SPACE USE BY VERVET MONKEYS (Cercopithecus aethiops) AND ITS CONSEQUENCES FOR THE GENETIC STRUCTURE OF THE BARBADOS POPULATION

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ABSTRACT

The space use by vervet monkeys (Cercopithecus aethiops) and its consequences for the genetic structure of the population of vervet monkeys in Barbados was investigated. The distribution of vervets in Barbados was not uniform across the island, vervets being more abundant in parishes with high vegetative cover and low human population density. The home range size for 4 troops in Barbados was among the smallest ever reported for vervets. Ranging patterns for 4 troops of vervets in Barbados were shown to be influenced by the maximum daily temperature and the mean daily humidity. Given that vervets in Barbados used a single sleeping site, the daily pattern of space use within a home range was consistent with the predictions of the central place foraging model. The frequency of use of an area decreased with increasing distance from the sleeping site, and the duration of use increased with increasing distance from the sleeping site. An interpopulation comparison of home range size and ranging patterns of vervet populations from Africa and St. Kitts, showed a positive correlation between home range size and group size and a negative correlation between home range size and population density. Furthermore, home range size was significantly smaller for populations of vervets which were not limited by the availability of food at a given site, than for population which were limited, suggesting that food availability influences space use of vervets.

Serum protein electrophoresis and ABO blood typing were used to investigate genetic variation in the Barbados vervet population, and genetic differentiation between groups. The genetic structure of the Barbados population was characterized by relatively high levels of heterozygosity and gene diversity at the group level, and small genetic distances between groups indicating adequate gene flow between groups. The genetic distance between vervet groups, as indicated by either Nei's or Roger's genetic distances, was not correlated with the geographic distance between the groups. This may be because intergroup movement of vervets is restricted to specific "dispersal routes", such as vegetated gullies. If so, the probability of movement between groups may not be a simple function of their proximity. The north-east area of Barbados differs markedly from the rest of the island in geology, soil type, and vegetative composition, and few gullies run continuously from the east to the west of the island. Three of the 6 polymorphic loci investigated showed differences in allele frequency between east and west sub-populations of vervets, indicating some genetic differentiation. However, the genetic distance between the subpopulations was similar to the mean for the island population.

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RÉSUMÉ

L'utilisation de l'éspace par les singes vervet (Cercopithecus aethiops) et ses consequences sur la structure génétique de la population de singes vervet a la Barbade a été éxaminée. La repartition des vervet sur l'île n'était pas uniforme, ceux ci etant plus abondants dans les communes au couvert de végétation élevé et la faible densité de population humaine. Les aires vitales de 4 bandes de vervets étaient parmi les plus petites jamais signalées pour les singes vervets; il a montre que les modalites de depalcement de ces 4 bandes de vervets a la Barbade etaient influencées par la temperature maximale quotidienne et le degre d'humidité moyen journalier. Etant donne que les vervet n'utilisaient qu'un seul dortoir, les tendances quotidiennes d'utilisation de l'espace a l'interieur de l'aire vitale etaient compatible avec les predictions des modeles de retour au gite et de "central place foraging". A mesure que la distance entre le dortoir et une region augmentait durée d'utilisation augmenmtait. Une etude comparative des aires vitales et des tendances d'utilisation de l'espace des populations de l'Afrique et de St. Kitts a montre une correlation positive entre les tailles de l'aire vitale et du groupe ainsi qu'une correlation negative entre la taille de l'aire vitale et la densite de la population. Par ai'leurs, la taille de l'aire vitale etait significativement plus petite chez les populations de vervets qui n'etaient pas limitees par la disponibilite de nourriture dans un site donne par rapport aux populations exposees a un stock limite de nourriture, ceci suggerant une

influence de la disponibilite de nourriture sur l'utilisation de l'espace par les vervets.

L'éléctrophorese des proteins seriques et la determination du groupe sanguin (ABO) ont ete utilisees afin d'examiner la variation genetique a l'interieur de la population des vervets de la Barbade, ainsi que la differenciation génétique entre les groupes. La structure génétique de la population de la Barbade etait caracterisée au niveau du groupe par des taux relativement éléves d'heterozygosité et de diversite des genes, ainsi que par de courtes distances génétiques entre les groupes, ceci indiquant une circulation adequte des genes entre les groupes. La distance génétique entre les groupes de vervets, telle qu'indiquée par les distances génétiques de Nei et Roger n'était pas correlée avec la distance geographique entre les groupes. Cela pourrait etre du au fait que les mouvements entre les groupes sont limites a certaines "voies de dispersion" specifiques, tels que les ravins boises. S'il en est ainsi, la probabilite de mouvement entre les groupes pourrait ne pas etre une simple fonction de leur proximite. Le nord-est de la Barbade differe nettement du reste de l'fle de par sa geologie, son type de sol, et la constitution de sa végétation; de plus peu de ravines traversent l'île d'est en ouest sans interruption. Trois des 6 loci polymorphiques examines montraient des differences de frequences alleliques entre les sous-populations de l'est et celles de l'ouest, signes de differentiation genetique. Cependant, la distance génétique entre les sous-populations etait semblable a la moyenne pour la population de l'île.

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PREFACE

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Statement of contribution to original knowledge:

To the best of my knowledge, the material presented in this thesis is an original contribution to knowledge of the ecological, and genetic characteristics of the vervet monkey (*Cercopithecus aethoiops sabaeus*) in Barbados.

Thesis format:

In accordance with Section 1 of the Thesis Guidelines, this thesis has been prepared as 2 chapters for future publication. Therefore each chapter contains an introduction, methods, results, and discussion. However, to provide cohesion to the thesis, one overall abstract, a general introduction, and one overall reference section are provided.

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1. INTRODUCTION

Barbados is a coralline island of 430 km^2 which was first colonized by the British in 1627. Eighty-seven percent of the island is covered by a thin layer of Pleistocene limestone, while the remaining 13% on the north-east coast is covered by the tertiary sediments found elsewhere under the limestone (Denham 1987). This has resulted in a difference in the soil and vegetative composition of the two geological areas (Watts 1966). By 1665, virtually all of the island's arable land had been cleared for agricultural use (Watts 1966). The mesophytic woodland on the island was cleared mostly for sugarcane and subsistence crops, whereas most of the xerophytic shrub on the island was cleared for pastureland (Watts 1966). Presently, over 50% of the island is used for agriculture, mostly sugarcane, and the human density on the island is among the highest in the world (580/km²; Espenshade and Morrison 1987). A series of gullies on the island provide natural boundaries between areas of agricultural land. The vegetation in these gullies is not cleared, and they therefore act as vegetated corridors connecting the few remaining patches of natural woodland on the island.

Vervet monkeys (*Cercopithecus aethiops sabaeus*) were introduced to Barbados during the 17 th century (Horrocks 1984). The exact origin and number of vervet monkeys brought to the island is poorly documented. However, the most likely scenario is that vervets came to Barbados as pets during the slave trade from sub-Saharan Africa, probably from the West Coast of Africa or the Cape Verdes Islands (Horrocks 1984, Denham 1987). By 1682, the

population of monkeys on the island was large enough to warrart issuing an official bounty for their extermination (Horrocks 1984). In spite of the scarcity of woodland habitat, and in spite of several attempts to reduce the vervet numbers, they remain an agricultural pest on the island. The attempts at population reduction are summarized in C.A.R.D.I. (1982) and Horrocks and Baulu (1988). A long-term study of the behavioural ecology of vervets in Barbados has been underway since 1979 (Horrocks and Hunte 1983a, b, Horrocks 1984, Horrocks 1986, Hunte and Horrocks 1987). These studies have focused primarily on the life history and social behaviour of vervets on the island.

Vervet monkeys (*Cercopithecus aethiops*) are semi-terrestrial, old world monkeys who live in mixed and savannah habitats across sub-Saharan Africa and in addition to Barbados, on the Caribbean islands of St. Kitts and Nevis. Vervets are polygamous and live in either multi-male or single male groups which vary in size from 12-76 animals (Kavanagh 1981, Melnick and Pearl 1987). They have been described as generalized feeders, with leaves and fruit as the main constituents of their diet, and insects being occasionally consumed (Harrison 1983a, Melnick and Pearl 1987).

Although not quantitatively studied in vervets, intra - and interspecific comparisons not surprisingly suggest that the abundance and distribution of food resources influences the distribution and ranging patterns of primates (Melnick and Pearl 1987, Oates 1987). In general, the wider the area over which a group's required food resources are spread, the greater the annual home range size and day range length of the group (Clutton-Brock

and Harvey 1977a, Oates 1987). Conversely, home range sizes tend to be smallest when food is most abundant (Clutton-Brock and Harvey 1977b). This pattern has also been observed in the context of seasonal variation at a given site, home range size being largest at times of the year when food is least abundant (Clutton-Brock and Harvey 1977b).

Several general characteristics of primate species may be the consequence of effects of food availability on home range size. For example, food may be less available for terrestrial primates than aboreal primates, and the former have larger annual home ranges and longer day range lengths. Moreover, primates which are predominantly frugivores have larger home ranges and longer day range lengths than folivores, presumably because fruit is more clumped and sporadically distributed than leaves (Clutton-Brock and Harvey 1977b, Milton and May 1976). The above relationships are complicated by factors such as body weight, group size, population density, competition for food resources, and the abundance and fluctuation of resource types at a given site. For example, interspecific comparisons suggest that home range size in primates has been shown to be positively correlated with individual body weight (Milton and May 1976) and population group weight (i.e. the total weight of a social group of primates) (Clutton-Brock and Harvey 1977a). This suggesting that in primates all things being equal, home range size is positively correlated with group size (Clutton-Brock and Harvey 1977a).

Whether the distribution and abundance of vervets in Barbados is limited primarily by availability of food, or by availability of cover,

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and hence refuge from human predators; and the implications of this for their home range size and ranging patterns relative to vervet populations elsewhere, have not been investigated. These issues are addressed in Section 2 of the thesis through use of capture records to investigate distribution of vervets on the island, radio telemetry to investigate home range size and ranging patterns of 4 troops in Barbados, and intraspecific comparisons with populations outside of Barbados to comment on factors affecting home range size of vervets.

The observation that much of the natural vegetation in Barbados has been cleared and that over 50 % of the island is under cultivation, may have implications, not only for home range size and ranging patterns of vervets, but also for the genetic structure of the vervet population on the island. The degree of genetic differentiation between groups within a population is largely determined by the amount of gene flow (migration) between groups. Restricted gene flow facilitates differentiation. Dispersal in vervet monkeys is limited to males leaving their natal troops at sexual maturity or breeding males transferring between troops (Pusey and Packer 1987). This, along with the patchy distribution of remaining woodland in Barbados, may constrain gene flow between groups of vervets throughout the island. This constraint may be potentially overcome by the vegetated gullies on the island which may act as dispersal corridors facilitating gene flow. Limited gene flow between groups may not only increase the probability of genetic differentiation, but may result in reduced genetic variability and inbreeding depression within groups. Beyond this, genetic variability in the Barbados vervet population as a whole may be low, given the

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probability of a small founding population at colonisation. Denham (1987) suggests that as few as 50 monkeys may have originally colonised the island. Genetic variability and genetic differentiation in the vervet population in Barbados have not previously been investigated. These issues are addressed in Section 3 of the thesis through blood group analyses and electrophoretic analyses of serum proteins. Results of both types of analyses were used to calculate heterozygote frequencies and hence comment on genetic variability of vervets in Barbados. Results of the serum protein analyses were used to calculate fixation indices, genetic distances between groups, and differences in allelic frequencies between groups, and hence comment on genetic differentiation between groups of vervets in Barbados.

