University of Alberta

Foraging Strategies, Group Size, and Food Competition in the Mantled Howler Monkey, *Alouatta palliata*

by

François Larose ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Anthropology

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Foraging Strategies, Group Size, and Food Competition in the Mantled Howler Monkey, *Alouatta palliata* submitted by François Larose in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Linda Fedigan
Dr Linda Fedigan

Dr Owen Beattie

Dr Nancy Lovell

Pamela Willoughby
Dr Pamela Willoughby

Cynthia Paszkowski
Dr Cynthia Paszkowski

Milton Freeman
for Dr Peter Waser

Aug. 9, 1996

ABSTRACT

A thirteen month study of the foraging strategies of the mantled howler monkey (*Alouatta palliata*) was carried out in Santa Rosa National Park, Costa Rica, to investigate the relationship between group size, resource availability, and the intensity of food competition. Four groups of different sizes, ranging from six to forty-five animals, were followed simultaneously during this study. Quantitative descriptions of diet, ranging patterns, time budget, and patch use are presented for each group to provide a basis for comparing the intensity of food competition within each group.

Dietary overlap was generally low on a monthly, seasonal, and annual basis. Variability in abundance and density of plant species explained some of these differences. However, similarities were found in the number of food species used on a daily basis, and in the preference for large feeding trees. Results also demonstrate the preference for seasonal items such as flowers, fruits, and young leaves when these are available. Results also show that ranging patterns increased as a function of group size providing evidence that competition for resources forced animals in larger groups to spend more energy looking for food. Analyses of time budget provided more evidence of increased food competition. Groups BH45 and BH18 fissioned during the dry season when they were forced to remain active during the intense midday heat to find food. The results also showed that seasonal and annual variability of food items greatly influenced time budget and ranging patterns of howlers.

Analyses of aggression over food items also showed that howlers competed for preferred food items such as fruits and flowers. Evidence is presented suggesting that females, juveniles, and low-ranking animals incur most of the costs of aggressive competition over food. Analyses of food patch use also suggest that although large groups deplete food patches more often than small groups, most food patches used by howlers may not be depleted. The availability of "super-productive" food patches may reduce the intensity of food competition within groups and allow for larger group sizes.

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I. INTRODUCTION

Recent models to explain the diversity of social organization in animal communities have focused on the benefits and the costs of living in groups as opposed to solitary life (Bradbury and Vehrencamp 1976; Bertram 1978; Wrangham 1980; Terborgh and Janson 1986; Dunbar 1988). Although protection against predators is widely accepted as a benefit of group life, and a factor favoring large group size, variability in social organization is usually explained by competition for limited resources (Bradbury and Vehrencamp 1976; Wrangham 1980; Pulliam and Caraco 1984; Janson and van Schaik 1988).

The most comprehensive models so far have emphasized competition for mates and food, as those are thought to be the primary resources that govern animal grouping patterns (Wrangham 1980; Janson and van Schaik 1988). For instance, Wrangham (1980) and Gaulin and Sailer (1985) have argued that females distribute themselves in the environment based on the distribution of food resources while males distribute themselves according to female grouping patterns. Furthermore, Wrangham (1980) suggested that when the distribution of food makes it possible to defend these resources, females should form cooperative social groups based on kinship ties to exclude other groups from access to food resources. Thus, if resources occur in relatively small and discrete patches, and if females forage as a cohesive unit, a single male can attempt to monopolize access to females by excluding other males from the group. When resources are too scattered and females are forced to spread out while foraging, several males can join the group and cooperate to attempt to prevent other males from entering the group. Wrangham (1980) also suggested that the presence of several males would benefit the group as they would raise the competitive ability during intergroup encounters.

Although Wrangham's (1980) model has been criticized on several grounds (see van Schaik 1983 and Moore 1984), most researchers believe that the availability and the distribution of food resources are key determinants in the evolution of group size, and ultimately, of social organization (Bradbury and Vehrencamp 1976; Andelman 1986;

Janson and van Schaik 1988). Because food sources occur in limited quantities and are usually found in relatively small and discrete patches, natural selection has favored the evolution of strategies that maximize the individual's chances of finding and harvesting those resources. For instance, several researchers have argued that social groups increase the likelihood of detecting patchy resources (Horn 1968; Ward and Zavahi 1973), and allow more efficient monitoring of the environment by decreasing the likelihood that an individual will travel to a food patch that has already been depleted (Cody 1971). Although there are benefits to group living, there are also costs associated with foraging in groups. Competition for food is widely accepted by researchers as a major cost of foraging in groups. Competition between groups favors large groups because they can force smaller groups to leave a food source or prevent them from exploiting it. Such a gain is a determinant factor in Wrangham's (1980) model of the evolution of social groups (see above). However, these gains can be offset by competition within groups. First, large groups have to travel farther than small groups to find enough food to sustain their members , thus increasing the energy expenditure of each individual (scramble or exploitation competition). Second, some individuals may prevent their fellow group members from achieving access to resources by the use of threats or aggression (contest or interference competition). As a result, the costs and benefits of competition may not be equally shared by all group members.

Consequently, group size can be understood as a compromise between the benefits and the costs of competing for limited resources on an individual basis. Recent studies have attempted to measure the costs and benefits associated with group life by measuring the intensity of food competition within and between groups of different size. For this purpose, particular attention has been given to the relationship between food competition, group size, and the distribution of food resources (Bradbury and Vehrencamp 1976; Pulliam and Caraco 1984; Janson 1988; Chapman et al. 1995).

Based on preliminary studies, several assumptions have been made about the relationship between group size, food competition, and food density and distribution. One of the first discoveries was the correlation between group size and broad diet categories

(Clutton-Brock and Harvey 1977). A number of studies have reported that folivores do not suffer the same costs associated with food competition as do frugivores because the resources used by folivores occur at high density, are evenly distributed, and occur in relatively large patches (Clutton-Brock and Harvey 1977; Isbell 1991). As a result, folivores tend to live in larger groups than frugivores and to have lower levels of interference and exploitation competition. Furthermore, the diet of folivores, which is low in energy, may limit the amount of energy that can be used in competition with other group members, and may limit the energy that can be expended in the search for food (Jones 1980; van Schaik 1989). Consequently, interference competition has often been considered to be absent or very rare in folivorous species (van Schaik 1989; Isbell 1991).

However, most of these assumptions about folivores have not been tested systematically in the field and have been based on indirect measures in a small number of species. Also, very few studies have attempted to measure the intensity of both exploitation competition and interference competition in folivorous species across a range of group sizes (Watts 1985). This is particularly surprising in light of the fact that several studies have disputed the assumptions that food sources used by folivores are abundant and evenly distributed (Glander 1975; Milton 1984; Mowry et al. 1996).

The objective of this study was to examine the relationship between group size and food competition in a folivorous species, the mantled howler monkey (*Alouatta palliata*). Howler monkeys are large arboreal folivores and are among the best studied neotropical primates (see Crockett and Eisenberg 1986). The genus *Alouatta* has a wide geographical range, from southern Mexico to northern Argentina. Howlers are also found in a wide range of habitats, from wet evergreen forests to highly seasonal semi-deciduous forests (Crockett and Eisenberg 1986). Much variation has been reported in their diet, and although leaves are an important part of their diet on an annual basis, the amount of fruits and flowers consumed varies from site to site, and from season to season (see chapter 2). The genus *Alouatta* is also characterized by intra and inter-specific variation in group size and composition. The reasons for this variation are still unclear, although reproductive strategies and the availability of food resources are considered to be important factors

(Jones 1980; Crockett 1984). Howlers also exhibit a relatively unusual dispersal pattern among primates. Both males and females migrate from their natal group, a pattern rarely found in primates, most species of which tend to have male-biased dispersal (Glander 1992). Hence, howler groups are generally composed of unrelated adult males, unrelated adult females, and their offspring.

The best-studied species of howlers is the mantled howler, *Alouatta palliata*. Mantled howlers have been studied in a wide range of habitats, from tropical rain forests in Panama (Smith 1977; Milton 1980), to dry deciduous forests in Costa Rica (Glander 1975; Chapman 1988). Despite the number of studies on mantled howlers, and despite the variation in group size and composition found in this species, very little is known about the causes of this variation. In this study, I test the hypotheses that food competition and the distribution of resources are determinant factors that influence group size in *Alouatta palliata*. For this purpose, I studied four groups of mantled howler monkeys in a tropical dry forest in Costa Rica. The main objective of this study was to measure the intensity of exploitation competition and interference competition in groups of different sizes. In chapter 2, I describe the variation in diet within and among groups and I examine whether differences in dietary composition can be explained by annual and seasonal variation in resource availability and distribution, and whether some differences in dietary composition can be explained by group size. In chapter 3, I compare the intensity of exploitation competition among my study groups to determine whether individuals living in large groups incur higher foraging costs than individuals living in smaller groups. I also document the annual and seasonal variation in the intensity of exploitation competition within groups as well as the effects of other ecological variables such as patch size and seasonal variation in temperature. In chapter 4, I examine the relationship between group size and interference competition and I test the hypotheses that aggression over food is rare among folivores and that the costs of foraging in large groups are shared equally by all group members. Finally, in chapter 5, I examine the relationship between group size and food patch size. In this chapter, I document the differences in the use of individual food patches and how group size may be influenced by the availability of large, high-quality food patches.

Santa Rosa National Park in Costa Rica offers an excellent opportunity to study mantled howlers. First, several groups of howlers have been studied since 1983 by Fedigan (1986) and individuals in several groups have been captured and marked to allow recognition and to facilitate studies of the different groups (Glander et al. 1991). Several studies have been conducted on the phenological patterns of various plant species (Daubenmire 1972; Bonoff and Janzen 1980; Janzen 1983) as well as on the distribution and density of plant species (Chapman and Chapman 1990). Chapman (1987) studied the foraging strategies of one group of howler monkeys in Santa Rosa and his work served as a reference for this study. Santa Rosa also offers excellent opportunities to study the relationship between group size and food competition in howlers for several reasons. Howlers in Santa Rosa live in a wide range of group sizes, ranging from 6 to 45 individuals for the groups in this study. This variation represents almost the total range of group sizes found in all other howler studies. Santa Rosa is composed of a mosaic of different forest types, from pristine semi-evergreen forest to young successional semi-deciduous forest, and the area experiences distinct dry and rainy seasons, each of which lasts approximately six months. This allows comparisons of resource availability across seasons and examination of the effects of seasonal changes on foraging strategies in howlers. Finally, the observation conditions in Santa Rosa are excellent, which facilitates the study of the behavior and ecology of the howler monkey population.

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II. Intergroup Variation in Diet in Four Groups of Howler Monkeys (*Alouatta palliata*) in Santa Rosa National Park, Costa Rica.

INTRODUCTION

Dietary composition is known to vary widely in primates species (Clutton-Brock 1977; Terborgh 1983). Although differences in diet are expected between species and within species living in different habitats, much variation is also known to occur from year to year (Hladik 1977; Kinzey 1977; Struhsaker 1975; Waser 1977) and between groups inhabiting the same area (Milton 1980; Watts 1984; Butynski 1990). For the latter, differences in diet may be explained in part by certain features in the environment which vary at a small scale, such as soil moisture (Jarman & Sinclair 1979) and nutrient content (Rhoades 1979; Mckey 1978; Gartlan et al. 1980) and which are known to influence the distribution of plant species and create a mosaic of microhabitats. However, as numerous studies have demonstrated, differences in diet composition cannot always be explained by the presence, absence, or overall availability of plant resources in time and space (Hladik 1977; Richard 1977; Struhsaker 1975; Waser 1977; Chapman & Fedigan 1989). Other factors such as scramble and contest competition are also known to influence access to certain foods for some individuals (S. Altman 1974; Robinson 1981; van Schaik et al. 1983, Janson 1985) and groups competing for the same resources (Wrangham 1980; Janson 1986). In habitats where the amount of food is limited, the intensity of scramble and contest competition may limit group size by forcing lower ranking individuals to leave the group thereby reducing the intensity of competition, even if they may be more vulnerable to predation by doing so or suffer a reduction in their reproductive success (Dunbar 1988). Consequently, several hypotheses have been proposed suggesting that group size may be a compromise between the need to balance the costs and benefits of within- and between-group competition for food and other factors such as access to mates and predator-avoidance (van Schaik 1983; Terborgh & Janson 1986; Dunbar 1988; Janson & van Schaik 1988).

Other factors, such as density and distribution of food resources, may set upper limits on group size by reducing foraging efficiency in large groups (Altman 1974; Bradbury & Vehrencamp 1976; Terborgh 1983; Wrangham 1980; Pulliam & Caraco 1984; Janson 1988; Chapman 1990; Chapman et al. 1995). Because individuals have to travel in search of food to meet their nutritional requirements and must maintain a positive energy budget (i.e., the energy acquired during the day must exceed or equal the energy expended searching for food for that same time period), larger groups will have to travel farther and cover a larger area than smaller groups to satisfy these demands . Furthermore, group size may vary according to how these resources are distributed. In a study of spider monkeys (*Ateles geoffroyi*)and chimpanzees (*Pan troglodytes*), Chapman et al. (1995) suggested that when resources occur at low density and are uniformly distributed, groups should be small; when resources occur at high density and/or are clumped, groups should be large. Intermediate group size should occur when the pattern of density and distribution of resources is also intermediate.

No studies existing have attempted to study the relationship between group size and diet composition *per se* because of the difficulty in separating the effects of food availability at different sites and the influence of group size. Almost all studies have concentrated on one or two groups and/or have studied groups of similar sizes (e.g., Milton 1980). Others have been concerned with the relationship between group size and measures of foraging effort, such as day range (Clutton-Brock & Harvey 1977; Waser 1977; Janson 1988; van Schaik & van Noordwijk 1988), and the relationship between patch size and foraging subgroup size (Leighton & Leighton 1982; Chapman 1988; White & Wrangham 1988; MacFarland-Symington 1988), as well as the effect of group size on the intensity of contest and scramble competition (Wrangham 1980; van Schaik 1983; Whitten 1983; Terborgh & Janson 1986; Isbell 1991). In this chapter, I compare the diet of four groups of howler monkeys (*Alouatta palliata*) to determine whether similarities and differences can be explained by resource availability and whether some variation can be explained by group size. Other aspects of food competition are examined in subsequent chapters.

Much variation in diet has been reported for howler monkeys, and although leaves are known to be an important part of their diet, the percentage of leafy material varies from study to study, from group to group, and from season to season (Altmann 1959; Smith 1977; Glander, 1978; Milton, 1980; Gaulin & Gaulin, 1982; Braza et al., 1983; Estrada, 1984; Rumiz et al., 1986; Galletti et al., 1987; Chapman, 1988; Juliot & Sabatier, 1993). Howlers typically consume a wide variety of plant species, although a few species may comprise the bulk of the diet (Hladik & Hladik 1969; Glander 1978; Milton 1978; Gaulin & Gaulin 1982; Chapman 1988). Despite their classification as folivores, howlers do not possess specialized stomachs for digesting leaves like colobines and indriids (Hladik 1967; Cramer 1968; Bauchop & Martucci 1968). However, like the colobines and other "leafeaters", howlers are known to consume flowers and fruits in varying quantities. Altmann (1959) reported that during certain periods of the year, fruits may comprise up to 95% of the howlers' diet. Howlers also show a marked preference for seasonal items (young leaves, flowers and fruits) over perennial items (mature leaves) since the former are higher in protein & fiber content (Milton 1979) and are more easily digested (Glander 1981; Estrada 1984), while the latter may be higher in secondary compounds and undigestible material (Hladik 1978; Parra 1978; Milton 1979; Glander 1982). Although many differences in the howlers' diet can be explained by differences in plant species availability between sites, little correlation has been found between diet composition and relative density and availability of resources (Glander 1978; Milton 1980; Estrada 1984; Chapman 1988). Milton (1980) and Glander (1981) both reported that the most common plant species at their sites were not used as food sources by their study groups.

MATERIALS AND METHODS

Study Site

The research was conducted in Santa Rosa National Park on the northwestern coast of Costa Rica. The Park, situated 35 km northwest of Liberia in the province of

Guanacaste, covers approximately 10 800 ha consisting of a series of plateaus starting at an elevation of approximately 300 m and drops down to the ocean. Santa Rosa was created in 1971 and consists of a mosaic of grassland, dry deciduous forest and semi-evergreen forest (Bonoff & Janzen, 1980; Janzen, 1983). Common species in the dry deciduous forest are *Bursera simaruba*, *Chlorophora tinctoria*, *Enterolobium cyclocarpum*, *Luehea candida*, *Pithecellobium saman*, *Spondias mombin*, and *Guazuma ulmifolia*. Common species in the semi-evergreen forest are *Hymenaea courbaril*, *Ficus spp.*, *Manilkara zapota*, *Castilla elastica*, and *Masticodendron capiri*. Santa Rosa is characterized by a dry season extending approximately from December through May, and a wet season which extends from June through November with annual precipitation ranging from 900 to more than 2400 mm, almost all of which falls during the wet season (see Figure 1). During the dry season, deciduous trees lose their leaves and remain bare until the onset of the rainy season.

Since the creation of the park, several studies have been conducted on the primate population inhabiting the area (Freese, 1976; Fedigan, 1986; Fedigan & Baxter, 1984; Fedigan et al., 1985; Chapman, 1987; Chapman et al., 1989; Glander et al., 1991; Rose, 1994). Three species of primates are present in Santa Rosa: *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*. Several groups of each species have been followed since 1983 as part of an ongoing study on the demography and behavior of the three species (see Fedigan, 1986). Individuals of the species *Ateles geoffroyi* and *Alouatta palliata* have been captured and marked to allow recognition and to facilitate studies of the different groups. A system of trails covering approximately 20 km has also been made to facilitate access to the groups. A number of ecological studies have also been conducted in the park, facilitating the recognition of plant species and their phenological patterns (Daubenmire, 1972; Frankie et al., 1974; Bonoff & Janzen, 1980; Opler et al., 1980; Janzen, 1982).

Santa Rosa offers an excellent opportunity to study wild primate populations because of the good observation conditions, particularly during the dry season. Also, the marked seasonality offers the opportunity to study changes in food availability and their effect on foraging strategies within and among groups.

Study Groups

Three groups of howlers were studied during the first field season (1991) and a fourth group was added during the second field season (1992). The size and composition of each group is presented in Table 2-1. The changes in group size for groups San Emilio (SE), Exclosure (EX), and Sendero (SN) were the result of births and disappearances of some animals, possibly due to immigration, in the case of juveniles and adults, and deaths, in the case of infants. However, no cases of immigration or deaths could be confirmed. Group SN also varied in size due to the fission-fusion of this group. Because some individuals were often separated from the main group for several days, the number of monkeys in the study group varied daily. Similarly, early in 1992, the group Bosque Humedo (BH) fissioned into three distinct subgroups. This pattern had been observed previously by Chapman (1987) for the same group. In the five months following the fission, two subgroups reunited again as had happened in the past. However, the smaller subgroup remained separate even after encountering the parent group at least three times after the separation. Therefore, for the study period, the initial group of forty-five animals was followed for only three days before it fissioned. Subsequently, two subgroups were observed. One subgroup of 18 animals was observed for six days while the smaller group of six animals was followed consistently over the remainder of the field season. The results presented in this paper for group BH are for the smaller subgroup of six animals as not enough data was collected on the other two groups of 45 and 18 individuals. Therefore, in this study, groups SE and BH were the smallest groups with approximately six individuals each, whereas EX varied between ten and fourteen individuals. Group SN was larger and varied between 20 and 28 individuals.

The groups were located in the central area of the park and occupied relatively well defined and discrete home ranges, although some overlap existed with other groups for all four groups. Individual recognition was not possible for all group members, however, age/sex classes were easily recognized. In all groups, some adults were marked with collars or ankle bracelets of different sizes, shapes and colors (see Glander et al. 1991 for details). In each of the four groups, other animals could be recognized by discolorations of the skin under the hind feet and by permanent scars on the face and on the tail.

Sampling Methods

Groups were observed from January through June 1991 and from January through July 1992. No data was collected in January 1991, and during this time, the monkeys became habituated and were not alarmed by the presence of the observer after only a few days with each group. Whenever possible, each group was followed in a fixed rotation for five consecutive days over a period of three weeks from February through June 1991 and over four weeks from January through July 1992. Data on each group was collected between 0530 and 1800 hours. Groups were usually found in their sleeping sites early in the morning and were followed until they had reached the sleeping sites at the end of the day. A total of 2040 hours of data were collected on the four groups over 166 full days of observation (see Table 2-1).

For the first field season, the groups were followed using focal sampling sessions (J. Altmann 1974) of ten minutes in length on adults and juveniles. Focal animals were selected at random prior to the beginning of the day, and when possible, were alternated according to age and sex class. The order of rotation was then maintained for the rest of the day. For the second field season, one individual was followed for the whole day and data was collected on adults only, alternating between males and females. The full day focal sampling sessions provided detailed information on individual time budget and dietary composition.

Dietary composition was measured in terms of time spent feeding and foraging on the different plant species and food items for the groups as a whole. Feeding was defined as eating from food sources where the animals fed for several minutes without interruption as opposed to foraging which was defined as eating from food sources where the animal spent less than one minute before moving on to the next food source (van Schaik & van Noordwijk, 1988). Feeding and foraging consisted of reaching for, bringing to the mouth, and chewing food items.

For the purposes of this study, a tree was considered to be a patch for four reasons. First, all group members or most group members were usually seen feeding in the same tree or in neighbouring trees of different species. Second, food items in different tree species probably contribute different nutrient and/or have different secondary compounds that limit the quantity that can be ingested. Third, groups spent more time moving between patches than within patches when they were foraging. Finally, this allowed me to retain the same definition for all my study groups and also allowed meaningful comparisons with other studies. Time spent feeding in a patch was determined by recording the interval elapsed between the time when the first individual started feeding in the patch and the time the last individual left the patch (patch residence time). This is referred to as a feeding record throughout this paper. If no feeding was observed in that patch for thirty minutes after the last individual left, the feeding record was terminated. If feeding resumed before that time, the second patch residence time (PRT) was added to the first one and constituted only one feeding record. At least once per five minutes, I recorded the number of individuals feeding in the patch to estimate the total "individual-minutes" spent feeding in that patch (i.e., if two individuals fed in the patch for five minutes each, the total "individual-minutes" was ten minutes). When subgroups were feeding in more than one patch at a time, I was able to record the same information for a second patch. When more than two patches were used simultaneously, data was recorded for as many patches as possible and the number of patches used was counted.

For each feeding patch visited by the group, I recorded the plant species, the food type ingested, and the size of the patch. Each feeding patch was marked and given an identification number so that frequency of use and renewal rate of patch resources could be determined. Patch size was determined by measuring the diameter at breast height (DBH). Because several studies have demonstrated a strong correlation between DBH, crown size, and productivity for a number of tropical tree species (McDiarmid et al., 1977; Leighton & Leighton, 1982), DBH was used as an estimator of the number of items available in a patch. Five food types were recognized: fruits, flowers, mature leaves, young leaves, and leaf buds. For the analysis, leaf buds and young leaves were combined into one category. To compare diets across seasons I determined the onset of the rainy season to be the first day following the first rain which occured in the first two weeks of May for 1991 and 1992. To allow for meaningful comparisons, most results presented in this paper were carried out on three groups (SE, EX, SN) combining 1991 and 1992 and for the four groups for the 1992 season only.

Sample plots

Forest profile was examined in each group's home range to provide a profile of the species composition and biomass in each area of the study site. One plot in each group's home range was sampled. Each plot was 50m x 100m and was taken at random in the core area of each group's home range. The core area was defined as the area where the group spent more than 20% of its time during the study period. All trees $\geq$ 20cm DBH were measured and identified to the species level whenever possible. The limit of 20cm was chosen because howlers very rarely used trees of a smaller diameter (< 0.2% of total feeding time). Only species of *Ficus*, *Trichilia*, and *Casearia* could not be identified to the species level. Species diversity and diet diversity measures were calculated using the Shannon-Wiener function with the following formula: $H' = \Sigma (p_i)(\ln p_i)$ where p represent the proportion of time spent feeding on the $_i$th species for diet diversity measures (see Krebs 1989) or the percentage of the total biomass of the $_i$th species for the sample plots. Biomass and species composition of the plots were compared using the Percentage Similarity Index (PSI) and was calculated using the basal area of each tree species (see Krebs 1989). The PSI was also used to compare the overlap of diet between groups. The index was calculated using the following formula: $P_{jk} = [\ \Sigma\ (\text{minimum}\ p_{ij}, p_{ik})]100$ where P_{jk} is the percentage overlap between group (or species) j and k, and p_{ij} and p_{ik}, are the proportions of the resource i used by groups (or composed of species) j and k.

Densities of tree species were taken from a study conducted in the same area by Chapman and Chapman (1990). They measured density by using three 4-hectare grids located in the home range of my four study groups. Two of my study groups (BH and EX) had home ranges which overlaped two of these grids and the density used for this study was the average between the two 4-hectare grids. Based on Chapman and Chapman's data, density was calculated for a total of 21 species eaten by my study groups. Of that total, my groups used between 11 and 18 of those species and the total percentage of time spent feeding on those species contributed between 70.4% and 83.5% of their total diet. Individual species for which no density value were available did not contribute more than 3% of the total diet.

Statistical methods

Parametric statistics were used whenever possible over nonparametric tests. For all parametric tests, the distributions of all variables were tested for normality and homogeneity of variances. When values were not normally distributed, an appropriate transformation was applied (Sokal & Rolhf, 1981). The reverse transformations were applied to facilitate the presentation of the results. For multiple group comparisons, a oneway anova with range test (Scheffé's method) was used. All probabilities are two-tailed unless stated otherwise. All statistical procedures were carried out using the SPSS/PC statistical package.

RESULTS

Habitat Description

Sample plots

The composition of the four sample plots indicate that the home range of my study groups overlapped different successional forest types: pristine semi-evergreen forest (BH & EX), old successional semi-deciduous forest (SE & SN), and young successional semi-deciduous forest (BH; see Table 2-2). The profile of each plot clearly indicates the differences in species composition and biomass (Figure 2-2). The number of species present in each plot varied from 21 to 29 and the diversity index (H') varied from 2.49 to 2.92 (Table 2-2). Notable differences can be seen in the dominance of a few species in sample plots such as *Cochlospermum vitifolium* and *Slonea terniflora*. This is reflected in the total biomass of each species in the sample plots as well as the relative contribution of each species (Figure 2-2). A comparison of the plots using the Percentage Similarity Index, based on species' biomass, yielded relatively low indices (27% for EX-SE; 22% for EX-SN; 37% for EX-BH; 47% for SE-SN; 56% for SE-BH; and 29% for BH-SN). However, a comparison of the size of the trees using DBH (see Figure 2-3) revealed no significant differences in their distribution among the four sample plots ($\chi^2 = 20.35$, df = 18, P = 0.31).

Diet Description

Species Composition

A total of 45 identified tree species and 3 unidentified species were used as food sources as well as vines, lianas, and epiphytes which could not be identified (Table 2-3). A total of 24 families were used as food sources. The families Moraceae and Mimosaceae were by far the most important in number of species used and percentage of diet for all four groups. Considering identified food species, group SE used the fewest (n=25) and group BH used the most (n=33). The number of species which contributed 1% or more of the diet varied little for groups SE, EX, and SN (11, 13 and 12 respectively) with group

BH using by far the greatest variety with 23. In 1992, 12 to 14 plant species represented individually at least 1% of the total diet for groups SE, Ex, and SN compared with 23 for group BH. Only 15 species were used by all four groups and they contributed from 65.7 % of the diet for group BH, to between 82 and 84% of the diet for the other three groups. Diet diversity (H') varied from 2.24 for group SE to 2.93 for group BH (see Table 2-3). Similarly, the top ten species in the diet of each group make up almost 90 % of the diet for groups SE, EX, and SN but only 70% for group BH (Figure 2-4).

Food items

The number of food items (vines, lianas, and epiphytes excluded) did not vary greatly between groups, with 56 for group SN and 47 for each of the other three groups (Table 2-4). Mature leaves contributed from 20.9% (SN) to 31.5% (SE) of the total diet (Figure 2-5). Young leaves contributed between 24.7% (BH) to 37.3% (SN). The percentage of flowers varied from 19.7% (EX) to 33.5% (SE) with *Pithecellobium saman* contributing greatly to the overall diet (12.8%). For fruits, the percentage varied very little in 1991-92 from 17.2% to 17.7% for SE, EX, and SN, but varied substantially for 1992 from 11.0% (SE) to 26.0% (SN). This variation is primarily due to two species, *Ficus spp.* and *Sciadodendron excelsum*. The latter is rare and occured only in the home range of groups BH and SN. Annual variations in the use of fruits was striking for all groups (SE 25% and 11%; EX 12% and 19%; SN 5% and 25%). The variation for group SE was primarily due to the absence of fruits of *Manilkara zapota* during 1992 because of the lack of rain in the wet season in 1991 (see Figure 2-1; data from Janzen 1991). A large part of the variation in fruit consumption for all groups can be accounted for by the use of the fruits of *Bursera simaruba* in 1992 which was ignored in 1991 despite its abundance. Monthly variations in the use of each of these food categories show similar patterns (Figure 2-6).

Primary food species

Of all the species used , three species (*Ficus spp.*, *Bursera simaruba*, *Pithecellobium saman*) were far more important on an annual, monthly, and daily basis (Table 2-5). These species were considered primary food sources because they were used almost every month by each of the four study groups (Figure 2-7) and generally contributed more than 10% of the total diet with one exception (Table 2-5). *Ficus* was by far the most utilized food source (17.4 - 28.4% of the total diet) followed by *Bursera* (15.7 - 18.6%) and *Pithecellobium* (8.5 - 15.8%). One other species was important during the first field season (*Manilkara zapota*), but was rarely used the second year and was not considered to be a primary food source for that reason (see discussion).

Daily and Monthly Variation in Diet

Daily turnover of food species

There was no significant difference in the mean number of species used on a daily basis among the four groups (F=1.62, P=0.18, df [3, 150] Scheffé's P > .05; Table 2-6). The number of species used during the dry and the rainy season were not significantly different (see Table 2-6). Similarly, the mean daily turnover of food species (i.e., the percentage of food species used one day and not used again the next day) was not significantly different among groups (F=0.64, P=0.58, df [3, 110], Scheffé's P > 0.5) or between seasons (Table 2-7).

Similarity of diet

The mean monthly similarity index for consecutive months varied greatly (from 15.71 to 73.02, Table 2-8) as did the coefficient of variation (22.5% to 41.9%) but the overall mean similarity index was not significantly different among the four groups (F=1.81, P=0.16, df [3, 25], Scheffé's P > .05). When groups were paired to compare the similarity of their diet on a monthly basis (Table 2-9), again , no significant differences were found between all possible pairs (F=0.23, P=0.87, df [3, 26], Scheffé's P > .05) although the coefficient of variation varied somewhat less for some groups (EX-SE 22.3% and BH-SE 26.9%).

Habitat variability and diet

Three measures of the habitat of each group can be compared with the data on diet. The first is the relation between the relative proportion of the diet of each species and the density of that food species. No significant correlations could be found for any of the four study groups (BH, r = 0.19, n=18, P= .44; SE, r = 0.14, n=11, P= .66; EX, r = 0.39, n=15, P= .14; SN, r = 0.31, n=11, P= .31). If the analysis is repeated by weighting the density by the biomass for each species (density x DBH), no significant correlations were found (BH, r=0.21, P=.39; SE, r=0.04, P=.89; EX, r=0.45, P=.08; SN, r=0.33, P=.31). If only the primary food species are used and the four groups combined, no significant correlations could be found (r = - 0.11, n=12, P= .72). Density weighted by biomass did not reveal any significant correlations (r=-0.10, P=.75). It is worth noting that of the three species, only *Bursera simaruba* had a relatively high density in all four home ranges (13.7 to 35.3 trees/ ha) compared to 0.3 to 0.9 trees / ha for *Ficus* and 0.6 to 1.3 trees /ha for *Pithecellobium saman.*

The second measure is the comparison of the similarity index for diet (Table 2-9) and the similarity of the sample plots (see above) for paired groups. These indices were not significantly correlated (r_s = 0.02, n= 6, P= .95). Finally, I examined the size of the trees used as food sources and the size of the trees in the sample plots to see if the size of feeding trees was determined by the size of trees available in the environment (Figure 2-3). A one-tailed Chi-square test for goodness of fit revealed a strong preference for the larger trees for all four groups (BH $\chi^2 = 476.2$, 6 df, P < 0.001; SE $\chi^2 = 229.6$, 6 df, P < 0.001; EX $\chi^2 = 146.8$, 6 df, P < 0.001; SN $\chi^2 = 253.9$, 6 df, P < 0.001).

DISCUSSION

The results presented in this study emphasize the variability of the diet within and among groups. Monthly and annual variability are too often overlooked or masked by categorizing species as folivores or frugivores. The oversimplification of dietary patterns is clear when we look at the variability in the use of food types (fruits, flowers, leaves) or the use of food species on a monthly or annual basis presented in this study and others (Gautier-Hion 1980; Struhsaker 1975; Waser 1977). Annual variation in the use of some species can be explained by the lack of rain during the rainy season in 1991 (Figure 2-1) which likely affected the production of fruits of *Manilkara zapota* which was a major source of food in 1991 but totally absent in 1992. However, despite of this variability, the diet of the four groups in this study fall within the range found by others for howlers (Smith 1977; Glander 1978; Milton 1980; Gaulin & Gaulin 1982; Estrada 1984; Juliot & Sabatier 1993). The number of food species used by the groups in this study is comparable with other studies in dry tropical forests. Glander (1978) found that his groups used 61 species compared with 45 in this study. The difference in the number of plant species used between this study and others is likely due to the fact that very little data was collected during the rainy season in this study compared to other studies. It is also interesting to note that the number of species eaten varies for studies conducted in different types of forests such as dry tropical forests (mentioned above), tropical rain forests (109 species, Milton 1980; 195 species, Juliot & Sabatier 1993), and cloud forests (34 species, Gaulin & Gaulin 1982). Tropical rain forests are known for their great diversity in plant species and this is reflected in the diet of howlers. Juliot & Sabatier (1993), for example, found that the top 40 species accounted for only 50% of the total diet of red howlers (*A. seniculus*). The three primary species in the present study generally accounted for > 50% of the diet . However, all studies of howlers have found that they tend to be selective in that they often use species that are relatively rare in the environment.

The preference for seasonal items (fruits, flowers, and young leaves) over perennial items (mature leaves) in this study also corroborates what has been found in other studies of howlers. The choice of these food items is probably related to their higher nutritive value and the lower amounts of secondary compounds (Glander 1978; Milton 1980). However, the availability of seasonal items is not always correlated with their use. In this study, fruits of *Ficus* were always used when available but the same was not the case for fruits of *Bursera simaruba*. Groups often fed heavily in *certain Bursera* trees bearing fruits while ignoring all other trees of *Bursera* which also had fruits and were presumably at the same stage of ripeness. Estrada (1984) also observed that groups would feed in specific trees of certain species and ignore neighbouring trees of the same species. This is likely due to variations in the amount of secondary compounds between trees (Glander 1978). In the present study, only one of two large *Manilkara zapota* trees, only 20 meters apart, was used while the other was systematically ignored even though howlers often had to enter that tree to travel along their arboreal pathways. The same behavior was observed for flowers of *Cochlospermum vitifolium* and *Cecropia peltata*.

