B = adult sex ratio, 1981 census; (i) constant birth ratio 1:1 (from best-fit model); (ii) alternating birth ratio 1:1.5 (60%, 40%); (iii) 1 year (1973) of 0:1 birthrate (all males).

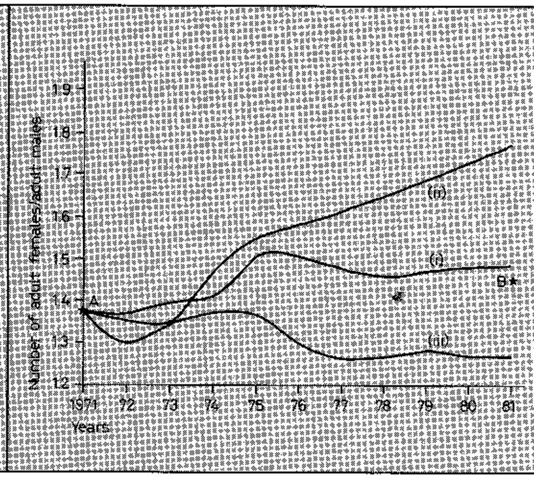

Fig. 2. Models showing relation of infant mortality to adult sex ratio. *A = Adult sex ratio, 1971 census; *B = adult sex ratio, 1981 census; (i) equal infant and juvenile mortality (from best-fit model); (ii) male infant and juvenile mortality = 15%, female infant and juvenile mortality = 5%; (iii) male infant and juvenile mortality = 5%, female infant and juvenile mortality = 15%.

during the 10 years were very inaccurate in predicting the age/sex class distribution and population total in 1982. The model which produced the 'best-fit' (within 10% for all but 1 age/sex class category) was very conservative, with natality dropping steadily and gradually from b = 1.00 in 1971 to b = 0.50 in 1981, and with mortality remaining low and constant for each age/sex class (adult female 5%, subadult females, juveniles, infants, 10% subadult and adult males 15%).

Of the models based upon the other pattern, that is, on a pattern of overall constant birthrate with year-to-year fluctuations (e.g. considering the 1971 values, b = 1.0, and the 1981 value, b = 0.45, to be fluctuations around a long-term mean b = 0.75), none produced a fit approaching that of the best-fit declining natality model described in the preceding paragraph. Using b = 0.75 as a steady birthrate for 10 years did predict a good fit for the total population as would be expected, but 2 of the 6 age/sex classes were inaccurately predicted by more than 20%. Models with birthrates fluctuating around a mean of 0.75 (e.g., 0.5 one year and 1.0 the following year) produced even more inaccurate age/sex class predictions as well as poor total population predictions. Table I (column 3) shows the predictions of the best-fit model compared to the enumeration figures from 1981.

Projections from the Model

(1) Future Growth: If the model is allowed to run with the 'best-fit' specifications, the population total begins to stabilize when natality reaches approximately 0.20 per annum.