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2. SPACE USE BY VERVET MONKEYS

2.1 INTRODUCTION

Within the limits set by suitability of climatic or abiotic conditions, two major factors can be expected to control the distribution and abundance of large, mobile animals. The first is the distribution and abundance of food in their environment, areas of higher food availability supporting larger numbers of animals (Alcock 1984, Brown 1964, Oates 1987). Lack of a correlation between the abundance of animals and abundance of their food is expected if animals are maintained by predator pressure below the carrying capacity set by food availability. A second major factor that may influence the distribution and abundance of animals is therefore the availability of cover for predator protection and the abundance of predators (Cheney 1981). Effects of interspecific competition on the distribution and abundance of animals typically act through altering access to food or cover. Much of the original mesophytic woodland and xerophytic shrub characteristic of Barbados has been cleared for agriculture and pastureland. Over 50 % of the island is currently under cultivation. Much of this area is used for sugarcane, which is consumed by vervets. Other food products include papayas, cassava, cucumbers, peas and bananas, and many of these are preferred food items of vervets (Horrocks 1984). The diet of vervets ensures that they are competitors of humans for food in Barbados. Beyond this, and as an extension of the interspecific competition, humans, occasionally supplemented by trained dogs, are the exclusive predators of vervets in Barbados. Human predation

pressure on vervets is strong and has been actively encouraged by a legislated bounty for over 300 years.

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The first part of the present section uses data from an extensive trapping program to investigate the distribution of vervets in Barbados and comment on whether their abundance at different locations is affected primarily by availability of food, availability of cover, or abundance of humans at the locations.

Primates living in social groups tend to restrict their normal activities of food gathering, mating and caring for their young to particular group-specific home ranges (Oates 1987). Increasing evidence suggests that food availability may not only influence the distribution and abundance of animals, but may also influence their home range size and ranging patterns. The rationale is that when food density is high, animals can find adequate food by moving around a relatively small home range area. With lower food density, animals must move around a larger area to satisfy their food requirements (Brown 1964, McNab 1963, Oates 1987). Home range size of primates may therefore depend upon resource availability. For primates, resources that might be expected to influence ranging patterns include the availability of food and water, the availability of vegetative cover as predator protection, and the availability of sleeping trees (Cheney 1981, Gartlan and Brain 1968, Struhsaker 1967a, 1969, 1973, Wrangham 1981).

Support for the influence of resource availability on ranging patterns of primates has typically come from intraspecific studies of feral populations living in habitats that consistently differ in the amount of food available, or habitats that show strong seasonal variation in resource availability (e.g. Cords 1987, Gartlan and Brain 1968, Struhsaker 1967b, c). These studies have typically verified that populations living in areas of low food availability tend to have larger home range sizes than populations living in areas where food is more abundant (Clutton-Brock and Harvey 1977b, Struhsaker 1967b); and that home range size is largest at those times of the year when food is least available (Clutton-Brock and Harvey 1977b).

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Interspecific comparisons of primates have also been used to comment on factors affecting home range size. These studies have shown a positive correlation between home range size and feeding group weight (or group size at the intraspecific level, assuming a constant species weight) and a negative correlation between population density and feeding group weight (Clutton-Brock and Harvey 1977a). The correlation between home range size and group size can presumably emerge through the media of food availability i.e. at a similar food density, and assuming food to be limiting, larger groups will have to range over a wider area to satisfy food requirements. Alternatively, the correlation may emerge through the availability of other potentially limiting resources such as safe sleeping sites and water, or predation pressure. The negative correlation between population density and feeding group weight is likely the product of differences in food availability for primate populations (Clutton-Brock and Harvey 1977a).

Resource availability may not only influence home range size but may also influence the ranging patterns of primates within their home ranges. Ranging patterns of primates are typically described in terms of the mean day range length, i.e. the average distance a group

moves in its range over a day, or in terms of the location and amount of time spent in different parts of the home range or in terms of the amount of time spent in different parts of the home range. Interspecific studies have shown that variation in day range length within and between populations of primates is dependent on the density of food in the home range (Clutton-Brock and Harvey 1977b). Consistent with the rationale for the effects of food abundance on home range size, day range length appears to be longer in primate groups living in areas of low food density than in areas of high food density (Struhsaker 1967c), and is longer during times of the year when food availability is reduced (Clutton-Brock and Harvey 1977b). Through interspecific comparisons, day range length has been found to be positively correlated with feeding group weight for frugivores (Clutton-Brock and Harvey 1977b), although a similar relationship was not found for folivores. The rationale for frugivores, is that larger groups must move over more area per day in their home ranges than smaller groups, to meet their food requirements. Variation in the location and amount of time spent in a particular area of the home range appears to be influenced by climatic variables, such as temperature and amount of rainfall (Harrison 1983a, Oates 1987), as well as by habitat type (Sigg and Stolba Variation in the amount of time spent in particular areas of 1981). the home range may be influenced by several quite distinctive types of factors. An obvious example is habitat type, as demonstrated by Sigg and Stolba (1981) for hamadryas baboons. Climatic variables, such as temperature and rainfall, may also influence time spent in particular areas (e.g. Harrison 1983a for the green monkey,

Cercopithecus sabaeus, in Senegal). Finally time spent in particular areas of the home range may be influenced by the energetics of foraging in the home range within the constraint of having to return to a fixed sleeping site every night (Anderson 1984). Returning to a fixed sleeping site is common in many primates (Anderson 1984). Two types of models may be relevant to the ranging patterns of animals which return to a fixed sleeping site; namely the central place foraging models (Orians and Pearson 1979, Schoener 1979) and the refuging model (Hamilton and Watt 1970). The essence of these models is an attempt to predict how animals might maximize their net rate of energy intake while foraging, when under the constraint of returning to a central resting or refuging site. For primates that use a single sleeping site, the two types of models make some simple predictions about movement away from the sleeping site, i.e. animals should spend more time per visit in areas which are further from the sleeping site than those which are close. The rationale in the context of central place foraging is that they must compensate for the greater costs of travel to distant sites by feeding longer at that site, once they have arrived (Orians and Pearson 1979). The rationale in the context of the refuging model is that areas farther away from the central site may be less frequently visited, and may therefore contain higher densities of resources. The animals may therefore stay longer in distant areas since more food is available there (Hamilton and Watt 1970). Several studies have found that the foraging behaviour of animals away from central areas is consistent with predictions of central place foraging and refuging models (e.g. Kramer and Nowell 1980, Brooke 1981, Tinbergen 1981, Carlson and

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Moreno 1982 and Kacelnick 1984). Only one study, that by Sigg and Stolba (1981) on hamadryas baboons has attempted to investigate whether patterns of home range use in primates using a fixed sleeping site are consistent with the predictions of the models. They found a weak tendency for the mean time spent in an area to increase with the distance from the sleeping site, as predicted by both models.

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The central place foraging model and refuging model make the same prediction about movement patterns within the home range, but the rationale for the prediction differs between the models. This may make it possible to determine which model more appropriately explains the movement patterns of vervets in Barbados. For example, if the vervets do spend more time per visit in areas farther from the sleeping site, as predicted by both models, but the frequency of visits to distant areas is not lower, the data would be more supportive of the central place foraging model than the refuging model.

The objectives of the second part of this section are to use radio telemetry to describe home range size and ranging patterns of four groups of vervet monkeys in Barbactos, to determine whether movement patterns within the home range are consistent with the predictions of the central place foraging and refuging models and comment on which of these models more appropriately explains the movement patterns, and to use an intraspecific comparison approach based on populations in Barbados, St. Kitts, and Africa to comment on factors affecting home range size of vervet monkeys.

2.2 METHODS

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2.2.1 Distribution of vervets in Barbados

To investigate the distribution of vervets across the island, a trapping program was conducted in conjunction with trappers working for the Barbados Primate Research Center. Monkeys were humanely trapped in large wire-mesh traps baited with bananas. Traps were preferentially placed at sites around the island where complaints of monkey crop damage by local farmers were frequent, and where monkeys have historically been known to be abundant. The location of capture, the number of monkeys caught, and the number of traps used at each trapping site were recorded. Traps were used continuously throughout the period of data collection and were checked twice a day at each trapping site. The trapping effort at each site was supervised as frequently as possible to ensure consistency of trapping between sites. The 82 trapping sites finally used provided good coverage of the entire island (Fig. 1).

From the catch and trap number data collected at the 82 sites an abundance index was calculated for each of the 82 trapping sites. The abundance index was calculated as the sum of all monkeys caught at each capture site over the period April 1987-April 1988, divided by the number of traps at each site. It is subsequently referred to as catch/effort (CPUE) for that site.

Annual rainfall, density of agricultural land, density of vegetative cover and human population density were the environmental parameters quantified to access their possible effects on the Figure 1- Map of Barbados showing the eleven parishes and the 82 trapping sites for vervets.

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distribution of vervets in Barbados. For several reasons, these variables were quantified at the parish level (Fig. 1). In the case of annual rainfall, there was inadequate variation on a local scale to justify individual monitoring at the trapping site level. In the case of agricultural land, vegetative cover and human density, it was difficult to objectively determine what area of land surrounding a trapping site should be considered as having potential impact on that site. The logistics of having to quantitatively determine agricultural land, vegetative cover and human density over some pre-determined area surrounding each trapping site for each of the 82 sites was daunting.

Annual rainfall data for the last 50 years were obtained by parish from the Barbados Meteorological Station, and human population density by parish from the Barbados Office of Statistics. The amount of agricultural land in each parish was obtained from the Barbados Lands and Surveys Office, and the density of agricultural land was calculated by dividing this by parish area. The amount of vegetative cover in each parish was calculated from a series of aerial photographs of the island. This included woodland patches as well as the heavily vegetated gullies that traverse the island. The area of each section of woodland was calculated from the photos using a digitizer and was plotted on a 1:10,000 map of the island. Density of vegetative cover was calculated as vegetative cover in a parish divided by parish area.

2.2.2. Home range size and ranging patterns of vervets

2.2.2.1. Home range size and ranging patterns in Barbados

Four vervet troops from geographically distinct areas of Barbados were chosen to investigate home range size and ranging patterns. The areas were Sailor's Gully, Mt. Brevitor, Bath and St. Simons (Fig. 2). The Sailor's Gully site consisted of a plateau running along a cliff 20 meters high. The terrain was composed of sour grass (Andropogon intermedius) and low shrubs (56 % of total area) crossed by three densely vegetated gullies, approximately 15m deep with trees up to 20 m high (29 % of total area) surrounded by two fields of sugarcane (15 % of total area). Human disturbance was minimal, as only an abandoned windmill and an infrequently used cart road impinged on Two agricultural fields, alternatively planted with the site. sugarcane and eddoes, were included in the troop's range. The gully vegetation was dominated by whitewood (Tabebuia pallida), fiddle wood (Citharexylum spinosum), and bearded fig (Ficus citrifolia). The sleeping site for the troop was several whitewood trees (Tabebuia pallida), located at the northeastern end of the home range.

The Mt. Brevitor site surrounded a plantation house. A portion of a gully was used for refuge and sleeping, but most of the home range was comprised of the woodland and shrubs that bordered the plantation house. Planted fruit trees (primarily banana and mango trees), sugarcane, and whitewood were distributed throughout the home range. The sleeping site was located in a group of whitewood trees in the gully situated in the west corner of the home range.