Is there a relationship between group size and diet?

Although some differences were found in dietary composition among the four study groups, group size did not provide an adequate explanation for these differences. Other factors may provide more probable explanations. First, differences in species composition for the four groups can be explained in part by the sampling regime. Groups were observed for a maximum of five consecutive days once a month and food items which are only available for brief periods of time (fruits, flowers) would be missed. Variations in the use of flowers of *Tabebuia ochracea* fall in this category. The flowers, which appear in the days following the first rain, are eaten extensively by howlers and depleted in a manner of days. Flowers not eaten in those first few days of availability are thereafter ignored. The same pattern was observed for *Cochlospermum vitifolium* early in the dry season. Secondly, variation in the diet of the howlers can be explained by the absence of certain food species in their home range. *Sciadodendron excelsum* was a major source of fruits during 1992 for group SN (9.7%) but only 0.8% for group BH which only had one representative of that species in its home range (> 90cm DBH) compared to three for group SN (>120cm DBH; > 90cm DBH and 32cm DBH). *Sciadodendron excelsum* was absent in the home range of groups SE and EX. Similar differences were found for *Manilkara zapota*, *Inga vera*, *Spondias mombin*, *Lonchocarpus minimiflorus* and *Casearia sp.*. These differences in presence and absence are explained in large part by the age of the forests in the home range of the study groups. Although groups occupied home ranges which overlapped several successional forest types, certain species were relatively rare and were not likely to be a major part of the diet of some groups.

In spite of some differences, there are far more similarities in the use of resources between the four groups. Not surprisingly, the primary food sources are the same for all four groups. *Ficus* is commonly found in the diet of many species particularly because of their nutritious fruits and their widespread distribution in the tropics (Janzen 1979). Gaulin et al. (1980) reported that howler group size at Barro Colorado Island was highly correlated with density of *Ficus*. Although no such correlation was found in the present study, *Ficus* remained an important food source despite a much lower density of *Ficus* at Santa Rosa. *Pithecellobium saman* are mostly used for their flowers which are produced in great quantities (tens of thousands) once or twice during the dry season (Janzen 1983). Mature trees of this species are relatively large (>90cm DBH) and are abundant in some parts of Santa Rosa. *Bursera simaruba*, which are among the most abundant trees, were used heavily in this study although howlers were selective in their choice of individual trees used.

Similarities were also found in the average number of species consumed on a daily basis with an overall average of 3.7 species. The lack of differences may reflect the need to obtain the necessary nutrients which cannot be found in only one or two species. Milton (1980) found that howlers at Barro Colorado Island (BCI) used on average 7 to 8 species *per* day. BCI has a much higher diversity of plant species with an H' of 3.9 (Shannon-Wiener's H') compared to 2.9 for Santa Rosa. Howlers at BCI also used a total of 109 species compared with 45 in Santa Rosa. Santa Rosa also has a marked dry and wet season compared with BCI which may limit the number of available food sources when deciduous species lose their leaves during the dry season. However, no significant differences could be found between the rainy season and the dry season. Similarities were also found in the turnover of food species on a daily basis with an average of 54%. These results are very similar to the turnover rates found by Milton (1980), who reported turnover rates of 51%. These similarities may be explained by the fact that howlers use seasonal items (flowers, fruits, young leaves) and that they are more likely to be depleted rapidly. However, the lack of difference between small and large groups may be more easily explained by the need to patrol the home range and often leave behind patches that are not depleted and find new food sources elsewhere.

Another similarity with findings of other studies was the preference for large feeding trees (>60cm DBH) by all groups. Large trees are relatively rare compared to other trees in most areas of Santa Rosa but are used preferentially by howlers. Leighton & Leighton (1982) have reported that the number of individuals feeding in a tree (feeding aggregates) was limited by the number of food items available in the feeding tree and that groups should apportion themselves among feeding trees according to the size of feeding trees. Although this may be the case for large groups, small groups should also use large feeding trees and thereby limit the distance traveled each day in search of food. In addition, primary food sources in Santa Rosa tend to be large trees and because howlers use preferentially those trees, this may further explain the similarity in the size of feeding trees among groups. Under certain conditions however, large groups may have to bear the burden of having to feed more individuals and may compensate by travleeing longer distances on a daily basis in search of food or by switching to less nutritious food sources.

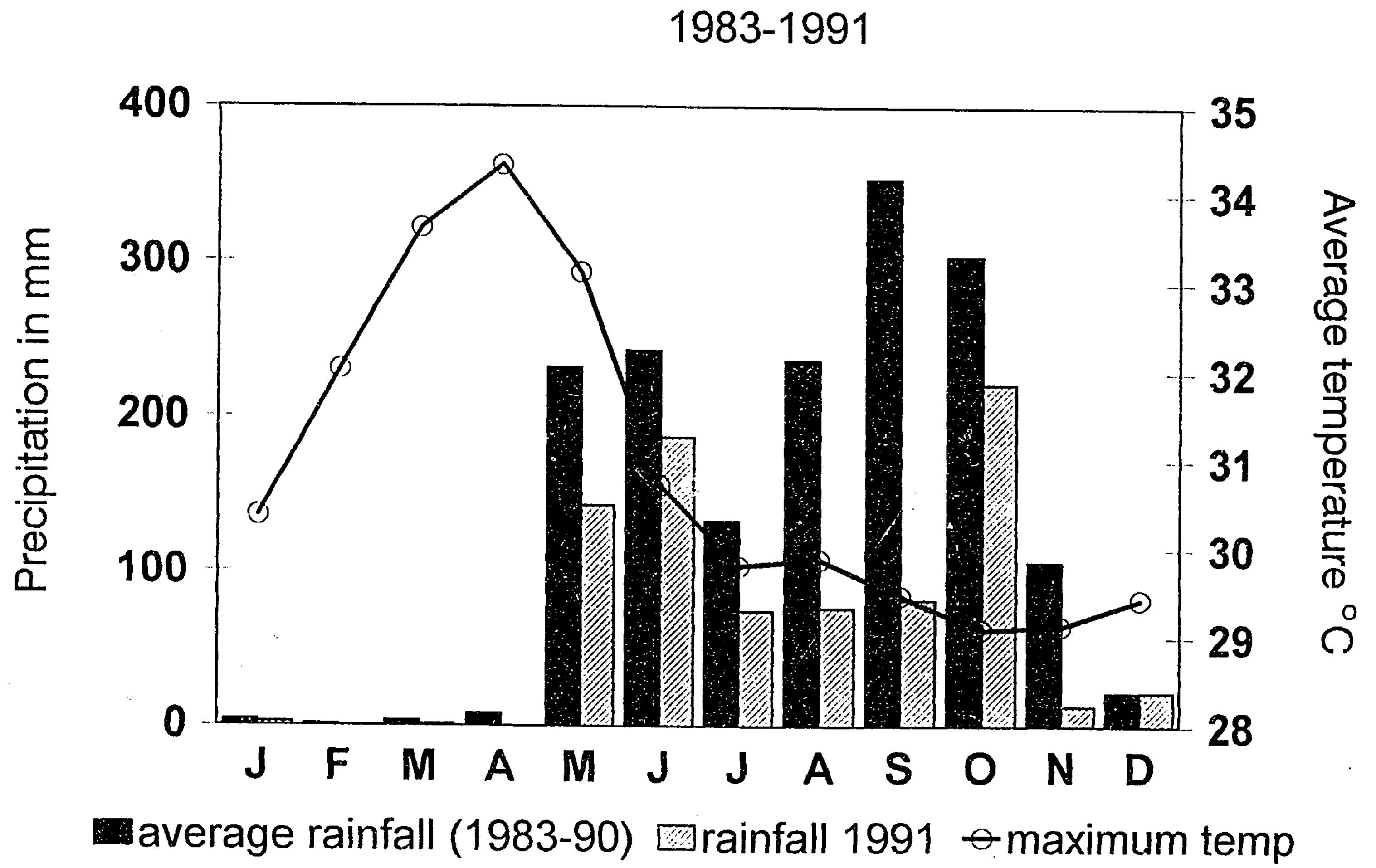


Figure 2-1. Average monthly maximum temperature and precipitation for 1983-1991 for the administration area of Santa Rosa National Park.

Table 2-1. Composition of the four study groups and the breakdown of sampling time spent with each group.

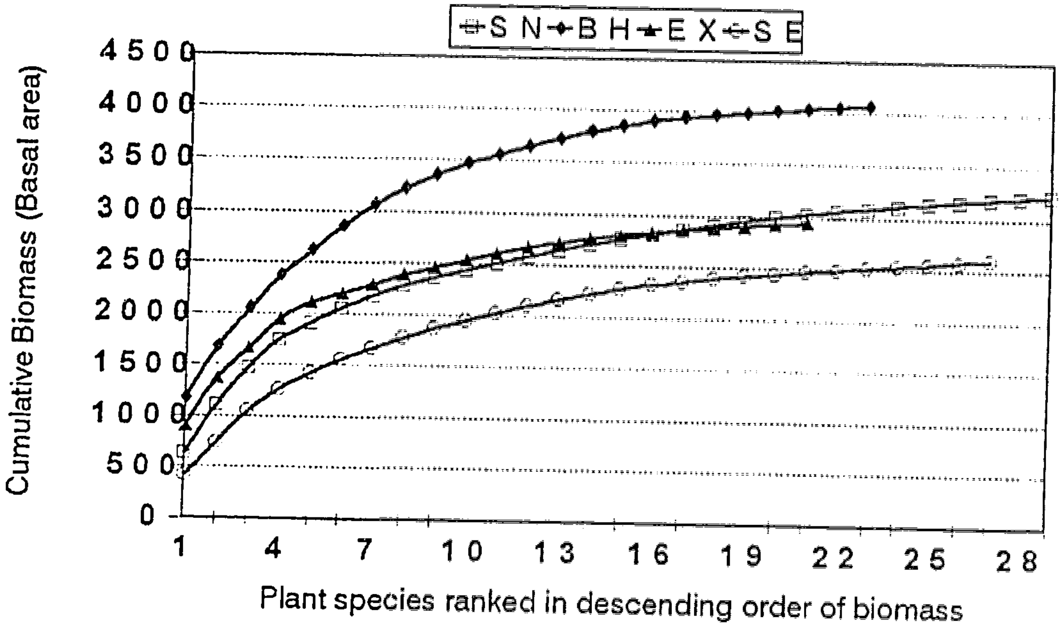
	Group Composition					**Sampling Time**	
Group	Males	Females	Juveniles	Infants	Total	# hours	# days
SE 1991	2	2 (1)	1 (0)	2 (1)	7 (4)	275	22
1992	2	2	1	1	6	302	25
EX 1991	2	5 (4)	2 (1)	5 (4)	14 (11)	241	18
1992	1	5	1	3	10	291	24
SN 1991	5	12	2	9	28	324	27
1992	3	12	4	1 (3)	20 (22)	304	25
BH 45[a]	7	22	5	11	45	37	3
BH 18	3	9	2	4	18	73	6
BH 6	2	3	1	0	6	193	16
TOTAL						2,040	166

( ) number in parentheses represent the number of individuals at the end of the field season if the number changed

[a] see text for explanation

Table 2-2. Number of trees of each species and family for each sample plot.

Species	Family	BH	SE	EX	SN
Albizzia caribea	Mimosaceae			10	
Annona purpurea	Annonacaceae			3	3
Annona reticulata	Annonacaceae			1	
Apeiba tibourbou	Tiliaceae		2		
Astronium	Anacardiaceae		4	2	2
Bombacopsis	Bombacaceae	8	2		
Brosimum	Moraceae		1		1
Bursera simaruba	Burseraceae	17	5		3
Bursera tomentosa	Burseraceae	1			
Calycophyllum	Rubiaceae	8	5		2
Capparis indica	Capparidaceae				4
Casearia spp.	Flacourtiaceae		3		
Cecropia peltata	Moraceae	2	4	3	
Cedrela mexicana	Meliaceae				1
Chimarrhis	Rubiaceae			2	1
Chlorophora	Moraceae	2		1	8
Chomelia spinosa	Rubiaceae	5	1		2
Cochlospermum	Cochlospermaceae	39	13		1
Cordia panamensis	Boraginaceae	1	1		2
Erythroxylon spp.	Erythroxylaceae				1
Exostema mexicana	Rubiaceae	1	2	1	16
Ficus spp.	Moraceae	1		1	
Guazuma ulmifolia	Sterculiaceae	1			
Guettarda	Rubiaceae	1	1		1
Hemiangium	Hippocrataceae	5			
Hymenaea	Caesalpiniaceae	9	1	1	
Inga vera	Mimosaceae		1		
Jacarandia copaia	Bignoniaceae				1
Licania arborea	Chrysobalanaceae		2		1
Lonchocarpus	Fabaceae	3	3		2
Luehea candida	Tiliaceae	8	9	7	16
Luehea speciosa	Tiliaceae	2	1	2	1
Manilkara zapota	Sapotaceae	1	2	12	2
Mastichodendron	Sapotaceae		1	2	2
Ocotea veraguensis	Lauraceae		3	1	1
Sapium	Euphorbiaceae		1	1	4
Schoepfia schreberi	Olacaceae		1	2	
Sciadodendron	Araliaceae	2	1		
Slonea terniflora	Elaeocarpaceae			23	
Spondias mombin	Anacardiaceae	6	9		8
Swietenia	Meliaceae				5
Tabebuia ochracea	Bignonicaeae	1		1	
Tabebuia rosea	Bignoniaceae	3		1	3
Trichilia spp.	Meliaceae			2	3
Zuelania guidonia	Flacourtiaceae		2		1
Total # of species		23	27	21	29
Diversity Index H'		2.49	2.92	2.49	2.9



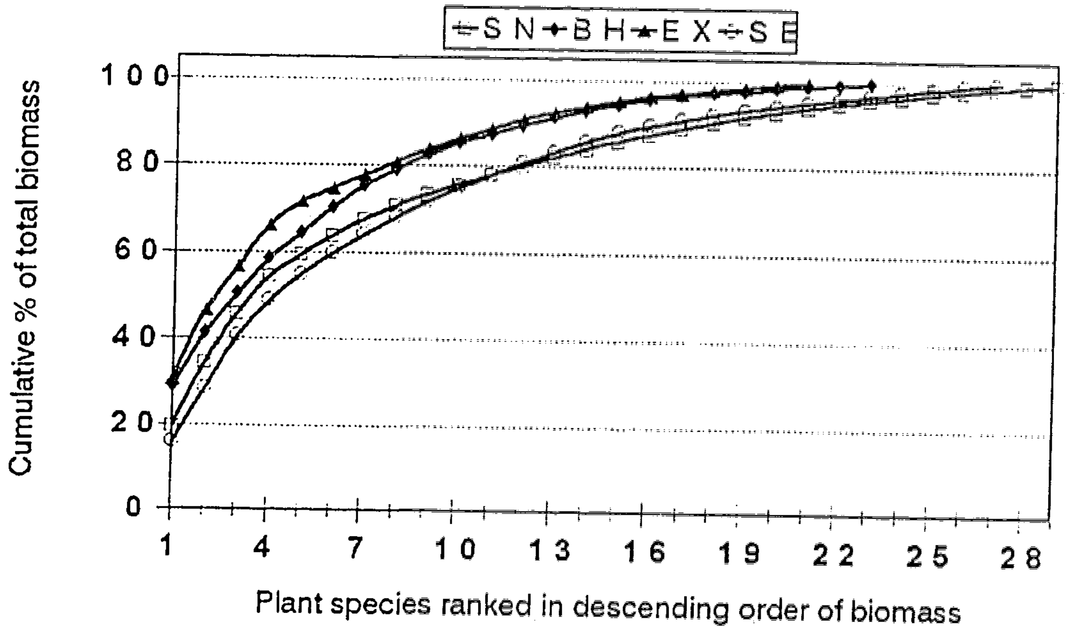


Figure 2-2. Cumulative plots of plant species' biomass expressed as total basal area and percentage of biomass for each sample plot.

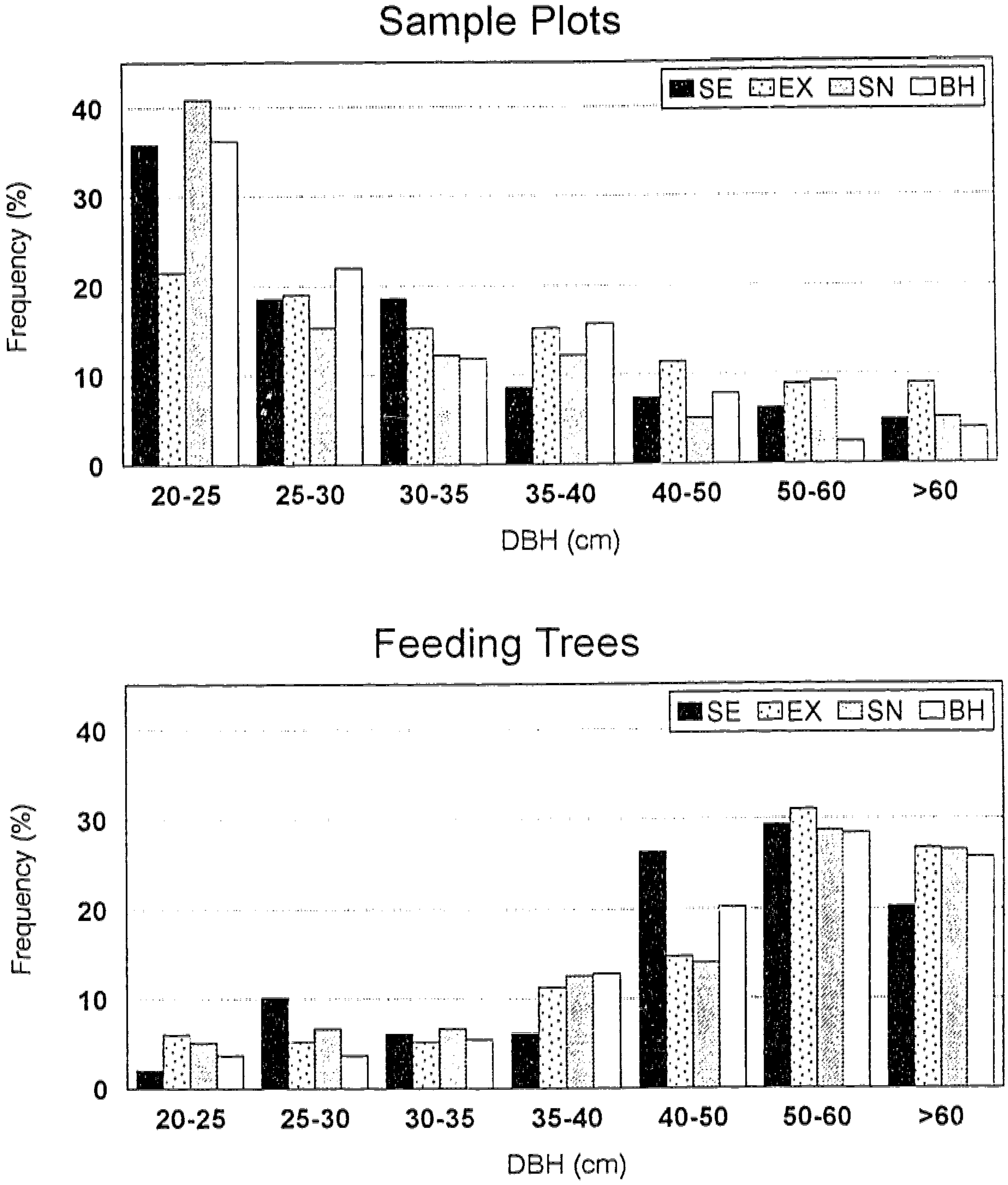


Figure 2-3. Relative frequency of the size of trees in each sample plots and feeding trees used by each group.

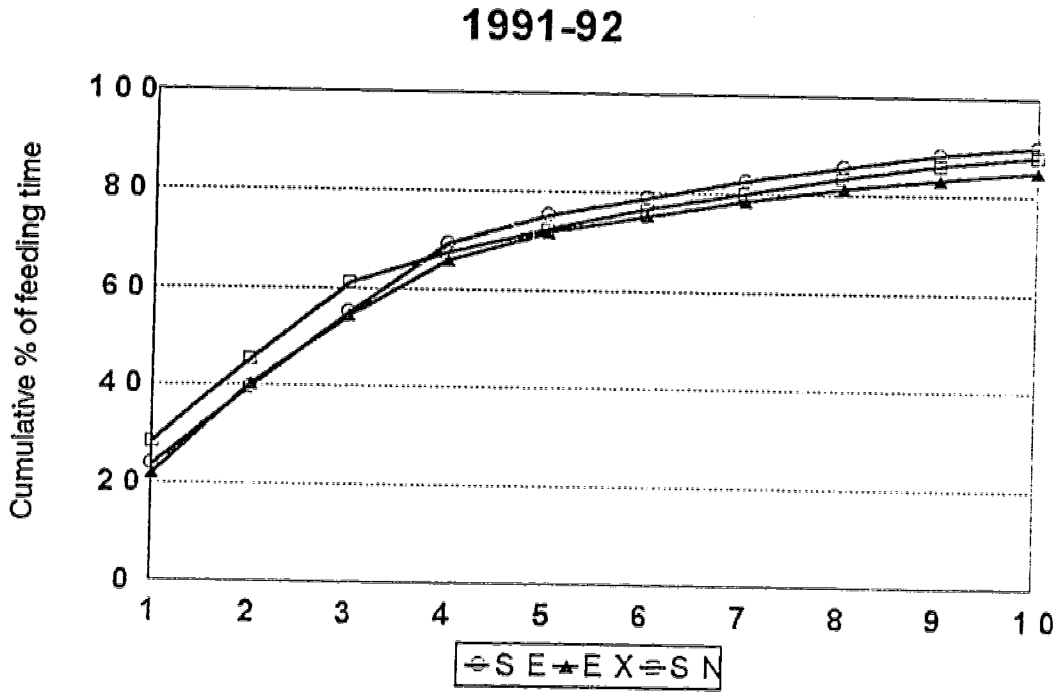
Table 2-3. Diet composition expressed as a percentage of feeding time for the duration of the study for each study group.

Family/species	BH	SE	EX	SN	ALL	items used	# days used
Anacardiaceae							
Astronium graveolens	2.2	0	0	0.5	0.5	yl,ml	3
Spondias mombin	2.3	0.6	0	0	0.5	fl	3
Spondias purpurea	0.4	0	0.4	0.8	0.5	fr,ml	5
Araliaceae							
Sciadodendron excelsum	0.8	0	0	6.3	2.5	fr	7
Bignoniaceae							
Tabebuia ochraceae	0	0	2.1	3.4	2.5	fl	5
Tabebuia rosea	1.8	0	0	0	0.3	yl	1
Bombacaceae							
Bombacopsis quinatum	2.3	0	0.7	0.5	0.7	fl,ml	6
Boraginaceae							
Cordia panamensis	1.4	0.8	0.9	2.0	1.4	ml	10
Burseraceae							
Bursera simaruba	18.6	15.7	18.3	17	17.2	fr,yl,ml	96
Caesalpiniaceae							
Hymenaea courbaril	2.0	3.8	3.2	4.4	3.7	fl,yl,ml	29
Swartzia cubensis	0.0	0.0	3.5	0.0	0.8	fr	3
Capparidaceae							
Capparis indica	0.8	0.0	0.0	0.0	0.1	ml	1
Chrysobalanaceae							
Licania arborea	0.3	3.1	11.5	3.4	4.6	yl,ml	29
Cochlospermaceae							
Cochlospermum vitifolium	5.3	0.0	0.0	0.5	1.0	fl	5
Elaeocarpaceae							
Muntingia calabura	1.7	5.7	0.3	0.0	1.8	fl,ml	17
Slonea terniflora	0.0	0.0	0.5	0.0	0.1	yl	1
Euphorbiaceae							
Sapium thelocarpum	0.0	0.8	0.5	0.0	0.3	ml	6
Fabaceae							
Andira inermis	0.9	0.2	0.0	0.5	0.4	yl,ml	4
Gliricidia sepium	0.0	0.5	0.0	0.4	0.3	fl	2
Lonchocarpus minimiflorus	2.4	0.0	0.9	0.0	0.6	fl,ml	4
Flacourtiaceae							
Casearia sp.	0.0	3.6	1.5	0.0	1.2	fl,yl,ml	13
Zuelania guidonia	0.4	0.0	0.0	0.0	0.1	ml	1
Hippocrataceae							
Hemiangium excelsum	0.0	0.0	0.0	0.2	0.1	ml	1
Meliaceae							
Trichilia sp.	1.4	0.3	0.7	1.2	0.9	ml	7

Table 2-3. (continued)

Family/species	BH	SE	EX	SN	ALL	items used	# days used
Mimosaceae							
Albizzia caribea	0.0	0.4	0.0	0.9	0.5	yl,ml	6
Enterolobium cyclocarpum	1.5	0.3	0.5	0.1	0.5	fl,ml	4
Inga vera	1.8	1.8	0.4	4.7	2.6	fl,yl,ml	10
Lysiloma semanii	1.5	0.2	1.5	0.0	0.6	fl,yl,ml	3
Pithecellobium saman	8.5	14.2	14.3	15.8	13.9	fl,yl,ml	69
Moraceae							
Brosimum alicastrum	0.4	0.3	1.7	0.8	0.8	yl,ml	8
Castilla elastica	2.7	0.0	0.2	0.0	0.5	yl	6
Cecropia peltata	0.3	0.0	0.0	0.0	0.1	fl	2
Chlorophora tinctoria	5.8	0.6	2.8	2.8	2.7	fr,yl,ml	20
Ficus sp.	17.4	23.7	21.8	28.4	24.1	fr,yl,ml	85
Rubiaceae							
Calycophyllum candidissimum	0.0	0.0	0.0	0.2	0.1	ml	2
Chomelia spinosa	0.6	1.0	0.7	0.9	0.8	yl,ml	8
Exostema mexicana	0.0	0.0	0.0	0.1	0.1	ml	1
Sapindaceae							
Dipterodendron costaricense	1.8	0.0	0.0	0.0	0.3	fr	2
Thouinidium decandrum	0.0	2.6	0.4	0.3	0.9	yl,ml	7
Sapotaceae							
Manilkara zapota	3.9	15.6	5.8	0.7	6.1	all	31
Mastichodendron capiri	2.2	0.0	1.4	0.0	0.7	yl,ml	6
Simaroubaceae							
Simarouba glauca	1.1	0.3	0.0	0.3	0.3	ml	3
Sterculiaceae							
Guazuma ulmifolia	1.6	0.5	0.3	0.4	0.6	fr,yl,ml	5
Sterculia apetala	0.0	0.0	0.6	0.0	0.1	ml	1
Tiliaceae							
Luehea candida	0.5	0.5	0.2	1.6	0.9	fl,yl,ml	12
Unidentified							
Vines, lianas, epiphytes	0.9	2.4	2.4	0.8	1.5	leaves	19
unidentified (3 species)	2.0	0.3	0.0	0.0	0.4	ml	5
Total Feeding Minutes (PRT)	3,257	5,293	4,613	7,839	21,002		
Diversity Index H' (1992)	2.93	2.24	2.51	2.30			
Diversity index H' (1991-1992)	--	2.38	2.51	2.40			

fl=flowers fr=fruits yl=young leaves ml=mature leaves



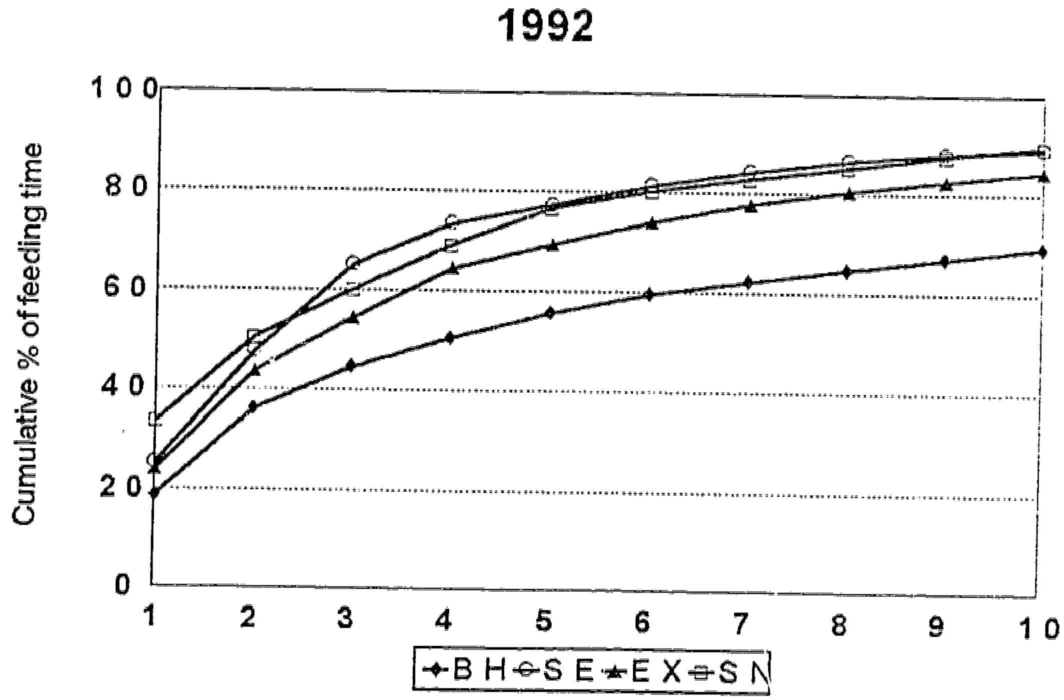
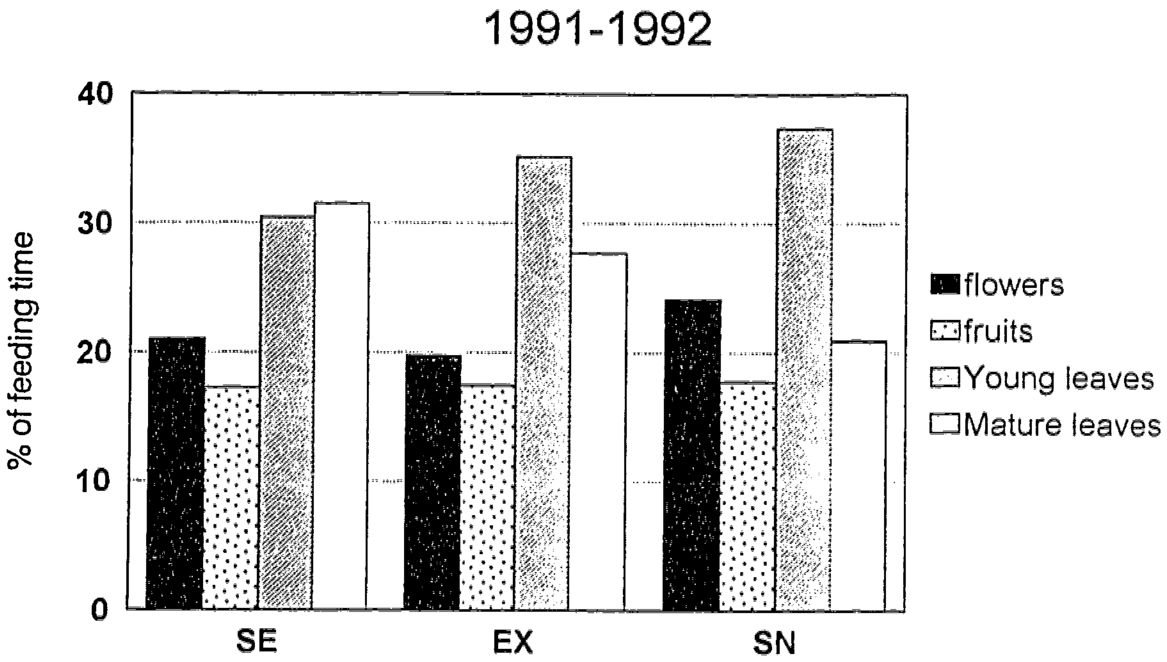


Figure 2-4. Relative contribution of the top 10 species to the overall diet of each group (expressed as percentage of feeding time) for 1991-1992 and 1992. The top 10 species plotted for each group are the species which contributed the most to the diet of each group individually and are not necessarily the same for each group (see Table 2-3).

Table 2-4. Number of food species and food items eaten overall and for each season.

	Group				
Food Source	BH	SE	EX	SN	ALL
Total					
Species	33	25	29	30	46
items	47	47	47	56	84
Dry Season					
Species	21	20	26	29	41
items	29	36	39	49	83
Rainy Season					
Species	19	15	15	12	33
items	27	23	20	19	52



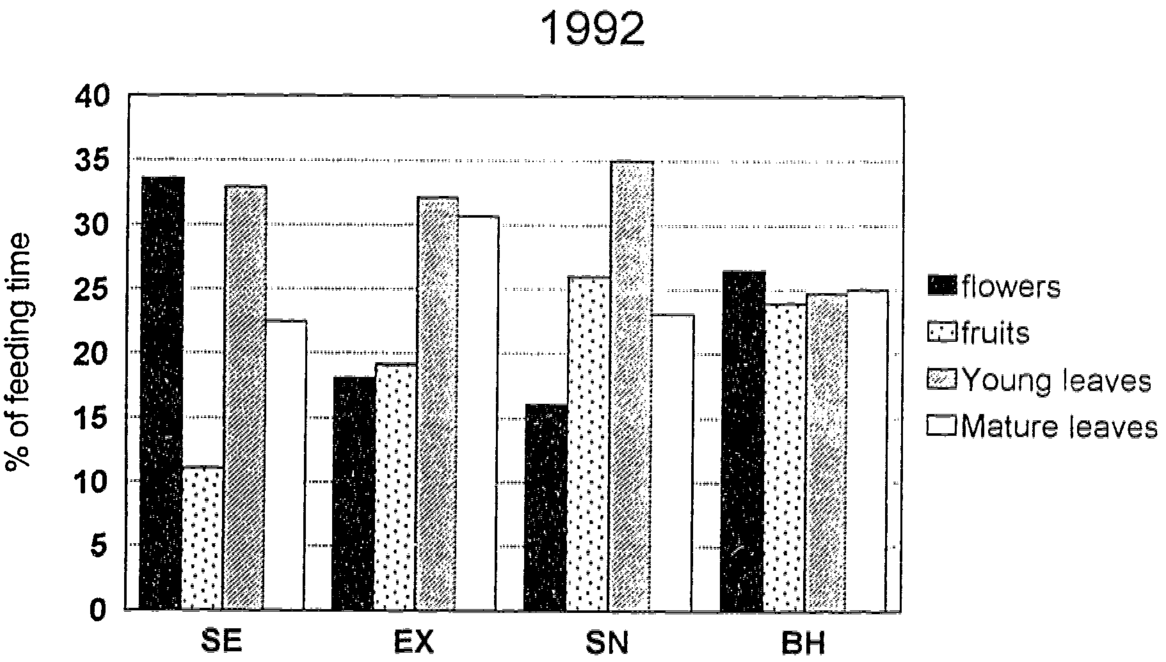


Figure 2-5. Percentage of time spent feeding on each food item for 1991-1992 and 1992.

