SHORT COMMUNICATION

Ecological and Demographic Influences on the Pattern of Association in St. Kitts Vervets

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ABSTRACT. A group of St. Kitts vervets (*Cercopithecus aethiops*) were observed to have an association pattern which involved the formation of spatially separated subgroups which were unstable in composition. Five types of subgroups are described which account for 94% of the associations observed. The size of the subgroups changed when the abundance and distribution of the available resources changed. Based on this observation and on an analysis of the diurnal patterning of subgroups, we suggest that the association pattern of the vervets is a response to the distribution of food resources and that it arose under specific demographic conditions.

Key Words: Association patterns; Social organization; Vervets; *Cercopithecus aethiops*.

INTRODUCTION

There have been numerous attempts to identify factors that influence social organization and association patterns in primates. Most notably, the abundance and distribution of food resources (ALTMANN, 1974; WRANGHAM, 1986) and demographic characteristics of populations (ALTMANN & ALTMANN, 1979) have been suggested to determine association patterns. Briefly, the abundance and distribution of resources can influence association patterns when group size influences foraging efficiency. Animals must forage over an area which meets their energetic and nutritional needs. It follows that an increase in group size will increase the area that must be travelled to find adequate food supplies. With an increase in the time spent travelling, some point will be reached at which the energy spent in travel exceeds that obtained from the environment, and a smaller group size will be advantageous. Demographic conditions, such as population density, can set the size and composition of social groups, which in turn affects the behaviour of the animals concerned, thereby influencing association patterns. DUNBAR and DUNBAR (1976) demonstrated this process by documenting demographic and behavioural differences between groups which corresponded to differences in group structure.

In this paper we examine the association pattern of a group of vervet monkeys living on the savanna-like peninsula of St. Kitts, West Indies. The study group had a very fluid pattern of association in which animals were found in unstable subgroups that were spatially dispersed across their home range. This pattern is interpreted in terms of an ecological model which examines responses to the abundance and distribution of food resources, and the demorgraphic history of the group during the previous ten years.

METHODS

This research was conducted from April to December of 1982 on a group of 50 vervet monkeys (*Cercopithecus aethiops*) living on the savanna-like peninsula of St. Kitts. The majority of the group's home range was on the slope of a hill which supported a fire-affected plant community dominated by clumps of *Acacia farnesiana* scattered throughout grass covered slopes. Ravines coming down from the hill contained trees which reached a height of 15 m, such as *Bursera simaruba*, *Tabebuia pallida*, and *Hippomane mancinella*. Throughout the group's home range were stands of *Cordia obliqua*, *Coccolobo uvifera*, and coconut palms (*Cocos nucifera*).

The association pattern of the group was studied by recording the composition of subgroups every 5 min. Once a subgroup was located, it was followed as long as possible. If the group was lost, a search was made until another subgroup was found, where upon its composition was recorded. An attempt was made to search all habitats in the group's home range so that no bias was introduced by over-sampling accessible habitats. The group's association pattern was observed approximately equally in every hour of the day, so as not to introduce a diurnal bias.

The behaviour of the vervets was recorded using a focal animal sampling regime. If the subject of the focal animal session was lost prior to the end of the 5-min session, the session was terminated and the data discarded. The movement patterns of the subgroups were described by estimating the location of the center of the subgroup every 5 min in relation to a 100 m by 100 m grid established throughout the group's home range.

RESULTS

TYPES OF SUBGROUPS

All group members were rarely seen together in a cohesive unit, except at night when they all came into the area of the sleeping trees. Five types of subgroups accounted for 94% of the total 2,591 associations seen (Table 1). Eleven percent of the sightings were of solitary animals, the majority (71%) of which were of adult males. However, 18% were of adult females, and 12% were of subadult males. The age and sex distribution of solitary animals differed significantly from that expected if adult and subadult animals had an equal chance of being solitary ($\chi^2 = 363, p < 0.001$). Solitary animals tended to be seen in peripheral areas of the group's home range.

Of the 2,591 subgroups observed, 7.9% were all-male subgroups, and 2.5% were all-female subgroups. As with the solitary animal sightings, all-male subgroups tended to occur on the

Table 1. The frequency of occurrence of different types of subgroups seen in a group of St. Kitts vervets over the entire day and at different times of the day.

Subgroup type	All day	6:00–8:00	9:00–11:00	12:00–14:00	15:00–17:00
Solitary animals	8.7	7.8	7.9	8.5	13.6
All male subgroups	7.9	8.1	7.4	1.6	9.3
All female subgroups	2.5	0.9	2.4	2.4	4.5
Adult males and females	4.2	4.9	4.7	4.8	5.2
Core subgroups	70.5	74.0	73.4	77.6	58.0
Sample size	2591	849	806	376	442

periphery of the group's home range. However, all-female subgroups tended to be seen in the core area (CHAPMAN & FEDIGAN, 1984). Subgroups composed of only adult males and adult females were seen on 109 occasions (4.2%), of these, 65 subgroups contained only one adult male and one adult female.