Figure 2 - Map of Barbados showing the locations of the four study troops used to assess home range size

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BH = Bath MB = Mt. Brevitor SG = Sailor's Gully SS = St. Simons



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The Bath site covered most of the east side of a 100 m high hill. The hill was covered with scattered planted fruit trees (primarily bananas, ackee, and mango trees) and woodlands (primarily whitewood and casurina), and coconut trees were common at the base. Houses were common in the area, with five lying within the home range itself. Human interference was high as the hillside was used to graze sheep, cows, and goats. Refuge and sleeping trees were restricted to scattered fruit trees and one large whitewood tree in the middle of the home range.

The St. Simons site consisted of a dry river bed and a wide gully that branched off the river bed. The site extended to a secondary road where human habitation was high. A banana plantation impinged on the site, along with several small fields with fruit (primarily mango trees) and other food crops. Other vegetation included whitewood and fiddle wood trees. The sleeping site was a group of whitewood trees in the southeastern section of the home range.

To investigate home range size and ranging patterns, a monkey from each troop was caught using a large wire-mesh cage (60 X 60 X 90 cm). At each trapping site, cages were baited before dawn every morning and left untriggered for several weeks to familiarize the monkeys with the traps. Once a monkey was trapped, it was immobilized with an injection of 5 ml/kg of Ketamine hydrochloride. A radio collar, 140g in weight and designed specifically for vervet monkeys, was placed around the neck of the monkey. The animal was released approximately 20 minutes after capture at the exact location of capture. In 3 of the 4 troops (Sailor's Gully, troop size 15; Mt. Brevitor, troop size 16; and Bath, troop size 9), the animal radiocollared was an adult male. Since uni-male troops are typical in Barbados (Horrocks 1986), this animal was probably the dominant or alpha male in the troop. In the fourth troop, (St. Simons, troop size 8), the radio collared animal was a large adult female.

Monkeys were radio-tracked using a Customs Electronic receiver, model CE12, and a Yagi directional antenna. A tracking day involved monitoring the movement of the radio-collared animal from its departure from the sleeping tree area, until its return at dusk. Periodic checks were made at night to ensure that night movement did not occur. The position of the radio-collared monkey was recorded every half hour by triangulating from two fixed stations. Α minimum of ten fixed stations was used at each site to record position, and an effort was made to maximize the angle of triangulation for each fix taken. The location of the monkey at each half hour interval was then plotted on a 1:2500 map of the area using a compass. The error in triangulation was estimated from visual censuses at no greater than three degrees, which amounted to approximately 20 meters in mapping the home range. An average of 154 hours (range 100 - 248 hours) of home range data was collected for each radio-collared animal. Finally, observational data were used to supplement radio telemetry data in determining the home range. The location of other troop members was recorded when sighted and the number of troop members observed travelling with the radiocollared animal was recorded when possible.

Home range size was calculated as the smallest convex polygon that connected the farthest points of the range, and the area was calculated by summing the number of 25 m X 25 m grids used by the troop.

Ranging patterns were investigated for all four troops of vervets in which individuals were radio-collared. However, the number of full day observations of movement patterns was much greater for the troop of vervets at Sailor's Gully. An aerial photograph of the home range of the Sailor's Gully troop is shown in Fig. 3. Seventeen full-day movements were recorded for the Sailor's Gully troop; 4 full-days for the troop at Mt. Brevitor; 3 full-days for the troop at St. Simons; and 4 full-days for the troop at Bath.

The home range for each troop was divided into grids of 25 m X 25 m, this allowed the frequency and duration of use in each grid to be quantified The frequency of use of each grid was scored as the total number of times the monkey entered the grid over the study period. The duration of time spent in each grid was taken as the total amount of time, summed in half hour intervals, that the monkey spent in the grid over the study period. The day range length was the total distance travelled over the day. In generating this, it was assumed that the distance moved within a half hour period was a straight line between consecutive locations. The angle of turning was calculated at each half hour interval, as the angle the radio-collared monkey deviated from its previous course.

The effect of climatic variables on daily activity was investigated only for the troop at Sailor's Gully. On each of the 17 days on which full-day observations were conducted, temperature and percent

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cloud cover at the site were recorded every two hours. Daily rainfall and humidity data were obtained from the Barbados Meterological Station for the Warleigh station, the nearest point of data collection to the study site.

2.2.2.2. Interpopulation differences in home range size and ranging patterns

A review of the literature was conducted to obtain information on home range size, group size, day range length, resource availability, rainfall and population density for populations of vervet monkeys outside of Barbados. The relevant data were obtained for 9 populations in Africa and 3 populations in St. Kitts. If several populations had been studied at a given site, means were taken to obtain home range size, group size and day range length characteristic of that site. Populations were scored as "food-limited" or "not food-limited" from statements in the literature which specifically described the availability of resources to a population.

2.2.3 Data analysis

Normality for all variables was examined. For non-normal distributions, the variables were log transformed (Sokal and Rohlf 1981). Variables which were ratios or percents were arcsine transformed (Sokal and Rohlf 1981). The abundance of vervets in Barbados was examined by testing the abundance (CPUE) of vervets against a Poisson distribution for randomness. An analysis of variance was then used to examine the variance of the CPUE within

Figure 3 - Aerial photograph of the home range of a troop of vervet monkeys at Sailor's Gully, Barbados

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and between parishes. Finally, a multiple regression analysis was used to examine the influence of several environmental parameters on the abundance of vervets around the island of Barbados.

The ranging patterns of vervets on Barbados were examined using linear regression and multiple regression analysis to look at the relationships of the day range length and climatic variables. Predictions from the central place foraging model and the refuging model were tested using simple linear regressions and multiple regressions analyses to examine the relationships of the distance from the sleeping site and the frequency and duration of use of areas in the home range.

Finally, the influence of several factors on the home range of populations of vervets was examined by simple linear regression and multiple regression analyses. Populations were divided into two categories; "food-limited" and "not food-limited" from statements in the literature. An analysis of covariance was used to examine the relationship of range size and several other parameters for "foodlimited" and "not food-limited" populations. Data were tested for homegeneity of slopes prior to considering potential differences in the y-intercepts (Sokal and Rohlf 1981). Lastly, a t-test was used to test the differences in parameters measured for both categories of populations.

2.3 RESULTS

2.3.1 Distribution of vervets in Barbados

A total of 732 monkeys was trapped at the 82 sites around the island from April 1987-April 1988. The index of abundance at each trapping site is shown in Table 1 and the environmental parameters characteristic of each parish in Table 2. The abundance of vervets (CPUE) at trapping sites was significantly clumped (Poisson test, Coefficient of dispersion>1; $X^2=946.7$, p<0.001). Consistent with this, as analysis of variance on CPUE data at trapping sites indicated significant variation in abundance between parishes (ANOVA, F=3.13, p<0.005).

The effects of the environmental variables on vervet abundance at trapping sites were investigated by regression analysis. All trapping sites within a parish were given the values of the environmental variable characteristic of that parish. In simple linear regression analyses, CPUE at trapping sites was positively correlated with density of vegetation (r=0.62, p<0.05), but not with density of agricultural land (r=-0.17, p>0.05), human population density (r=-0.30, p>0.05) or annual rainfall (r=0.11, p>0.05). In a multiple regression analysis used to partial out the interactive effects of the environmental variables, the strength of the positive correlation between CPUE and density of vegetative cover improved (r=0.78, p<0.001). Moreover, CPUE was negatively correlated with human population density (r=-0.45, p<0.05) i.e. controlling for the effects of vegetative cover, monkeys are more scarce where human density is

Table 1 - Number of monkeys caught, number of traps set and the abundance index (CPUE i.e. No. of monkeys/No. of traps) at each of the 82 trapping sites in Barbados.

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PARISH	SITEN	O. MONKEYS	NO. TRA	PS CPUE
		1	2	0.22
ST. JAMES	DI LIMTREE	1	5	0.35
ST. JAMES		2	12	0.10
ST. JAMES		0	5	05
SI, JAMES	SANT LANE	1	2	0.5
ST. JAMES	SIUN HILL		4 01	0.23
ST JAMES	SPRING PLIN	5	21	0.24
SI, JAMES	IAIIIS UDDED CADITON	10	2	2.20
ST IAMES	WESTMODEL AND	5	5	1 2
ST. JAMES	UICUCATE CADDE	NIC 1	2	1.2
ST. MICHAEL		1 CM	2 5	0.5
ST. MICHAEL		2	5	0.4
ST. MICHAEL	WANGIEAD	1	5	0.2
SI. PEIEK	DLACK DESS	1	6	0.17
ST. PEIER		5	5	0.0
ST. PEIER	FRENCH VILLAGE	1 1	12	0.08
ST. PEIER	CURRS	42	0	5.25
ST. PETER	GIBD3		/ E	0.14
SI, PEIER	MAINAKUS	2	5	0.4
ST. PETER	KIJK NOAD VIEW	2	4	0.5
ST. PEIER		2	4	0.5
ST. LUCY	BROMEFIELD	1	2	0.2
ST, LUCY	CAVE HILL	1		0.14
ST. LUCY	CHECKER HALL	2	0	0.33
ST. LUCY	CKAB HILL	6	6	1
ST. LUCY	FUSTICK	U	4	0
ST. LUCY	HALFMOON	1	5	0.2
ST, LUCY	JOSEY HILL	6	6	1
ST. LUCY	NORTH PT.	4	5	0.8
ST. LUCY	ROCK HALL	4	4	1
ST. LUCY	SPRING HALL	11	5	2.2
ST. ANDREW	BAWDENS	20	15	1.33
ST. ANDREW	BELLEPLAINE	14	3	4.66
ST. ANDREW	BOSCOBELLE	13	9	1.44
ST. ANDREW	CANE GARDEN	131	11	11.9
ST. ANDREW	CHERRY TREE	44	10	4.4
ST. ANDREW	ROCK HALL	5	10	0.5
ST. ANDREW	SEDGE POND	2	5	0.4
ST. ANDREW	ST. SIMONS	35	35	1
ST. ANDREW	TRIO PATH	6	10	1.5
ST. ANDREW	TURNERS HALL	5	4	0.5
ST. ANDREW	WHITE HILL	20	4	5
ST. JOSEPH	BATHSHEBA	2	3	0.67
ST. JOSEPH	BLACKMANS	34	4	8.5
ST. JOSEPH	BONWELL	9	5	1.8
ST. JOSEPH	CATTLEWASH	2	2	1
ST. JOSEPH	LARK HOLE	5	10	0.5

ST IOSEDU	EACY HALL	1	5	0.2
ST. JUSCPH	LADI HALL	14	5	25
ST. JUSEPH	IORSE HILL	10	10	5.5
ST JOSEPH	IW DADKO	20	12 5	4
ST. JUSEPH		20	2	1 2 2
ST. JUSEPH	MELLOWS HILL	7	2	1.55
ST. JOSEPH	MI. DARERS	2	L E	1
ST. JUSEPH	PAIRS HILL	10	5	1 42
ST. JOSEFH	ST REDNADDS	10	5	2
ST. JOSEFH	ST ELIZABETU	21	2	297
ST. JUSEFII	DELAID	1	0	5.07
ST. GEORGE		1	4	0.25
ST. ODOROD	TRANCIA DATU	12	11 6	0.09
ST. JOHN		15	5	2.10
ST. JOHN		12	2	0.4
ST. JOIN		15	5	4.33
ST. JURN		44	0	2.2
ST. JUHN	GLENBURNIE	0	4	0
ST. JUHN	NEW CASILE	9	4	2.25
ST. JUHN	SEALE I HALL	1	4	0.25
ST. JUHN	WILSON HILL	I	5	0.33
ST. PHILIP	MARLEI VALE	9	4	2.25
ST. PHILIP	SAM LURDS	2	8	0.25
ST. PHILIP	THICKEITS	4	8	0.5
ST. THOMAS	BARKERS CR.	0	6	0
ST. THOMAS	CHAPMAN VILLAGE	4	5	0.8
ST. THOMAS	DUNSCOMBE	8	7	1.14
ST. THOMAS	FARMERS	14	17	0.82
ST. THOMAS	HILLABY	2	2	1
ST. THOMAS	ROCK HALL	6	6	1
ST. THOMAS	SHOP HILL	1	4	0.25
ST. THOMAS	VAULT RD.	3	6	0.5
CHRIST CHURCH	DOVER	1	5	0.2
CHRIST CHURCH	GRAEME HALL	1	3	0.33
CHRIST CHURCH	KENT	1	6	0.17
CHRIST CHURCH	MAXWELL RD.	2	2	1
CHRIST CHURCH	WELCHES	4	3	1.33

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Table 2 - Annual rainfall (mm), density of vegetative cover (area of vegetation/parish area in km^2), density of agricultural land (area of agricultural land/parish area in km^2), and human population density (no./parish area in km^2) for each of the 11 parishes of Barbados.