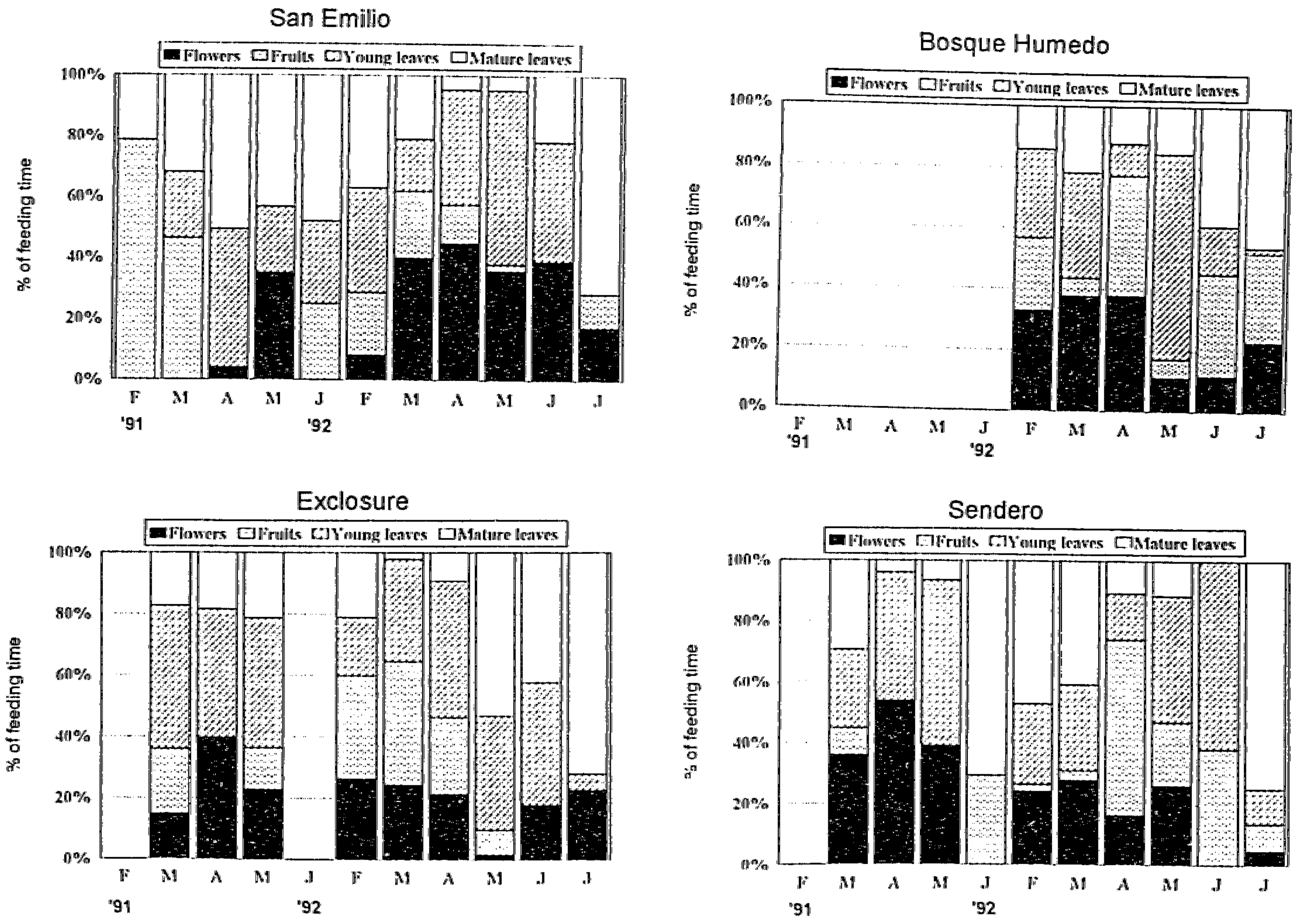


Figure 2-6. Monthly variations in time spent feeding on each food item (expressed as percentage) for each group over the study period.

Table 2-5. Utilization of primary food species by each study group.

Species/group	% of feeding time	mean daily % of diet when used	# trees used	# times used	% days used	items used
Bursera simaruba						
BH	18.6	29.0	25	29	69.5	fr,yl,ml
SE	15.7	25.3	19	46	52.2	fr,yl,ml
EX	18.3	25.6	28	48	75.7	fr,yl,ml
SN	17.0	27.8	28	52	57.1	fr,yl,ml
ALL	17.2	26.7	97	175	61.9	fr,yl,ml
Ficus spp.						
BH	17.4	33.3	8	17	43.5	fr,yl,ml
SE	23.7	37.0	6	40	41.3	fr,yl,ml
EX	21.8	37.7	7	29	67.6	yl,ml
SN	28.4	37.8	12	55	63.2	fr,yl,ml
ALL	24.1	37.1	30	141	54.8	fr,yl,ml
Pithecellobium saman						
BH	8.5	29.3	7	19	43.5	fl,yl
SE	14.2	29.7	10	37	39.1	fl,ml
EX	14.3	31.2	8	33	54.0	fl,yl
SN	15.8	39.8	7	40	42.8	fl,yl,ml
ALL	13.9	33.2	29	129	44.5	fl,yl,ml

fr=fruits yl=young leaves ml=mature leaves fl=flowers

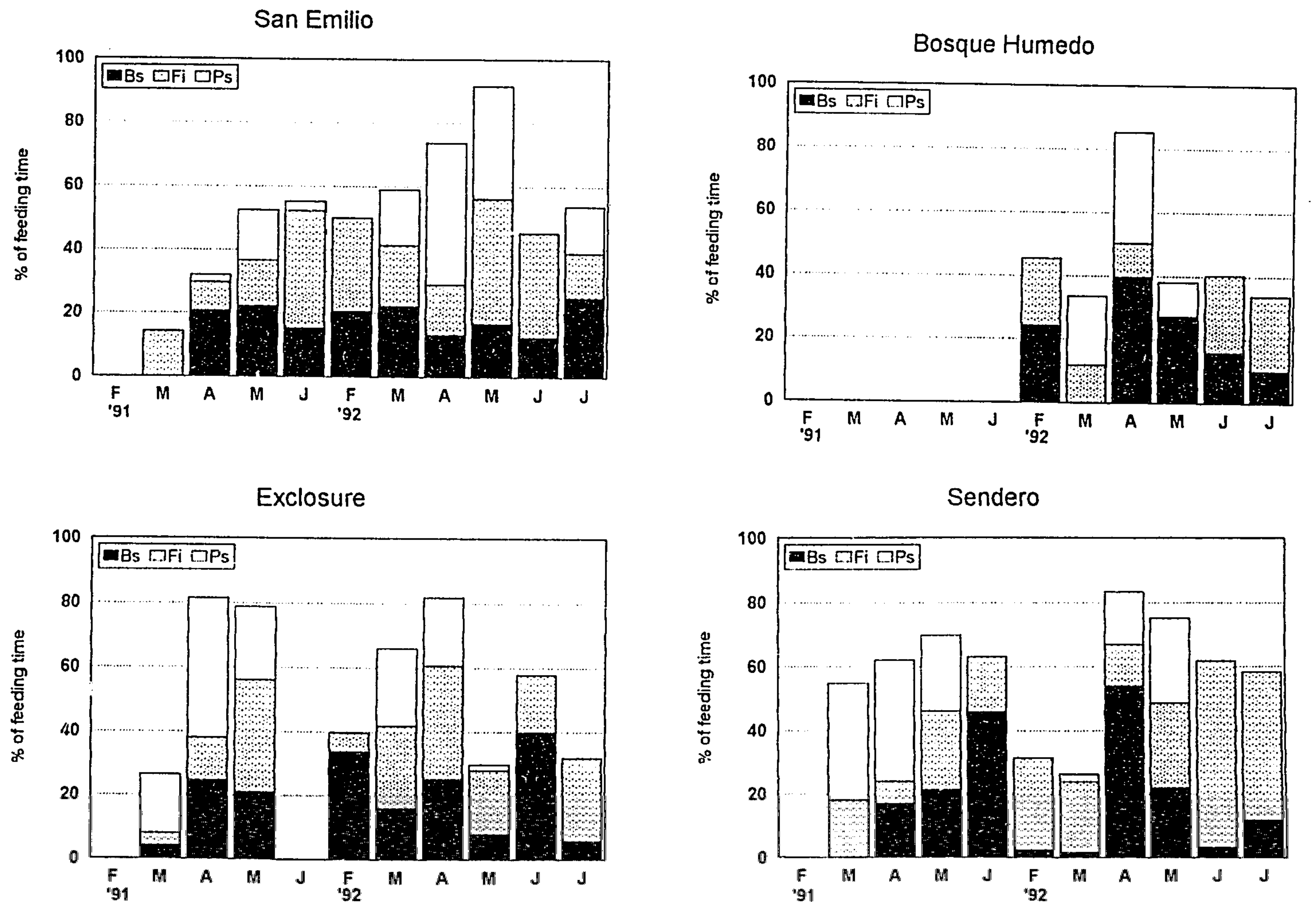


Figure 2-7. Percentage of time spent feeding on *Bursera simaruba* (Bs), *Pithecellobium saman* (Ps), and *Ficus spp.* (Fi) over each month of the study period.

Table 2-6. Number of food species used on a daily basis.

Group	Total				Dry season				Rain Season				Dry vs Rain season		
	mean	s.d.	s.e.	cv	mean	s.d.	s.e.	cv	mean	s.d.	s.e.	cv	t-test	df	P=
BH	4.34	1.79	0.37	41.20	4.46	1.71	0.47	38.30	4.20	1.98	0.62	47.10	-0.34	21	0.73
SE	3.58	1.35	0.20	37.70	3.45	1.30	0.22	37.70	3.92	1.49	0.41	38.00	1.05	44	0.29
EX	3.75	1.44	0.23	38.40	3.62	1.39	0.25	38.40	4.25	1.58	0.55	37.20	1.10	35	0.28
SN	3.54	1.62	0.23	45.70	3.79	1.66	0.28	43.80	2.92	1.38	0.37	47.30	-1.71	46	0.09
ALL	3.72	1.54	0.12	41.40	3.72	1.50	0.14	40.30	3.73	1.64	0.24	43.90	-0.03	152	0.97

s.d .= standard deviation s.e. = standard error of the mean cv = coefficient of variation

Table 2-7. Daily turnover rate of food species. Numbers represent the percentage of species used one day and not the next day.

Group	Total				Dry season				Rain Season				Dry vs Rain season		
	mean	s.d.	s.e.	cv	mean	s.d.	s.e.	cv	mean	s.d.	s.e.	cv	t-test	df	P=
BH	45.62	31.29	7.59	68.60	53.80	35.15	11.11	65.30	33.92	22.07	8.34	65.10	1.32	15	0.20
SE	55.19	28.17	4.83	51.00	58.79	28.61	5.72	48.70	45.18	25.75	8.58	56.90	1.25	32	0.21
EX	57.15	30.41	5.85	53.20	52.85	28.49	6.21	53.90	72.22	34.82	14.21	48.20	-1.40	25	0.17
SN	56.90	30.87	5.14	54.30	51.86	31.26	6.13	60.30	69.99	26.98	8.53	38.50	-1.61	34	0.11
ALL	54.77	29.90	2.80	54.60	54.47	29.84	3.29	54.80	55.54	30.50	5.39	54.90	-0.17	112	0.86

s.d. = standard deviation s.e. = standard error of the mean cv = coefficient of variation

Table 2-8. Percentage of diet overlap for each group on consecutive months and seasons. Diet overlap was measured using the Percentage Similarity Index (PSI).

Group	Feb Mar '91	Mar Apr	Apr May	May June	Feb Mar '92	Mar Apr	Apr May	May June	June July	mean	Dry Rain
BH	--	--	--	--	21.66	34.88	38.00	15.71	49.28	31.90	41.61
SE	46.96	33.27	57.98	40.81	50.89	50.92	73.02	46.89	45.61	43.68	58.87
EX	--	32.52	62.46	--	23.43	64.76	46.90	32.44	43.28	49.59	58.37
SN	--	65.16	55.64	38.51	42.99	19.48	53.57	32.14	49.85	44.66	46.75

-- not enough consecutive days to measure diet overlap

Table 2-9. Percentage of diet overlap for paired groups for each month. Diet overlap was measured using the Percentage Similarity Index (PSI).

Paired Groups	Mar '91	Apr	May	June	Feb '92	Mar	Apr	May	June	July	mean	Plots' Index of similarity
EX-SE	47.00	42.45	66.38	--	36.18	52.73	52.61	31.38	47.78	57.77	48.25	27.10
EX-SN	47.93	64.11	73.93	--	12.29	28.16	55.68	39.14	21.18	39.95	42.48	22.20
SE-SN	28.42	34.57	57.08	37.15	40.10	27.13	42.44	71.82	36.30	30.66	40.57	47.20
BH-EX	--	--	--	--	30.00	35.56	59.16	20.05	60.06	55.69	43.42	37.10
BH-SE	--	--	--	--	43.96	50.85	63.87	27.34	49.67	39.01	45.78	56.10
BH-SN	--	--	--	--	51.57	23.28	66.57	38.27	32.54	43.72	42.66	29.30

-- not enough data to measure diet overlap

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III. The effects of group size on time budget and ranging patterns in four groups of howler monkeys (*Alouatta palliata*) in a tropical dry forest.

INTRODUCTION

Attempts to understand the evolution of sociality in primates have focused on the costs and benefits of group life (S. Altmann 1974; Bradbury and Vehrencamp 1976; Clutton-Brock and Harvey 1977; Wrangham 1980; van Schaik 1983; Terborgh and Janson 1986; Dunbar 1988). Several studies have suggested that the major benefit of group life is protection against predators (Pulliam 1973; Alexander 1974; Treisman 1975; Hoogland and Sherman 1976; Taylor 1977; Bertram 1978; van Schaik et al. 1983). According to this hypothesis, larger groups have a greater likelihood of detecting predators and may deter attacks on the group through the use of mobbing behavior. Other studies have suggested that the main benefit of group life is an increase in foraging success by members of the group. Among the benefits are an increase in the detection of patchy resources (Horn 1968; Ward and Zavahi 1973), more efficient use of their home range (Cody 1971), and cooperative defense of resources (Schoener 1971; Wrangham 1980). However, regardless of the benefits, researchers agree that the costs of group living set limits to group size and that most of the variation in group size can be explained by the costs (Clutton-Brock and Harvey 1977; Terborgh and Janson 1986).

The major cost of group life is a reduction of foraging efficiency because of increasing competition for food among group members. Nicholson (1954) recognized two forms of competition. Exploitation competition occurs when individuals use resources, thereby reducing the amount of food available to other group members. As a result, groups have to travel further to satisfy their food requirements (Clutton-Brock and Harvey 1977; Waser 1977; Terborgh 1983; Dunbar 1988; Wrangham et al. 1993; Janson and Goldsmith 1995). Interference competition is the result of direct competition (by aggression or threats) between individuals and may reduce the foraging efficiency of subordinate group members (Post et al. 1980; Robinson 1981; Janson 1985). However, the intensity of both types of competition is determined by a number of ecological and social variables such as the type of resources used, the density and distribution of these resources, and group size (Clutton-Brock and Harvey 1977; Dunbar 1988; Chapman 1990; Wrangham et al. 1993; Chapman et al. 1995; Janson and Goldsmith 1995).

In this chapter, I examine the intensity of exploitation competition in four groups of howler monkeys. More specifically, I test the hypothesis that larger groups suffer a reduction in foraging efficiency. A number of studies have previously reported that folivorous primates do not suffer the same costs of group life because the resources they use occur at high density, are evenly distributed, and occur in relatively large patches (Clutton-Brock and Harvey 1977; Isbell 1991).

Measures of exploitation competition

Because it is difficult to measure directly the costs incurred by individual group members, researchers have relied upon a number of indirect measures of exploitation competition. One such measure is the size of the home range. As group size increases, larger groups must use a larger area to compensate for the food used by additional group members (Clutton-Brock and Harvey 1977). A number of studies have demonstrated that home range size increases with group size regardless of diet or distribution of resources (McNab 1963; Milton and May 1976; Clutton-Brock and Harvey 1977). Although home range size reflects the area needed to support a group on an annual basis, the distance travelled each day has also been used as a measure of exploitation competition. Larger groups may travel further on a daily basis to meet the energetic requirements of each group member. As group size increases, so does the distance travelled daily (Clutton-Brock and Harvey 1977; Waser 1977; Dunbar 1988). However, Clutton-Brock and Harvey (1977) reported that day range length increased as a function of group size in frugivorous species but not in folivorous species.

Another indirect measure of exploitation competition is the amount of time devoted to major activities each day. Diurnal species have a limited number of hours to carry out their daily activities (active period) before settling for the night (and *vice versa* for nocturnal species). Because the survival of the individual depends on finding food, we can expect that feeding activities and the search for food will have the highest priorities. Since the resources used by primates tend to occur in relatively small and discrete patches, the time spent in search of food will increase as group size increases because the patches will yield fewer food items *per capita* and will force groups to move in search of new patches. Consequently, the amount of time spent travelling during the day in search of food should increase as a function of group size (van Schaik et al. 1983). However, because the time devoted to one activity will reduce the time available for other activities, a reduction in the time devoted to other behaviors will also reflect the intensity of exploitation competition. Altmann (1980) and Dunbar and Dunbar (1988) have reported that as the energetic demand on an animal increases, they are forced to spend less time engaged in social activities.

A number of studies have shown that other factors limit the amount of time individuals can be active. High midday temperatures in the tropics often coincide with periods of rest in primates who must regulate their body temperature (Clutton-Brock 1977). In seasonal environments, thermoregulation may be particularly difficult during the dry season and may further reduce the active period (Oates 1987). Conversely, Iwamoto and Dunbar (1983) reported that in gelada baboons (*Theropithecus gelada*), low temperatures resulted in increased time spent feeding, to attempt to regulate the gelada's body temperature. Rain may also affect the time budget of animals particularly during periods of heavy rain. Raemaekers (1980) reported that some species are not affected by the rain but that others halt their activities for some time.

Another cost to group living is the synchronization of behaviors between group members. Group life requires a certain amount of coordination of activities in spite of differences in energetic demands. Group members have different food requirements based on their size and reproductive condition. However, to function as a unit, certain activities such as travelling and feeding will have to be more or less synchronized. Green (1978) reported that larger groups of *Macaca silenus* had less synchronized feeding bouts than smaller groups. The lack of synchronization may be a strategy to avoid direct competition for limited resources when food items occur in small and discrete patches. Reduced synchronization may also be a strategy created by the number of "feeding spaces" in patches. Certain individuals may have to wait until other group members leave the patch before they can start feeding. Consequently, when the group moves away, individuals may have to choose between staying behind to feed or moving with the group, particularly if the animal may be vulnerable on its own.

In this paper, I present evidence that individuals in larger groups of howler monkeys incur higher costs than individuals in smaller groups as measured by the intensity of exploitation competition. Larger groups have larger home ranges, longer day range length and are less synchronized. Larger groups are also forced to reduce the time spent resting which is crucial for folivorous species. I also discuss the relationship between group size, exploitation competition and the availability of resources.

MATERIALS AND METHODS

Study Site

The research was conducted in Santa Rosa National Park on the northwestern coast of Costa Rica. The Park, situated 35 km Northwest of Liberia in the province of Guanacaste, covers approximately 10 800 ha consisting of a series of plateaus starting at an elevation of approximately 300 m and drops down to the ocean. Santa Rosa was created in 1971 and consists of a mosaic of grassland, dry deciduous forest and semi-evergreen forest (Bonoff & Janzen, 1980; Janzen, 1983). Common species in the dry deciduous forest are *Bursera simaruba, Chlorophora tinctoria, Enterolobium cyclocarpum, Luehea candida, Pithecellobium saman, Spondias mombin*, and *Guazuma ulmifolia*. Common species in the semi-evergreen forest are *Hymenaea courbaril, Ficus spp., Manilkara zapota, Castilla elastica*, and *Masticodendron capiri*. Santa Rosa is characterized by a dry season extending approximately from December through May, and a wet season which extends from June through November with annual precipitation ranging from 900 to more than 2400 mm, almost all of which falls during the wet season.

During the dry season, deciduous trees lose their leaves and remain bare until the onset of the rainy season.

Since the creation of the park, several studies have been conducted on the primate population inhabiting the area (Freese, 1976; Fedigan, 1986; Fedigan & Baxter, 1984; Fedigan et al., 1985; Chapman, 1987; Chapman et al., 1989; Chapman & Fedigan 1990; Glander et al., 1991; Rose, 1994). Three species of primates are represented in the Santa Rosa population: *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*. Several groups of each species have been followed since 1983 as part of an ongoing study on the demography and behavior of the three species (see Fedigan, 1986). Individuals of the species *Ateles geoffroyi* and *Alouatta palliata* have been captured and marked to allow recognition and to facilitate studies of the different groups. A system of trails covering approximately 20 km has also been made to facilitate access to the groups. A number of ecological studies have also been conducted in the park, facilitating the recognition of plant species and their phenological patterns (Daubenmire, 1972; Frankie et al., 1974; Bonoff & Janzen, 1980; Opler et al., 1980; Janzen, 1982).

Santa Rosa offers an excellent opportunity to study wild primate populations because of the good observation conditions, particularly during the dry season. Also, the marked seasonality offers the opportunity to study the changes in food availability and its effect on foraging strategies within and among groups.

Study Groups

Three groups of howlers were studied during the first field season (1991) and a fourth group was added during the second field season (1992). The changes in group size for groups San Emilio (SE), Exclosure (EX), and Sendero (SN) were the result of births and disappearances of some animals, possibly due to immigration in the case of juveniles and adults, and deaths in the case of infants. However, no cases of immigration or deaths could be confirmed. Group SN also varied in size due to the fission-fusion of this group. Because some individuals were often separated from the main group for several days, the number of monkeys in the study group varied daily. Similarly, early in 1992, the group

Bosque Humedo (BH) fissioned into three distinct subgroups. This pattern had been observed previously by Chapman (1987) for the same group. In the five months following the fission, two subgroups reunited again as had happened in the past. However, the smaller subgroup remained separate even after encountering the parent group at least three times after the separation. Therefore, for the study period, the initial group of forty-five animals was followed for only three days before it fissioned. Subsequently, two subgroups were observed. One subgroup of 18 animals was observed for six days while the smaller group of six animals was followed consistently over the remainder of the field season. The results presented in this paper for group BH are for the smaller subgroup of six animals (BH6) except where noted. The two larger BH groups are referred to as BH18 and BH45. Therefore, in this study, groups SE and BH6 were the smallest groups with approximately six individuals, whereas EX varied between ten and fourteen. Group SN was larger and varied between 20 and 28 individuals (see Table 2-1 in Chapter 2).

The groups were located in the central area of the park and occupied relatively well defined and discrete home ranges although some overlap existed with other groups for all four groups. Individual recognition was not possible for all group members, however, age/sex classes were easily recognized. In all groups, some adults were marked with collars or ankle bracelets of different sizes, shapes and colors (see Glander et al. 1991 for details). In each of the four groups, other animals could be recognized by discolorations of the skin under the hind feet and by permanent scars on the face and on the tail.

Sampling Methods

Groups were observed from January through June 1991 and from January through July 1992. No data was collected in January 1991, and during this time, the monkeys became habituated and were not alarmed by the presence of the observer after only a few days with each group. Whenever possible, each group was followed in a fixed rotation for five consecutive days over a period of three weeks from February through June 1991 and over four weeks from January through July 1992. Data on each group was collected between 0530 and 1800 hours. Groups were usually found in their sleeping sites early in the morning and were followed until they had reached the sleeping sites at the end of the day. A total of 2040 hours of data were collected on the four groups over 166 full days of observation.

For the first field season, the groups were followed using focal sampling sessions (Altmann 1974) of ten minutes in length on adults and juveniles. Subjects were selected at random prior to the beginning of the day, and when possible, were alternated according to age and sex class. The order of rotation was then maintained for the rest of the day. For the second field season, one individual was followed for the whole day and data was collected on adults only, alternating between males and females. Scan sampling was used to determine the time spent in all major activities for each group. Instantaneous scans were taken at ten minute intervals and one activity was scored for the group. Because howler groups are highly synchronous in their activities, the results of the scan sampling is an accurate method for howlers. The behavioral categories used for the scans were feeding (i.e., eating from large food sources), foraging (i.e., eating from small, dispersed food sources), resting, travelling, and other. The above definitions for foraging and feeding were the same as those used by van Schaik & van Noordwijk (1988). To measure the degree of synchrony within groups, I scored a second behavior during the scans when at least twenty percent of the group was engaged in a different activity. This second score was not used to determine the time budget of the study groups.

Daily ranging patterns were measured by recording the direction of group movements and by recording the location of the group on a map made from aerial photographs of the research area. Distances were measured by pacing and measuring with forester's tape the distance from tree to tree. Because howlers often use the same paths to travel from one feeding tree to another, most distances were measured more than once. All daily ranging patterns were later plotted on a map for each group. Home range was then measured by tracing a taut line around the contour of the area used and by superimposing on the map a grid of 1mm x 1mm (equal $100m^2$) and by counting the number of quadrants within the contour of the home range.

Statistical methods

Parametric statistics were used whenever possible over nonparametric tests. For all parametric tests, the distributions of all variables were tested for normality and homogeneity of variances. When values were not normally distributed, an appropriate transformation was applied (Sokal & Rolhf, 1981). The reverse transformations were applied to facilitate the presentation of the results. For multiple group comparisons, a oneway anova with range test (Scheffé's method) was used. Least squares regression analysis was used to examine the relationship between daily and monthly time budget, and diet and environmental variables (temperature). Most variables used in regression analyses were transformed in an attempt to obtain linear models. All probabilities are two-tailed unless stated otherwise. All statistical procedures were carried out using the SPSS/PC statistical package.

RESULTS

Home range and day range

Although most groups had a clearly defined territory, some overlap existed between groups (Figure 3-1). The overlap areas usually centred around large food patches such as *Ficus spp*. and *Manilkara zapota* species. Measurements of home range size were as follows: SE = 17.75 ha, BH6 = 14.25 ha, EX = 46.02 ha, SN = 30.5 ha, BH18 = 94.00 ha and Bh45 = 108.25 ha. Home range size increased as a function of group size (Figure 3-2). Additional variation in home range size may be explained by food density and dispersal. Although I did not attempt to analyze their effects here, the study groups occupied different successional forest types with groups BH18 and BH45 using a young successional semi-deciduous forest with some overlap in pristine semi-evergreen forest. Group BH6 spent most of its time in the pristine semi-evergreen forest after its separation from the main group. However, both forest types have lower food species density than older successional forest types occupied primarily by group SE and SN (see Discussion).

Day range also showed an increase as a function of group size (Figure 3-3). The three larger groups (SN, BH18 and BH45) had significantly longer day ranges than other groups while BH18 and BH45 also had longer day ranges than group SN ($F= 30.25$, $P < .001$, df[5, 161] Scheffé's $P < .05$). Day range was also significantly positively correlated with time spent travelling for all groups except group BH6 (SE, $r^2 = .14$ df[1,35], $P = .10$; EX, $r^2 = .24$ df[1,43], $P = .002$; SN, $r^2 = .08$ df[1,47] $P = .05$; BH6, $r^2 = .01$ df[1,14] $P = .63$). Sample size for groups BH18 (n=6) and BH45 (n=3) precluded meaningful regression analyses. The low coefficient of determination shows that although day range is partly determined by time spent travelling, it is influenced by other variables. However, no consistent patterns emerged in the analysis of the relationship between daily ranging patterns and the percentage of the different food items in the daily diet. No significant correlations were found either with the number of patches used on a daily basis (SE, $P = .14$; EX, $P = .97$; SN, $P = .14$; BH6, $P = .21$) or with patch size (SE, $P= .41$; EX, $P = .32$; SN, $P = .68$; BH6, $P = .83$). Furthermore, between group comparisons of average patch size used on a daily basis did not reveal any significant differences with one exception ($F= 4.02$, $P= .001$ df[5,161] Scheffé's $P < .05$). The only significant difference found was between group SN which used slightly larger patches than group SE (DBH= 72.1 vs 61.2 respectively). Group SN used larger food patches than all other groups and group SE used smaller patches than all other groups.

Seasonality also played a role in daily ranging patterns (Figure 3-4). All four study groups for which seasonal data was collected had shorter day ranges during the rainy season (SE, $t = 2.30$ n=45 $P = .026$; EX, $t = 1.40$ n=41 $P = .179$; SN, $t = 4.51$ n=50 $P < .001$; BH6, $t = 2.90$ n=15 $P = .01$). Group EX used certain areas of its home range during the rainy season which were not used during the dry season. This may explain the lack of a significant difference although day range was still shorter in the rainy season. Shorter day range in the rainy season is likely explained by the distribution of food items used in the rainy season (mostly young leaves and mature leaves, see chapter 2). Annual variations in day range length were also found for groups SE, EX, and SN (Figure 3-4). Precipitation during the rainy season in 1991 was far below average (see chapter 1) and resulted in a much drier season than normal in 1992. As a result, groups SE and EX used parts of their home in 1992 they did not use in 1991 to meet their nutritional requirements, despite the fact that group size had declined for Se, Ex, and SN (see Table 2-1, chapter 2). Groups SE and SN had longer day ranges in 1992 although the difference was significant for group Se only (SE, $t = -5.32$, df, 45 $P < .001$; SN, $t = -1.33$, df, 50 $P = .190$) whereas EX had a shorter day range although the results were not significant ($t = 1.38$, df 41, $P = .176$). It is important to note that both groups EX and SN had fewer group members in 1992 than in 1991 (EX 10 vs 14; SN 20 vs 28) but group SN still utilized the same areas of its home range while EX utilized only parts of it.

Time budget

Figure 3-5 presents the time budget for all six groups for 1992. With the exception of groups BH18 and BH45, the groups spent approximately 70% of their time resting. The remaining time was spent engaged in feeding, foraging, and travelling. The time spent engaged in social behaviors is not included here as it contributed less than 2% of the total activity budget for all groups. It is of interest to note that groups BH18 and BH45 spent only between 55 and 58% of their daily time budget resting. Group BH45 fissioned into three subgroups after only three days of observation (see Methodology). Group BH18 also fissioned a few weeks later. Oneway analyses of variances were carried out to determine if differences existed in the amount of time engaged in different activities between groups (Table 3-1). For 1991, the smaller group (SE) spent more time feeding and less time foraging than the two larger groups EX and SN. Group EX also spent less time foraging than the larger group SN. Since smaller groups do not use significantly smaller food patches than larger groups, they do not deplete patches as fast and may therefore spend more time feeding (eating from large food sources). Consequently, smaller groups also spent less time foraging (eating from small and dispersed food sources) than larger groups. Time spent travelling was also related to group size, as the larger group SN spent more time travelling than the two smaller groups. No differences were found in time spent resting.

Similar results were found for 1992. Smaller groups generally spent more time feeding and less time foraging. Group BH6 was an exception, spending less time feeding than SE and EX and more time travelling than SE, EX, and SN. When groups BH18 and BH45 were included in the analysis, there was a tendency for them to spend more time feeding, more time foraging, and less time resting. The increased time spent feeding and foraging by those two groups can be explained by the increase in time spent active as opposed to time resting (see Discussion).

Regression analysis was also used to examine which variables were important in determining the time spent engaged in different activities (Table 3-2). Time spent travelling and feeding was in large part determined by the time spent resting and was not related to the food items used either on a daily or monthly basis with only a few exceptions. Foraging was not significantly determined by any other behaviors or by diet composition. This suggests that group size may be more important in determining time spent foraging. Because time budget is expressed as a percentage, an increase in time engaged in one activity will result in less time available for other behaviors. However, feeding, foraging, and travelling behaviors were more influenced by the time spent resting than any other activity. Time spent resting in turn was influenced by average maximum temperature although no significant correlations were found on a daily basis or monthly basis (Figure 3-6).

Some seasonal and annual variations in time budget did exist (Figure 3-7), but only a few significant differences were found (Table 3-3). Although groups SE and EX spent less time resting during the rainy season, only group EX exhibited significant differences. Because the dry season begins sometime in May, this does mask part of the differences. The time spent resting in June and July is much lower than previous months (Figure 3-6). The smaller groups (SE and BH6) also spent less time travelling but more time foraging during the rainy season. Annual differences were also found pertaining to resting time.

All three groups (SE, EX, SN) spent more time resting in 1992 while SE and SN also spent less time feeding.

Synchronicity of behavior

Larger groups were significanlty less synchronous in their activities than smaller groups (Figure 3-8; $r^2 = .90$, $P < .001$). Asynchronicity was measured as the percentage of scans where more than 20% of the group was engaged in different activities than the majority of the group. SE and BH6 were asynchronous 10% of the time while members of the larger group BH45 were asynchronous more than 60% of the time. A oneway anova revealed that each of the larger groups (SN, BH18 and BH45) were less synchronous than the three smaller groups ($F = 65.77$ $P < .001$ df[5,93] Scheffé's $P < .05$). Asynchronicity of behaviors varied annually and seasonally for each group (Figure 3-9). Annual differences also showed that groups were more asynchronous in 1992 (SE, $t = 7.10$ n=46 $P < .001$; EX, $t = 6.60$ n=40 $P < .001$; SN, $t = 5.10$ n=50 $P < .001$). Groups were more asynchronous during the rainy season except for group SE. Only group SN was significantly more asynchronous in the rainy season ($t = 2.80$ n=50 $P = .007$).

DISCUSSION

Variations in group size in primates have been explained in large part by the foraging costs as measured by day range and time budget (van Schaik et al. 1983; Dunbar 1992; Wrangham et al. 1993; Chapman et al. 1995). In several studies, the intensity of exploitation competition, i.e., the increase in foraging costs due to additional group members, has also been linked to the distribution of resources (Terborgh 1983; Chapman et al. 1995). However, most studies have concluded that the intensity of exploitation competition could explain some variation in group size among frugivores but not among folivores (Clutton-Brock and Harvey 1977; Isbell 1991; Janson and Goldsmith 1995). The food sources used by folivores have often been described as abundant, evenly distributed, and occurring in large patches, in spite of the number of studies that have shown folivores to be very selective in the choice of plant species used (Milton 1979;

Oates et al. 1980; Glander 1982; Mowry et al. 1996). The results for howlers presented in this chapter indicate clearly that individuals in larger groups tend to incur higher foraging costs than individuals in smaller groups. Larger groups have larger home ranges, longer day ranges, and suffer other indirect costs related to time budget and synchronization of group activities.

Previous studies have reported that home range increases as a function of group size for frugivores and folivores (Milton and May 1976; Clutton-Brock and Harvey 1977). The results presented here corroborate these findings. Although home range appears to be a linear function of group size, some deviations from the expected values may be explained by the distribution of food items rather than by the density and the size of patches used. For example, both group BH18 and BH45 utilized the same territory and had similar home ranges despite their considerable difference in size. Since no differences were found in the size of patches used, the difference in home range size can be attributed to the distribution of the resources. Group EX also had a larger home range than the larger group SN. Furthermore, groups SE and BH6 had similar home ranges despite the fact that they occupied different forest types and were approximately the same size.