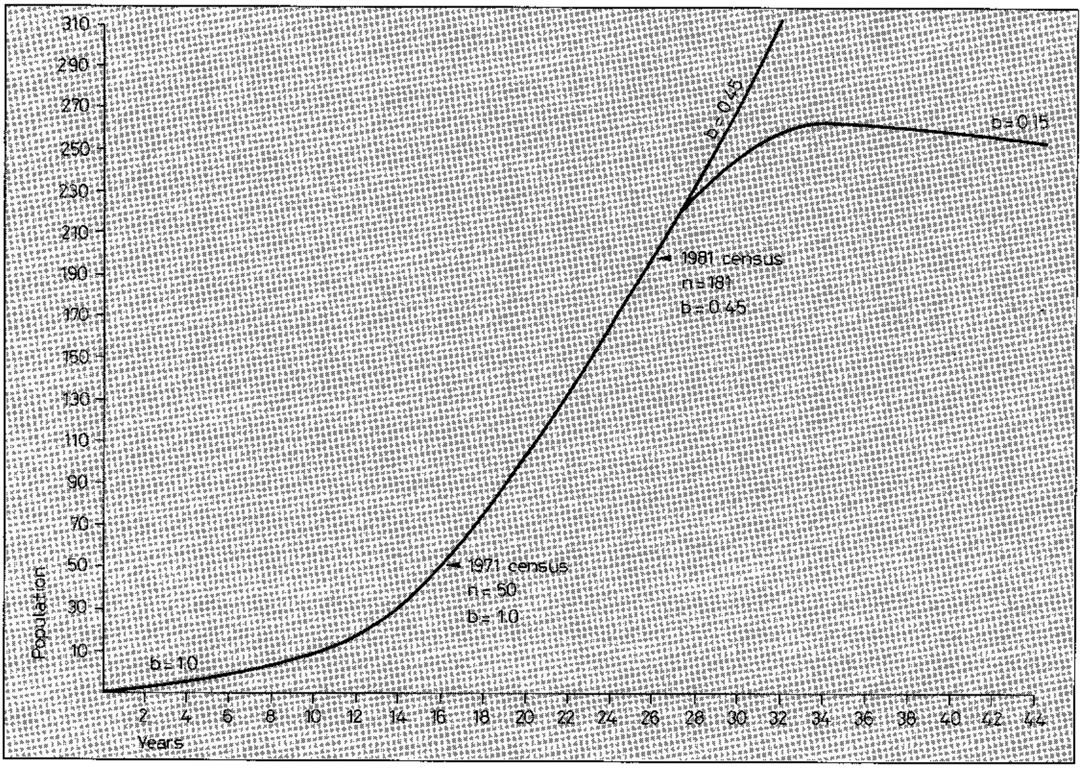

Fig. 3. Model of the population growth of vervet monkeys on Sir Timothy Hill, St. Kitts.

Table I. Census by enumeration, and model population estimates for the Sir Timothy Hill vervet monkeys

Age/sex	Census 1971–72 b = 1.0	Census 1981–82 b = 0.45	Best-fit model projected 1981	Projected stable population b = 0.15 1990	Projected doubling b = 0.45 1988
Adult female	11	59	63.7	121.5	126
Subadult female	5	11	11.95	8.8	20
Adult male	8	41	39.29	61.7	87
Subadult male	3	12	11.95	8.8	20
Juvenile	12	31	27.99	15.3	50
Infant	11	27	29.33	17.5	60
Total	50	181	184.21	233.6	363

Natality: b = 1.00 in 1971, b = 0.45 in 1952. Best-fit model reduces natality by 5% per annum.

Mortality: infant, juvenile, subadult female = 10% (all models) adult female = 5%; subadult male = 15%; adult male = 15%.

The age/sex class structure has become very different, representing an 'old' population. Table I (column 4) shows the population and age/sex class distribution of a stable population predicted in 1992 by the model. At this point the population declines very slowly because of the higher mortality rate fixed for subadult and adult males in the model. In contrast, if natality remains at the 1981 rate of 0.45, growth remains exponential, with the population doubling in 6 years (column 5).

(2) Reconstructing Early Population Growth: The troop fissions and common sleeping areas described by McGuire for 1970–1971, the high rate of natality and the age/sex class distribution suggest a young and rapidly growing population at that time. Assuming an original colonizing population of 1 adult male and 1 adult female vervet, the best-fit model was used to project population growth to the point at which a total population size and age/sex distribution similar to that recorded in 1971 was obtained. The only change made to the model was to keep the natality level high (b = 1.00) on the assumption that a colonizing population would maintain a high reproductive rate. The model predicted that within 18 years the original 2 vervets would produce a population very close in numbers and age/sex class distribution to that observed in 1971 (within 10% for all but one age/sex class). Table I (columns 6–9) shows the projected population history of the Sir Timothy Hill population from a colonizing pair in 1953 to a population total and composition comparable to that recorded in 1971. When combined, the best-fit estimates from the model produce the population curve shown in figure 3.

Predicted growth from colonizing populations (b = 1.0)				
year 1 1953	year 5 1960	year 10 1965	year 18 1971	
1	1.49	3.67	12.01	(11)
	0.37	1.03	4.72	(5)
1	1.24	2.80	8.91	(8)
	0.37	1.03	3.5	(3)
	1.10	2.80	8.22	(12)
1	1.50	3.70	12.01	(11)
3	6.07	15.03	49.37	(50)