Parish	Annual Rainfall	Density of Vegetative Cover	Density of Agricultural Land	Human Density
St. John	145.00	0.037	.850	302
St. Thomas	145.28	0.065	.971	311
St. Joseph	147.82	0.088	.526	277
St. Andrew	144.55	0.082	.606	187
St. George	132.30	0.010	.724	287
St. Philip	114.30	0.004	.754	417
St. James	134.28	0.086	.666	546
St. Peter	162.45	0.079	.823	312
St. Michael	133.37	0.012	.472	2485
St. Lucy	123.85	0.020	.649	257
Christ Church	118.05	0.006	.547	705

highest. CPUE was not correlated with the density of agricultural land (r=-0.14, p>0.05) or with annual rainfall (r=0.13, p>0.05).

2.3.2 Home range size and ranging patterns of vervets

2.3.2.1 Home range size in Barbados

The home range sizes for 4 troops of vervet monkeys in Barbados are shown in Table 3. The average home range size for the four troops was 6.4 ha. (range 3.6-9.5 ha.). This is substantially below the mean home range size of 50.5 ha. that can be calculated for the species from the literature, but is similar to the mean home range size reported by McGuire (1974) for vervets in St. Kitts (6.0 ha.) (Table 4).

2.3.2.2 Ranging patterns in Barbados

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2.3.2.2.1 Variation in movements within days

Movement patterns of vervets at Sailor's Gully varied over the 17 full observation days within the two month study period. Typically, the troop left the sleeping site at dawn (6:30-7:15, mean 7:00), and moved away from their sleeping site. On average, the troop returned to their sleeping site at 18:00 (range 17:30-18:45). When the troop moved, the course taken in the following half hour interval differed from the previous course by an angle greater than Table 3 - Home range size and troop size for four troops of vervet monkeys in Barbados

Location	Home range size (ha)	Troop size
Bath	3.6	9
Mt. Brevitor	4.5	16
Sailor's Gully	9.5	15
St. Simons	8.1	8

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Table 4 - monkeys	Home (Cercop	range size, <i>ithecus ae</i> MEAN	troop s ethiops)	ize, day in diffe	range rent loc AY RANGE	length cations ANNUAL	and pop	ulation	density of vervet
CTUDY					LENGIH	HAINFALL	DENSITY		
GALAT & GALAT-LOUNG (1976)	2	138.0		33	<u> </u>	(//////.)	23.6	MIXED	SENEGAL
. ,	_								
KAVANAGH (1981)	1	13.5	LIMITED	15		3580	112.6	MIXED	CAMERCON
KAVANAGH (1981)	1	102.5	LIMITED	18	2267	1450	18.0	MIXED	CAMEROON
CHENEY									
(1981)	6	28.0	LIMITED	20		1040	103.0	SAVANNA	KENYA
STRUHSAKER (1967c)	4	41.8	LIMITED	24	1400	1040	104.0	SAVANNA	H KENYA
HARRISON (1983a)	2	178.0	LIMITED	26	1515		14.3	MIXED	SENEGAL
HALL & GARTL/ (1964)	AN 2	15.0	LIMITED	12	500		88.8	SAVANNAH	l Lolui-Island
CHAPMAN & FEDIGAN (1984)) 3	32.0	NOT LIMITE	D 56	2400	1396	236.2	SAVANNAH	I ST. KITTS
McGUIRE(1974)	4	19.0	NOT LIMITE	D 21		1396	135.0	SAVANNAH	ST. KITTS
KAVANAGH (1981)	1	56.5	NOT LIMITE	D 76	939	650	149.0	SAVANNAH	
RICHARDSON (This Study)	4	6.4	NOT LIMITE	D 12	1530	1364	213.0	MIXED	BARBADOS
DUNBAR(1974)	1	20.0	NOT LIMITE	D 12	550	2390	60.0	MIXED	SENEGAL
McGUIRE(1974)	4	6.0	NOT LIMITE	D 13		1396	255.0	MIXED	ST. KITTS

5° on 83% of the occasions. On 50 % of the occasions, the angle of turning from one half hour period to the next was greater than 45° . The mean angle of turning during a day's travel was 67° (range 0 - 180°).

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The distance moved by the Sailor's Gully troop during a half hour interval varied, with the mean distance being 54 m (range 0 - 277 m). When periods with no movement were excluded, the mean distance moved per half hour interval was 78 m (Fig. 4). The number of full-day observations of the Bath, Mt. Brevitor and St. Simon's troops were combined to give a total of 11 fullday observations. As for the Sailor's Gully troop, the distance moved by the 3 troops during a half hour interval varied, with the mean distance being 49 m (range 0-230). When periods with no movement were excluded, the mean distance moved by the 3 troops per half hour was 72.1 m (Fig. 5). This did not differ significantly from the mean of 78 m travelled per half hour by the Sailor's Gully troop (t-test, t=1.51, p>0.05). This suggests that the rate of movement during a day does not differ significantly between troops.

Movement within the home range at Sailor's Gully was greatest in the early morning and late afternoon (Fig. 6), and this movement was usually associated with observed foraging behaviour. A similar pattern of diurnal variation in movement within the home range was observed for the Bath, Mt. Brevitor and St. Simons troops combined (Fig. 7). This suggests that the pattern of greatest movement being in the early morning and late afternoon may be common to all vervet troops in Barbados. Figure 4 - Frequency histogram of the distance travelled in a half hour interval by the vervet troop at Sailor's Gully, Barbados.

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Figure 5 - Frequency histogram of the distance travelled in a half hour interval by the vervets troops at Bath, Mt. Brevitor and St. Simons.

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Figure 6 - The mean distance moved in a half-hour interval versus the time of day for a troop of vervets at Sailor's Gully.

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Figure 7 - The mean distance moved in a half-hour interval versus the time of day for the vervets troops at Bath, Mt. Brevitor and St. Simons.

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In the Sailor's Gully troop, the two half-hour intervals prior to and following the bi-hourly recording of temperature and cloud cover were used to examine the relationship between climatic variables and mean distance moved during various times of the day. Considering 16 of the 17 observation days (data for June 28 was not available, Table 5), the distance moved during any half-hour interval was not correlated with the percent of cloud cover, but was negatively correlated with bi-hourly temperature (linear regression; r=-0.16, p<0.05). Consequently, in a multiple regression analysis, controlling for the effects of cloud cover the relationship between the distance travelled and the temperature did not greatly improve (multiple regression; r=-0.29, p<0.05). The negative correlation with temperature is not surprising, given the observed tendency of the troop to be less active in the early afternoon (see Fig. 6).

2.3.2.2.2 Variation in movement between days

On average the troop at Sailor's Gully travelled 1.53 km (range 0.83 - 1.57 km) each day. Travel paths usually had an eliptical shape with an average maximum distance from the sleeping site of 0.30 km (range 0.13 - 0.40 km). The location of movement in the home range varied daily, such that most areas of the home range were visited over approximately a week. This daily variation in location is illustrated in Fig. 8, which presents the range use for 4 sequential observation days. The tendency to shift the daily location of movement was consistent with the observation that the troop used most of its home range in a short period of time. From the first day

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TABLE	5 -	Daily	distanc	es travelled	by	a	troop	of	vervets	at	Sailor's	Gully	and	climatic
factors	meas	sured	at the	site.								-		

Observatic Day	on Daily distance travelled (m)	Mean distance travelled in a 1/2 hour (m)	Max distance travelled in a 1/2 hour (m)	Max. temp. (^o C)	Mean temp. (^O C)	Min. temp. (^o C)	Mean percent of cloud cover	Rain (mm)	Humidity (%)
1	900.0	72.2	182.5	31.0	29	27	45.0	0.01	70
2	967.5	87.3	137.5	30.5	28	26.5	66.6	0	74
3	855.0	59.2	135.0	28.5	27.5	26	38.75	2.47	97
4	1327.5	101.8	165.0	29.0	28.5	25.5	33.3	0.02	73
5	1237.5	74.8	205.0	31.0	29	27	45.5	0.009	76
6	1002.5	71.8	167.5	30.0	28	26	43.3	0.001	84
7	830.0	62.5	122.5	30.0	27.5	25.5	48.3	0.06	75
8	870.0	61.8	215.0	25.0	25	25	00.0	0.02	84
9	1325.0	82.2	152.5	31.0	29	27	62.5	0	71
10	1192.5	84.8	197.5	31.0	28.5	26.5	61.6	0.01	76
11	1125.0	66.5	155.0	31.0	30	26	44.0	0.04	78
12	1185.0	71.5	162.5	31.0	30	27	72.5	0.71	71
13	1395.0	99.8	277.5	28.5	27	26	72.5	0.03	74
14	1567.5	92.2	195.0	27.0	26	25.5	72.5	0	78
15	1435.0	85.5	275.0	29.0	28	26	41.3	0.10	80
16	1232.5	74.5	195.0	30.0	28	26	62.5	0.04	75

*Note data not available for June 28.

Figure 8 - The travel paths of the troop of vervet monkeys at Sailor's Gully, over 4 sequential observation days.

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of observation, the number of new areas (25 m X 25 m grid cells) within the home range increased rapidly up to day 7; by which time the troop had already visited approximately 67 % of its home range (Fig. 9). This then slowly increased to 84 % over the 17 days.