Many of these differences may be explained by the fact that the groups occupied different successional forest types. Group BH45's home range overlapped both the pristine semi-evergreen forest and the young successional semi-deciduous forest although the pristine semi-evergreen forest accounted for less than 20% of their total home range. Chapman & Chapman (1990) reported that the density of food sources used by primates in the same area was lowest in the young successional forest and intermediate in the pristine semi-evergreen forest. In this study, the highest density was found in the older successional forest occupied by groups SE and SN. Chapman and Chapman (1990) also demonstrated that these different habitats varied in the temporal distribution of their resources. This may explain why groups BH45, BH18 and EX had relatively large home ranges compared to the other groups. These groups may have to use different habitats in their home range when resources are scarce in one habitat or another. The large home range may be necessary to encompass sufficient areas or different habitats to sustain the group year-round.

Group EX and BH18 had the lowest density of individuals per hectares (home range / group size) with 5.22 hectares per individual for group BH18 and 3.28 for group EX. Group EX was also the only group whose home range overlapped all three forest types. Variation in home range of groups SE and SN may be largely a function of group size, as they both occupied patches of old successional forest. It is interesting to note that the boundaries of their home range corresponded with the presence of large trees of *Ficus*. Also, the areas of overlap in the home range of the groups usually contained at least one large *Ficus*.

Day range length also varied as a function of group size. A number of other factors are known to influence day range within and between species. Wrangham et al. (1993) reported that both food density and travel efficiency (i.e., distance travelled per fitness cost) were correlated with day range and ultimately, group size. At a given level of food density and travel efficiency, day range should increase as a function of group size, provided that food patch size remains constant. Janson and Goldsmith (1995) analyzed the relationship between group size and foraging costs and determined that one of the most important variables influencing group size may be the increase in individual foraging cost. An increase in day range length caused by adding group members should limit group size when the additional distance that must be travelled exceeds the benefits individuals gain by finding new food sources. In this study, variations in day range may be partly explained by group size. Although the differences in average distance travelled increased with group size, all groups occasionally travelled well beyond that distance as demonstrated by the maximum day range observed for each group. This suggests that some variation in day range may be attributed to other factors. Because no differences were found in average food patch size, the remainder of the variation may be explained by density and distribution of food patches. Annual and seasonal variations in day range provide evidence that changes in density and distributions of food sources affect daily path length. Another indirect indicator of increased exploitation competition is that day range increased in 1992 even though groups EX and SN had significantly fewer members (14 vs 11 for EX and 28 vs 22 for SN). Although I could not determine the reason for the changes in group size for group SN, it is possible that increased food competition may have forced some individuals to leave, or for parts of the group to fission. Since this study has ended, group SN fissioned permanently (Fedigan, pers. comm.).

Further evidence of an increase in exploitation competition as a function of group size is provided by the analysis of time budget. Overall, larger groups spent less time feeding and more time foraging. Because all groups fed preferentially in the largest feeding trees (see chapter 1), larger groups may have depleted the patches more rapidly than smaller groups. Also, as the number of feeding spaces in a patch is limited, members of larger groups were often feeding in nearby trees, usually waiting for "spaces" to open up in the preferred feeding trees. Furthermore, if day range is limited by energetic costs and travel efficiency, larger groups may have to spend more time feeding from smaller, less desirable feeding trees to compensate for the diminished food intake caused by the presence of additional group members. In this study, larger groups often stopped briefly while on the move to feed from small trees while this was rarely the case for the smaller groups. The latter usually travelled directly to other food patches using the shortest path. Evidence of this kind of mental map has been reported for a number of species (*Alouatta palliata*: Milton 1980; *Colobus badius:* Marsh 1981; *Papio hamadryas*: Sigg and Stolba 1981; *Papio cynocephalus*: Altmann and Altmann 1970; *Pan troglodytes*: Wrangham 1977). Van Schaik et al. (1983) found that larger groups spent more time travelling in long-tailed macaques (*Macaca fascicularis*). Although there was a tendency for larger groups to spend more time travelling in this study, few significant differences were found. This may be explained by the increase in time spent foraging by larger groups. Because travelling represents the greatest foraging cost, larger groups may have other strategies to limit these costs, such as a greater degree of dispersion while travelling, which would increase the likelihood of detecting food patches (even small ones). This pattern was observed for the larger groups in this study (particularly SN and BH45).

Time spent resting did not vary significantly for the four main study groups. In the tropics, intense midday heat may force some species to halt their activities to prevent problems of thermoregulation. The slow metabolic rate and digestive efficiency of howlers (Nagy and Milton 1979) coupled with a leafy diet may restrict their ability to be active during that period. Capuchin monkeys and spider monkeys in Santa Rosa have much longer active period than howlers. Sesonal variation also indicates that midday temperature may affect the active period, as time spent resting generally decreased in the rainy season. Another explanation may be that the greater density of their food sources allows them to travel less to feed. Furthermore, the rainy season not only offers a greater density of food but also provides more shade to protect them. Time spent resting was correlated with average maximum temperature in this study, although not significantly. I did not expect significant correlations on a daily basis as many other factors probably influence time budget such as food patch size and distribution. However, no single variable could account for the time spent resting for any of the groups, possibly because small groups can easily terminate their feeding bouts long before the midday heat forces them to halt. The reverse may explain the lack of significant correlations for the larger groups. It is also possible that confounding factors not analyzed in this study play an important role such as relative humidity, cooling effects of the wind (particularly during the dry season), time budget of previous days, and so forth.

Two groups however provided evidence that larger groups may find it difficult to remain active long enough for their members to meet their nutritional requirements. Groups BH45 and BH18 spent significantly less time resting and had longer day ranges than all other groups. This very likely explains the fact that group BH45 fissioned (as it had been doing for many years during the dry season, see Chapman 1987). Group BH18, which was subsequently followed for six days, also fissioned. Group BH6 which was a splinter group of BH45 reverted to a time budget which mirrored that of the three other groups. Annual variation in time budget also suggests that temperature along with a decrease in food density (1992 being much drier than 1991) affects the length of the daily active period. Contrary to other species, howlers have very little social time that can be given up when their time budget is being compressed. Dunbar (1992) observed that in the gelada, time devoted to social behaviors such as grooming was time that could be used for more important activities when necessary, although there is a limit to how much social time can be sacrificed particularly if group unity is to be maintained. Consequently, group size may vary because of the constraints on time budget by environmental variables.

Another cost associated with a reduction of the active period is the synchronization of group activities. Several studies have reported that groups are not always synchronous in their activities. This pattern has been observed in *Macaca silenus* (Green 1978), *Colobus badius* (Clutton-Brock 1974) and *Cercopithecus aethiops tantalus* (Kavanagh 1978). In this study, larger groups exhibited less synchronized feeding and travelling activities than smaller groups. Coincidently, groups BH45 and BH18 fissioned while group SN was frequently more scattered while feeding and travelling. When behaviors cannot be synchronized within groups and the time that can be devoted to searching for food and feeding is limited, groups may benefit by separating to avoid being active during the midday period.

Although it is difficult to separate the effects of food density and distribution from the effects of group size, several findings in this study suggest that howler monkeys do incur increased costs as group size increases. The fission and fusion of group BH45 has previously been observed in spider monkeys and chimpanzees and has been related to size, density and distribution of their food sources (McFarland 1986; McFarland-Symington 1988; Chapman et al. 1995). Several findings in this study also contradict previous assumptions about the intensity of food competition in howlers (Isbell 1991; Janson and Goldsmith 1995). More detailed studies on the effects of food density and distribution are needed to determine how they influence group size in folivores.

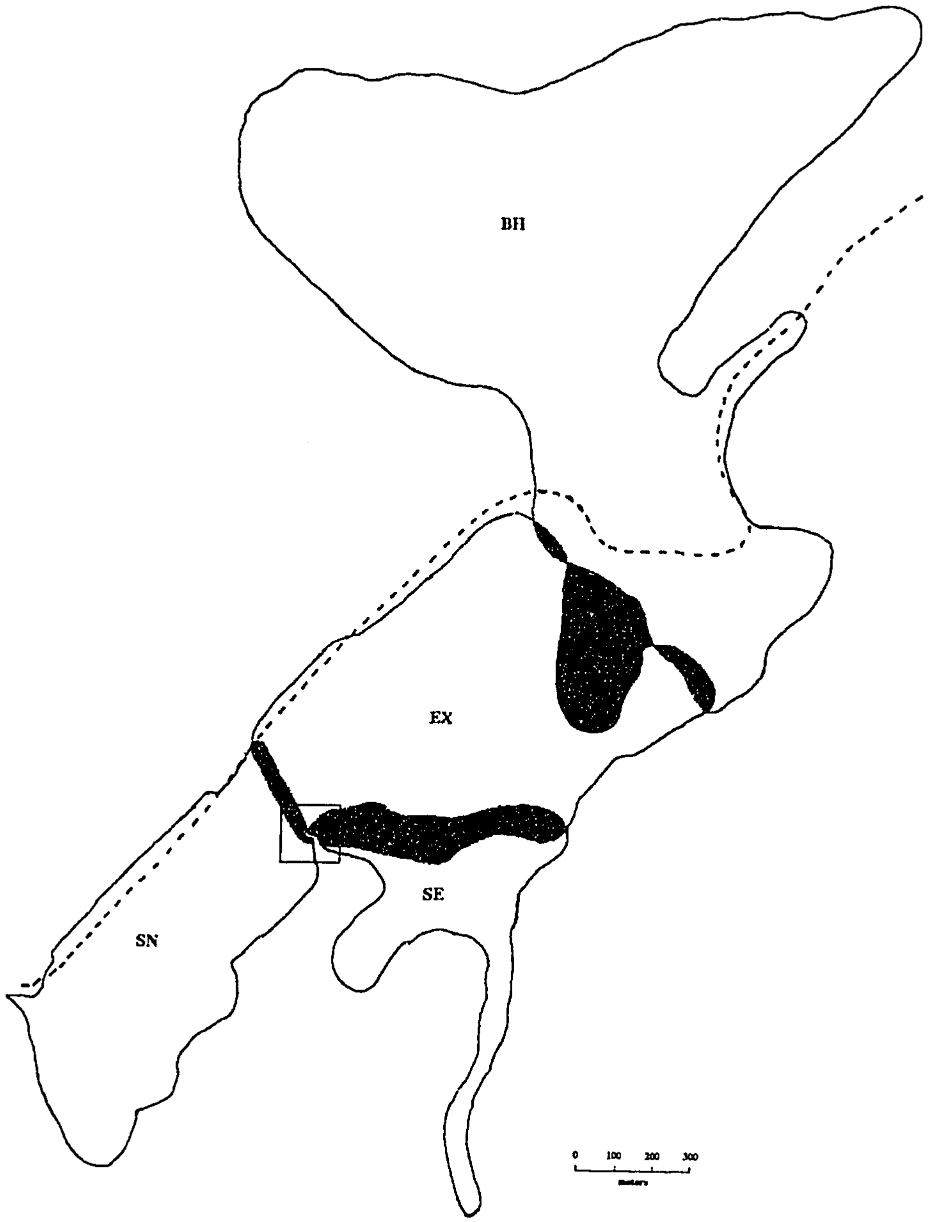

Figure 3-1. Map of the home range of the study groups. The dotted line represents a paved road that runs through the park. Grey areas represent arreas of overlap in home ranges. The dark area on the map was not utilized by any of the groups. The area marked by a square represents an area used by three groups, SE, EX, and SN.

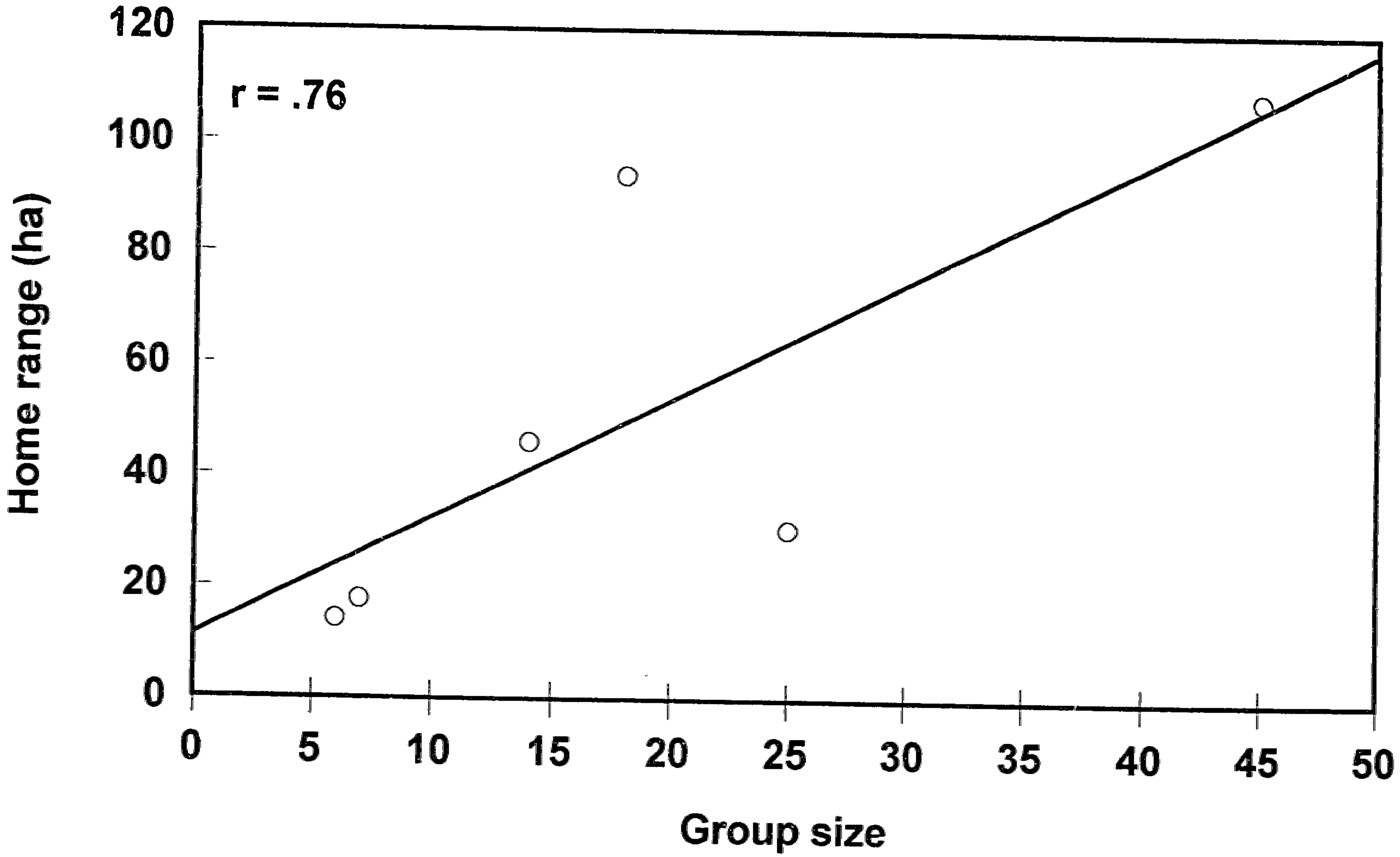

Figure 3-2. Home range area plotted against group size. The six data points represent groups SE, EX, SN, as well as group BH45 and the two subgroups which were followed after BH45 fissioned: BH18 and BH6. The three groups above the regression line occupy more productive forest types than the three groups below the regression line.

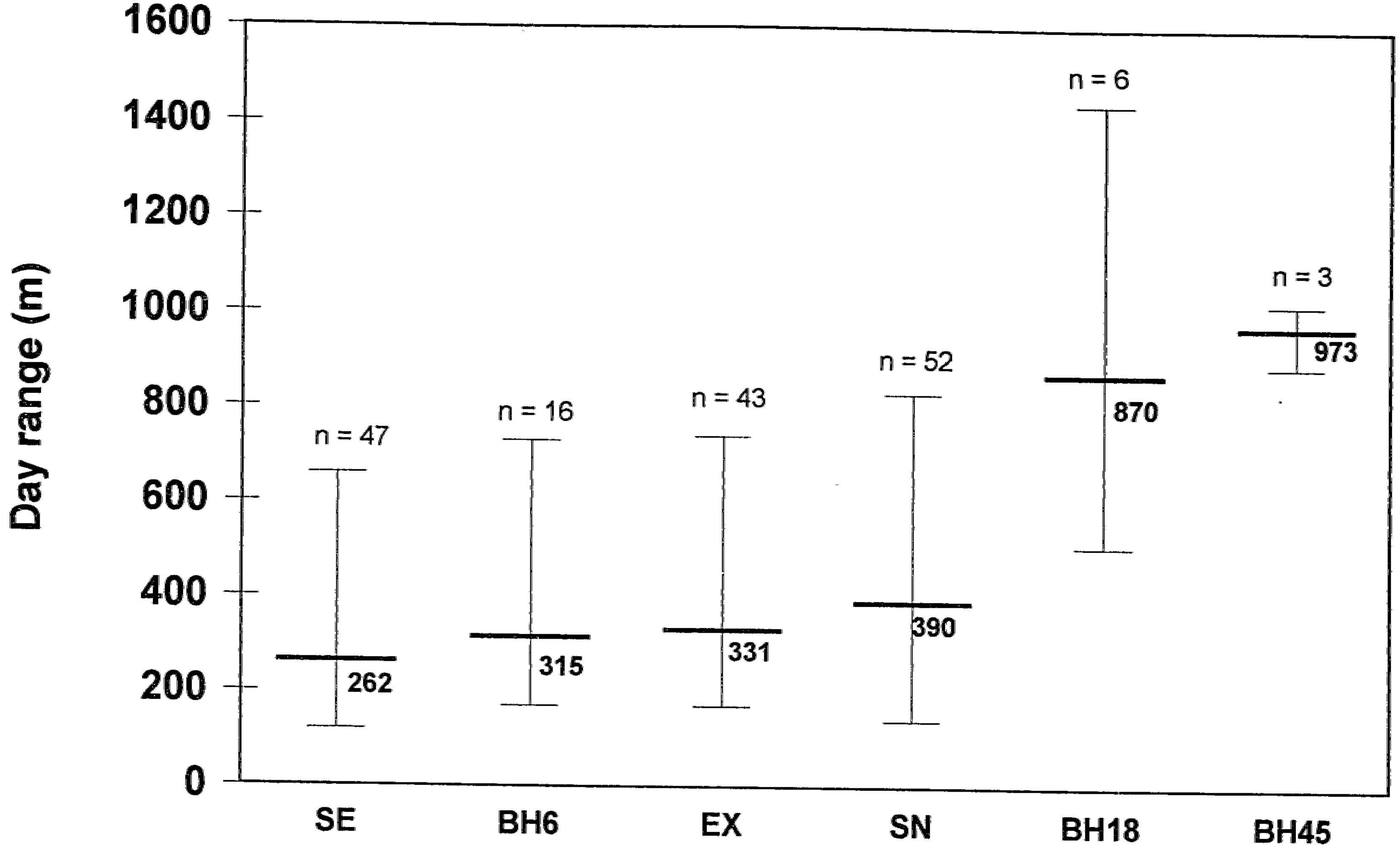

Figure 3-3. Plot of day range for all six study groups. Indicated are the mean, minimum and maximum day range. Numbers indicate the mean. n = sample size.

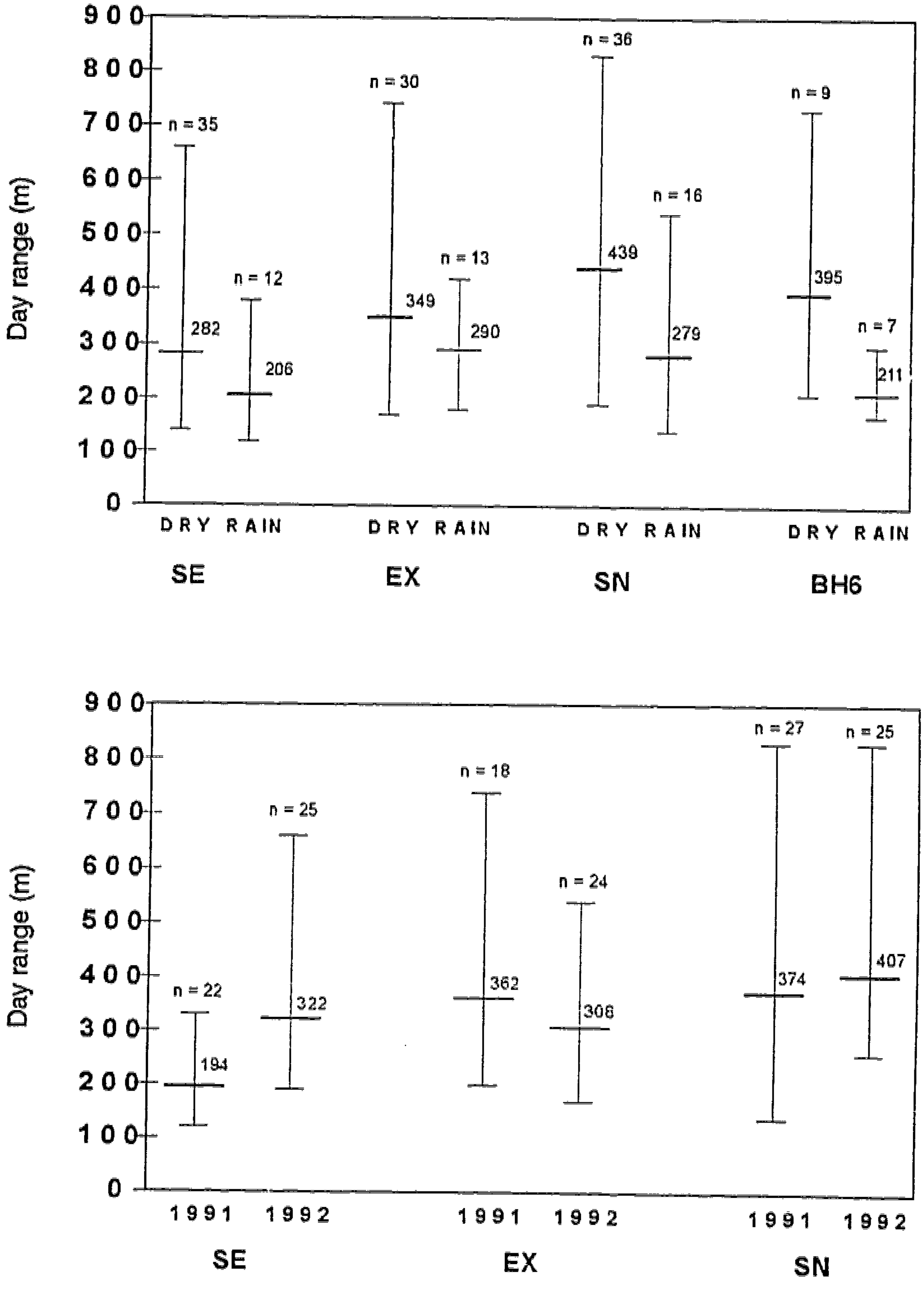

Figure 3-4. Seasonal and annual variations in day range length. Indicated are the mean, minimum and maximum day range. Numbers indicate the mean. n = sample size.

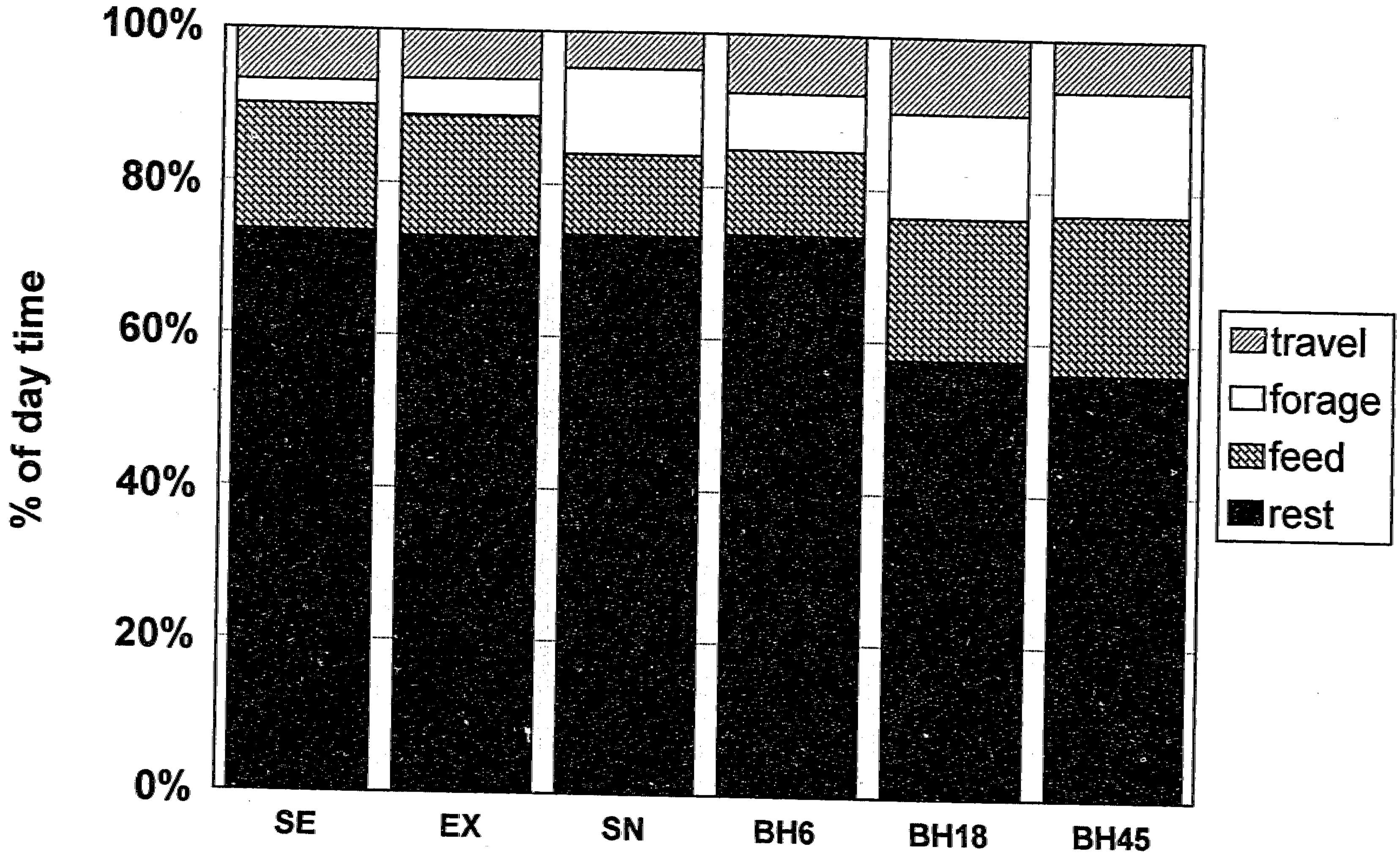

Figure 3-5. Time budget for all six study groups for 1992.

Table 3-1. Between group comparisons of time budget activities for 1991 and 1992.

1991 (SE, EX, and SN only)				
Feeding	SE > EX, SN	f= 13.69	df 2,64	P < .001
Foraging	SE < EX < SN	f= 28.57	df 2,64	P < .001
Resting	no differences	f= 0.41	df 2,64	P = .66
Travel	SE, EX < SN	f= 6.03	df 2,64	P = .004
1992 (excl. BH18 and BH45)				
Feeding	SE, EX > SN, BH6	f= 8.77	df 3,86	P < .001
Foraging	SE, EX < BH6 < SN	f= 20.76	df 3,86	P < .001
Resting	no differences	f= 0.04	df 3,86	P = .98
Travel	SE, EX, SN < BH6	f= 3.10	df 3,86	P = .03
1992 (incl. BH18 and BH45)				
Feeding	BH18, BH45 >	f= 7.59	df 5,93	P < .001
Foraging	BH6, SE, EX < SN, BH18, BH45	f= 16.95	df 5,93	P < .001
Resting	BH18, BH45 <	f= 10.32	df 5,93	P < .001
Travel	BH45 > SN	f= 3.43	df 5,93	P = .006

> and < indicate significant differences at the .05 level

Table 3-2. Daily and monthly determinants of time budget activities.

Group	Daily correlations					
	Dependent variable	Independent variable	Slope (+,-)	r^2	df	P
SE	% travel	% rest	-	0.390	1,42	< .001
	% feed	% rest	-	0.480	1,42	< .001
	% travel	% fruits	+	0.240	1,42	< .001
	% travel	% flowers	-	0.110	1,42	= .028
EX	% travel	% rest	-	0.560	1,34	< .001
	% feed	% rest	-	0.300	1,34	< .001
SN	% travel	% rest	-	0.150	1,46	= .01
	% feed	% rest	-	0.500	1,46	< .001
BH6	% feed	% rest	-	0.480	1,13	= .004
	Monthly Correlations					
SE	% travel	% rest	-	0.370	1,9	= .047
	% feed	% rest	-	0.350	1,9	= .054
	% travel	% fruits	+	0.707	1,9	= .001
EX	% travel	% rest	-	0.773	1,7	= .002
	% feed	% rest	-	0.614	1,7	= .002
	% travel	% yleaves	-	0.499	1,7	= .033
SN	% travel	% rest	-	0.319	1,8	= .088
	% feed	% rest	-	0.768	1,8	= .001
	% travel	% mleaves	+	0.503	1,8	= .021
	% travel	% yleaves	-	0.342	1,8	= .075
BH6	% travel	% flowers	+	0.987	1,2	= .006

yleaves= young leaves mleaves= mature leaves

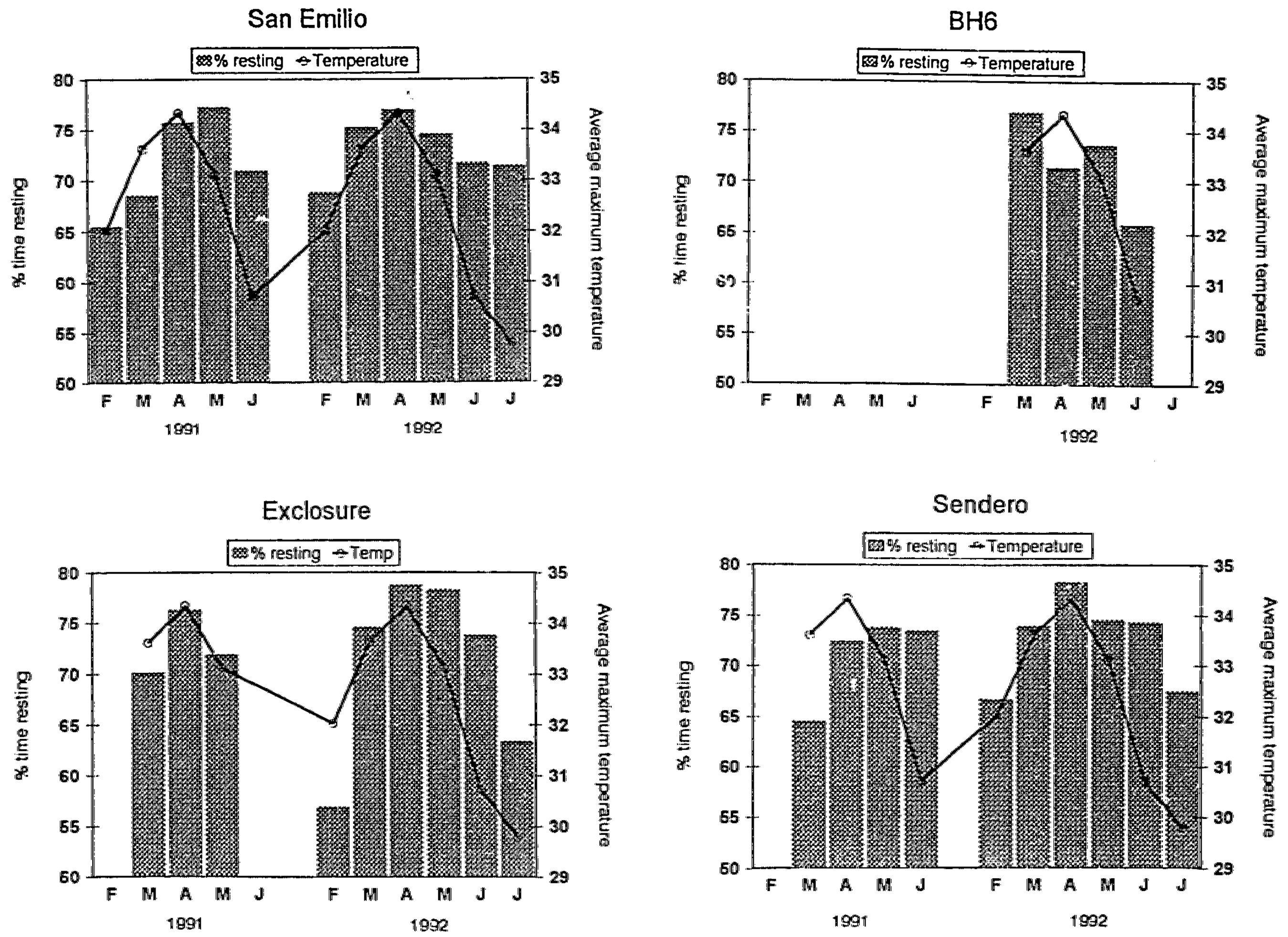

Figure 3-6. Time spent resting on a monthly basis (expressed as percentages) plotted against the average maximum temperature.