Discussion

The significant increase in total population between 1971 and 1981, together with the apparent decrease during that period in natality, and the apparent good fit with a model postulating a colonizing pair of vervets around 1953, all suggest that continuous occupation of the Sir Timothy Hill area is fairly recent. This suggestion is supported by records showing that until the period between 1945 and 1950, the hill and the neighboring ones were regularly burnt to improve pasturage. Although monkeys were known to be in the area at that time, the regular seasonal burning would have made the continuous occupation of any hill impossible. If permanent colonization of Sir Timothy Hill did begin about 1950, then we postulate a 20-

year period of rapid population growth, with the original group perhaps fissioning just prior to McGuire's original study. This might explain the common sleeping site of the groups he reported upon, and the subsequent fission he observed, resulting in the 4 groups which still appeared to be occupying much the same ranges during our study in 1981–1982. While the ranges of the groups have stayed quite stable, the numbers have more than tripled, going from 50 in 1971 to 181 in 1981. However, the natality rate appears to be declining (from 1.0 in 1972 to 0.45 in 1981), and if it continues to do so would result in a stable population in another 10 years. There are no indications that carrying capacity is being reached; the monkeys are in good physical condition [c.f. Galat and Galat-Luong, 1977], show no food or water stress and little territorial defence [Chapman, 1983; Chapman and Fedigan, in press]. There are, as yet, no signs of this population being resource-limited. At the time of the first census in 1971, some 200 goats were grazing the top of Sir Timothy Hill, and remained there until 1978–79. The area grazed by the goats was little used by the monkeys in 1971 [McGuire, 1974], and remains little used now after the departure of the goats [Chapman, 1983]. The present vervet density on Sir Timothy Hill is 169 monkeys/km^2, which is towards the high end of reported vervet populations. The high numbers of adult and subadult males may reflect the growing isolation of Sir Timothy Hill, and their inability to emigrate, suggesting that development has created a bottleneck for the rapidly expanding vervets.

Demographic theory predicts that natural populations in fairly stable environments will tend toward an equilibrium state. Minor perturbations will be quickly absorbed, while major events may have a severe or lasting effect. Field studies on a variety of primate species have reported increasing and decreasing, as well as stable populations [e.g., Dunbar, 1979; Struhsaker, 1976; Dittus, 1980; Jolley et al., 1982a, b].

Colonizing species are thought to show different patterns from noncolonizers (e.g. greater niche breadth [Crowell, 1962]). Although it has been suggested that many or all species can temporarily exhibit a colonizing pattern, some primates, such as macaques and vervets, may show a special ability to move into and rapidly populate newly available areas, as demonstrated by their historically recent and successful occupation of islands in the Caribbean, the Pacific, and the Indian Ocean. It has been postulated in general that island colonizing species will initially show rapid growth, especially where predator pressure is low [Wallace, 1978; Ricklefs and Cox, 1972; MacArthur and Wilson, 1967]. Following an initial growth spurt, two patterns have been suggested: a slow down in population growth caused by a switch from an r-selected reproductive pattern to a k-selected pattern [e.g. Wallace, 1978]; or continued rapid population growth followed by rapid decline [e.g. Krebs, 1978]. The 'best-fit' model of population growth for the Sir Timothy Hill vervets reported in this paper would conform more to the first pattern of slowly declining birthrates, rather than to the 'boom and bust' model.

In order to produce a rapid decline or 'crash' in the Sir Timothy Hill vervet population it would be necessary to envision large increases in mortality, or the cessation or reversal of the decline in natality, resulting in a continued rapid population growth until carrying capacity is exceeded. If birthrate were to remain at the 1981 level of approximately

0.45, the population would double by 1988 (table I, column 5), resulting in the extremely high density of individuals 390/km^2. This is close to the previous highest density reported for vervets of 386/km^2 [Jolly, 1972]. That the best-fit model described here, of declining natality is correct, gains some support from birth data collected for one of the Sir Timothy Hill groups in 1982. In this group, the birth-rate in 1982 was 0.26; lower than the predicted rate for the whole population of 0.40.

If the model is correct, and Sir Timothy Hill was colonized in about 1950, then our results can be said to describe a very rapid expansion or 'boom'. And if fissioning of groups and range expansion has been the method of colonizing the hill which has allowed the continuing high growth rate, the present isolation of the hill may indeed represent a major environmental stress to which the response may be reduced natality, or continued rapid growth to the breaking or 'bust' point. Should the natality level continue to decline, a stable 'old' population will emerge in about another 10 years. It would, however, contain large numbers of 'surplus' adult males and females; the average interbirth interval would be very long, almost 5 years, and productivity would be for replacement only. What the mechanisms, environmental or social, might be that would bring and maintain the Sir Timothy Hill vervets to this theoretical carrying capacity, are not apparent [however, see Rowell, 1969; Dunbar, 1979]. On the other hand, should the population continue to grow at the present rate, doubling in 6 years, one can readily imagine resource limits being rapidly exceeded, with serious dislocations resulting. Unfortunately the rapid human development of the area at this time may make the 'natural' evolution of the Sir Timothy Hill population academic.

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