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The day range length was not correlated with any of the climatic variables measured (linear regression; daily maximum temperature: r=-0.042, p>0.5; daily mean temperature: r=-0.046, p > 0.50; daily minimum temperature r=-0.053, p > 0.50; mean cloud cover: r= -0.041, p > 0.5; mean humidity: r = -0.337, p > 0.1; daily rainfall: r = -0.3370.16 p > 0.5; Table 5). In a multiple regression analysis, day range length was still not correlated with any climatic variable, although the climatic variable measured at the site were correlated with each other (Table 6). The mean distance travelled in a half hour interval and the maximum distance travelled in a half hour interval over a day away from the sleeping site were not correlated with any of the climatic variables measured (linear regression; mean distance: maximum daily temperature: r=-0.025, p > 0.5; mean daily temperature: r=-0.038, p > 0.5; minimum daily temperature r=-0.014, p > 0.5; mean daily cloud cover: r = 0.006, p > 0.5; daily rainfall: r=-0.16, p > 0.5; mean humidity r=-0.46, p>0.05; maximum distance: maximum daily temperature: r=-0.35, p > 0. 1; mean daily temperature: r=-0.30, p>0.1; minimum daily temperature: r=-0.11, p>0.5; mean cloud cover: r=0.25, p>0.1; mean humidity: r=-0.06, p>0.10.5; daily rainfall: r=-0.31, p > 0.1). In a multiple regression analysis,

Figure 9 - The percentage of home range used by the troop of vervet monkeys at Sailor's Gully over the 17-day observation period.

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Table 6 - The correlation coefficients (r) between the climatic variables measured at Sailor's Gully for 16 observation days

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	Maximum daily temp. (C ⁰)	Mean daily humidity (%)	Mean daily cloud cover (%)	Mean daily rainfall (mm)
Max. daily temp		-0.47	-0.49*	-0.74**
Mean daily humidity	-0.47	• • •	-0.12	-0.19
Mean daily cloud cove	-0.49* r	-v.12		0.79**
Mean daily rainfall	-0.74**	-0.19	0.79**	

* indicates a probability level of <0.05

** indicates a probability level of <0.001

there was no correlations between mean daily distance and maximum daily distance and the climatic variables measured, although there were correlations between the climatic variables (Table 6).

2.3.2.2.3 Applicability of the refuging and central place foraging models

The refuging model assumes that the frequency of use of a grid will decrease with increasing distance of the grid from the sleeping site, and that grids which are used less often will be used for longer duration. It therefore predicts that the duration of time spent in a grid should increase with increasing distance from the sleeping site. The frequency of use of a grid was negatively correlated with its distance from the sleeping site (linear regression; r=-0.31, p < 0.05), the duration of use of a grid was negatively correlated with its frequency of use (linear regression; r=-0.86, p<0.001), and the duration of time the troop spent in a grid was positively correlated with its distance from the sleeping site (r=0.24, p < 0.05). These relationships are all consistent with the assumptions and predictions of the refuging model and central place foraging model. Interestingly, the duration of use of a grid was still correlated with the distance of the grid from the sleeping site in a multiple regression which controlled for the effect of frequency use on duration of use (r=0.32, p < 0.05), although when distance was controlled for, there was no relationship between the duration of use and the frequency of use of a grid (r=0.21, p>0.05). This suggests that factors other than frequency of use (and hence presumably food availability) may play a role in generating the positive correlation

between distance from the sleeping site and duration of use. These observations are consistent with the central place foraging model which predicts longer use of preferred grids based on the greater cost of travel to such grids, but not with the refuging model which predicts that the frequency of use of areas further away from the sleeping site should be lower than areas closer to the sleeping site. The above analyses were re-done excluding grids in which the monkeys did not stay longer than one 30 minute period, since this may have reflected movement through an area rather than a foraging bout. This exclusion did not change the relationships found between the frequency of use, duration of use, and distance of the grid from the sleeping site. When days in which the mid-day resting site was used were removed from the analyses, the same relationships were again found; and the correlation between duration of use of a grid and its distance from the sleeping site, when the effects of frequency of use was controlled, became stronger (r = 0.40, p < 0.05, n=9).

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Data on ranging patterns from the 3 other troops studied were used to test the predictions of the central place foraging and refuging models. The data from all 3 troops were combined due to small sample size of daily movements recorded from each troop. Before combining the data, the predictions were tested for each individual troop, and in all cases, except the distance from the sleeping site and the frequency of use of a grid at Mt. Brevitor (p=0.102) the correlations were significant. For the combined data, the frequency of use of a grid was negatively correlated to the distance from the sleeping site (r=0.41, p<0.01). The duration of time spent in a grid was positively correlated to the distance from the sleeping site (r=0.33, p<0.01), and the duration of use was negatively correlated with the frequency of use of a grid (r=-0.70, p<0.01). In a multiple regression controlling for the effects of frequency use on duration use, the frequency of use and the distance from the sleeping site were negatively correlated (p<0.01) and the duration of use and the distance from the sleeping site mere negatively correlated (p<0.01) and the duration of use and the distance from the sleeping site were positively correlated (p<0.01). Thus, patterns of movement around a home range in Barbados appears to be consistent between troops.

2.3.2.2.4 Effects of habitat on ranging patterns

For the Sailor's Gully troop, a preference for habitat type in the home range was tested by scoring the number of half hour intervals the troop spent in the wooded gullies, grassland areas, and cultivated fields and comparing the time spent in each habitat type with the amount of each habitat in the home range. Monkeys spent more time in the wooded gully areas than expected ($X^2=12.24$, d.f.=1,p < 0.001), and less time in the cultivated crops areas ($X^2 = 14.63$, d.f.=1, p < 0.001). The amount of time spent in the grassland areas did not deviate from the expected time ($X^2 = 0.26$, d.f.=1, p>0.05). In order to ensure that the frequency of use of an area and the duration of time spent in an area in relation to its distance from the sleeping site was not influenced by the habitat type of a grid, the home range was divided into three equal concentric circles around the sleeping site. The amount of each habitat type in each of the circles was scored and then compared against the expected distribution. There was no difference in the amount of wooded gully between circles $(X^2=0.34,$

d.f.=1, p>0.05), cultivated crop area ($X^2=1.82$, d.f.=1, p>0.05) or grassland ($X^2=0.27$, d.f.=1, p>0.05). This suggests that habitat type did not influence the frequency of use or duration of time spent in a grid with the distance of the grid from the sleeping site.

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For the other three troops combined, monkeys spent more time in the wooded gully areas than expected ($X^2=10.13$, d.f=1,p < 0.001). Although, the amount of time spent in the cultivated crops areas (X^2 =0.78, d.f.=1, p>0.05) and grassland areas did not deviate from the expected time ($X^2 = 0.54$, d.f.=1, p>0.05). There was also no difference in the amount of wooded gully area ($X^2=1.31$, d.f.=1, p>0.05), cultivated crop area ($X^2=0.98$, d.f.=1, p>0.05) and grassland ($X^2=0.46$, d.f.=1, p>0.05) in each of the concentric circles surrounding the sleeping sites, suggesting that habitat type did not influence movement to areas far from the sleeping site.

2.3.2.3 Interpopulation differences in home range and ranging patterns

Interpopulation differences in home range size and ranging patterns were examined by looking at the social and environmental factors which might influence home range size and ranging patterns. Home range size increased with increasing groups size (linear regression; n=13, r=0.557, p<0.05), and decreased with increasing population density (linear regression; n=13, r=-0.81, p<0.001). In a multiple regression controlling for the effects of group size on population density, there was a positive relationship between home range size and group size and a negative relationship between home range size and population density (group size; n=13, p<0.001, population density; n=13, p<0.001).

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There was no relationship between home range size and the day range length or the amount of rainfall at a site (a possible measure of 'habitat productivity') (Table 4).

Populations of vervet monkeys were divided into two classes; populations which were "food-limited" and populations which were "not food-limited" in order to examine the influence of resource availability on home range size. The home range size of the populations which were "food-limited" was significantly larger than the home range size of the populations which were "not food-limited" (t-test; t=2.22, p<0.05). When food availability for populations (i.e. limited or not limited) was factored out in the regression of home range size and group size, no significant differences occurred between the slopes of the regressions (ANCOVA, F=3.55, p>0.05), but there was a significant difference in intercepts (ANCOVA, F=11.09, p<0.05) (Fig. 10). Therefore, for a given home range size, group size was larger for "not food-limited" populations than for "food-limited" populations, although there was no difference in group size for the two types of populations (t-test, t=.81, p>05). There was no difference in elevation for the regression of home range size and population density, when food availability was controlled for (slope ANCOVA, p>0.5, intercept ANCOVA, p>0.5). However, the population density was significantly higher for populations of vervets which were "not food-limited" (t-test; t=2.52, p<0.05) than for populations which were "food limited".

Figure 10 - The relationship of home range size and group size for "food limited" and "not food limited" populations of vervet monkeys from various locations.



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There was no relationship between the day range length, group size or population density, as might be expected if larger groups of animals have to move farther to obtain their daily food requirements. Day range length did not differ between populations which were "food-limited" and populations which were "not foodlimited" (p>0.5).

2.4 DISCUSSION

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Two major factors may influence the distribution and abundance of large, mobile animals; the distribution and abundance of food in an environment, and the abundance of predators and availability of predator refuge. The influence of each of these factors is difficult to evaluate as most populations of large animals are limited by food availability, thus creating an empirical relationship between abundance of animals and abundance of food, in which the influence of predator pressure may be hard to measure.

Vervet monkeys in Barbados are under strong predator pressure by humans, and the only apparent refuges from humans on the island are the densely vegetated gullies which traverse the island, and the small patches of remaining woodland. Cultivated crops, which comprise approximately 70 % of the diet of vervets, are widespread across the island (C.A.R.D.I. 1982) and are predictable throughout the year. Data collected from an extensive trapping program, showed that the distribution of vervets in Barbados appears to be affected primarily by the density of vegetative cover and the abundance of humans in a location, rather than the availability of food, as measured by the density of agricultural land. This suggests that the abundance of vervets in Barbados is not limited by food availability, but rather by the distribution of predator refuge and the density of possible predators in an area. These findings are consistent with Horrocks' (1984) finding that when agricultural land only is considered, the abundance of vervets is correlated with the vegetative cover rather than the total cultivated acreage. Several other populations of vervets have been described as "not food limited" in their environment (Chapman and Fedigan 1984, Dunbar 1974, Kavanagh 1981 and McGuire 1974), although similar relationships between the distribution and abundance of vervets, the amount of vegetative cover and predator density at a location have not been tested for these populations.

Home range size in Barbados is very small compared to populations of vervets from various locations in Africa. The only population which exhibits a similar home range size, is a population of vervets living in a mixed habitat in St. Kitts (McGuire 1974). Both of these populations of vervets live in areas of high food density, thus can presumably find adequate food by moving around a relatively small home range, and are under strong predator pressure, as the same actively encouraged bounty on vervets is also in existence in St. Kitts. Home range size for both populations may be a function of the distribution and abundance of predator refuge, as vegetative cover in St. Kitts and Barbados, is clumped around and in gullies which act as natural boundaries between areas of agricultural land. Home range size may be correlated with the available cover in an area, home range size being small in areas of high density of

cover. From the limited descriptions of home ranges in Barbados, this appears to be the case. The smallest home range (Bath) had the highest density of vegetative cover. Because the vegetative cover in both Barbados and St. Kitts is not continuous due to the clearing of the islands for agricultural use, vervets may have to exist in home ranges comprising small, fragmented pockets of vegetation and this may limit the size of a group in a home range which can avoid being detected by predators and can seek refuge in the available cover. The average group size for both of these populations is relatively low (mean=12.5 for St. Kitts and Barbados, mean= 26 for all vervet populations studied), suggesting that predation pressure may have some influence on the relationship between home range size and group size for populations which are not food limited.