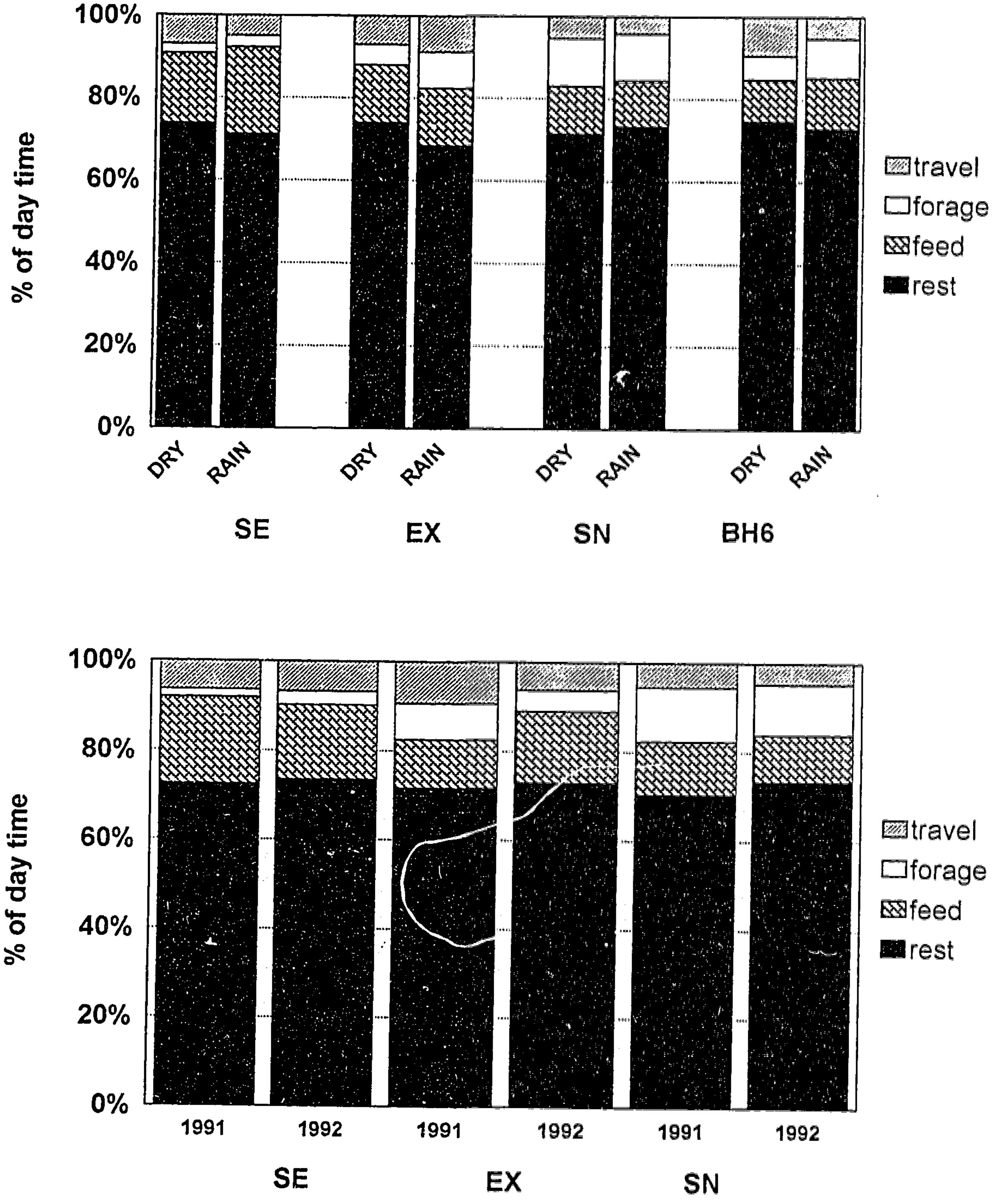

Figure 3-7. Seasonal and annual variations in time budgets.

Table 3-3. Annual and seasonal variations in time budget.

	Feeding	Foraging	Resting	Travel
1991 vs 1992				
SE	92 < 91 P = .064	92 > 91	92 > 91	92 = 91
EX	92 > 91 P = .003	92 < 91 P = .017	92 > 91	92 < 91 P = .015
SN	92 < 91	92 = 91	92 > 91 P = .087	92 = 91
Rainy vs Dry				
SE	R > D P = .009	R = D	R < D	R < D P = .026
EX	R = D	R > D P = .011	R < D P = .028	R > D
SN	R = D	R = D	R > D	R < D
BH6	R < D	R > D P = .073	R = D	R < D P = .006

P values are given if P < .10

= indicates a difference of 1% or less

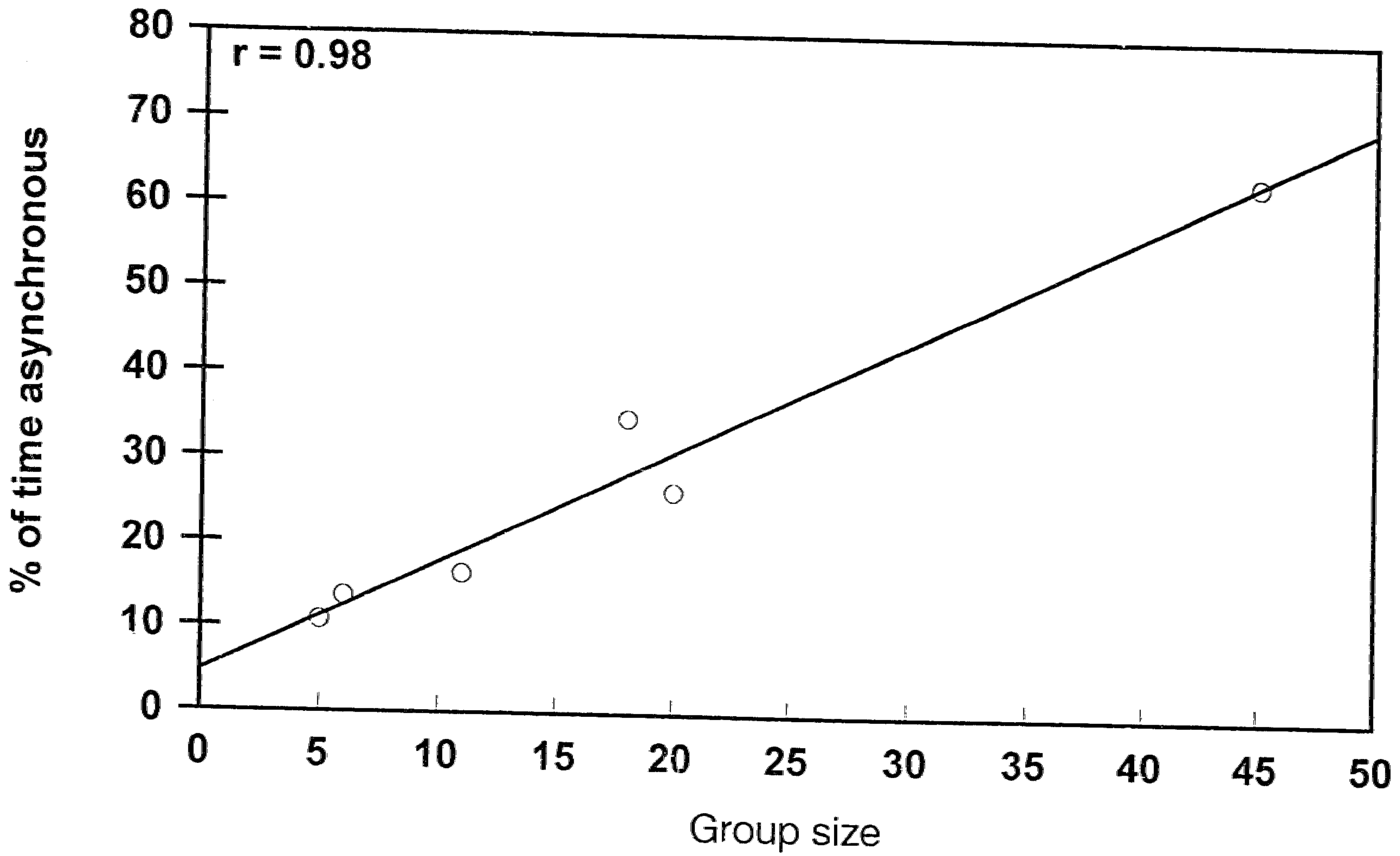

Figure 3-8. Plot of the percentage of time at least twenty percent of the individuals in each group were not engaged in the same activity as the rest of the group.

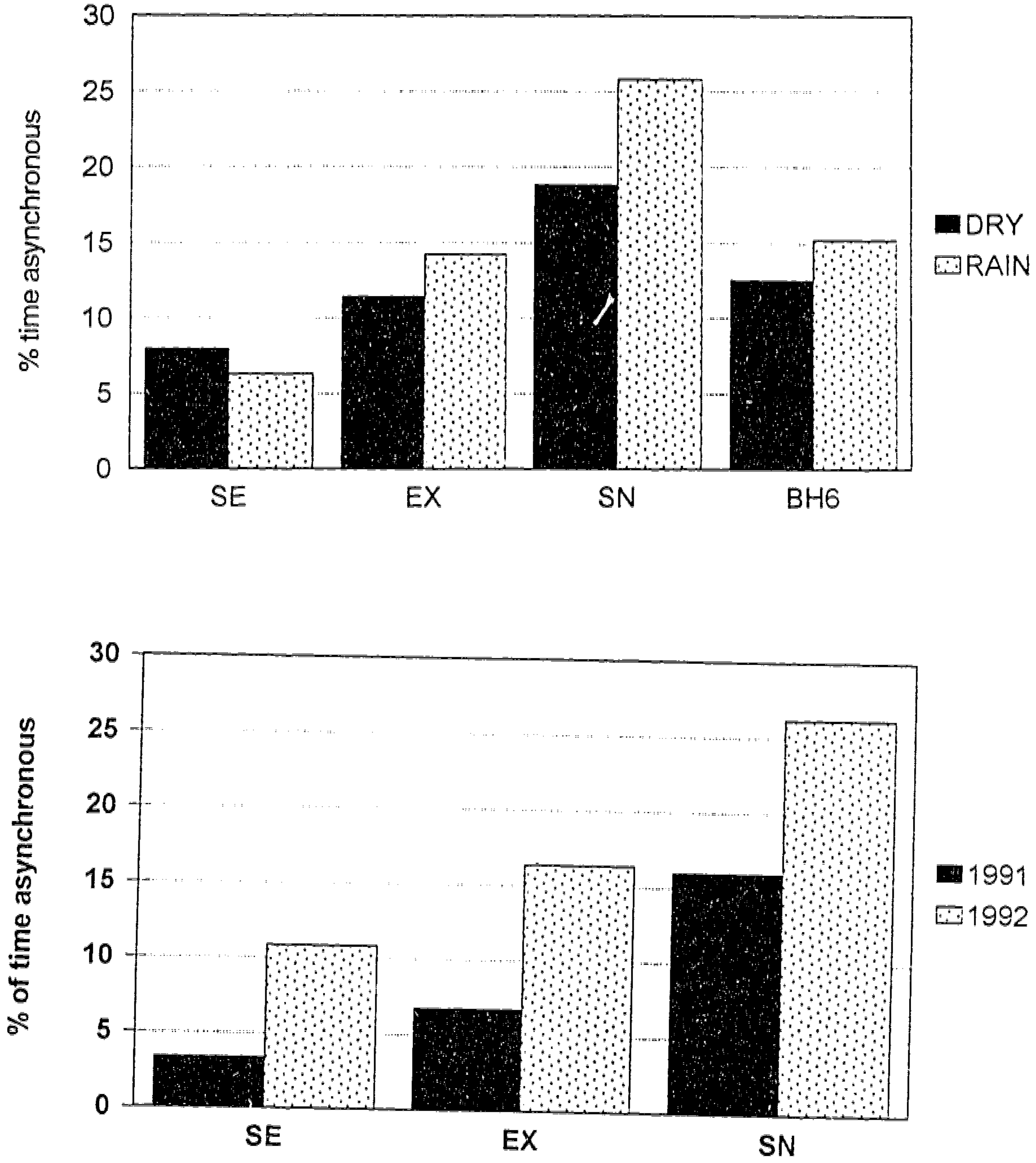

Figure 3-9. Seasonal and annual variations in time spent asynchronous for each group.

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IV. The effects of group size on contest competition and foraging efficiency in howler monkeys (*Alouatta palliata*).

INTRODUCTION

Attempts to understand the variation in group size and composition in primates have focused on the costs and benefits of living in groups. Many researchers agree that one of the most important costs is the increase in feeding competition within groups. Several studies have shown that the intensity of competition for food is an important determinant of group size (Clutton-Brock and Harvey 1977; Terborgh 1983; Dunbar 1988; Wrangham et al. 1993). Most of the early studies have relied almost exclusively on indirect measures of feeding competition such as home range size (Milton and May 1976; Clutton-Brock and Harvey 1977), day range length (Waser 1977; Terborgh 1983; Dunbar 1988; Wrangham et al. 1993) and time budget (van Schaik et al. 1983; Altmann 1980; Dunbar and Dunbar 1988; Dunbar 1992). More direct measures estimate the costs and benefits on a *per capita* basis rather than on group averages (Post et al. 1980; Whitten 1983; Janson 1985; Stacey 1986; Watts 1985; Janson 1988). When groups reach a certain size, the benefits gained may be negated by the increased costs. Thus, it is widely believed that there is an optimal group size where the ratio of benefits over costs reaches a maximum (Charnov 1976; Pyke et al. 1977; Krebs 1978; Cant and Temerin 1984; Stephens and Krebs 1986). When the intensity of food competition reaches a certain level, i.e., when the costs exceed the gains, two possibilities are available. One is to fission (Wrangham 1980; McFarland 1986) and the other is for individuals to switch groups (Brown 1982). Group fission should occur when the costs are shared more or less equally between all group members (McFarland-Symington 1988) while emigration should occur when the costs of competition affect certain group members more than others (Vehrencamp 1983). Several studies have reported differences in food intake rate based on dominance rank (Whitten 1983; Janson 1985), the amount of aggression received (Plotnick 1968; Dittus 1977; Robinson 1981), age-sex classes (Dittus 1977; Robinson 1981) and group size (Caraco 1979; Leighton and Leighton 1982).

Differences in food intake rates are usually the result of subordinates avoiding dominant individuals (Robinson 1981) or supplantation of subordinates by dominant individuals (Kurland 1977). High rates of aggressive competition for food is a consequence of living in groups and has been reported for a number of species (*Papio cynocephalus*: Altmann and Altmann 1970; Altmann 1980; Post et al. 1986; *Macaca sinica*: Dittus 1977, 1979; *Cercopithecus aethiops*: Cheney et al. 1981). The resulting differences in food intake rate may have important consequences for overall reproductive success of individual group members (Whitten 1983; Harcourt 1987). In this chapter, I examine the effects of group size on the rate of agonistic interactions over food. I also test whether differences in individual food intake rate exist within and between groups of mantled howler monkeys.

Howler monkeys are large neotropical folivores and have been characterized as having weak linear hierarchies and low rates of aggression over food. This has often been explained by their folivorous diet which may limit the amount of energy available for aggressive interactions (Jones 1980; Isbell 1991; van Schaik 1989). Maynard-Smith (1974) suggested that the need to minimize the energy invested to resolve conflicts under such conditions should give rise to highly 'ritualized behaviors'. Howlers use vocalizations during group encounters and advertize their positions by using loud morning choruses. These behaviors offer the advantage of reducing the potential costs of escalating conflicts which may lead to severe injuries or even death. However, male howlers have been known to fight and give chase and even inflict serious injuries (Glander 1975). It has also been argued that contest competition over food is often absent in folivores because their food sources are large enough to accomodate all group members (van Schaik 1989). However, groups living in habitats where food is limiting have higher levels of agonistic behaviors (Jones 1980) and may form stronger linear dominance hierarchies (Glander 1975). Furthermore, because both males and females migrate in howlers (a trait common among arboreal folivores), groups are usually composed of unrelated males and females. This pattern of migration may explain the absence of strong linear and stable hierarchies and the individualistic nature of howlers. Howler females rarely form coalitions within groups (however see Jones 1980) unlike female-bonded groups where males leave their natal groups and females remain to form the stable core of the group (Wrangham 1980).

Using data on agonistic interactions and ingestion rates, I test the hypotheses that contest (or interference) competition is rare in howler monkeys and that no significant differences exist in feeding efficiency (food intake rate) within and between groups of different sizes. I also examine the influence of rank, age, and sex on food intake rate. I conclude by re-examining the importance of feeding competition in folivores.

MATERIALS AND METHODS

Study Site

The research was conducted in Santa Rosa National Park on the northwestern coast of Costa Rica. The Park, situated 35 km Northwest of Liberia in the province of Guanacaste, covers approximately 10 800 ha consisting of a series of plateaus starting at an elevation of approximately 300 m and drops down to the ocean. Santa Rosa was created in 1971 and consists of a mosaic of grassland, dry deciduous forest and semi-evergreen forest (Bonoff & Janzen, 1980; Janzen, 1983). Common species in the dry deciduous forest are *Bursera simaruba*, *Chlorophora tinctoria*, *Enterolobium cyclocarpum*, *Luehea candida*, *Pithecellobium saman*, *Spondias mombin*, and *Guazuma ulmifolia*. Common species in the semi-evergreen forest are *Hymenaea courbaril*, *Ficus spp.*, *Manilkara zapota*, *Castilla elastica*, and *Masticodendron capiri*. Santa Rosa is characterized by a dry season extending approximately from December through May, and a wet season which extends from June through November with annual precipitation ranging from 900 to more than 2400 mm, almost all of which falls during the wet season. During the dry season, deciduous trees lose their leaves and remain bare until the onset of the rainy season.

Since the creation of the park, several studies have been conducted on the primate population inhabiting the area (Freese, 1976; Fedigan, 1986; Fedigan & Baxter, 1984; Fedigan et al., 1985; Chapman, 1987; Chapman & Fedigan 1990; Chapman et al., 1989;

Glander et al., 1991; Rose, 1994). Three species of primates are represented in the Santa Rosa population: *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*. Several groups of each species have been followed since 1983 as part of an ongoing study on the demography and behavior of the three species (see Fedigan, 1986). Individuals of the species *Ateles geoffroyi* and *Alouatta palliata* have been captured and marked to allow recognition and to facilitate studies of the different groups. A system of trails covering approximately 20 km has also been made to facilitate access to the groups. A number of ecological studies have also been conducted in the park, facilitating the recognition of plant species and their phenological patterns (Daubenmire, 1972; Frankie et al., 1974; Bonoff & Janzen, 1980; Opler et al., 1980; Janzen, 1982).

Santa Rosa offers an excellent opportunity to study wild primate populations because of the good observation conditions, particularly during the dry season. Also, the marked seasonality offers the opportunity to study the changes in food availability and its effect on foraging strategies within and among groups.

Study Groups

Three groups of howlers were studied during the first field season (1991) and a fourth group was added during the second field season (1992). The changes in group size for groups San Emilio (SE), Exclosure (EX), and Sendero (SN) were the result of births and disappearances of some animals, possibly due to immigration in the case of juveniles and adults, and deaths in the case of infants (see Table 2-1, chapter 2). However, no cases of immigration or deaths could be confirmed. Group SN also varied in size due to the fission-fusion of this group. Because some individuals were often separated from the main group for several days, the number of monkeys in the study group varied daily. Similarly, early in 1992, the group Bosque Humedo (BH) fissioned into three distinct subgroups. This pattern had been observed previously by Chapman (1987) for the same group. In the five months following the fission, two subgroups reunited again as had happened in the past. However, the smaller subgroup remained separate even after encountering the parent group at least three times after the separation. Therefore, for the study period, the initial group of forty-five animals was followed for only three days before it fissioned. Subsequently, two subgroups were observed. One subgroup of 18 animals was observed for six days while the smaller group of six animals was followed consistently over the remainder of the field season. The results presented in this paper for group BH are for the smaller subgroup of six animals (BH6) for the most part except where noted. The two larger BH groups are referred to as BH18 and BH45. Therefore, in this study, groups SE and BH6 were the smallest groups with approximately six individuals, while EX varied between ten and fourteen. Group SN was larger and varied between 20 and 28 individuals.

The groups were located in the central area of the park and occupied relatively well defined and discrete home ranges although some overlap existed with other groups for all four groups. Individual recognition of the animals was not possible for all group members, however age/sex classes were easily recognized. In all groups, some adults were marked with collars or ankle bracelets of different sizes, shapes and colors (see Glander et al. 1991 for details). In each of the four groups, other animals could be recognized by discolorations of the skin under the hind feet and by permanent scars on the face and on the tail.

Sampling Methods

Groups were observed from January through June 1991 and from January through July 1992. No data was collected in January 1991, and during this time, the monkeys became habituated and were not alarmed by the presence of the observer after only a few days with each group. Whenever possible, each group was followed in a fixed rotation for five consecutive days over a period of three weeks from February through June 1991 and over four weeks from January through July 1992. Data on each group was collected between 0530 and 1800 hours. Groups were usually found in their sleeping sites early in the morning and were followed until they had reached the sleeping sites at the end of the day. A total of 2040 hours of data were collected on the four groups over 166 full days of observation.

For the first field season, the groups were followed using focal sampling sessions (Altmann 1974) of ten minutes in length on adults and juveniles. Subjects were selected at random prior to the beginning of the day, and when possible, were alternated according to age and sex class. The order of rotation was then maintained for the rest of the day. For the second field season, one individual was followed for the whole day and data was collected on adults only, alternating between males and females. During each focal session, the main activity in which the subject had engaged was recorded for each two minute period at the end of each time interval. Thus, five behaviors were scored for each focal session in the first year. In the second year, behaviors were scored every two minutes from the first contact in the morning until the end of the day. Because howlers have a relatively limited behavioral repertoire and engage in each behavior for relatively long periods of time, a two minute period was adequate. Behavioral categories for the focals were: rest, play, travel, manipulate (substrate), scan, feed (bringing food to the mouth, chewing, and swallowing), vocalize (for males only), social (sexual behaviors), and 'other'. Ingestion Rates were also recorded for each focal animal. I counted the number of food items ingested or the number of bites taken during each two minute period . The ingestion rates presented in this paper represent the average rate per minute. Scan sampling was used to determine the time spent in all major activities for each group. Instantaneous scans were taken at ten minute intervals and one activity was scored for the group. Because howler groups are highly synchronous in their activities, the results of the scan sampling is an accurate method for howlers. The behavioral categories used for the scans were feeding (i.e., eating from large food sources), foraging (i.e., eating from small, dispersed food sources), resting, travelling, and other. Definitions for foraging and feeding were the same as those used by van Schaik & van Noordwijk (1988).

For each feeding tree visited by the group, I recorded the plant species, the food type ingested, and the size of the patch. Each feeding tree was marked and given an identification number so that frequency of use and renewal rate of patch resources could be determined. Patch size was determined by measuring the diameter at breast height (DBH). Because several studies have demonstrated a strong correlation between DBH, crown size, and reproductive capacity for a number of tropical species (McDiarmid et al., 1977; Leighton & Leighton, 1982), DBH was used as an estimator of the number of items available in a patch. Five food types were used for this study: fruits, flowers, mature leaves, young leaves, and leaf buds. For the analysis, leaf buds and young leaves were combined into one category. To compare diets across seasons I determined the onset of the rainy season to be the first day following the first rain, which occurred in the first two weeks of May for 1991 and 1992. To allow for meaningful comparisons, most results obtained in this paper were carried on three groups (SE, EX, SN) combining 1991 and 1992 and on the four groups for the 1992 season only.

All aggressive interactions were recorded *ad libitum*. Because of the good observation conditions (particularly during the dry season), I was able to record most of the aggressive behaviors in my study groups. Aggressive interactions usually involved vocalizations and rapid flight and were therefore highly noticeable. Focal and *ad libitum* data were combined in this analysis. The identity of the animals involved as well as the context and the outcome were recorded whenever possible. I did not include in this analysis aggression between mother and infant when it involved the weaning process. For this study, I regrouped all aggressions into three contexts: feeding, sexual, and 'other'. Aggression was recorded as having occurred in a feeding context when the 'aggressor' replaced the 'aggressee' at the latter's feeding spot (supplantation) or if an animal moved away when another approached (avoidance) and the latter proceeded to feed. In this analysis, supplantation and avoidance are combined. I also recorded the plant species, the food item, the diameter at breast height (DBH) and the number of individuals in the patch where the aggression occured. Aggression in a sexual context was recorded if one of the participants was observed in a consortship at any time during that day and if the 'aggressor' did not replace the 'aggressee' at the latter's feeding spot. If the context could not be determined, or if the aggression occurred in another context, the context was classified as 'other'.

To compare the rates of aggression between groups and within groups across seasons, I used the rates of aggression per hour of observations for each group (number of aggressive behaviors / number of hours). However, to control for the differences in group size, I divided the aggression rates by the number of individuals in the group during that month to get average individual aggression rates. Yearly and seasonal rates represent the average rates for that period. To compare rates across food items or food species, I calculated the rates as the number of aggressive acts divided by the total time spent feeding on that food item or food species. I used the patch residence time (PRT) as an estimate of the total time spent feeding (see chapter 2).

Statistical methods

Parametric statistics were used whenever possible over nonparametric tests. For all parametric tests, the distributions of all variables were tested for normality and homogeneity of variances. When values were not normally distributed, an appropriate transformation was applied (Sokal & Rolhf, 1981). The reverse transformations were applied to facilitate the presentation of the results. For multiple group comparisons, a oneway anova with range test (Scheffé's method) was used. Chi-squares tests for goodness-of-fit were used on frequencies of aggressions across age-sex classes and food items. All probabilities are two-tailed unless stated otherwise. All statistical procedures were carried out using the SPSS/PC statistical package.

RESULTS

Overall rates of aggression

A total of 387 aggressions were observed (Table 4-1). However, 143 of these were dominance related, i.e., the 'aggressor' was targetting an individual and was repeatedly displacing the subordinate (up to 17 times a day) without replacing that subordinate at the resting spot or feeding spot, i.e., the reason for the aggression was not for immediate access to resources. These 143 cases were used to determine a dominance hierarchy but were not used in calculating the rates of aggression. These dominance-related acts of aggression were not included in any of the analyses below. A total of 244 aggressive interactions (or supplantations) remained in feeding, sexual or 'other' contexts which were recorded during 2040 hours of observations. This represents a rate of 0.119 interactions per hour of observation. Of that total, 176 interactions were food related (72.1%), 18 were in a sexual context (7.4%) and 50 occurred in other contexts (20.5%). Of the latter, in 28 cases out of 50, I could not determine the context. For the remaining 22 cases, 8 (36.4%) occurred during play bouts (all involving at least one juvenile), 12 (54.5%) occurred over resting spots, and 2 (9.1%) occurred during group encounters (within-group aggression). Of the 244 agonistic acts, only 28 (11.5%) involved physical contact (grabbing, biting, hitting). Of the 28, all but one involved females against females and only one involved a male biting a female. Of the 28, 19 (67.8%) occurred in a feeding context.

The effects of age and sex classes on aggression

In feeding contexts, adult males were the aggressors more often than expected and juveniles far less than expected ($\chi^2 = 37.8$ df 2, $P < .001$; Figure 4-1). Conversely, adult males were on the receiving end less than expected (n=0) whereas females were the target more often than expected ($\chi^2 = 45.51$ df 2, $P < .001$). Based on these interactions, it was clear, that in all contexts, adult males were dominant over adult females and adult females were dominant over juveniles. In only one case was a juvenile aggressive towards an adult female. All other aggressive behaviors directed by juveniles were towards other juveniles. In feeding contexts, mothers displaced their own offspring on 8 occasions.

The effects of rank on aggression

Because of the low frequency of aggression in this study, I could not determine a complete dominance hierarchy in any of the groups except for the smaller group SE. Only two adult females were present in this group, and of the 20 aggressive interactions over food, 13 occurred between the two females, two between an adult male and an adult female, and 5 between adult females and juveniles. Of the 13 interactions between the two females, 11 were won by the same female and two reversals were observed. For the other groups, although I was able to determine the relative rank between several female pairs, I could not determine the absolute rank within the group. Consequently, I could not determine whether dominants were involved more frequently in aggressive interactions than subordinates. However, it is interesting to note that males were rarely involved in aggressive interactions and I never observed two males of the same group acting aggressively toward each other. In the group where I could determine the hierarchy among adult males (group SE, two males), the dominant and the subordinate were involved in aggressive interactions as expected ($\chi^2 = 1.12$ df 1, P = .29).

The effects of group size

In 1991, aggression rates did increase slightly as a function of group size, but not so in 1992 (Figure 4-2). The year 1992 was a much more stressful period for each group because of the lack of rain in the previous rainy season. Interestingly, two groups (EX and SN) had fewer members that year. The rates of aggression in 1992 were 8 to 9 times higher for the smaller groups SE and EX than in 1991. Group BH6, which was originally part of group BH45, had a much lower rate of aggression after the separation whereas group BH18, which also separated from group BH45, retained a relatively high aggression rate. Group BH18 subsequently fissioned into two smaller groups. The same pattern is found if only the aggressive interactions in a feeding context are considered (Figure 4-3). Rates increased as a function of group size in 1991 but not in 1992. The increase in the rates of aggression in 1992 compared to 1991 for groups SE, EX, and SN was due almost entirely to aggression over food (Figure 4-4). Aggression rates were much higher in the dry season than in the rainy season. In all cases, the rates were approximately three times higher in the dry season (SE=3.26; EX=3.31; SN=2.88). The howlers' diet contains a much higher proportion of mature leaves in the rainy season and much higher proportions of fruits and flowers in the dry season (see below).

The effects of diet and patch size

Seasonal items like fruits and flowers were more often contested than mature leaves in each group except BH6 (n = 3; Figure 4-5). Flowers and fruits were contested more often than expected whereas young leaves and mature leaves were contested less often than expected (all groups combined, $\chi^2 = 14.25$, df 3, $P = .002$; Figure 4-6). Expected frequencies were based on their relative contributions to the diet. Aggressive behaviors occurred over 15 food species for all data combined. A Spearman's rank correlation between the frequency of aggressive interactions and the relative contribution of each species to the diet was significant ($r_s = .5229$, $n = 15$, $P = .045$) indicating that favorite species (and food items) are more contested than other foods. The three most important species in the diet (*Bursera simaruba*, *Ficus spp.*, and *Pithecellobium saman*) were by far the most contested (Figure 4-7) and were major sources of fruits and flowers.

I analyzed the distribution of aggressive interactions across patches of different sizes to see if food items were more likely to be contested in small patches or in large patches (Figure 4-8). More contest occured in larger patches than in smaller patches ($\chi^2 = 60.6$, df 6, $P < .001$). This can be explained by the fact that groups spent more time feeding in large patches and that more individuals are feeding at the same time, which would result in higher rates of aggression. Also, large patches like *Ficus*, and *Pithecellobium* were major sources of fruits and flowers which were more often contested.

Ingestion Rates

I also wanted to see if ingestion rates were influenced by variables such as sex, age, rank patch size,, and group size. Food items and food species do not take the same amount of time to process, so to control for these differences, I selected food items for which I had a sample large enough to compare the ingestion rates across the different categories. Because ingestion rates may diminish as the patch is being depleted, I used only the first ten minutes spent feeding in a patch by a group. First, I tested to see if adult males, adult females and juveniles had different ingestion rates. I was able to use only seven food items for this analysis (Table 4-2). Not surprisingly, the food items included were from the three most important food species in the diet (*Bursera simaruba*, *Ficus spp.*, and *Pithecellobium saman*). In all cases where there are significant differences in ingestion rates, adult males had higher ingestion rates than adult females, and adult females had higher ingestion rates than juveniles. When no significant differences existed, adult females had slightly higher ingestion rates than males. In two of three cases, the food items for which no significant differences were found were mature leaves. The third food item was among the most palatable (figs). The differences in ingestion rates may be explained by the fact that mantled howlers are sexually dimorphic and the differences may represent allometric differences. Analysis of the time budget of males and females showed that females spent more time feeding (eating from large food sources) than males (+ 2.09 %, t = 1.93, df 97, P = .056) whereas males spent more time foraging (eating from small and scatterred food sources) than females (+ 1.90 %. t = 1.67, df 97, P = .099).

Sex and body size may also be confounding variables in the analysis of rank differences in ingestion rates since males are dominant to females in mantled howlers. To control for this, I used pairs of same sex individuals for which I was able to determine their relative rank (at least 6 interactions with at least a two to one ratio of wins over losses). I did not use females who were nursing an infant. The comparisons between pairs were made on food items for which I had a large enough sample. Although no significant differences were found for any of the pairs, in 5 out of 6 cases dominants had a slightly higher feeding rate (Table 4-3). I also tested to see if the number of individuals feeding in a patch (NBF) affected ingestion rates. I only used adult females for this analysis, to control for differences in body size, and I used similar food items for which I had a large enough sample. I found no significant differences for the three food items (*Bursera* fruits: F = .334 df 5,90 P = .89; *Ficus* young leaves: F = 1.83 df 4,55 P = .13; *Pithecellobium* flowers: F = .95 df 4,111 P = .43).

No significant correlations were found either between the size of patches and ingestion rates except for two groups (EX and BH18), or between the size of feeding trees and the number of individuals feeding in a patch (Table 4-4). It is important to note, however, that in almost all cases there is a negative correlation between ingestion rates and patch size. The same relationship was found when patches were further categorized based on the type of food items being exploited (Table 4-4). More interestingly, no significant relationship was found between ingestion rates and the number of individuals feeding in a patch (Table 4-4). The only significant relationship was between ingestion rates and the number of individuals feeding in a patch when howlers fed on fruits (r = -.1821 n=109 P= .058).

DISCUSSION.

The results presented in this study corroborate the hypothesis that contest competition is relatively rare among folivores compared to other species (see below). However, the rate of aggression did increase as a function of group size for 1991. Although no data are available to compare behaviors from previous years, the lack of rain in the 1991 rainy season resulted in drier conditions in 1992, and may have certainly affected the foraging strategies of howlers during the dry season. This resulted in conditions which were much more stressful for the howlers at Santa Rosa in 1992. Evidence for this was presented in the previous chapters, and more evidence is presented here by the fact that aggression rates were much higher in 1992 than in 1991 (up to nine times higher). Further evidence is found when we compare the differences in rates of aggression between the dry season and the rainy season. Rates during the dry season were up to three times higher than during the rainy season. Finally, the fission of group BH45 into several subgroups resulted in much lower aggression for the smaller BH6 subgroup but higher rates or subgroup BH18. The higher rates for BH18 may have been the result of even more difficult conditions as the dry season continued. Group BH18 subsequently fissioned into two smaller subgroups a few weeks later. However, no data are available for these subgroups.

Variations in rates of aggression between years and between seasons (and possibly between groups) may be explained by the relative availability of certain food items in the howlers' home range. The results of this study show that seasonal items such as fruits and flowers are more often contested than expected while leaves are less often contested than expected based on their relative contribution to the diet. Several studies have shown that howlers prefer seasonal items when they are available because of their higher protein content and because they are more easily digested (Milton 1979; Glander 1981). Thus, reports that folivores have low rates of aggression can be explained in part by the amount of seasonal items in the diet. Such items were more important in the diet during the dry season while leaves and particularly mature leaves were more important during the rainy season. Howlers may be more willing to contest resources when resources are limited. Rates of aggression were also higher than expected in large patches, possibly because these patches are often the source of seasonal items such as figs. Another explanation may be that the greater number of individuals that can feed in large patches increases the likelihood of food-related aggression. A study conducted at Barro Colorado Island by Leighton and Leighton (1982) showed that the number of howler monkeys feeding in *Trichilia cipo* trees bearing fruits was correlated with the size of the feeding trees. The authors suggested that the number of spaces in a patch was limited and that howlers apportioned themselves based on the size of feeding trees. The same pattern was observed in this study where the larger groups were often observed feeding in several patches simultaneously with individuals going back and forth between patches so that the whole group was rarely feeding in the same patch simultaneously except for very large feeding trees like *Ficus*, *Pithecellobium saman* or *Manilkara zapota*. This mechanism may contribute to lower rates of aggression over food.

Who contests the resources?

The results presented here show that almost all food-related aggression occurred among females. Females were not the 'aggressor' more frequently than expected but were the 'aggressee' more often than expected. This suggests that females may bear the burden of contest competition. This is further substantiated by the fact that males are dominant to females and were never displaced by females in feeding contexts. Juveniles on the other hand were rarely involved in food-related aggression but when they were, they were on the receiving end. Males in this study never displaced other males in feeding contexts or in any contexts. Because males are dominant over females, it is probably less risky for them to displace females than to engage in a fight with another male. Although aggression between males is relatively rare, it can lead to serious injuries (Crockett 1984).