The majority (70.5%) of the subgroups were considered to be "core" subgroups. Core subgroups normally contained the majority of the adult females, their associated juveniles and infants, most, if not all, of the subadult females, and a variable number of adult and subadult males. Fifty percent of the core subgroups had only one adult male.

THE DISPERSION OF SUBGROUPS

The group's home range was divided into 100 m by 100 m quadrats, thus by comparing the occupational density of the quadrats, an estimate of the dispersion of the group was determined for different time periods. The coefficient of variance (C.V., the ratio of the standard deviation of the number of animals seen in each quadrat divided by the mean for the quadrats, RASMUSSEN, 1980) was used to represent the dispersion of the group. This index is zero if all quadrats have the same number of observations and increases as the use of quadrats becomes more variable.

The vervets were most spatially clumped (C.V. = 3.82) in the late morning, when they were spending the majority of their time resting. Subgroups were most dispersed (C.V. = 1.56) in the late afternoon, when they were foraging and travelling back to the sleeping site. At this time, observations of solitary animals increased, and the number of observations of core subgroups decreased, implying that the larger subgroups had split (Table 1). In the early morning and early afternoon the vervets were clumped (C.V. = 2.68), although they were engaged in different activities (A.M.: principally foraging, P.M.: principally resting).

ASSOCIATION PATTERNS AND ECOLOGICAL CONDITIONS

While there was no quadrat that did not contain food plants, the favoured plant foods often had a clumped distribution. For example, *C. obliqua* trees were found in only 4 out of the 51 quadrats used by the group (C.V. of food plants at this time was 4.38). The fruits of this tree were a favourite food item, comprising 34% of the vervet's feeding time (CHAPMAN, 1985). All types of subgroups were commonly seen in the area containing *C. obliqua* trees, but the core subgroup was most closely associated with them, often staying near one of the stands all day. The use of these trees appeared to involve dominance interactions; males in the core subgroup would displace and chase males of other subgroups that were attempting to enter the groves. The solitary animals or small subgroups which were displaced from the *C. obliqua* tree were often seen in them after the core subgroup had moved on, and they frequently left the sleeping site early and travelled rapidly to the stands of *C. obliqua*, fed there until the core subgroup arrived, where upon, they abandoned the trees.

Vervets responded to changes in the abundance of food resources. *C. obliqua* trees bore fruit in seven out of the eight months of the study. In the month where no *C. obliqua* trees bore fruit, the vervets rapidly altered their diet. They foraged mainly on *Acacia farnesiana* and *Coccolobo uvifera*, but they also used seven new plant species. With the diversification of their diet and the use of *Acacia farnesiana*, which was abundant throughout the group's range (at least one tree was in each 100 m by 100 m quadrat), the vervets were using more dispersed food resources. During this month the distribution of the vervets food resources was more evenly dispersed than in any preceding month (C.V. of food plants during this month was 0.82). At this time the proportion of sightings of core subgroups rose while the proportion of sightings of solitary subgroups and all-male subgroups declined.

In the late morning when the vervets were resting and presumably least affected by the dispersion of food resources, they were the most cohesive. In contrast, in the late afternoon when they were foraging, and presumably more affected by the dispersion of food resources, they were more dispersed than at any other time of the day (Table 1).

DISCUSSION

The vervet monkey study group formed subgroups which frequently changed composition and were widely spatially dispersed. This form of association pattern is a departure from the stable relatively cohesive pattern typically described for vervets (STRUHSAKER, 1967; CHENEY, 1981; HARRISON, 1983). However, some studies have made observations similar to the ones made here. For instance, the vervets of Chobi, studied by GARTLAN and BRAIN (1968) were observed to be spread out over 0.5 km.

We suggest that the association pattern of the vervets described here is a response to the distribution of food resources and that it arose under specific demographic conditions. The vervets used food resources that occurred in small patches. Because of the large group size and the small size of the food patch it was not possible for the whole group to be in the food trees simultaneously. Either the trees were too small for all of the animals to be in the one location at the same time and interact amicably, or there was not enough food for all group members. This resulted in the core subgroup having priority of access to these trees and smaller subgroups being excluded. The importance of the distribution of food resources to association patterns was demonstrated when the distribution of resources naturally varied when the *C. obliqua* did not fruit. This natural experiment demonstrates that when the distribution of food resources changes, association patterns may change.

The demographic history of the group may also have been a factor influencing the adoption of this association pattern. In 1971 and 1972, MCGUIRE (1974) censused the area presently occupied by the study group. Since then there has been a rapid increase (362%) in the vervet population (FEDIGAN et al., 1984). This population growth has resulted in a population density of 96 individuals per km², which is high compared to most other density estimates for vervets (JOLLY, 1972). Thus, we suggest that since the vervet's population density was high and food resources were at times clumped and scarse, it became advantageous to adopt the observed pattern of association.

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