Ranging patterns of vervets in Barbados were examined in detail for the troop of vervets at Sailor's Gully and more generally for three other troops on the island. The climatic changes at Sailor's Gully did not appear to have a strong influence on the ranging patterns of vervets at the site. The distribution of movement throughout the day for troops in Barbados showed two peaks of activity; one in the early part of the morning and one in the later afternoon. These peaks tend to coincide with changes in temperature and thus, suggest that temperature may have a slight influence on ranging patterns. The influence of weather on the ranging patterns of primates has been shown to produce differing results. The presence of rain appears to halt all activity in siamangs, but not influence the activities of leaf monkeys (Raemaekers 1980). Increases in temperature have been shown to either increase activity levels, as in

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gelada baboons living at high altitudes (Oates 1987) or decrease activity levels, as in blue monkeys and colobus monkeys in Uganda (Oates 1987). For vervets living in Senegal, the mean hourly distance travelled by vervets decreased with increasing temperature in hot months, but increased with increasing temperature in cold months (Harrison 1983b). It is possible that the influence of temperature and other climatic factors on the daily movement of vervets at Sailor's Gully may be more pronounced during the extremes of the dry (January - May) and wet (June - December) seasons in Barbados; periods which were not sampled in this study. Daily variation in climatic factors is more marked during the seasonal extremes.

The movement of vervets in their home range at Sailor's Gully appeared to be influenced by the travel pattern of previous days. Vervets visited approximately 70 % of their home range every 7 days, and on most days, the movement included a visit to a boundary area of the range. Given the existence of a single sleeping site, use of the home range for all four troops of vervets in Barbados, was consistent with predictions of the central place foraging (Orians and Pearson 1979) model. The frequency of use of an area decreased with increasing distance from the sleeping site, the duration of use of an area increased with decreasing frequency of use, and the duration of use increased with increasing distance from the sleeping site. This later observation is a prediction of both the refuging and central place foraging models. The refuging model predicts longer use with increasing distance on the basis that distant areas will be used less frequently (an assumption borne out by the present results), and that infrequently used areas will have higher food availability. The

central place foraging model predicts longer use of distant areas on the basis that animals must compensate for the greater cost of travel to a distant area by remaining there longer. This idea was supported by the present results since duration of use of an area increased with increasing distance of the area, even when effects of frequency of The lack of relationship between the duration use were controlled. of use and frequency of use of an area when distance is controlled for, suggests that the refuging model may not be appropriate to describe the ranging patterns of vervets in Barbados, as the frequency of visits to farther areas should be lower to satisfy the assumption of greater resource availability with increasing distance from the sleeping site. An alternative explanation for the relationship between the duration of use, frequency of use and distance from the sleeping site could be the influence of habitat type. Sigg and Stolba (1981) suggested that for hamadryas baboons the weak relationship between the mean time spent in an area and the distance from the sleeping site, was due in part to the preferential use of wooded areas and the higher abundance of wooded areas at the outer edges of the range. Vervets in Barbados both at Sailor's Gully and the three other sites studied, show a preference for wooded gully areas over grassland and cultivated crop areas. The conclusions for vervets in Barbados differ from those for the hamadryas baboons studied by Sigg and Stolba (1981), as there was no difference in the amount of wooded gully area with increasing distance from the sleeping site, thus ruling out the possibility that vervets were spending more time in areas further away from the

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sleeping site because they consisted of greater amount of preferred habitat type.

An interpopulation comparison of home range size, group size and population density showed a positive correlation between home range size and group size and a negative correlation between home range size and population density. Both of these relationships are expected if food availability is limited, as larger groups will have to range over larger areas to satisfy their food requirements. If group size is held constant, than the relationship between home range size and population density is an empirical necessity, as there will be fewer animals per unit area i.e. population densities would have to be lower at larger home range sizes. Only 54 % of the vervet populations examined in this study were limited by food availability, implying that the limitation of food alone cannot explain the relationships of home range size, group size and population density. As suggested earlier, two main factors main influence the distribution and abundance of vervets, food availability and predation pressure. Vervets in most natural habitats are either under natural predation pressure or human predator pressure (Cheney and Wrangham 1987). For a particular habitat and home range size, there is probably an optimal group size for vervets. Below this optimum, the sensitivity of vervets to predators and the ability to escape them maybe inadequate. Above this optimal group size for a given range size, the increased conspicuousness of vervet groups to predators may nullify the positive features of the group (Cheney and Wrangham 1987, Strushaker 1967b). The comparison of home range size and group size for "food limited" and "not food

limited" populations revealed a significant difference in the elevation of the lines describing the relationship. For a given home range size, group size was larger for "not food limited" populations than for "food limited populations". This finding is consistent with the idea that food availability limits the number of animals an area can support. However, home range size should not be related to group size for "not food limited" populations if food availability is the only factor influencing the number of animals which can be supported by an area. Several other resources have been suggested in the literature as having minor influences on the relationship of ranging patterns and group size. For macaques and yellow baboons, safe sleeping sites and water holes replace food as the factor limiting group movement and home range size during the dry season (Altmann and Altmann 1970, DeVore and Hall 1965). To date, no study has suggested that vervets have a difficult time securing safe sleeping sites or finding adequate water. In yellow baboons, home range size increases when male immigration is highest and this is highly correlated with the estrus cycle of females (Rasmussen 1979). For vervets, groups are usually a fixed reproductive unit with male emigrations occurring only at sexual maturity or during breeding transfers. Thus, the most plausible explanation for the relationship of home range size and group size in vervets appears to be a combination of the influences of predation pressure and food availability. Seventy percent of all vervet mortality in Amboseli, Kenya, is estimated to be due to predation. For groups of vervets in Amboseli which appear to be food limited, it has been suggested that predation holds group size below the limit set by the food supply

(Cheney and Wrangham 1987). The findings of this study also suggest that for populations of vervets in Barbados, the amount of available predator refuge and predator presence in an area is more important than the density of food sources. In summary, although predation rates and the influence of predation are difficult to measure in most populations, it appears that for vervets, predation may be as or more important than food supply in regulating or limiting population size for a given area.

3. GENETIC CONSEQUENCES OF SPACE USE OF VERVETS IN BARBADOS

3.1 INTRODUCTION

The degree of genetic differentiation between groups within a population is determined largely by the amount of gene flow (migration) between the groups, which constrains differentiation, and by genetic drift and local selection pressure, which facilited differentiation. Limited gene flow between groups may in turn result in increased homozygosity and inbreeding depression within groups. Migration, on the other hand, tends to reduce genetic differentiation among groups that exchange individuals and their genes. The greater the level of migration, or gene flow, the more closely the genetic diversity of a social group will approach the genetic diversity of a population (Nei 1977).

Studies of the genetic structure of non-human primate populations have produced differing results. In the rhesus macaques of Cayo Santiago (Cheverud et al. 1987, Duggleby 1978), Pakistan rhesus monkeys (Melnick, et al. 1984a), Japanese macaques (Nozawa et al. 1982) and vervet monkeys in Ethiopia (Turner 1981), individual social groups have been found to include over 90 % of the genetic diversity of the local population, suggesting high intergroup migration rates. For Japanese macaques, where dispersal has been documented, migration appears to occur primarily between troops within groups, and groups become more genetically different with increasing geographic distance (Nozawa et al. 1982).

For vervet monkeys, only males migrate between groups (Pusey and Packer 1987). If dispersion of natal males in a vervet population is nearly complete (i.e. all males leave their natal group), then almost all paternally contributed genes in any social group should come from immigrant males. Assuming complete dispersion of natal males, then migration rates should approach 50 % per generation, and the genetic makeup of groups in adjacent home ranges should be very similar (Melnick 1987).

From previous studies of non-human primates, the predicted levels of genetic differences between groups as measured by a deterministic model of migration, consistently underestimate the observed levels of differences seen between groups of rhesus macaques (Duggleby 1978, Melnick et al. 1984b), Japanese macaques (Nozawa et al. 1982) and Ethiopian vervet monkeys (Turner 1981). The best explanation of this to date, is the non-random migration of males to groups. Cheney and Seyfarth (1983) have described the migration pattern of male vervet monkeys as an age-dependent polymorphism involving natal and breeding transfers. Natal transfers refer to the movement of males between birth site and breeding site at the age of sexual maturity. Cheney and Seyfarth (1983) suggest that these are nonrandom transfers to adjacent troops, usually in the company of brothers or peers. Breeding transfers refer to the movement of solitary breeding males between successive troops. Cheney and Seyfarth (1983) suggest that these are random movements, and that the coexistence of nonrandom and random dispersers may minimize the potential inbreeding depression, while maximizing the social benefits of initially

transferring to a potential breeding site in the company of brothers or peers. Such non-random, kin-structured migration should result in higher levels of overall differentiation between groups than might be expected if migration was random (Melnick 1987). To examine this, the genetic structure of groups living in close and distant proximity to each other are examined and the genetic composition of adjacent and non-adjacent home ranges are compared.

A second potential source of increased genetic differentiation between groups could be due to geographic barriers restricting movement of individuals to an area. In Japanese macaques, interpopulation differentiation may be elevated due to restrictive migration routes caused by urban areas and islands (Nozawa et al. 1982). To examine the influence of geographic barriers to the dispersal patterns of a population, groups from both sides of a potential barrier can be examined.

In Barbados, eighty-seven percent of the island is covered by a thin layer of Pleistocene limestone, while the remaining 13 % on the north-east coast is covered by the tertiary sediments found elsewhere under limestone (Denham 1987). This has resulted in a difference in the soil and vegetative composition of the two geological areas (Watts 1966). A series of gullies traverses the island and provides natural boundaries between areas of agricultural land. The distribution of vervet monkeys appears to be influenced by the distribution of these gullies (Section 2). Moreover, the gullies in Barbados are predominantly east-west, but few are continuous from the east to the west (e.g. note the discontinuity of gullies near the borders of St. Andrew and St. Joseph with the borders of St. Peter, St.

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James, St. Thomas, and St. John; Fig. 11). This discontinuity may constrain the movement of vervets between the east and west areas of the island.

Finally, genetic variability in the Barbados population of vervets may be low due to the effects of a small founding population. Vervet monkeys were introduced to Barbados during the British slave trade of the 17 th century, presumably as pets. The exact origin and founding number is not known, although as few as 50 animals may have founded the population (Denham 1987). If genetic variability is low in the overall population, it should be expressed as a low level of heterozygosity in the population.

This section describes the genetic composition of groups of vervet monkeys in Barbados and examines the genetic variability and differentiation in the population which may be a result of a small founding population, non-random dispersal between groups and geographic barriers within the island.

4.2 METHODS

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Vervet monkeys were trapped throughout Barbados from October 1987 - April 1988 using large, baited, wire-mesh cages. Monkeys were immobilized with an intramuscular injection of 5 ml/ kg of Ketamine hydrochloride and were immediately transported to the Primate Research Center. Each monkey captured was weighed and sexed. Protein electrophoresis and A-B-O blood typing have been shown to be the easiest and most effective methods of determining genetic differentiation between populations in feral

Figure 11 - The distribution of gullies across the island of Barbados (from Horrocks, 1984).

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primates (Byles and Sanders 1981, Lucotte et al. 1982, Melnick et al. 1984a, b, Nozawa et al. 1982, Turner 1981). Blood was therefore drawn from the femoral vein of each individual into 7-ml Vacutainers containing anticoagulant solution (sodium heparin). Blood samples (N = 248) were centrifuged for 20 minutes at 1500 rpm, until the plasma and red cells could be separated. Red cells were washed three times with 0.9% saline solution and frozen. The serum samples were immediately tested for blood type. Each serum sample was titrated with human O blood to remove non-specific antihuman heteroagglutinins and then tested against human red cells of groups O, A and B. If unclear or weak reactions were obtained, the test for agglutinins was repeated after the samples were diluted (1:3) with a 0.9% saline solution (Moor-Jankowski et al. 1964, Socha et al. 1972, 1977, and Wiener and Moor-Jankowski 1969).