A complete dominance hierarchy could not be established for all individuals in my study groups because of the duration of the study. However, it was clear that young females often targeted older females in the group and that younger females were generally higher ranking than older ones. This inverse relationship between age and rank has been observed in other studies of howlers (Glander 1975; Jones 1980) and langurs (Hrdy 1977). Jones (1980) also reported that groups living in less seasonal environments had weaker linear hierarchies than groups who lived in more seasonal habitats. Glander (1975) studied groups in a dry tropical riparian forest in Costa Rica and found a strong linear hierarchy in his study groups. Both studies reinforce the hypothesis that dominance hierarchies tend to evolve in environments where resources are limited (Emlen 1973). Santa Rosa is a dry tropical forest near Glander's study site and howlers should also exhibit a clear linear hierarchy in areas where food is limiting. Further studies are needed in Santa Rosa to test this hypothesis.

The consequences of contest competition are helpful in determining the effects on individual group members, and ultimately, on group size. The results presented in this study showed that males had higher ingestion rates than females, particularly when highly preferred foods were involved. Adult females also had higher ingestion rates than juveniles. Because ingestion rates (number of bites taken per minute) are not direct measures of energy intake, it is difficult to draw firm conclusions from these results. However, because the same measurements were made throughout the study, they allow for interesting comparisons. First, the differences in ingestion rates may be explained in part by the effects of body size. Males are approximately 20% larger than females and therefore require more energy to sustain their metabolic needs. Differences between females and juveniles may also be explained by these allometric differences. However, the energy required by females nursing or carrying infants and by juveniles to support their growth should reduce the effects of body size. Juveniles in this study rarely engaged in play bouts compared to young infants. This may suggest that they also have a low surplus energy budget. Second, the differences in feeding rate may underestimate the energy intake if males also take in more food (i.e., energy) per bite than females and females take in more than juveniles. Ingestion Rates were significantly different for small clumped food items (*Pithecellobium* flowers, *Bursera* fruits) but not for large or scattered food items (figs, leafbuds, mature leaves). This suggests that males may be able to obtain more food per bite than females and feed faster.

Although in five of six cases in this study, dominants had slightly higher rates than subordinates, the differences were not significant. It is difficult to determine how important these differences are in terms of energy intake and their long term effects on individual fitness. However, because subordinates are more likely to have their feeding bouts interrupted than dominants, particularly over high quality food items such as fruits and flowers, it may have important consequences during food shortages. This may explain the fission of group BH45 or the loss of several group members in group SN in 1992. Further studies are needed to compare ingestion rates across a wider range of food sources and more individuals.

Group size did not affect ingestion rates in this study. No significant differences were found although smaller groups did spend more time feeding than large groups (see Chapter 3). However, overall ingestion rates for all groups were affected by the size of the patches and by the number of individuals feeding in a patch. The correlations were not significant with a few exceptions (see Table 4-4). Nevertheless, for all groups combined, there was a negative correlation between ingestion rates, patch size and number of individuals feeding in a patch. These correlations were significant for fruits. This suggests that individuals are able to feed faster in small patches, possibly due to the fact that they only have to move short distances to resume their feeding bouts within small patches as opposed to large patches. The negative correlation between ingestion rates and the number of individuals feeding in a patch indicate that individuals have fewer options to move around in patches where many individuals are feeding and when they do, they have to spend more time moving within a patch. This latter effect may have a greater impact on subordinate individuals who are not able to displace others at a food source. This may explain the observation that several group members often fed in nearby trees until spaces became available in the larger food patches. Furthermore, this may corroborate the findings of Leighton and Leighton (1982) on the relationship between patch size and feeding aggregates in howlers at BCI. The same relationship was found in this study for all groups combined ($r = .254$, $P < .001$) but not within groups (see chapter 2). Small groups in this study (SE and BH6) had positive correlations between ingestion rates and the number of individuals feeding in a patch (NBF), possibly because of the lack of competition within larger food patches. The larger groups SN and BH45 also had positive correlation for ingestion rates and NBF. This may reflect the fact that under a tighter energy budget, individuals may compete by feeding faster and may deplete patches quickly so that contest competition does not occur (see chapter 4).

Comparisons with other species

The only folivorous species for which there exists data to compare with the results of the present study are for the mountain gorillas (*Gorilla gorilla beringei*). Watts (1985) reported similar supplantations rates (251 supplantations in 2400 hours of focal data) for his groups of mountain gorillas in the Parc National des Volcans in Rwanda. Silverback males were also responsible for a larger proportion of the supplantations and females were involved in aggression over food more often than expected. Watts also reported an increase in supplantation rates as a function of group size. High-ranking female gorillas were also less frequently supplanted than low-ranking females. Watts also reported that mother-daughter pairs also supplanted each other in feeding contexts. The similarities between gorillas and howlers may be explained by their primarily folivorous diet and by the dominance of males over females in both species. However, the intensity of contest competition in both species is relatively low compared to other species. Studies of yellow baboons (*Papio cynocephalus*) by Lee and Oliver (1979) and by Post et al. (1980) show higher rates of food related aggression in their study groups. Lee and Oliver (1979) recorded 598 acts of aggression in 630 hours of observation among 23 juveniles. Post et al. (1980) reported that feeding bouts were interrupted on average 4.47 times per hour in a group of 33 adult and juvenile baboons. Teas et al. (1980) reported rates of 1.71 acts of aggression *per* hour *per* monkey in their study of rhesus monkeys (*Macaca mulatta*) in

Nepal. The rates for baboons and rhesus macaques are very high compared to the 387 acts of aggression in 2040 hours reported in this study.

Several studies have shown correlations between aggression rates between females and fecundity (Dunbar 1980; Clutton-Brock et al. 1982). Although no data is available to test this idea directly in mantled howlers, several studies on this species have reported an inverse relationship between female rank and reproductive success (Jones 1980; Clarke and Glander 1984). Young females often lose their infants and this may be because young females usually rise in rank at that time and may invest more energy to achieve this. Once established in the group, their reproductive success increases as the need to compete to remain in the group is less intense (Glander 1992).

Stacey (1986), in his study of foraging efficiency in yellow baboons (*Papio cynocephalus*), showed that there were no differences in energy intake between individuals living in groups of different sizes, although smaller groups had higher ingestion rates and spent less time feeding than large groups. There were also no differences in energy intake based on rank. The author suggested that because there were no differences in foraging efficiency as a function of group size, the primary benefit of living in large groups for baboons was for protection or detection of predators. Studies on brown capuchin monkeys *(Cebus apella)* by Janson (1985) showed that energy intake varied according to rank, aggression received and the rate of fighting at a food tree. Dominant individuals had up to 37% higher energy intake than subordinates. Energy intake was also similar for food items which were not disputed. Janson concluded that the intensity of within-group competition was ten times more intense than between-group competition. Therefore, the benefits of living in large groups may not be equal for all group members. The decision of group members to stay in large groups even when their energy intake is relatively lower than other members of the group may be based on how much better the animal could do by switching groups.

Models to understand the benefits of sociality in primates often argue that folivores show low rates of within-group competition and that contest competition is frequently absent (see van Schaik 1989 for review). These models also suggest that the costs of living in large groups are minimal for folivores. The results presented in this chapter indicate that there may be low rates of aggression over food in howlers but that competition usually occurs over high-quality food items as it does in frugivores. Furthermore, howlers show the type of fission and fusion usually associated with chimpanzees and spider monkeys, two highly frugivorous species (McFarland 1986). This study also indicates that high rank may confer an advantage to certain individuals particularly during times of food shortages. Further studies are needed to measure exactly the differences in energy intake between groups and within groups and to determine if emigration and immigration in howlers may be linked to differential foraging efficiency.

Table 4-1. Frequency of aggressive interactions by context for each study group.

Group	Context				Total # hours of observation
	Feeding	Sexual	Other	Total	
SE	20	4	4	28	577
EX	42	7	9	58	532
SN	78	7	25	110	628
BH6	3	0	2	5	193
BH18	20	0	5	25	73
BH45	13	0	5	18	37
Total	176	18	50	244	2,040

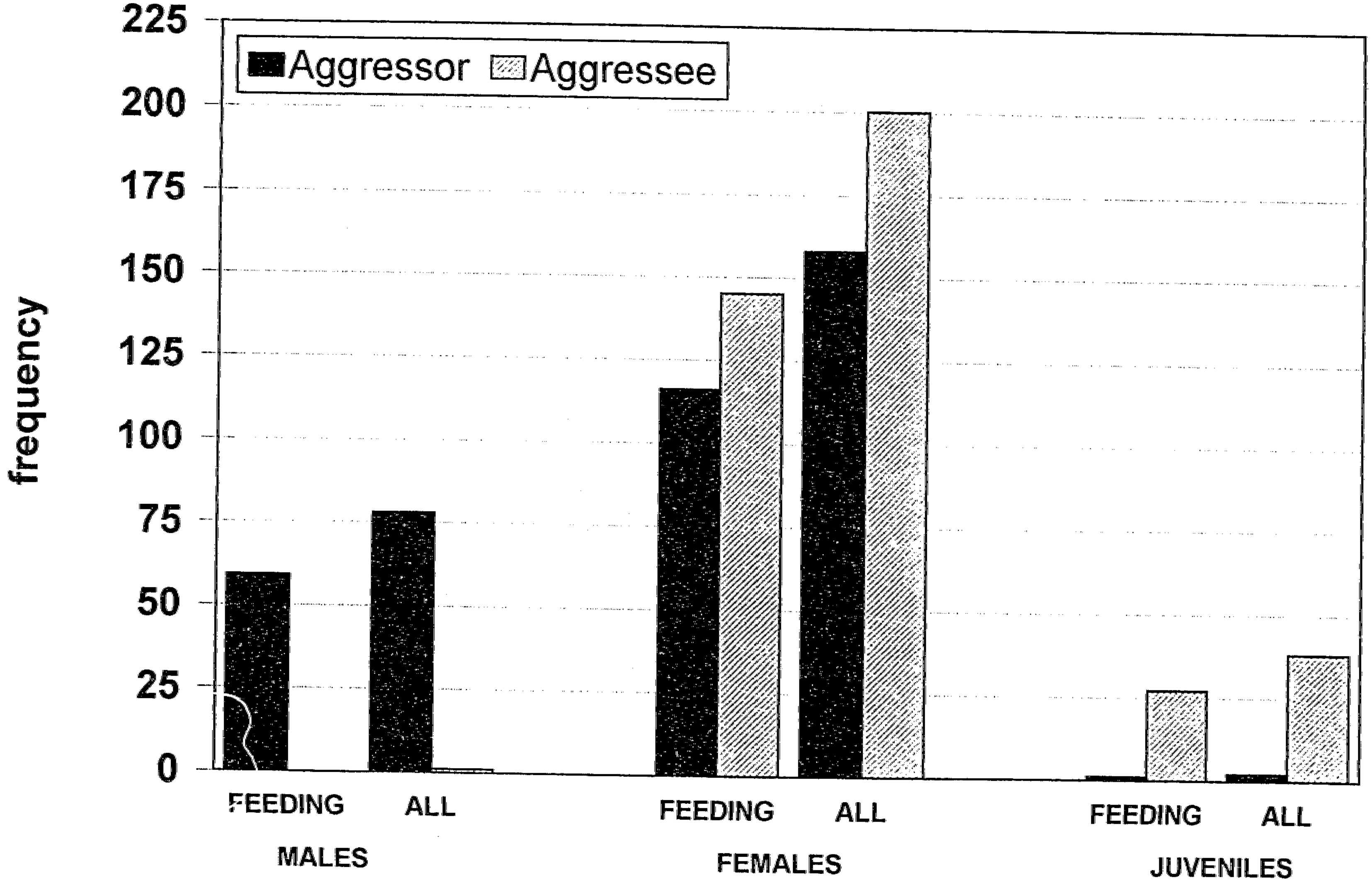

Figure 4-1. Frequency of aggression given and received in feeding context and overall for adult males, adult females, and juveniles.

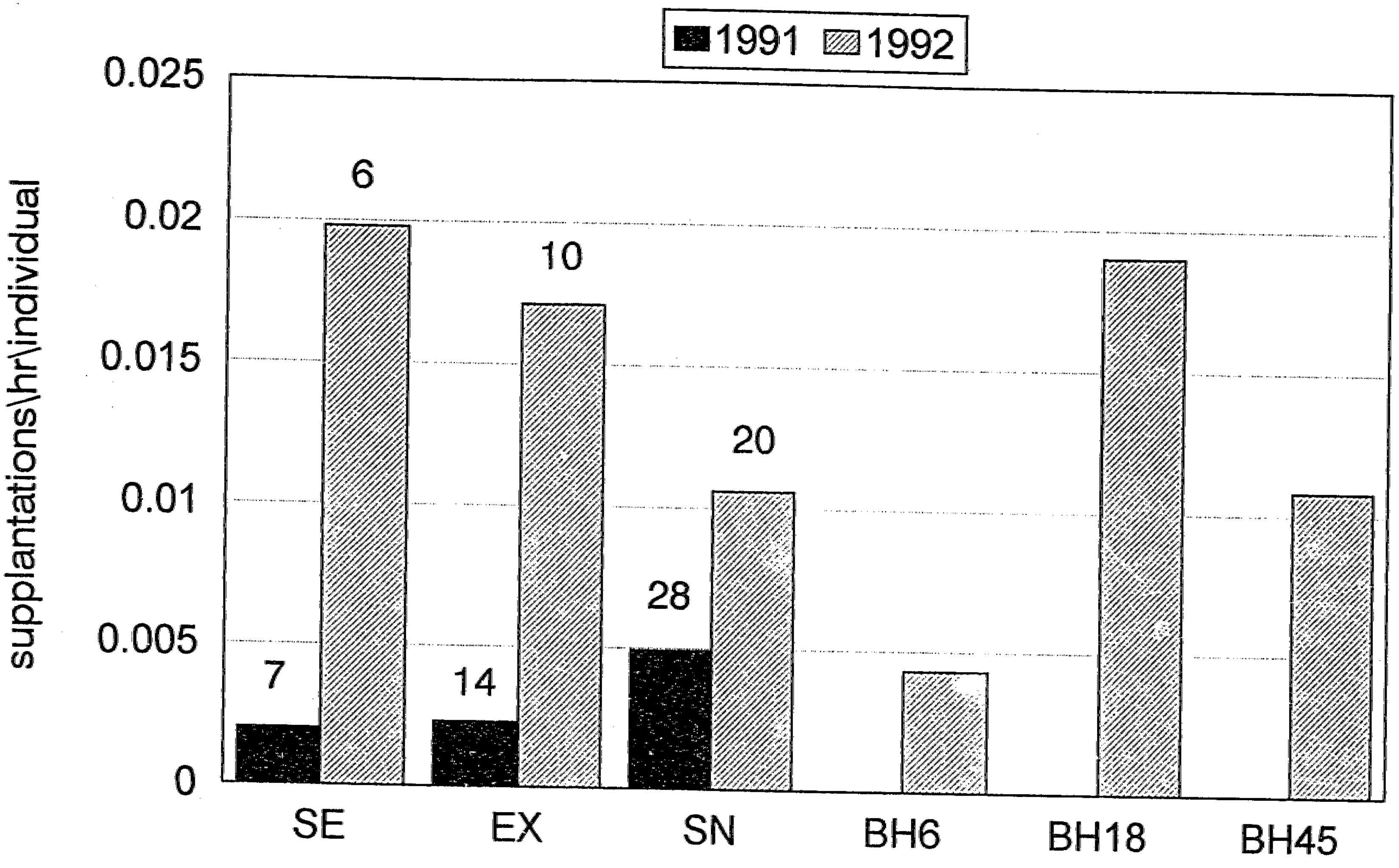

Figure 4-2. The relation between group size and overall rates of aggression for 1991 and 1992. Numbers indicate the number of individuals in the group for 1991 and 1992.

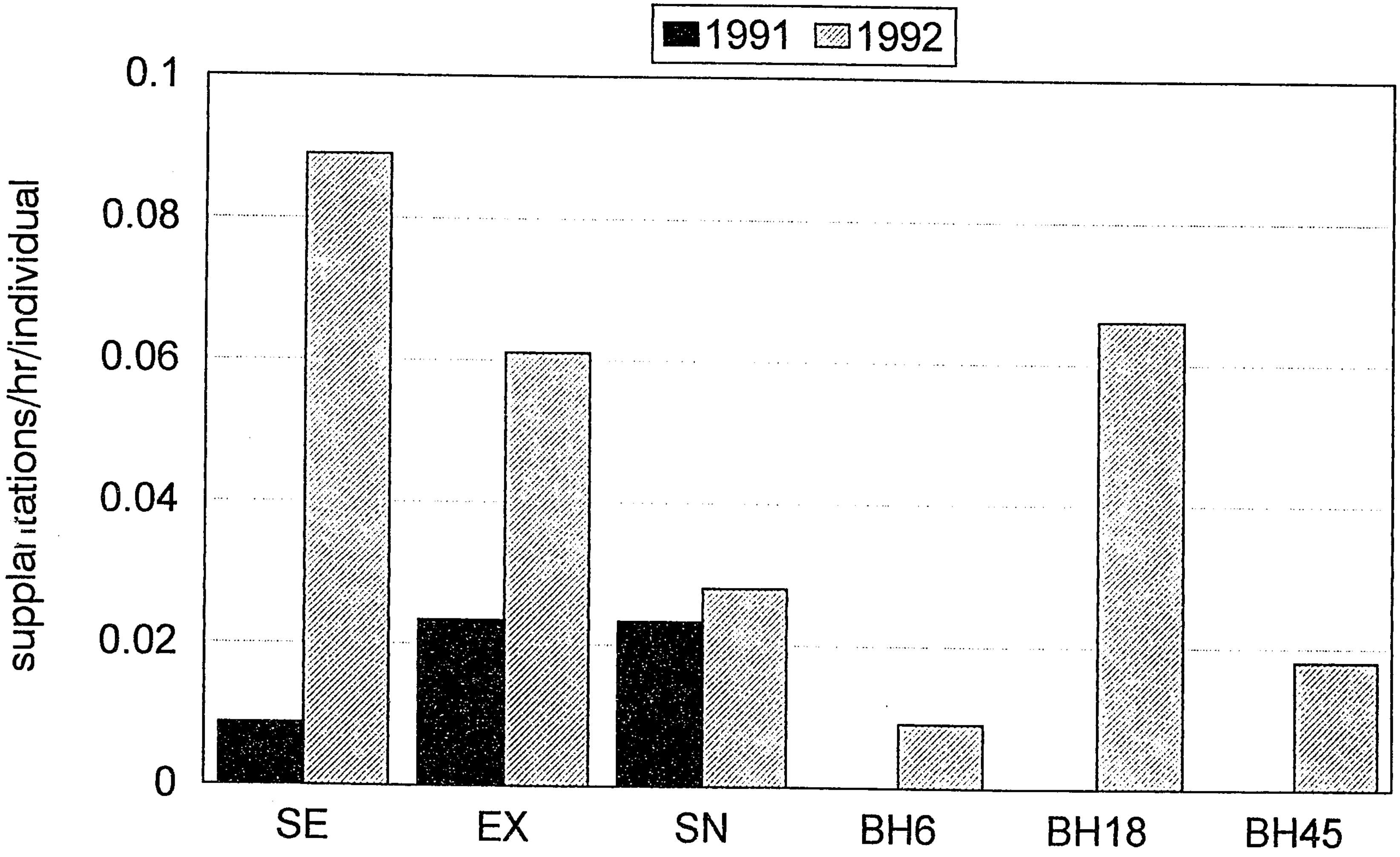

Figure 4-3. The relation between group size and rates of aggression in feeding context for 1991 and 1992.

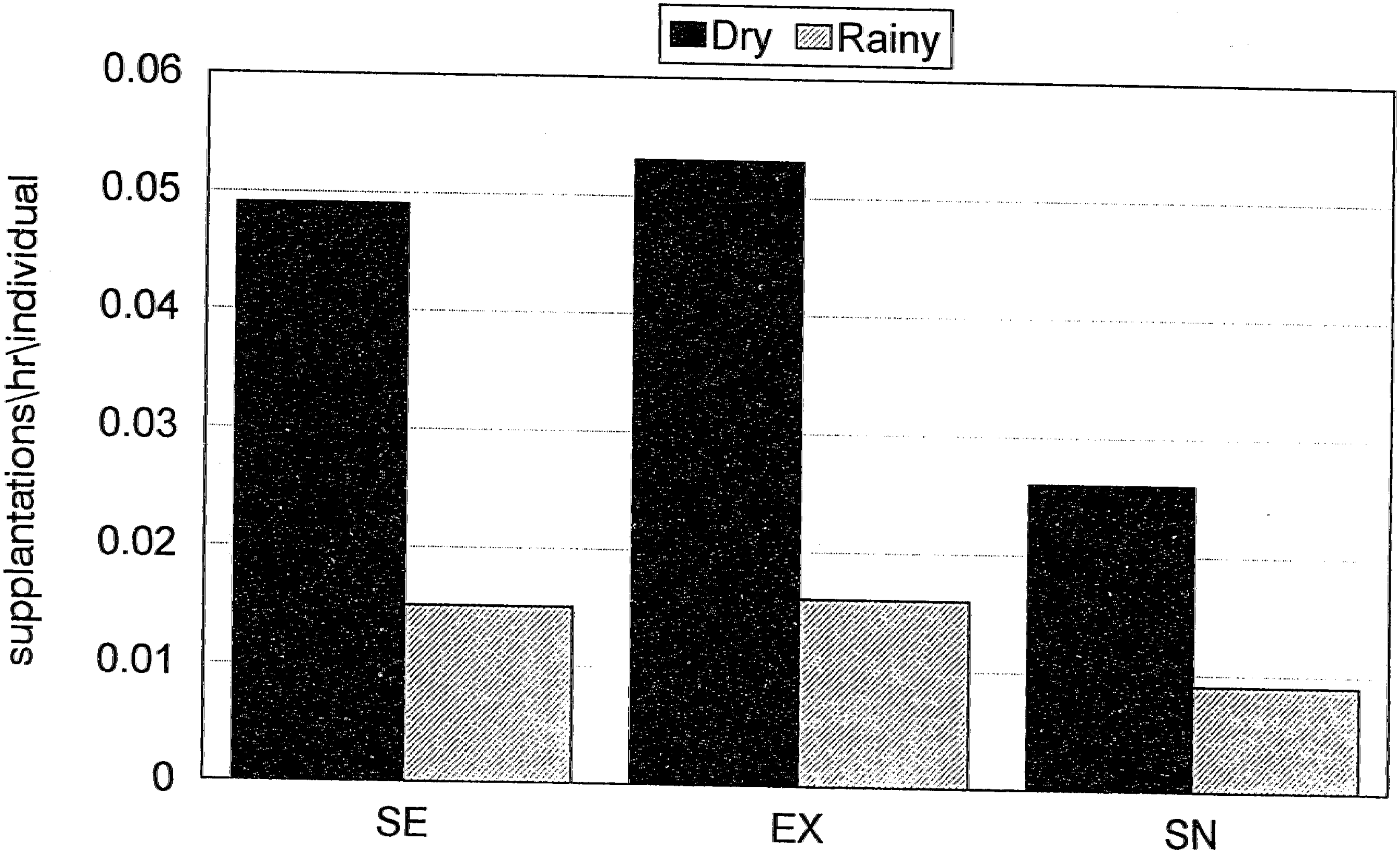

Figure 4-4. Comparison of aggression rates between the dry season and the rainy season.

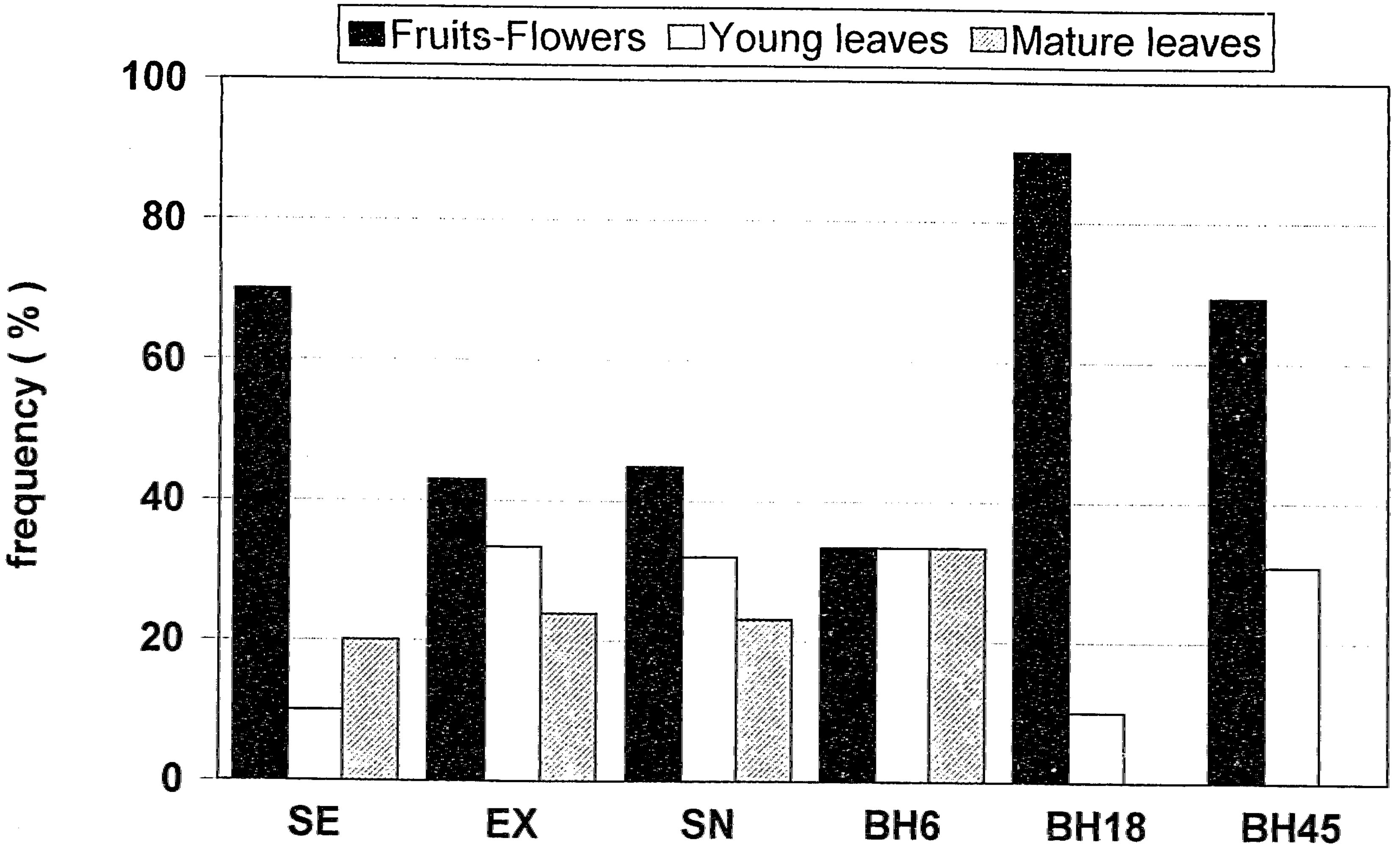

Figure 4-5. Relative frequency of supplantations over different food items for each study group.

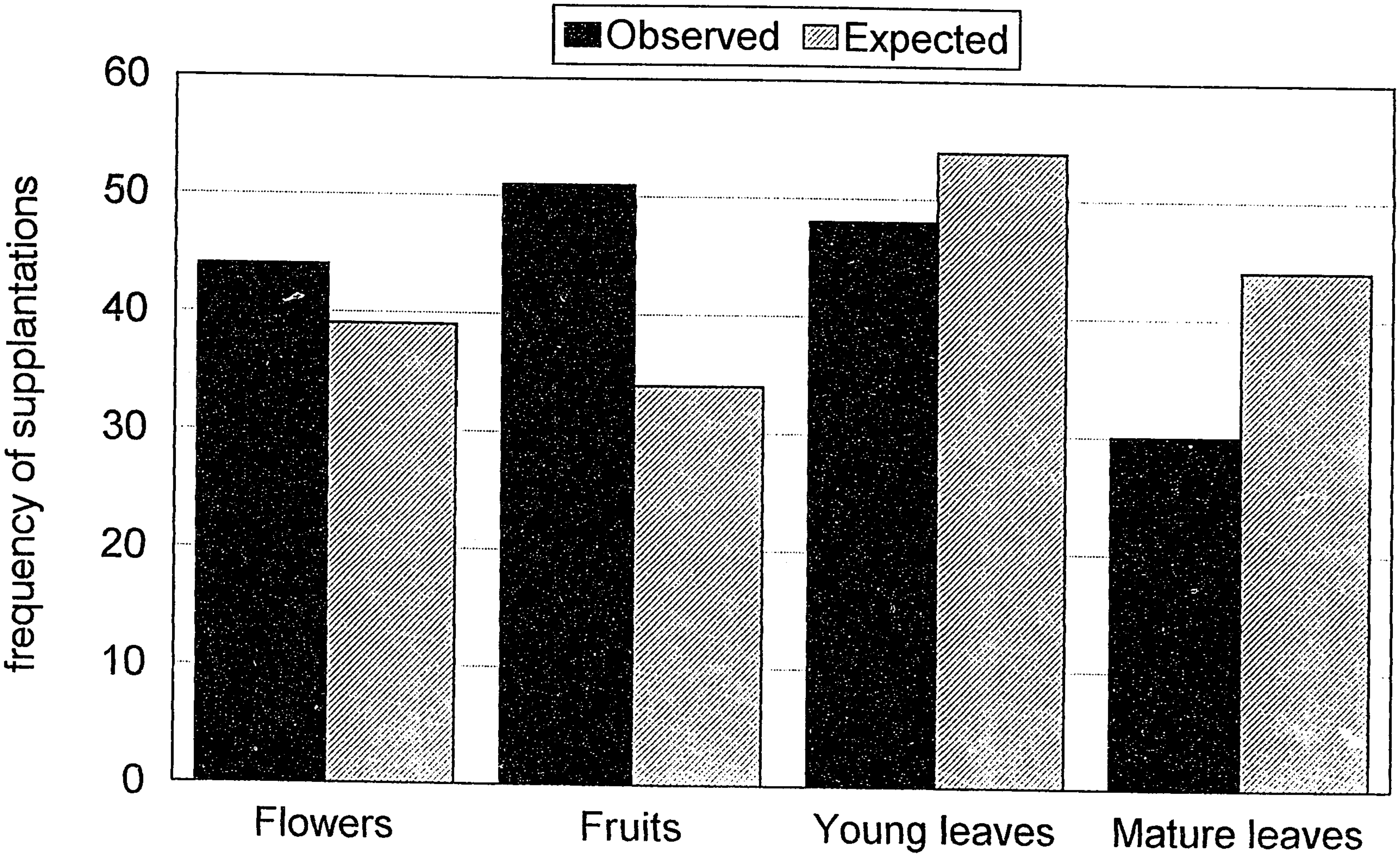

Figure 4-6. Frequency of observed and expected supplantations over different food items (all data combined).

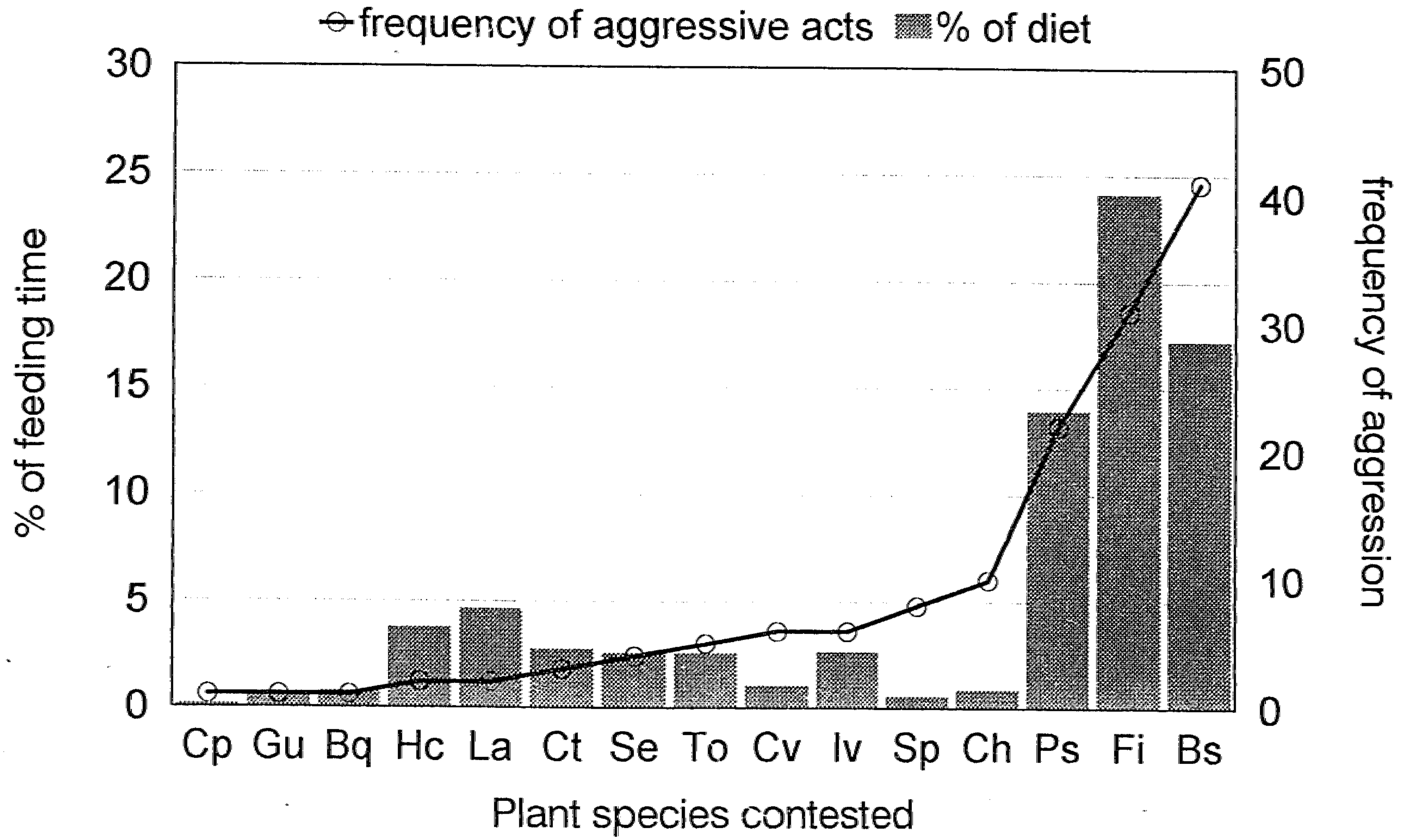

Figure 4-7. The relation between relative contribution of diet and frequency of aggressive acts in plant species where supplantations were observed (all data combined). Abbreviations for the plant species' names are for the genus and species, i.e., Bs = *Bursera simaruba*. See Table 2-3, Chapter 2 for the names of each species.