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Serum samples were transported to McGill University, Montreal on dry ice and kept frozen at -20 C until electrophoresis was performed. Samples were subjected to electrophoresis in horizontal 12 % starch gels (Connaught Laboratories). The proteins examined, buffer systems, and stains used are summarized in Table 7. Serum proteins were stained following the procedures of Barnicott and Hewett-Emmett (1971), Lucotte et al. (1982), McDermid and Ananthakrishnan (1972), McDermid et al. (1973) and Turner (1981).

The vervet population in Barbados was divided into groups according to geographic distance and vegetative cover. All troops sharing a continuous vegetative cover, whether this was continuous forested area or a continuous gully, were considered as one group. Using this criterion, the minimum distance that separated two groups was 1.4 km. The average troop's home range size in Barbados was 0.064 km^2 (Section 2). The opportunities for interaction between troops from different groups were therefore negligible (Section 2). The locations of the different groups are shown in Fig. 12. Only 12 of the 20 groups were used in the serum protein analysis due to storage problems of blood from certain populations.

The vervet population in Barbados was also divided into two larger units, an east sub-population and a west sub-population. The rationale for this was the sharp discontinuity in geology, and hence in soil and vegetative composition, between the north-east area and the rest of the island (Watts 1966; Section 1). Moreover, the gullies in Barbados are predominantly east-west, but very few are continuous from the east to the west (e.g. note the discontinuity of gullies near the borders of St. Andrew and St. Joseph with the borders of St. Peter, St. James, St. Thomas, and St. John; Fig 11). This discontinuity may constrain the movement of vervets between the east and west areas of the island. The groups included in the east sub-populations were Bathsheba, Bawdens, Bonwell, Boscobelle, Cane Garden, St. Simons, and Turner's Hall; those in the west subpopulation were Airy Cot, Cherry Tree Hill, Farmers, Four Hill, Free Hill, Lion Castle, and Rock Hall (Fig. 12).

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Table 7 - The buffer systems and staining methods used in electrophoresis of serum proteins of vervet monkeys in Barbados.

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| Protein C          | ode  | Buffer       | Specific Stain  |
|--------------------|------|--------------|-----------------|
| Albumin            | Alb  | Tris Borate  | Giblett (1969)  |
| Alkaline Phosphate | AlPh | Tris Borate  | Giblett (1969)  |
| Ceroplasmin        | Ср   | Tris Borate  | Giblett (1969)  |
| Cholinesterase     | CEst | Lithium      | Giblett (1969)  |
| Haptoglobin        | Нр   | Tris Borate  | Giblett (1969)  |
| Macroglobulin      | Mg   | Tris Borate  | Giblett (1969)  |
| Prealbumin         | РА   | Tris Citrate | Fagerhol (1969) |
| Transferrin        | Tf   | Tris Borate  | Giblett (1969)  |

Figure 12 - Map of Barbados showing the locations of the 20 vervet groups. Asterisks indicate the groups (n=12) used for serum protein analysis.

## Legend

AC = Airy CotBA = Bathsheba $BL = Blackmans^*$ BN = Bonwell\* BP = BelleplaineBS = Boscobelle\* BW = BawdensCG = Cane Garden \* CH = Cherry Tree Hill CT = Connell Town\* FH = Four Hill\* FM = Farmers\* FR = Free Hill\* JH = Josey Hill LC = Lion Castle\*NC = New Castle\* RH = Rock Hall  $SS = St. Simons^*$ TR = Turner's Hall\*WH = White Hill



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The average heterozygosity (H) measures the amount of heterozygosity in a group, and provides an indication of the genetic variability in the group. The average heterozygosity was calculated as the total number of heterozygotes observed for each locus, divided by the total number of individuals in the sample, and averaged over all loci (Hartl 1981). The average heterozygosity was calculated for the entire population of Barbados, for the east and west subpopulations, and for each group.

The fixation index ( $F_{ST}$ ) measures the degree to which the groups within a larger population differ from each other. The theoretical minimum of the fixation index is 0 (i.e. all fixed alleles are identical between groups) indicating no genetic differentiation, and the theoretical maximum is 1 (i.e. fixation for alternative alleles between groups), indicating extreme genetic differentiation (Hartl 1981). The fixation index ( $F_{ST}$ ) was calculated using the following formulae:

$$F_{ST} = \frac{Var^2}{pq}$$

where  $Var^2$  is the mean square of the variance in allele frequency minus the squared mean, p and q are the average frequencies of the two alleles per locus. And by :

where HT represents the heterozygosity of the total population calculated from the average allele frequency across groups as the Hardy-Weinberg expectation of heterozygosity with random mating, and HS is the heterozygosity of a group (Hartl 1981). The first

formula was used to calculate the fixation index for loci having 2 alleles, the second for loci having 3 alleles.

The genetic distance between two groups was calculated using Nei's (1972) formula and Roger's (1974) formula.

4.3 RESULTS

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4.3.1. Genetic variability in Barbados

Blood group frequencies were analysed for 248 vervets in Barbados. Of these, 137 were group A, 65 were group B and 46 were group AB. No individuals with blood group O were found in the population. The observed number of heterozygotes (46) was significantly lower than that expected by Hardy-Weinberg equilibrium (133) ( $X^2 = 40.20$ , p<0.001, d.f =1).

Of the 8 loci examined in the serum of vervets from Barbados, 6 were found to be polymorphic. The expected number of heterozygotes, as predicted by Hardy-Weinberg equilibrium, was calculated and compared with the observed number of heterozygotes at each of the 6 polymorphic loci (Table 8). The observed number of heterozygotes was significantly lower than that expected for 4 of the 6 loci (Table 8). **Table 8 - Allele frequencies for serum proteins for vervet monkeys in Barbados.** HP: Haptoglobin; CP: Ceroplasmin; AKPH: Alkaline phosphatase; PA: Prealbumin; MG: Macroglobulin; TF: Transferrin.

| Locus |                | Allele n | Frequency |
|-------|----------------|----------|-----------|
| HP    | B              | 48       | .235      |
|       | C              | 156      | .765      |
|       | X2             |          | 11.59*    |
| CP    | В              | 44       | .231      |
|       | С              | 136      | .716      |
|       | D              | 10       | .053      |
|       | X <sup>2</sup> |          | 1.59      |
| AKPH  | В              | 137      | .796      |
|       | С              | 3 5      | .204      |
|       | X2             |          | 27.41*    |
| РА    | В              | 196      | .960      |
|       | С              | 8        | .040      |
|       | X2             |          | .431      |
| MG    | В              | 17       | .083      |
|       | С              | 187      | .917      |
|       | X <sup>2</sup> |          | 13.6*     |
| TF    | В              | 21       | .115      |
|       | С              | 145      | .797      |
|       | D              | 16       | .088      |
|       | <b>X</b> 2     |          | 12.0*     |

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\* indicates significant deviation from Hardy-Weinberg (P<0.05)

The heterozygosity (H) in groups ranged from 3.1% (S.E. 1.9%) (St. Simons) to 13.1% (S.E. 4.9%) (Boscobelle) with an overall heterozygosity for the island population of 8.9% (S.E. 4.6%). (Table 9).

The gene diversity, or average heterozygosity within a group (Hg) was calculated from the weighted mean gene frequencies from all groups. The average heterozygosity within a group was 0.074. The overall island heterozygosity (H<sub>t</sub>) was 0.089. Thus, the ratio of heterozygosity within groups (Hg) to heterozygosity of the total population (H<sub>t</sub>), was 0.83. This illustrates that 83 % of the gene diversity in the total population can be found in any one of the population's groups.

## 3.3.2 Genetic differentiation in Barbados

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## 3.3.2.1 Genetic differentiation between groups

The average fixation index ( $F_{ST}$ ) for the six polymorphic loci was 0.15 for the overall population in Barbados (range 0.089-0.257; Table 10). A fixation index between 0.05 and 0.15 is considered to indicate moderate genetic differentiation between groups for mammals (Hartl 1981).

The average genetic distance between pairs of groups, as indicated by Nei's formula, was 0.017 (range 0-0.066); the average, as indicated by Rogers' formula, was 0.121 (range 0.027-0.207) (Table 11). The genetic distances between groups were not correlated with the geographical distances between them (Nei's, r=0.08, p > 0.521; Rogers', r=0.18, p > 0.137; Fig. 13), i.e. genetic differentiation could not be predicted from geographical distance. Figure 13a Roger's genetic distance between 12 groups of vervets in Barbados versus the geographical distance between them. Each data point is the genetic distance between one pair of groups.

Figure 13b Nei's genetic distance between groups of vervets in Barbados versus the geographical distance between them. Each data point is the genetic distance between one pair of groups.



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Geographic distance (km)



Geographic distance (km)

To further examine genetic relatedness between groups, the number of neighbouring and non-neighbouring groups that were separated above and below the mean genetic distance for all groups (mean Nei's = 0.0173, Rogers' = 0.121) were calculated. Neighbouring groups were defined in two ways : 1) two groups that had no groups between them, and 2) groups which were separated by less than or equal to the average distance which separated groups in Barbados (8.53 km). Using the first definition of neighbours, 36% of neighbouring groups were above the mean genetic distance, 40% of non-neighbouring groups were above the mean distance. Using the second definition, 33% of neighbouring groups were above the mean genetic distance, 35% of non-neighbouring groups were above the mean distance.

# 3.3.2.2. Genetic differences between east and west subpopulations

The allele frequencies at the 6 polymorphic loci for serum proteins were compared between the east and west sub-populations of vervets, i.e. the sub-populations living in areas of the island which differ markedly in geology, soil composition, and vegetation; and between which gullies tend not to be continuous (see Section 3.2). Three of the 6 polymorphic loci were found to differ significantly (P<0.001; Table 12). However, the genetic distances which separated the two sub-populations (Nei's = 0.017, Rogers' = 0.119) were similar to the the averages for the island (Nei's = 0.017, Rogers' = 0.121). The fixation index for groups within sub-populations (i.e. east and west sub-populations) (F<sub>GS</sub>) was greater than the fixation index for

| Table | 9.     | The   | aver | age he | tero | zygosity | (H | )  | and   | standard |
|-------|--------|-------|------|--------|------|----------|----|----|-------|----------|
| error | (S.E.) | ) for | 12   | groups | of   | vervets  | in | Ba | rbado | DS       |

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| Location     | Н     | <u>S.E.</u> |
|--------------|-------|-------------|
| Cane Garden  | 0.033 | 0.025       |
| Farmers      | 0.010 | 0.060       |
| St. Simons   | 0.031 | 0.019       |
| New Castle   | 0.081 | 0.037       |
| Boscobelle   | 0.131 | 0.049       |
| Blackmans    | 0.113 | 0.075       |
| Connell Town | 0.033 | 0.033       |
| Lion Castle  | 0.111 | 0.056       |
| Four Hill    | 0.067 | 0.042       |
| Free Hill    | 0.056 | 0.056       |
| Bonwell      | 0.061 | 0.039       |
| Turners      | 0.067 | 0.067       |
| Barbados     | 0.089 | 0.046       |

# Table 10 - The fixation index (FST) of 6 polymorphic loci for serum proteins for vervets in Barbados

| Locus                | Fixation Index<br>(FST) |  |  |  |  |
|----------------------|-------------------------|--|--|--|--|
| Haptoglobin          | 0.109                   |  |  |  |  |
| Ceroplasmin          | 0.094                   |  |  |  |  |
| Alkaline phosphatase | 0.150                   |  |  |  |  |
| Prealbumin           | 0.089                   |  |  |  |  |
| Macroglobulin        | 0.257                   |  |  |  |  |
| Transferrin          | 0.222                   |  |  |  |  |

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Table 11 - Nei's and Rogers' genetic distances for groups of vervet monkeys in Barbados. Nei's distances are above the diagonal, Rogers' distances are below the diagonal. Key for the locations is as shown in Figure 10.

Pop CG FM SS NC BS BL CT LC FR FH BN TR .035 .044 .047 .008 .017 .004 .066 .049 .039 .036 .060 **G** -.136 -.000 .006 .014 .029 .027 .011 .000 .000 .000 .000 FM SS .147 .048 -.006 .017 .036 .017 .010 .024 .000 .000 .004 NC .161 .103 .104 - .039 .012 .028 .000 .012 .006 .005 .000 BS .073 .114 .114 .147 - .016 .000 .044 .032 .000 .010 .036 BL .116 .126 .151 .107 .117 -.012 .008 .021 .026 .032 .010 .078 .142 .117 .117 .056 .108 - .038 .053 .002 .016 .039 CT .203 .114 .108 .063 .168 .123 .151 - .015 .010 .009 .000 LC FR .169 .076 .118 .117 .145 .122 .173 .112 -.009 .011 .000 .194 .121 .114 .167 .147 .176 .153 .161 .138 -.000.000 FH .146 .029 .027 .108 .117 .126 .124 .102 .102 .109 -BN .000 .207 .104 .118 .081 .161 .132 .169 .048 .094 .133 .113 -TR

Table 12 - Allele frequencies for serum proteins for theeast and west sub-populations of vervets in Barbados.

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| Protein/allele | <u>n</u> | Eastern | area | <u>n</u> | Western | area | <u>d.f.</u> | <u>X</u> 2 |
|----------------|----------|---------|------|----------|---------|------|-------------|------------|
| Haptoglobin    | 42       |         |      | 30       |         |      |             |            |
| B              |          | 0.193   |      |          | 0.307   |      | 1           | 34.81**    |
| C              |          | 0.807   |      |          | 0.692   |      | -           |            |
| Ceroplasmin    | 42       |         |      | 30       |         |      |             |            |
| B              |          | 0.228   |      |          | 0.218   |      | 2           | 103.54**   |
| С              |          | 0.576   |      |          | 0.730   |      |             |            |
| D              |          | 0.196   |      |          | 0.051   |      |             |            |
| Alkaline Phos  | ohata    | se      |      |          |         |      |             |            |
|                | 42       |         |      | 30       |         |      |             |            |
| В              |          | 0.828   |      |          | 0.828   |      | 1           |            |
| С              |          | 0.172   |      |          | 0.172   |      |             |            |
| Prealbumin     | 42       |         |      | 30       |         |      |             |            |
| В              |          | 0.959   |      |          | 0.962   |      | 1           | 0.141      |
| С              |          | 0.041   |      |          | 0.038   |      |             |            |
| Macroglobulin  | 42       |         |      | 30       |         |      |             |            |
| B              |          | 0.919   |      |          | 0.871   |      | 1           | 12.26**    |
| С              |          | 0.081   |      |          | 0.129   |      |             |            |
| Transferrin    | 42       |         |      | 30       |         |      |             |            |
| В              |          | 0.104   |      |          | 0.125   |      | 2           | 2.74       |
| С              |          | 0.779   |      |          | 0.750   |      | _           |            |
| D              |          | 0.117   |      |          | 0.125   |      |             |            |

\*\* indicates a significant difference in allele frequency (P < 0.001).

groups across the whole population ( $F_{GT}$ ) ( $F_{GS}$ =0.100,  $F_{GT}$ =0.080) indicating greater differentiation between groups in the two sub-populations than for all the groups across the island.

## 3.4 DISCUSSION

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The natural vegetation in Barbados has been extensively cleared, and the distribution of vervets on the island is now strongly influenced by the availability and distribution of vegetative cover. The scarcity and patchy distribution of vegetative cover may constrain the movement of male vervets between groups, as males may be forced to restrict their movements to the wooded gullies that traverse parts of the island. The restricted movement may affect the amount of genetic differentiation in the vervet population, measured here by fixation indices and by the genetic distances of groups and sub-populations. In addition, genetic variability for the whole population may be low due to a small founding population.

## 4.4.1 Genetic variability in the Barbados population

Since the initial gene frequencies of the founding population of vervets in Barbados are not known, the heterozygosity that existed in the population 300 years ago can not be determined. However, present levels of heterozygosity and gene diversity can be considered by examining current gene frequencies in the population.

In a panmictic population, the number of observed heterozygotes should approximate the expected number of heterozygotes as predicted by Hardy-Weinberg equilibrium. The vervet population in Barbados showed a significant deviation from Hardy-Weinberg equilibrium for the blood group locus, as well as for 4 of 6 polymorphic loci for serum proteins examined. The deviation reflects a lower proportion of heterozygotes in the population than expected.

The levels of heterozygosity (H) from 12 vervet groups in Barbados ranged from 0.033 to 0.131 with an average of 0.089. This is above the 0.056 found by Turner (1981) for 7 populations of Ethiopian vervets, and above the 0.050 found by Dracopoli et al. (1983) for vervets caught in various locations in Kenya, although the difference between these populations is probably not significant.

The gene diversity of the population showed that 83 % of the diversity in the population can be attributed to differences within an individual group.

The basic genetic characteristics of the vervet population in Barbados are therefore a relatively high level of heterozygosity, although fewer than expected heterozygotes in the population, and a relatively high level of gene diversity at the group level. These characteristics do not appear to support the idea that the population is homogeneous due to a small founding population, as heterozygosity is quite high. The fewer than expected heterozygotes in the population may be better explained by a deviation from Hardy-Weinberg due to non-random mating in the population or genetic drift due to small troop sizes in Barbados.

## 4.4.2 Genetic differentiation between vervet groups in Barbados

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The average fixation index for the groups examined in Barbados was 0.15. This is greater than the 0.062 found by Turner (1981) for Ethiopian vervets, and the 0.034 found by Melnick et al. (1984a) for macaques. The relatively high fixation index observed here could be particular to the 8 loci examined. However, the number of polymorphic loci is comparable with that of other studies (see Turner 1981, Dracopoli et al. 1983, and Melnick et al. 1984a).

The possibility of limited movement of vervets between groups increases the probability of differentiation. The "stepping stone model" of population structure described by Kimura and Weiss (1964) and Wright's "isolation by distance model" (Wright 1978) states that, for discontinuous groups, individuals living nearby will be more genetically alike than those living far apart. Extending this to the genetic structure of a population, the genetic differentiation between two groups should be positively correlated with the geographic distance separating the groups. A correlation between genetic distance and geographic distance has been shown for groups of Japanese macaques (Nozawa et al. 1982). Dracopoli et al. (1983) have conducted the only similar study on vervets to date. They found a tendency for genetic distance to approximate geographic distance; but the correlation was not statistically significant.

The genetic distance between vervet groups on Barbados was not correlated with the geographical distance between the groups. One explanation for this may be that male vervets transferring between groups in Barbados are restricted to certain "dispersal routes", i.e. zones of dense vegetative cover such as gullies, which may connect two areas. In Barbados, where clearing of vegetation has been extensive, restriction of inter-group movement to specific dispersal routes is likely. If 2 areas that are relatively well separated geographically are connected by a dispersal route, the vervet groups in the areas may be more genetically related than 2 closer groups with no connecting dispersal route.

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Two types of male transfer between groups have been described These are nonrandom transfers at sexual maturity, the for vervets. transfer typically being to a familiar neighbouring group in the company of brothers or peers; and random transfers of solitary adult males between successive breeding sites (Cheney and Seyfarth 1983). Nonrandom transfers of males to familiar neighbouring groups has been also documented in macaques (Melnick et al. 1984a, b) and baboons (Packer 1985). The genetic consequences of these two types of transfer have been intensively examined for macaques (see Melnick et al. 1984a, b, Nozawa et al. 1982, Duggleby 1978), but only the studies of Turner (1981) and Dracopoli et al. (1983) have begun to address the influence of male transfers on the genetic structure of populations in vervets. An examination of the relatedness of neighbouring and non-neighbouring groups was therefore done to test whether the two patterns of male transfers characteristic of vervets influence the genetic structure of the vervet population in Barbados. The distribution of dispersing male vervets has not yet been documented in Barbados. However, Horrocks (1984) estimated a rate of dispersal for natal males leaving a troop

for the first time to be 0.625/year, and the average tenure of a breeding adult male in a troop was estimated to be 32 months (Horrocks 1984). Thus, the turnover of males between troops in Barbados appears to be rapid.

Analysis of the relatedness of neighbouring and non-neighbouring groups indicated that 33 % of neighbouring groups had genetic distances above the mean genetic distance for the island population, and 67% of neighbouring groups had genetic distances below the mean genetic distance. On its own, this tends to suggest an association between proximity and genetic similarity; an association that is expected if males transfer at maturity to neighbouring troops. However, only 38 % of non-neighbouring vervet groups in Barbados had genetic distances above the mean genetic distance for the population; 62 % below the mean distance. The difference between 67 % and 62 % may suggest some effect of proximity on genetic similarity; but the striking result is the high percentage (62 %) of non-neighbouring groups which are closely related. This suggests that there is no simple relationship between genetic similarity and geographical proximity, which is consistent with the earlier observation that genetic distance is not correlated with geographical distance for vervets in Barbados. The results strengthen the previous suggestion that inter-group movement of vervets in Barbados, whether it be first transfers at sexual maturity or subsequent transfers between breeding sites, may be restricted to specific dispersal routes such that the probability of movement between groups is not strongly dependent on group proximity. The groups with genetic distances below the mean for the island may be

those that are well connected by dispersal routes; the groups with genetic distances above the mean may be those that are poorly connected. The skewed distribution around the mean may suggest that those groups which are poorly connected by dispersal routes deviate markedly from the genetic distance separating most groups in the population.

The investigation of genetic differentiation between east and west sub-populations of vervets in Barbados lends partial support to the suggestion that vegetated gullies, as potential dispersal routes, may be important in influencing the genetic structure of the vervet population. The north-east area of the island differs markedly from the rest of the island in geology, soil type, and vegetative composition, and few gullies run continuously from the east to the west of the island. Three of the 6 polymorphic loci investigated showed significant differences in allele frequency between the east and west sub-populations. The fixation index of groups within subpopulations was greater than that of groups in the whole population indicating more differentiation between sub-population groups than between all the groups on the island. However, the genetic distance between the sub-populations was similar to the mean for the island population.

The genetic structure of the vervet population in Barbados is characterized by relatively high levels of heterozygosity and gene diversity at the group level, and small genetic distances between groups, indicating adequate gene flow between groups. The discontinuity of the vegetated gullies on the island appears to influence the genetic composition of the island, by possibly acting as

geographic barriers to dispersing males, and hence creating differences in the allele frequencies between the east and west sides of the island.

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