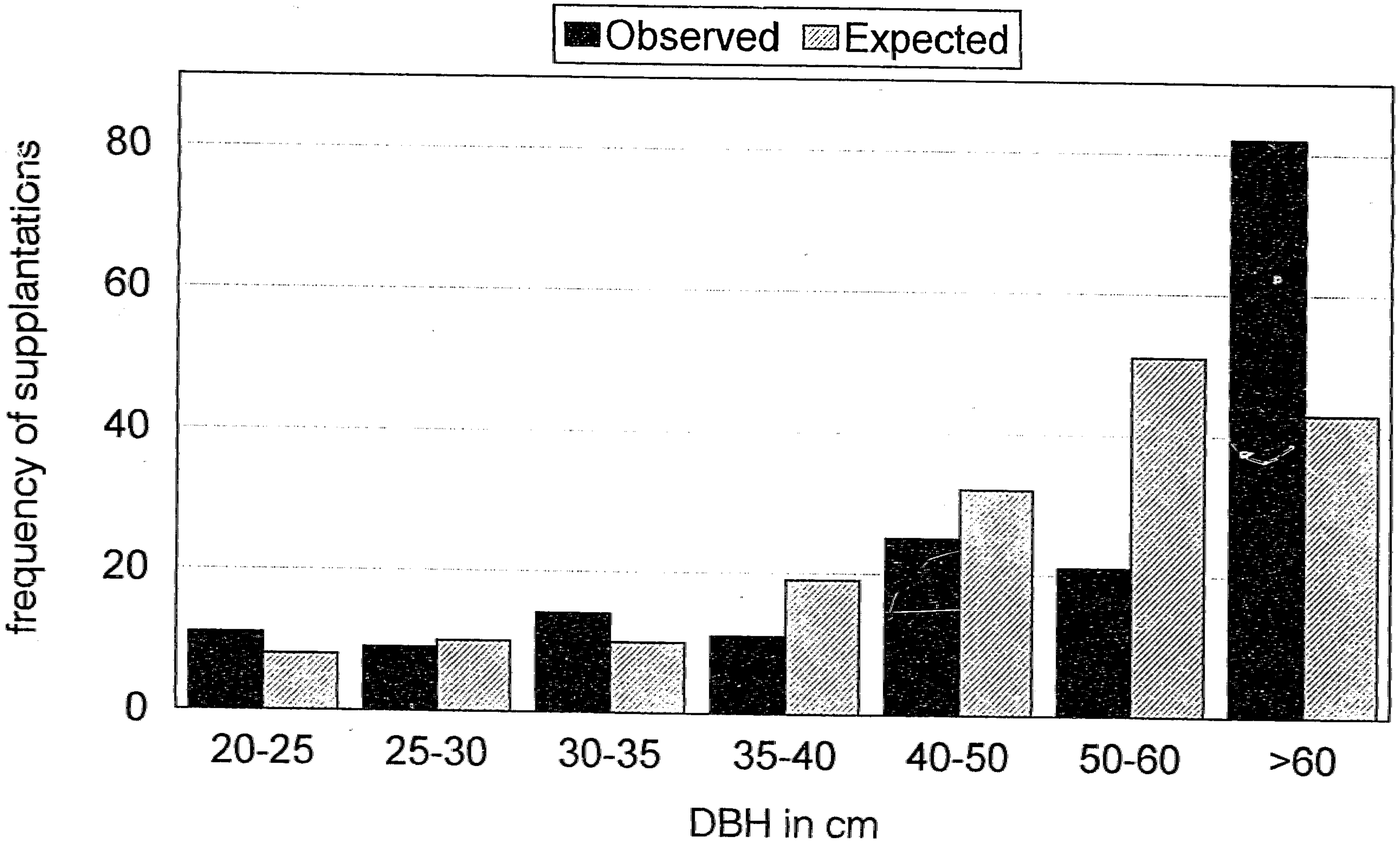

Figure 4-8. The relation between food patch size and frequency of aggression (all data combined). Presented are the observed frequencies and expected frequencies. Expected frequencies are based on the percentage of time spent feeding in patches of different sizes.

Table 4-2. Comparison of ingestion rates between adult males, adult females, and juveniles for selected food items.

Food items	Mean ingestion rates per minute[1]			Oneway anova		
	Adult males	Adult females	Juveniles	F	df	P
Bs-fr	9.53[a]	8.16	7.66	5.65	2,93	0.004
Bs-ml	5.25	5.54	3.66	2.95	2,19	0.076
Bs-yl	11.27[a]	9.80	8.00	9.34	2,54	0.003
Fi-fr	6.00	6.12	5.33	0.29	2,10	0.75
Fi-ml	3.75	3.63	3.16	0.94	2,24	0.40
Fi-yl	9.94[a]	8.72[b]	7.28	12.33	2,100	< .001
Ps-fl	10.38[a]	9.15[b]	7.87	12.46	2,113	< .001

Bs = *Bursera simaruba* Fi = *Ficus spp*. Ps = *Pithecellobium saman* fr = fruits fl = flowers yl = youngleaves ml=mature leaves

[1] rates are for the number of bites taken per minute

[a] males have significantly higher ingestion rates than females and juveniles

[b] females have significantly higher ingestion rates than juveniles

Table 4-3. Comparisons of ingestion rates between dominant and subordinate pairs within groups.

Group	Pair	Ingestion rate	t	n	P
SE	F 1 (D)	8.77	0.67	18	0.51
	F 2 (S)	8.22			
SE	M 1 (D)	8.64	0.49	26	0.63
	M 2 (S)	8.16			
EX	F 3 (D)	8.0	-0.38	20	0.71
	F 4 (S)	8.5			
SN	F RYC (D)	7.50	0.08	15	0.93
	F CAD (S)	7.42			
SN	F # 8 (D)	8.33	0.30	18	0.76
	F cafe (S)	7.88			
SN	F UN (D)	8.53	0.48	23	0.63
	F # 25 (S)	8.01			

F = female M = male D = dominant S = subordinate

Table 4-4. Correlations of ingestion rates with patch size (dbh) and number of individuals feeding in a patch (nbf) for each group and for each food item, all groups combined.

Group	Variables	r	n	P
SE	dbh-rate	-0.080	123	.376
	nbf-rate	.404		.658
EX	dbh-rate	-.2152	110	.024
	nbf-rate	-.1008		.295
SN	dbh-rate	-.0874	147	.292
	nbf-rate	.0400		.630
BH6	dbh-rate	.0292	33	.872
	nbf-rate	-.0495		.785
BH18	dbh-rate	-.4920	17	.045
	nbf-rate	-.0563		.830
BH45	dbh-rate	.2778	15	.316
	nbf-rate	.2347		.400
Food Items				
flowers	dbh-rate	-.0809	116	.388
	nbf-rate	-.0378		.687
fruits	dbh-rate	-.1881	109	.05
	nbf-rate	-.1821		.058
mature leaves	dbh-rate	-.4123	52	.002
	nbf-rate	-.1989		.157
young leaves	dbh-rate	-.1514	111	.113
	nbf-rate	-.0338		.725

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V. The relation between group size, patch size, and patch use in howler monkeys (*Alouatta palliata*) in a tropical dry forest in Costa Rica.

INTRODUCTION

Food resources used by primates tend to occur in relatively small and discrete patches particularly for frugivores and folivores, despite some claims that resources are superabundant for the latter (Coelho et al. 1976). Because there is a limit to the size of these patches, large groups and small groups should make differential use of patches. Since large groups require more food than small groups to sustain their members, there should be a positive relationship between group size and the total amount of food consumed. Thus, for a patch of a certain size and productivity, small groups should be able to spend more time feeding in the patch than larger groups if all the food items in the patch are consumed before all group members are satiated, i.e., until the patch is depleted. As a result, when patches are depleted, groups should move in search of another patch until satiation occurs. Theoretically, a patch is considered depleted when the intake rate of food items in a patch drops to the average intake rate for the habitat (Charnov 1976). However, this assumption is difficult to verify in field situations and has led to many criticisms of optimal foraging theories (Zach and Smith 1981). Furthermore, groups may leave a patch before it is operationally depleted for other reasons. The toxicity of certain plants, for example, may limit the quantity of food that can be ingested within a given time period particularly for generalist herbivores (Freeland and Janzen 1974; Feeny 1975; Rhoades and Cates 1976; Bryant and Kuropat 1980; Glander 1981). Other studies have shown that herbivores may need to consume a variety of plants to obtain complementary nutrients (Belovsky 1978; Rapport 1980) or to inhibit the action of other toxins (Freeland and Janzen 1974). Finally, groups may leave a patch because they are satiated.

In this chapter, I examine the relationship between the use of individual food patches and group size in the mantled howler monkey (*Alouatta palliata*). More specifically, I examine whether groups of howler monkeys deplete the patches they use. If patches are depleted, the rate of food intake should be lower towards the end of the feeding bout than at the beginning and the same patches should not be revisited until the patch has had time to be replenished. Furthermore, larger groups should use more patches on a daily basis and spend less time feeding in individual patches than smaller groups if patch productivity remains constant.

Several studies have examined the relationship between the size of food patches and group size in primates (Altmann S. 1974; Leighton and Leighton 1982; Whitten 1983; Janson 1985, 1988; McFarland 1986; Chapman 1988; Strier 1989). Leighton and Leighton (1982) reported a correlation between the number of howler monkeys feeding in a patch and the size of *Trichilia cipo* fruit trees. Other studies on the chimpanzees and spider monkeys have shown that the size and distribution of feeding trees was a determining factor in the size of feeding subgroups (Wrangham 1977; Klein and Klein 1977; McFarland 1986). Janson (1988) reported that groups of *Cebus apella* often used "super-productive" patches (i.e., large-crowned fruit trees), and that the intensity of interference competition was lower in these patches than in smaller patches. Strier (1989) also suggested that the difference between fission and fusion social systems and more cohesive and stable social groups may be determined by the availability of large patches of preferred foods. However, the difficulty in testing these hypotheses partly result from the definition of what constitutes a patch. Although several definitions have been used (S. Altmann 1974; Hassel and Southwood 1978; Chapman 1988), it is difficult to agree on a definition that can be used to compare across species and habitats. Furthermore, the type of food items consumed (fruits, leaves, insects) and their temporal and spatial distribution (fine-grained vs coarse-grained) make a definition even more difficult. For the purpose of this study, a tree was considered to be a patch for four reasons. First, in this study, all group members or most groups members were usually seen feeding in the same tree or in neighbouring trees of different species. Second, food items in different tree species probably contribute different nutrient and/or have different secondary compounds which limit the quantity that can be ingested. Third, groups spent more time moving between patches than within patches when they were foraging. Finally, this allowed me to retain the same definition for all my study groups and also allowed meaningful comparisons with other studies.

MATERIALS AND METHODS

Study Site

The research was conducted in Santa Rosa National Park on the northwestern coast of Costa Rica. The Park, situated 35 km northwest of Liberia in the province of Guanacaste, covers approximately 10 800 ha consisting of a series of plateaus starting at an elevation of approximately 300 m and drops down to the ocean. Santa Rosa was created in 1971 and consists of a mosaic of grassland, dry deciduous forest and semi-evergreen forest (Bonoff & Janzen, 1980; Janzen, 1983). Common species in the dry deciduous forest are *Bursera simaruba*, *Chlorophora tinctoria*, *Enterolobium cyclocarpum*, *Luehea candida*, *Pithecellobium saman*, *Spondias mombin*, and *Guazuma ulmifolia*. Common species in the semi-evergreen forest are *Hymenaea courbaril*, *Ficus spp.*, *Manilkara zapota*, *Castilla elastica*, and *Masticodendron capiri*. Santa Rosa is characterized by a dry season extending approximately from December through May, and a wet season which extends from June through November with annual precipitation ranging from 900 to more than 2400 mm, almost all of which falls during the wet season. During the dry season, deciduous trees lose their leaves and remain bare until the onset of the rainy season.

Since the creation of the park, several studies have been conducted on the primate population inhabiting the area (Freese, 1976; Fedigan, 1986; Fedigan & Baxter, 1984; Fedigan et al., 1985; Chapman, 1987; Chapman & Fedigan 1990; Chapman et al., 1989; Glander et al., 1991; Rose, 1994). Three species of primates are represented in the Santa Rosa population: *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*. Several groups of each species have been followed since 1983 as part of an ongoing study on the demography and behavior of the three species (see Fedigan, 1986). Individuals of the species *Ateles geoffroyi* and *Alouatta palliata* have been captured and marked to allow recognition and to facilitate studies of the different groups. A system of trails covering approximately 20 km has also been made to facilitate access to the groups. A number of ecological studies have also been conducted in the park, facilitating the recognition of plant species and their phenological patterns (Daubenmire, 1972; Frankie et al., 1974; Bonoff & Janzen, 1980; Opler et al., 1980; Janzen, 1982).

Santa Rosa offers an excellent opportunity to study wild primate populations because of the good observation conditions, particularly during the dry season. Also, the marked seasonality offers the opportunity to study the changes in food availability and its effect on foraging strategies within and among groups.

Study Groups

Three groups of howlers were studied during the first field season (1991) and a fourth group was added during the second field season (1992). The changes in group size for groups San Emilio (SE), Exclosure (EX), and Sendero (SN) were the result of births and disappearances of some animals, possibly due to immigration in the case of juveniles and adults, and deaths in the case of infants. However, no cases of immigration or deaths could be confirmed. Group SN also varied in size due to the fission-fusion of this group. Because part of the group was often separated from the main group for several days, the daily number of monkeys in the study group was variable. Similarly, early in 1992, the group Bosque Humedo (BH) fissioned into three distinct subgroups. This pattern had been observed previously by Chapman (1987) for the same group. In the five months following the fission, two subgroups reunited again as had happened in the past. However, the smaller subgroup remained separate even after encountering the parent group at least three times after the separation. Therefore, for the study period, the initial group of forty-five animals (BH45) was followed for only three days before it fissioned. Subsequently, two subgroups were observed. One subgroup of 18 animals (BH18) was observed for six days while the smaller group of six animals (BH6) was followed consistently over the remainder of the field season. The results presented in this paper for group BH are for the smaller subgroup of six animals (BH6) except where noted since not enough data was collected on the other two groups of 45 and 18 individuals. Therefore, in this study, groups SE and BH were the smallest groups with approximately six individuals, while EX varied between ten and fourteen. Group SN was larger and varied between 20 and 28 individuals (see Table 2-1 in Chapter 2).

The groups were located in the central area of the park and occupied relatively well defined and discrete home ranges although some overlap existed with other groups for all four groups. Individual recognition of the animals was not possible for all group members, however age/sex classes were easily recognized. In all groups, some adults were marked with collars or ankle bracelets of different sizes, shapes and colors (see Glander et al. 1991 for details). In each of the four groups, other animals could be recognized by discolorations of the skin under the hind feet and by permanent scars on the face and on the tail.

Sampling Methods

Groups were observed from January through June 1991 and from January through July 1992. No data was collected in January 1991, and during this time, the monkeys became habituated and were not alarmed by the presence of the observer after only a few days with each group. Whenever possible, each group was followed in a fixed rotation for five consecutive days over a period of three weeks from February through June 1991 and over four weeks from January through July 1992. Data on each group was collected between 0530 and 1800 hours. Groups were usually found in their sleeping sites early in the morning and were followed until they had reached the sleeping sites at the end of the day. A total of 2040 hours of data were collected on the four groups over 166 full days of observation.

For the first field season, the groups were followed using focal sampling sessions (Altmann 1974) of ten minutes in length on adults and juveniles. Subjects were selected at random prior to the beginning of the day, and when possible, were alternated according to age and sex class. The order of rotation was then maintained for the rest of the day. For the second field season, one individual was followed for the whole day and data was collected on adults only, alternating between males and females. During each focal sessions, the main activity in which the subject had engaged was recorded for each two minute period at the end of each time interval. Thus, five behaviors were scored for each focal session in the first year. In the second year, behaviors were scored every two minutes from the first contact in the morning until the end of the day. Because howlers have a relatively limited behavioral repertoire and engage in each behavior for relatively long periods of time, a two minute period was adequate. Behavioral categories for the focals were: rest, play, travel, manipulate (substrate), scan, feed (bringing food to the mouth, chewing, and swallowing), vocalize (for males only), social (sexual behaviors), and other. I also recording the ingestion rates for each focal animal whenever possible. I counted the number of food items ingested or the number of bites taken during each two minute period . The ingestion rates presented in this paper represent the average rate per minute. Scan sampling was used to determine the time spent in all major activities for each group. Instantaneous scans were taken at ten minute intervals and one activity was scored for the group. Because howler groups are highly synchronous in their activities, the results of the scan sampling is an accurate method for howlers. The behavioral categories used for the scans were feeding (i.e., eating from large food sources), foraging (i.e., eating from small, dispersed food sources), resting, travelling, and other. Definitions for foraging and feeding were the same as those used by van Schaik & van Noordwijk (1988).

Dietary composition was measured in terms of time spent feeding and foraging on the different plant species and food items for the groups as a whole. Feeding was defined as eating from large food sources as opposed to foraging which was defined as eating from small food sources where the animal spent less than one minute before moving on to the next food source. Feeding and foraging consisted of reaching for, bringing to the mouth, and chewing food items. In this chapter, I combined the feeding and foraging data for all analyses and I use only the term 'feeding' to signify both feeding and foraging as defined above.

Time spent feeding in a patch was determined by recording the interval elapsed between the time when the first individual started feeding in the patch and the time the last individual left the patch (patch residence time, PRT). This is referred to as a feeding record throughout this paper. If no feeding was observed in that patch for thirty minutes after the last individual left, the feeding record was terminated. If feeding resumed before that time, the second patch residence time (PRT) was added to the first one and constituted only one feeding record. At least once per five minutes, I recorded the number of individuals feeding in the patch (NBF) to estimate the "total feeding minutes" (TFM) spent feeding in that tree (i.e., if two individuals fed in the tree for five minutes each, the "total feeding minutes" was ten minutes). When subgroups were feeding in more than one tree at a time, I was able to record the same information for a second patch. When more than two patches were used simultaneously, data was recorded for as many patches as possible and the number of patches used was counted.

For each feeding tree visited by the group, I recorded the plant species, the food type ingested, and the size of the patch. Each feeding tree was marked and given an identification number so that frequency of use and renewal rate of patch resources could be determined. Patch size was determined by measuring the diameter at breast height (DBH). Because several studies have demonstrated a strong correlation between DBH, crown size, and reproductive capacity for a number of tropical species (McDiarmid et al., 1977; Leighton & Leighton, 1982), DBH was used as an estimator of the number of items available in a patch. Five food types were used for this study: fruits, flowers, mature leaves, young leaves, and leaf buds. For the analysis, leaf buds and young leaves were combined into one category. To compare diets across seasons I determined the onset of the rainy season to be the first day following the first rain, which occurred in the first two weeks of May for 1991 and 1992. To allow for meaningful comparisons, most results obtained in this paper were carried on three groups (SE, EX, SN) combining 1991 and 1992 and on the four groups for the 1992 season only.

Statistical methods

Parametric statistics were used whenever possible over nonparametric tests. For all parametric tests, the distributions of all variables were tested for normality and homogeneity of variances. When values were not normally distributed, an appropriate transformation was applied (Sokal & Rolhf, 1981). The reverse transformations were applied to facilitate the presentation of the results. For multiple group comparisons, a oneway anova with range test (Scheffé's method) was used. For all regression analyses, the data was log transformed to approximate linear relationships between the variables. Comparisons among groups are normally for all six groups (including BH18 and BH45) if sample size is adequate. When fewer groups are used, I indicated it in the text. All probabilities are two-tailed unless stated otherwise. All statistical procedures were carried out using the SPSS/PC statistical package.

RESULTS

If large groups deplete the patches they use, larger groups should use more patches on a daily basis than small groups. To control for changes in group size which occured between 1991 and 1992, I analyzed the data for each year separately. For 1991, there was a significant differences in the number of patches used on a daily basis ($F=26.58$, $P < .001$, df[5,61], Scheffé's $P < .05$). Larger groups used more food patches than smaller groups (SE=7.54, EX=12.22, SN=16.37). For 1992, groups BH18 and BH45 used significantly more patches than the other groups ($F=17.75$, $P < .001$, df[5,94], Scheffé's $P < .05$; BH6=6.93, SE=7.40, EX=8.28, SN=8.64, BH18=12.16, BH45=21.33). Although there were no significant differences between the other groups, the number of patches used did increase as a function of group size. There were also no significant differences in the size of feeding patches between groups (see Chapter 3).

Another test to determine if patches are depleted is to examine the time spent feeding in a patch (patch residence time, PRT) for each group. For a patch of a given size, larger groups should deplete the patch faster than small groups and therefore spend less time feeding in the patch than smaller groups. For my study groups, larger groups spent on average more time feeding in a patch than smaller groups ($F=9.26$, $P < .001$, df[5,863], Sheffé's $P < .05$). However, the only significant differences were between group SN (29.4 minutes) and the three smaller groups, SE (21.87), EX (21.86), and BH6 (18.26). The average PRT for groups BH18 and BH45 were also higher than the smaller groups, although not significantly (BH18 = 24.41, BH45 = 25.43). This could be explained by the fact that small groups may become satiated and may leave the patch before it is depleted whereas larger groups remain in the patch until satiation occurs or until the patch is depleted. Also, because animals often left the patch and were replaced by others (particularly in larger groups), PRT may not be an accurate measure of patch depletion. To control for this, I used the total feeding minutes spent feeding in a patch. Total feeding minutes was calculated by counting the number of individuals feeding in a patch (NBF) at least once every five minutes (see methodology). Using this measure, larger groups spent more time feeding in patches than small groups ($F=22.44$, $P < .001$, df[5,863], Scheffé's $P < .05$). The three larger groups spent significantly more time feeding than the three smaller ones (BH6 = 56.95, SE = 72.29, EX = 98.33, BH18 = 109.90, SN = 141.60, BH45 = 170.75). Total feeding minutes (TFM) represent not only the time spent feeding in a patch (PRT) but also the number of individuals feeding in a patch (NBF) and is therefore a more accurate estimate of the amount of food present in a patch.

I also tested to see if differences existed in the average number of individuals feeding simultaneously in a patch. Larger groups did have more individuals feeding in patches than small groups ($F = 66.27$, $P < .001$, df[5,863], Scheffé's $P < .05$). Most comparisons between pairs of groups revealed significant differences with two exceptions, group BH6 and SE (4.04 and 4.23 respectively) and group BH18 and SN (7.49 and 7.28 respectively). Group EX had an average of 6.17 individuals feeding in a patch, while the larger group BH45 had the most (11.18).

I also used multiple regressions to determine whether patch size and the number of individuals feeding in a patch explained patch residence time. For the multiple regression, I used PRT as the dependent variable and patch size (DBH) and number of individuals feeding in a patch (NBF) as the independent variables. When all the data is combined, NBF was a better predictor of patch residence time although it explained only 10 % of the variation (see Table 5-1). When both patch size and NBF are included, they explained only 13% of the variation in PRT. Partial correlations show that NBF is a better predictor of PRT when controlling for patch size ($r = .268$ $P < .001$) than patch size is when controlling for NBF ($r = .195$ $P < .001$). Comparisons of PRT and TFM by food items revealed that groups spent on average less time in patches when they were feeding on mature leaves than on other food items (PRT: $F = 5.42$, $P < .001$, df[3,865], Scheffé's $P < .05$; TFM: $F = 12.04$, $P < .001$, df[3,865], Scheffé's $P < .05$). There were no differences between other food items for either PRT or TFM.

I used the same regression analysis to determine if PRT was affected more by DBH and NBF for the different food items (see Table 5-1). When both independent variables are entered in the equation, they only explained 6% of the variation in PRT ($r^2 = .065$, $P < .001$) when the groups are feeding on mature leaves, compared with 18% for young leaves ($r^2 = .182$, $P < .001$), 11% for flowers ($r^2 = .118$, $P < .001$) and 20% for fruits ($r^2 = .197$, $P < .001$). For flowers, DBH did not explain any of the variation in PRT when controlling for NBF (partial correlation, $r = .009$, $P = .890$). A plot of the residuals of PRT and NBF controlling for patch size (Figure 5-1) and a plot of residuals of PRT and DBH controlling for NBF (Figure 5-2) clearly show that NBF is a better predictor of patch residence time than patch size. The greater contribution of NBF can be explained by the fact that most of the flowers eaten by howlers in this study came from large *Pithecellobium saman* trees which produce tens of thousands of small flowers over a few weeks at the end of the dry season and shortly after fruiting. Thus, these patches are rarely depleted (see below). Partial correlation analysis for each of the independent variables and for each food item are presented in Table 5-1.

I repeated the analysis for each group to determine if group size *per se* and not only NBF explained the use of patches (Table 5-2). Patch size and NBF explained more of the variation in PRT for larger groups (SN: $r^2 = .149$, BH18: $r^2 = .233$, BH45: $r^2 = .394$, all $P < .001$) than for small groups (SE: $r^2 = .112$, EX: $r^2 = .090$, $P < .001$; BH6: $r^2 = .009$, $P = .716$). However, DBH and NBF did not explain any of the variation in PRT for group BH6 (less than 1%). For most groups (except EX and BH6), NBF explained more of the variation in PRT than DBH (see Table 5-2). Plots of the residuals of PRT and NBF controlling for the patch size (DBH) for the three larger groups (SN, BH18, BH45) clearly show the influence of NBF (Figure 5-3, 5-4, 5-5 respectively).

It is also possible to determine if patches are depleted by looking at the frequency of use of the same patches on a daily and a monthly basis. If patches are depleted after the first visit, the patch should not be revisited until it has been replenished. This is unlikely to be the case when the patches are used more than once the same day, or several times over consecutive days. On a daily basis, patches were used more than once *per* day 125 times. Patches were used twice *per* day 103 times, three times *per* day 18 times, and four times *per* day 4 times (Table 5-3). All groups except BH18 and BH45 used some patches twice *per* day. Of the 125 times where patches were used more than once a day, 68.8% (86) were large patches (> 60 cm DBH). There were no significant differences between groups in the size of patches used more than once ($F = 2.72$, $P = .04$, df[3,121], Scheffé's $P > .05$). Of the 125 times when patches were used more than once a day, groups were feeding on flowers 31 times, 23 times for fruits, 40 times for young leaves, and 31 times for mature leaves. Most instances of feeding on fruits were for *Sciadendron excelsum* (7) and *Bursera simaruba* (12), which bear small fruits which grow in large clumps. Also, 20 of the 31 instances of feeding on flowers were in *Pithecellobium saman* trees. The species most frequently used more than once a day were *Ficus* (37 times), *Pithecellobium saman* 20 times, and *Bursera simaruba* 15 times.

On a monthly basis, all groups often used the same patches on consecutive days even if some were used more than once a day. The number of days of observations for each group never exceeded 7 days a month and some patches were used up to 10 times during that period, usually for the same food item. Most of these patches were preferred food species like *Pithecellobium saman*, *Ficus spp.*, and *Bursera simaruba*. To compare between groups, I counted the total number of feeding records and I divided by the total number of patches used for each group to estimate the average number of times patches were used. In 1991, group SE used 32 patches 102 times (102/32 = 3.18), group EX used 30 patches 63 times (63/30 = 2.1) and group SN used 44 patches 97 times (97/44 = 2.2). The smaller groups did use the same patches more often on average than large groups. Similar results were obtained for 1992 (SE = 2.05; BH6 = 1.71; EX = 1.72; SN = 1.83; BH18 = 1.24; BH45 = 1.12).

A final test to determine if patches were depleted is to look at ingestion rates for individuals at the beginning of feeding bouts and at the end of the feeding bouts. I was able to use 527 feeding records for which I had ingestion rates per minutes for the first five minutes feeding in a patch and for the last five minutes. Patch residence time for those feeding records was at least 10 minutes in duration. Paired t-tests were used for each group and the results show that ingestion rates at the end of the feeding bout were significantly lower for all groups (SE: $t = 9.73$ $P < .001$; EX: $t = 9.87$ $P < .001$; SN: $t = 13.27$ $P < .001$; BH6: $t = 5.73$ $P < .001$; BH45: $t = 2.82$ $P = .014$) except group BH18 ($t = 1.18$, $n = 17$, $P = .252$. I also carried out the analysis for each food item in the diet and all paired t-tests were significant at the .001 level (mature leaves: $t = 4.57$; young leaves: $t = 10.78$; flowers: $t = 11.74$; fruits: $t = 8.35$). The results show that ingestion rates are much lower at the end of the feeding bouts, suggesting that either food items are more difficult to find because they are becoming scarce, i.e., patches are depleted, or because individuals are satiated. To test the hypothesis that patches are depleted, I compared ingestion rates between the beginning and the end of the feeding bout with the feeding rate in patches that were used again the same day or the following day. I had a sample of 86 patches for which I had rates on consecutive feeding bouts (Table 5-4). In most cases, ingestion rates were lower at the beginning of the second feeding bout than at the beginning of the first feeding bout. However, ingestion rates were higher at the beginning of the second feeding bout than at the end of the first feeding bout. These results suggest that patches were not necessarily depleted when individuals stopped feeding since the second feeding bout in the same patch later the same day or the following day were higher. However, it is possible that some of the patches had produced more flowers overnight or that fruits had ripened hence the higher ingestion rates at the beginning of the second feeding bout. However, this is an unlikely explanation for patches used the same day (n = 51). I also did the same analysis for each group and obtained similar results suggesting the ingestion rates were usually higher at the beginning of the second feeding bouts than at the end of the first one. Ingestion rates were also usually lower at the beginning of the second feeding bout than at the beginning of the first one, confirming that fewer items were available the second time around.

DISCUSSION

Several results presented here indicate that larger groups may deplete patches more frequently than smaller groups. This agrees with a previous study done by Chapman (1988) in Santa Rosa on group BH45. Although no differences were found in the size of feeding patches used between small and large groups, the number of patches used increased as a function of group size for 1991 and 1992. The difference in the number of patches used however may not reflect the fact that patches were depleted but may be a strategy to minimize the amount of interference competition which would result if individuals are feeding in close proximity to one another, particularly when feeding on high-quality food items such as fruits or flowers. Thus, individual members of a group may feed in several neighbouring trees at once to lower the rate of aggression or may wait for "spaces" to open up in patches when others become satiated. This process was observed frequently in this study and by other studies on howlers (Glander 1975; Milton 1980; Leighton and Leighton 1982; Chapman 1988). Leighton and Leighton (1982) in studies of howlers at Barro Colorado Island, Whitten (1983) in a study of vervets (*Cercopithecus aethiops*) and Strier (1989) in a study of muriquis (*Brachyteles arachnoides*) reported that there was a positive correlation between patch size and the number of individuals feeding in a patch when feeding on fruits. Strier (1989) also reported that a greater number of individuals fed at leaf sources than expected from the size of the patches. This suggests that competition for leaves may be low compared to fruits and that more individuals may be able to feed simultaneously in a leaf patch without increasing the level of interference competition. Moreover, several findings in the present study suggest that leaf patches are seldom depleted, particularly mature leaf patches. An important difference between the present study and the three previously mentioned studies is that no significant correlation was found here between patch size and the number of individuals feeding in a patch when the data was analyzed separately for each group. A significant correlation was found however when all the data from each group were combined (see chapter 4).

Other evidence presented in this study suggest that larger groups deplete the patches they use more often than smaller groups. Larger groups used the same patches less often on a daily and monthly basis. Even if patches are somewhat replenished (new flowers or ripe fruits), the quantity of food required by large groups may be such that using the same food sources would still result in ingestion rates lower than could be achieved at other food sources. This would fit in with the patch depletion hypothesis of Charnov (1976). Another strategy is for groups to fission. This pattern has been observed for groups BH18 and BH45. There is considerable evidence in this study to suggest that groups BH18 and BH45 frequently depleted the patches they used. Both groups fissioned during the dry season, when food items occur in relatively small and discrete patches (fruits and flowers), and reunited in the rainy season when the diet is primarily composed of mature leaves. Furthermore, the absence of large *Pithecellobium saman* trees provided fewer flower sources than could be found in the other groups' home range. *Pithecellobium saman* trees produce tens of thousands of small flowers over several weeks twice during the year (Janzen 1983). These trees have large canopies (DBH > 60 cm) and thus may constitute "super-productive" patches (Janson 1988) which can be used for several days consecutively. This explains the high proportion of flowers of *Pithecellobium saman* in the diet of three of my study groups (SE, EX, and SN). Other trees can be included in the category of "super-patches". For instance, fig trees are also large food sources (DBH > 90 cm and > 120 cm) and produce flowers, fruits and young leaves during the year. Howlers feed on all of these food items. As a result, the same patch can be used several times a month and several times a year. More importantly, contrary to *Pithecellobium saman* trees which have more synchronized phenological cycles, fig trees are highly asynchronous in their production of fruits and leaves. This ensures an almost constant food supply throughout the year if several fig trees are present in a group's home range. In fact, fig trees were used as food sources every month in this study. Groups BH18 and BH45 also had the lowest density and the fewest fig trees in their home range compared to the other groups. These findings corroborate Strier's suggestion that the difference between species which exhibit a fission-fusion social system and species which have more stable groups may be determined by the availability of these "super-patches". In a study of *Cebus apella*, Janson (1988) also reported that his study group used "super-productive" patches. Janson noted that the level of interference and exploitation competition was lower in these patches than in smaller, less productive patches.

Nevertheless, although some patches may be depleted, several results in this study suggest that certain feeding trees or "super-patches" are often not depleted. First and foremost, patches are frequently used several times a day, particularly by small groups. It is unlikely that these sources renew themselves in a few hours (often in less than two hours). Still, howlers were often seen leaving a patch to resume their feeding in another patch, usually a different food species. Small groups often fed in the same two or three patches later in the day and the subsequent day. This is in accord with hypotheses which suggest that individuals may require several food sources, each providing different nutrients (Belovsky 1978; Rapport 1980). It may also be that the presence of secondary compounds limits the quantity of certain foods that can be ingested over short periods of time (for a review, see Freeland and Janzen 1974). Glander (1981) and Milton (1984) provided evidence that howlers choose their food sources based on the quality of the food (protein content and digestibility) and the avoidance of secondary compounds like tannins. This may explain the fact that the size of patches and the number of individuals feeding in a patch were poor predictors of time spent feeding in a patch. An important factor to consider may be individual tolerance to certain compounds or the amount ingested previously in the day, as well as gut capacity and digestion rate. More evidence of this comes from examination of daily combinations of food species and food items for each group and for the dry and rainy season (Table 5-5). All combinations of species or food items that were used in at least 10% of the sample days for each group are listed in the table. Groups usually fed on at least two of the three primary species (*Ficus*, *Pithecellobium saman* and *Bursera simaruba*) on a daily basis and usually included a mix of leaves and fruits or flowers.

Finally, the fact that individuals had lower ingestion rates at the end of feeding bouts than at the beginning may be explained in two ways. First, in the case of large groups, patches may be functionally depleted. Second, for small groups which return to feed in the same patch later that day, it may be that they have reached their satiation level for that food item, whether it is because they need other nutrients or because of the presence of toxins. This may explain the fact that ingestion rates were often higher when they returned to the patch later. Another explanation may be that patches are replenished between visits. Although this is unlikely to be the case when visits occur within hours, it may explain the visits to the same patches over consecutive days particularly for flowers, new leaves or ripe fruits

Do howlers deplete the patches they use?

The results presented in this study suggest that larger groups more often deplete the patches they use compared to smaller groups. The evidence for this can be summarized as follows: 1) large groups used more patches than small groups 2) large groups use the same patches less often than small groups on a daily and a monthly basis 3) ingestion rates for all groups were lower at the end of the feeding bout than at the beginning of the feeding bout 4) larger groups spent more time feeding in patches than smaller groups and 5) the number of individuals feeding in a patch and patch size were better predictors of time spent feeding in patches for larger groups than for smaller groups. However, some results presented here also suggest that some patches are not depleted by either small or large groups. First, patch size and the number of individuals feeding in a patch were extremely poor predictors of patch residence time when howlers were feeding on mature leaves. This suggests that time spent feeding on mature leaves may be limited by other factors such as satiation levels or the presence of toxins in mature leaves. Second, during consecutive visits to the same patches, ingestion rates were higher at the beginning of the second visit than at the end of the first visit. This can be explained in two ways: 1) lower ingestion rates mean that individuals were satiatied at the end of the first visit or 2) patches produced more food items between the end of the first and the second visit. The latter in unlikely to be the case however when visits occur the same day.

Finally, the evidence presented here strongly suggest that the presence of "super-patches" may reduce the effects of feeding competition within groups and may favor larger groups. When such patches are scarce or absent, at least temporarily, several options may be possible. One is to increase the level of interference competition so that some group members are able to maintain intake rates to sustain themselves at the expense of others (Janson 1988). The other option is to fission like chimpanzees and spider monkeys (McFarland 1986). Howlers in this study have demonstrated that it is a viable option even for more 'folivorous' species. Foraging models and hypotheses to explain the evolution of social systems will have to incorporate variables such as the presence or absence of these 'super-patches' and the renewal rate of patches, i.e., how long are patches productive and how often do they produce food items available for consumption. Furthermore, several assumptions about folivores and howlers will have to be reexamined in light of the findings presented here. First, the term folivore may not be accurate for howlers as their diet consists of seasonal items whenever they are available and should therefore be called "facultative" folivores to distinguish them from true folivores like Colobines and Indriids who possess specialized stomachs for digesting leaves. Second, the assumption that food is not a limiting factor in determining group size in howlers is contradicted in this study. Groups BH45 and BH18 fissioned during this study not necessarily because of a lack of food but primarily because of the absence of large feeding trees or 'super-patches'. Finally, the relationship between dietary composition and stable *versus* fission-fusion social groups may be less obvious than previously thought. Fission and fusion is also possible among 'facultative' folivores like howlers who feed primarily on high-quality seasonal food items.

Table 5-1. Regression equations and partial correlation analysis for all data combined and each food item. Independent variable is patch residence time (PRT) estimated from patch size (DBH) and the number of individuals feeding in a patch (NBF).

Dependent variable[1]	Independent variable[1]	r^2	P	Y-intercept	regression coefficient	partial correlation
PRT all data combined	NBF (only)[a]	.99	< .001	1.02	.385	
	DBH (only)	.66	< .001	.719	.328	
	NBF-DBH	.13	< .001	.629	NBF = .327	r = .268 P < .001[b]
					DBH = .244	r = .195 P < .001[c]
PRT mature leaves	NBF (only)	.032	= .004	1.08	.251	
	DBH (only)	.049	< .001	.809	.263	
	NBF-DBH	.065	< .001	.755	NBF = .180	r = .184 P = .003
					DBH = .222	r = .127 P = .042
PRT young leaves	NBF (only)	.133	< .001	1.03	.409	
	DBH (only)	.095	< .001	.610	.400	
	NBF-DBH	.182	< .001	.548	NBF = .341	r = .309 P < .001
					DBH = .296	r = .237 P < .001
PRT flowers	NBF (only)	.118	< .001	.976	.422	
	DBH (only)	.0003	= .802	1.26	.025	
	NBF-DBH	.118	< .001	.953	NBF = .422	r = .343 P < .001
					DBH = .012	r = .009 P = .890
PRT fruits	NBF (only)	.096	< .001	1.02	.395	
	DBH (only)	.151	< .001	.253	.594	
	NBF-DBH	.197	< .001	.206	NBF = .283	r = .232 P = .003
					DBH = .504	r = .334 P < .001

[1] see text for explanation [a] only one variable in the equation (all variables are log transformed)

[b] partial correlations are for regression of NBF on PRT when DBH is held constant

[c] partial correlations are for regression of DBH on PRT when NBF is held constant

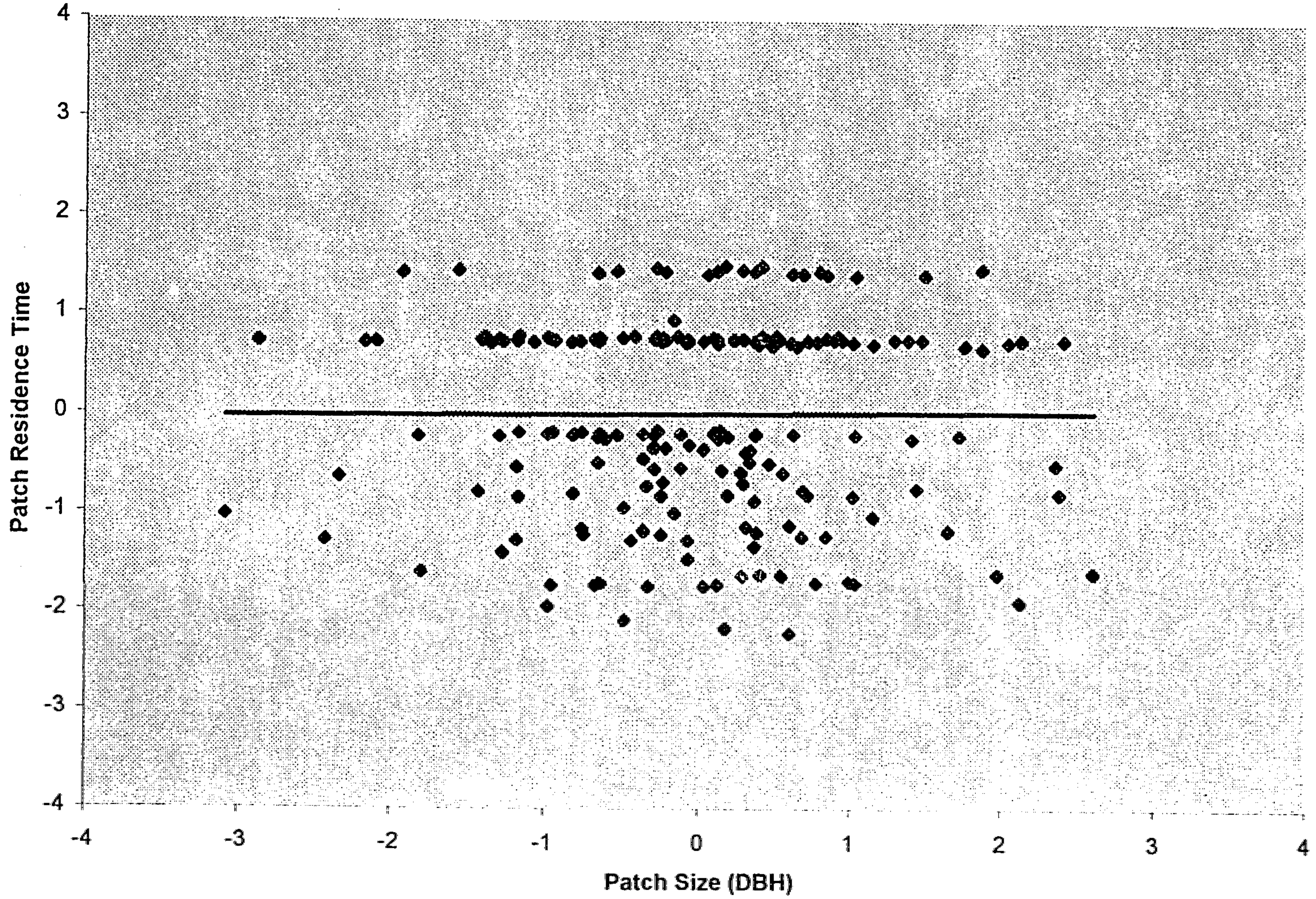

Figure 5-1. A standardized partial regression plot of the effects of patch size on patch residence time controlling for the effects of the number of individuals feeding in a patch. The data is for all groups combined and for time spent feeding on flowers.

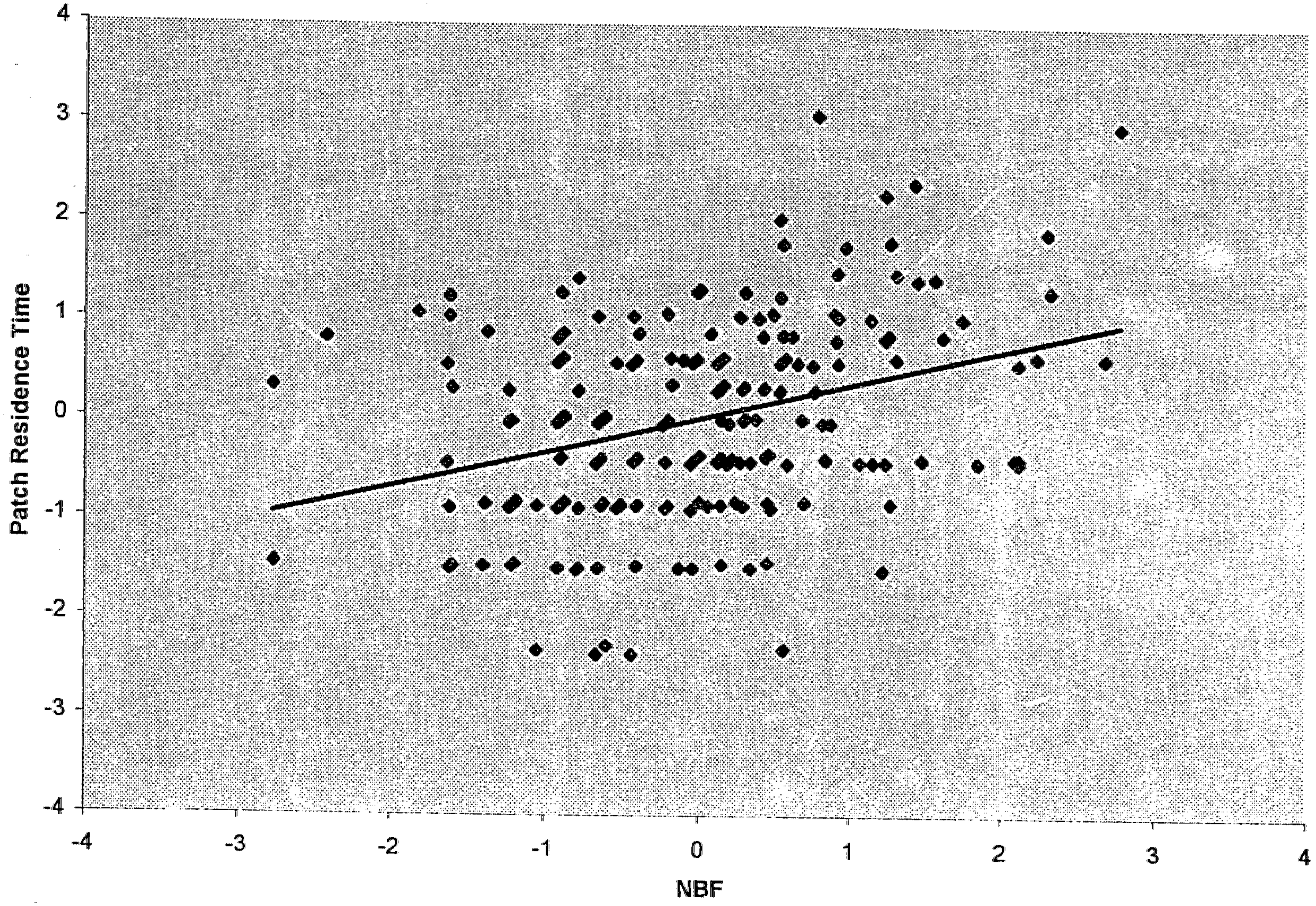

Figure 5-2. A standardized partial regression plot of the effects of the number of individuals feeding in a patch on patch residence time controlling for the effects of patch size. The data is for all groups combined and for time spent feeding on flowers.

Table 5-2. Regression equations and partial correlation analysis for each group[a]. Independent variable is patch residence time (PRT) estimated from patch size (DBH) and the number of individuals feeding in a patch (NBF).

Dependent variable	Independent variable[1]	r^2	P	Y-intercept	regression coefficient	partial correlation
PRT group SE	NBF(only)	.080	< .001	.927	.562	
	DBH (only)	.049	< .001	.715	.317	
	NBF-DBH	.112	< .001	.514	NBF = .502	r = .255 P < .001
					DBH = .256	r = .185 P = .003
PRT group EX	NBF (only)	.037	= .004	1.05	.282	
	DBH (only)	.077	< .001	.642	.349	
	NBF-DBH	.090	< .001	.588	NBF = .177	r = .120 P = .081
					DBH = .304	r = .235 P < .001
PRT group BH6	NBF (only)	.0001	= .978	1.22	.002	
	DBH (only)	.008	= .438	1.10	.069	
	NBF-DBH	.009	= .716	1.10	NBF = .031	r = .032 P = .788
					DBH = .079	r = .098 P = .415
PRT group SN	NBF (only)	.116	< .001	1.02	.430	
	DBH (only)	.058	< .001	.797	.317	
	NBF-DBH	.149	< .001	.621	NBF = .387	r = .311 P < .001
					DBH = .242	r = .192 P = .002
PRT group BH18	NBF (only)	.213	= .002	.779	.648	
	DBH (only)	.180	= .005	.485	.476	
	NBF-DBH	.233	= .006	.555	NBF = .454	r = .253 P = .110
					DBH = .219	r = .156 P = .330
PRT group BH45	NBF (only)	.333	< .001	.783	.580	
	DBH (only)	.306	< .001	.436	.537	
	NBF-DBH	.394	< .001	.452	NBF = .381	r = .354 P = .030
					DBH = .306	r = .301 P = .070

[a] see Table 5-1 for explanation (all variables are log transformed)

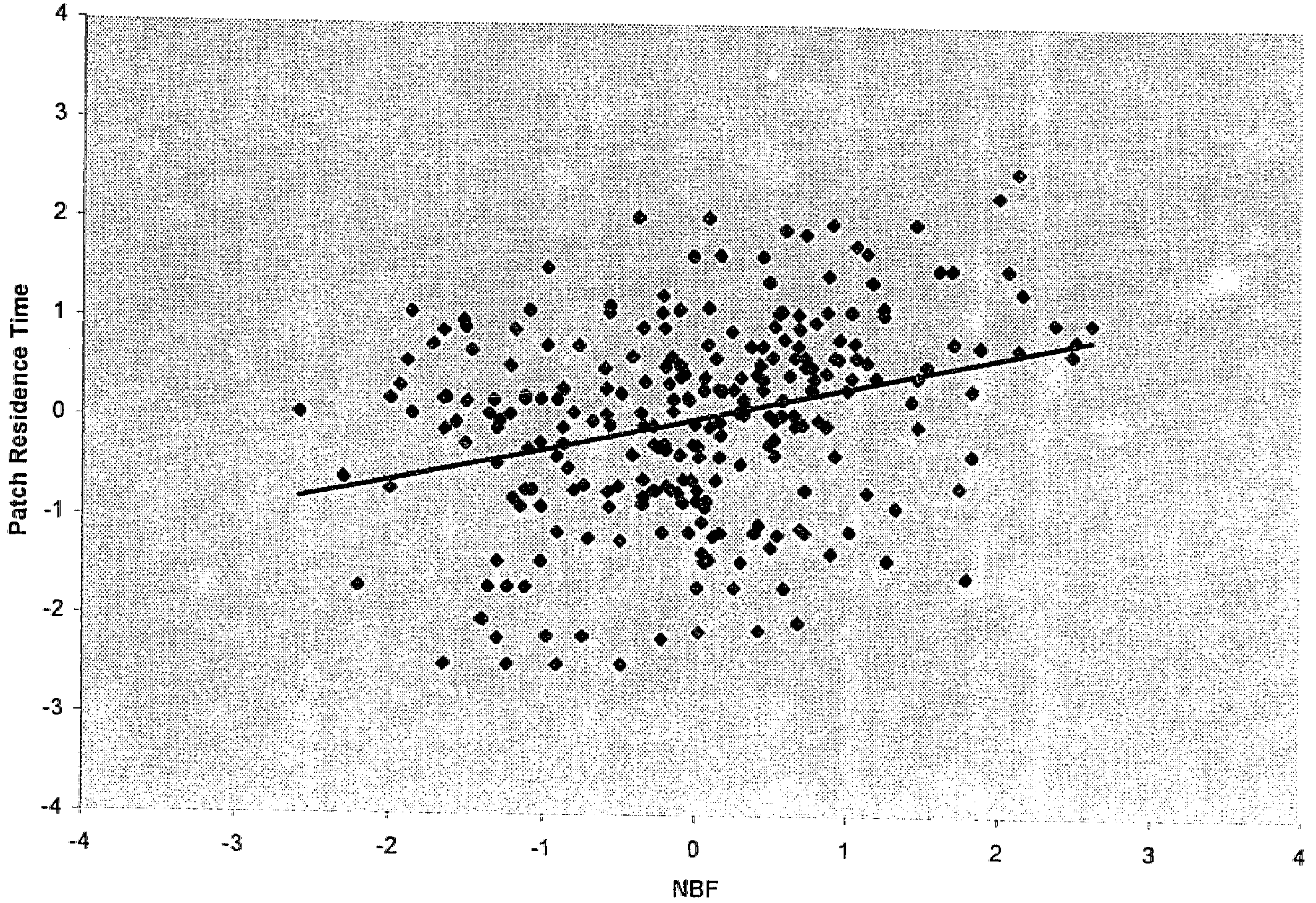

Figure 5-3. A standardized partial regression plot of the effects of the number of individuals feeding in a patch on patch residence time controlling for the effects of patch size. The data is for group SN, all food items combined.

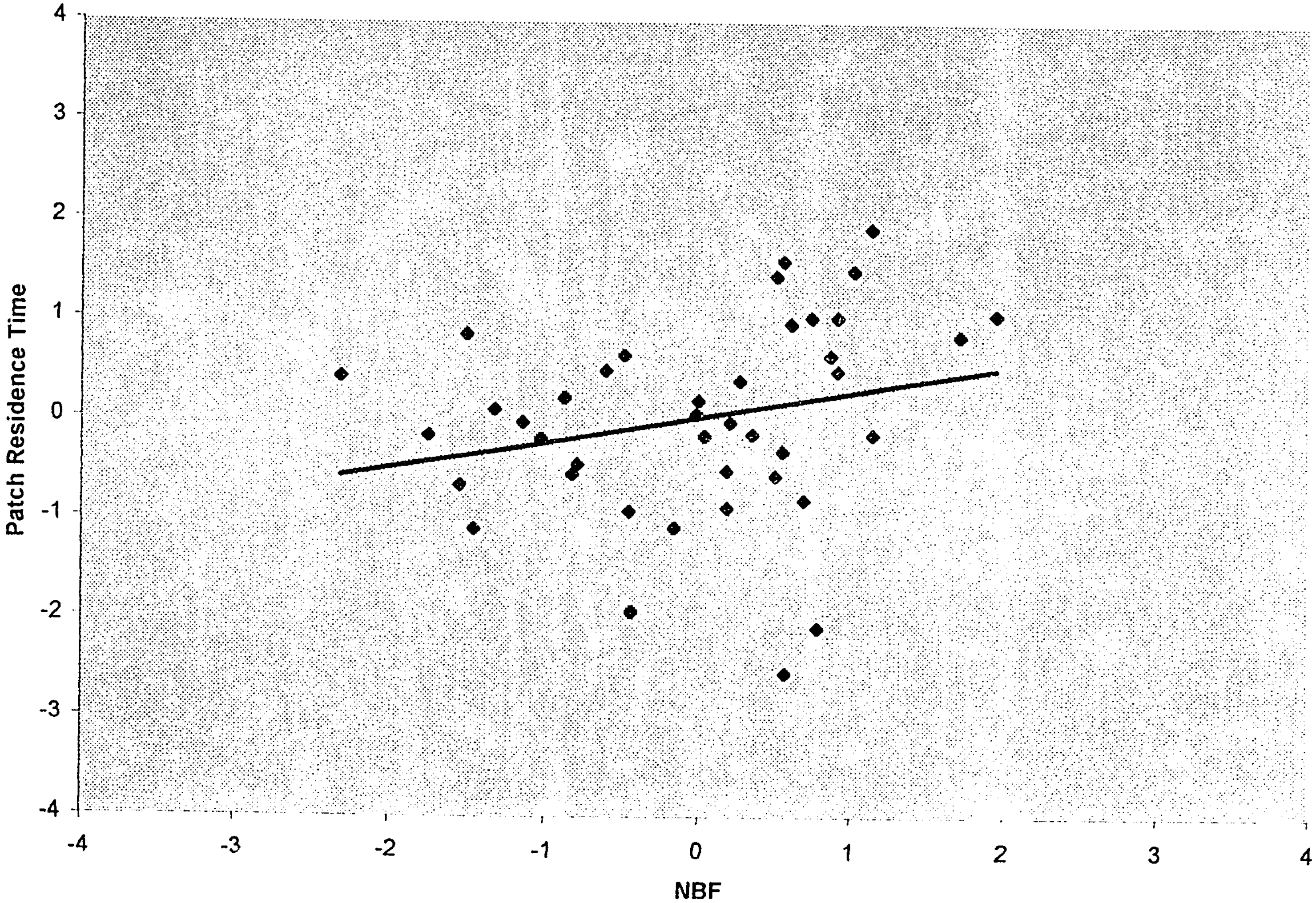

Figure 5-4. A standardized partial regression plot of the effects of the number of individuals feeding in a patch on patch residence time controlling for the effects of patch size. The data is for group BH18, all food items combined.

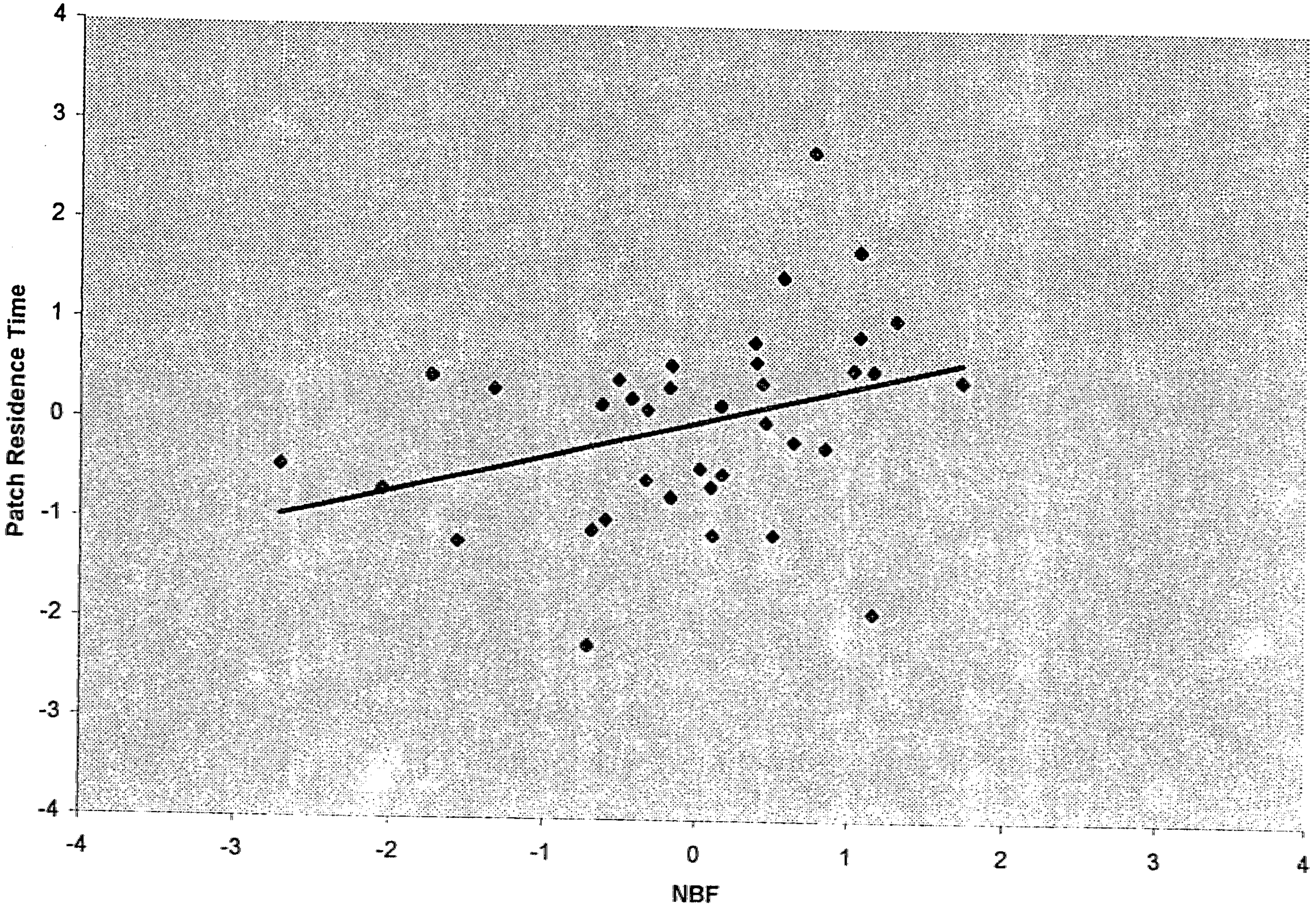

Figure 5-5. A standardized partial regression plot of the effects of the number of individuals feeding in a patch on patch residence time controlling for the effects of patch size. The data is for group BH45, all food items combined.

Table 5-3. Frequency of the number of times patches were used per day for each group.

Group	number of times patches were used per day			total	# of days sampled
	2	3	4		
SE	35	6	1	42	47
EX	22	3	0	25	42
SN	32	6	3	41	52
BH6	14	3	0	17	16
total	103	18	4	125	157

Table 5-4. Comparisons of ingestion rates at the beginning and the end of feeding bouts (Rate1 and Rate2) with ingestion rates at the beginning of the feeding bout on subsequent visit to the same patches (Rate3).

	variables tested	t	df	P
All data combined	Rate1 - Rate3 Rate2 - Rate3	5.11 -3.11	86 86	< .001 = .003
Fruits	Rate1 - Rate3 Rate2 - Rate3	0.91 -1.91	22 22	= .370 = .069
Flowers	Rate1 - Rate3 Rate2 - Rate3	6.53 -1.77	31 31	< .001 = .087
Young leaves	Rate1 - Rate3 Rate2 - Rate3	4.24 -0.87	20 20	< .001 = .397
Mature leaves	Rate1 - Rate3 Rate2 - Rate3	-0.40 -2.21	10 10	= .640 = .052
Group SE	Rate1 - Rate3 Rate2 - Rate3	1.09 -2.35	24 24	= .286 = .028
Group EX	Rate1 - Rate3 Rate2 - Rate3	5.54 -3.80	21 21	< .001 < .001
Group SN	Rate1 - Rate3 Rate2 - Rate3	3.24 -0.14	25 25	= .003 = .892
Group BH6	Rate1 - Rate3 Rate2 - Rate3	2.71 0.31	6 6	= .035 = .766

Table 5-5. Combination of food species and food items eaten on a daily basis.

Group	Species combination	% of days used	food item combination	% of days used	total # of days observed
BH[1]	Bs-Fi +	30.4	fl-fr +	60.9	n = 23[2]
	Bs-Ps +	26.1	fl-fr-yl-ml	30.4	
	Fi-Ps +	17.4	fl-fr-ml	13.0	
SE	Bs-Fi +	36.9	fl-fr +	21.7	n = 46
	Bs-Ps +	34.8	fl-yl-ml	10.9	
	Fi-Ps +	28.3	yl-ml	10.9	
	Bs-Fi-Ps +	23.9			
	Bs-Fi-Ps only	15.2			
EX	Bs-Fi +	37.8	fl-fr +	35.1	n = 37
	Bs-Ps +	35.1	fl-yl-ml	13.5	
	Fi-Ps +	32.4			
	Bs-Fi-Ps +	24.3			
	Bs-Fi-Ps only	18.9			
SN	Bs-Fi +	38.8	fl-fr +	20.4	n = 49
	Bs-Ps +	30.6	fl-yl-ml	10.2	
	Fi-Ps +	22.4			
	Bs-Fi-Ps +	16.3			
	Bs-Fi only	12.2			
	Bs-Fi-Ps-La only	10.2			
All groups combined	Bs-Ps +	32.2	fl-fr +	30.3	n = 155
	Bs-Fi +	30.3	fl-yl-ml	11.0	
	Fi-Ps +	25.8			
	Bs-Fi-Ps +	19.4			
	Bs-Fi-Ps only	11.6			
Dry season[3]	Bs-Ps +	41.8	fl-fr +	38.2	n = 110
	Bs-Fi +	33.6	fl-fr-yl-ml	11.8	
	Fi-Ps +	33.6	fl-yl-ml	10.0	
	Bs-Fi-Ps +	25.5			
	Bs-Fi-Ps only	16.4			
	Bs-Ps only	10.0			
Rainy season[3]	Bs-Fi +	44.4	fl-yl-ml	13.3	n = 45
	Bs-Fi-Mz +	17.8	fl-fr +	11.1	
	Bs-Fi only	11.1	fr-yl +	11.1	

Bs = *Bursera simaruba*, Fi = *Ficus*, Ps = *Pithecellobium saman*, La = *Licania arborea*
Mz = *Manilkara zapota*, fl = flowers, fr = fruits, yl = young leaves, ml = mature leaves

[1] includes BH6, BH18, and BH45

[2] some days were not used in the analysis when the I could not identify all the food items

[3] all groups combined

+ indicates items on the left plus other items not listed here

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VI. GENERAL DISCUSSION

In most models that attempt to determine the ecological variables important in structuring animal communities, food resources seem to be both a reason to aggregate (to increase foraging efficiency), and a constraint on the number of individuals which can coexist in a group (food competition), as well as an ultimate determinant of social organization. This study contributes to the understanding of how the availability and distribution of food resources influence group size and the intensity of food competition in an arboreal folivore, the mantled howler monkey (*Alouatta palliata*). The main objective of this study was to measure the intensity of food competition in four groups of howlers.

Because most models have relied on indirect evidence to explain the differences in group size and behavior between folivores and frugivores, several assumptions have been made about the relationship between group size and food competition in folivores. First, howler monkeys have been characterized as folivores, although the amount of leaves in their diet is highly variable, and despite the fact that they are reported to prefer more seasonal food items such as fruits and flowers when these are available. Second, it has been suggested that because of the abundance of leaves in the environment, competition for food is not a determinant factor of group size in howlers and that consequently, living in large groups does not significantly reduce the foraging efficiency of individual members of the group. The results presented in the preceding chapters do not corroborate the second assumption for the howler monkeys in Santa Rosa National Park.

In chapter 2, I demonstrated that howlers feed on a variety of food items and that although leaves are an important part of their diet, the seasonal and annual variation in their consumption of fruits and flowers justifies a re-evaluation of the label of 'folivore'. The more appropriate label of 'facultative folivores' may better represent the feeding habits of howler monkey populations. The results presented in chapter 2 also indicate that howlers are very selective in their choice of feeding trees. These results corroborate the findings of other studies and suggest that howlers seek highly nutritious and digestible food items and that the presence of toxic compounds may further reduce the number of plants species available for howlers. Variability in the abundance and density of certain plant species is also important in determining dietary composition in my study groups. Although similarities were found in the use of certain plant species and in the preference for large feeding trees, diet overlap was generally low within and between groups on a monthly, seasonal, and annual basis. Despite these differences, howler groups typically feed on three or four plant species on a daily basis, regardless of group size and food availability (see also chapter 4). This suggests that howlers may need to feed on different food sources to obtain the necessary nutrients needed for a balanced diet.

In chapter 3, I presented evidence to indicate that individuals living in large groups incur higher foraging costs than individuals living in small groups. Large groups have larger home ranges and travel farther on a daily basis than small groups. Forest productivity in different parts of the home range of my study groups could explain part of this variability. Large groups also spend more time feeding in small food sources and more time travelling in search of food. However, time spent resting did not vary significantly for most of the study groups. The groups in this study spent approximately 70% of their time resting, with the exception of groups BH18 and BH45, which spent approximately 55% of their resting. Because howlers have slow digestive systems, they require long periods of inactivity to digest their bulky diet. Furthermore, the midday heat in tropical forests, particularly during the dry season, forces howlers to interrupt their daily activities for several hours. The results presented in chapter 3 clearly demonstrate that groups BH18 and BH45 were forced to remain active for longer periods of time during the day to find food, and that ultimately, the increased costs incurred by the intense heat and the energy expended may have caused the two groups to fission. Evidence was also presented showing that seasonal and annual variability of food items greatly influenced the time budget and ranging patterns of howlers in this study, and ultimately, the foraging strategy of howler monkeys.

In chapter 4, I tested the assumption that the costs of foraging in groups were equally shared by all group members. The results indicate that although aggression over food is relatively rare in howlers, competition usually occurs over high-quality food items such as fruits and flowers, and very rarely over mature leaves. This suggests that the relative scarcity of certain food items during parts of the year may increase the intensity of interference competition over food. Thus, the amount and availability of fruits and flowers in the diet may determine the intensity of competition over food. It was also clear that aggression rates over food increased as a function of group size, although the behavioral and biological significance of such increases is difficult to determine. Evidence was presented suggesting that females and juveniles incur most of the costs of interference competition in howler groups and that competition over food between mother and infants may explain in part the dispersal pattern of young males and females from their natal group. Comparisons of food intake rates within groups showed that differences existed between age and sex classes but that no differences existed in ingestion rates between groups. Differences in ingestion rates were also found between high-ranking and low ranking individuals within groups. However, it is not clear whether differences in ingestion rates between males, females and juveniles, and between high-ranking and low-ranking individuals were biologically significant. Nevertheless, the results suggest that lower ranking individuals may suffer higher foraging costs particularly during periods of food shortages.

In the last chapter, I examined the relationship between group size and the use of individual food patches. An important assumption in foraging theory is that foraging groups deplete the patches they use and, as a result, larger groups should feed in larger patches or use more food patches than small groups. The results presented in chapter 5 suggest that although large groups deplete food patches more often than small groups, most food patches used by howlers may not be depleted. Evidence was presented to show that howlers leave patches before they are depleted for several reasons. First, the presence of toxic compounds in plants and the need to obtain a mix of nutrients may force howlers to feed on several food patches during the day. This is corroborated by evidence presented in chapter 2 on dietary composition. Second, the preference for large and renewable food sources may ensure a relatively stable food supply. The evidence presented here suggests that the availability of these 'super-patches' may play an important role in the evolution of group size and social organization not only in howlers, but also in other species.

The findings presented in this study hint at a more complex pattern of the behavioral ecology of howler monkeys than has previously been assumed. In addition to identifying important ecological variables such as the size, availability and distribution of food resources, the present study indicates that other variables such as temperature and digestion rates need to be incorporated in models to explain variation in group size in primates. Furthermore, the results presented here suggest that food competition is highly correlated with group size in howlers. Similar studies are also needed to test assumptions on feeding competition in other folivores. Most models in behavioral ecology lack detailed studies on foraging strategies, particularly on arboreal folivores. More systematic studies are needed to test assumptions about the relationship between diet and group size. A better understanding of the evolution of social organization will require validation of these assumptions and comparative data within and between species across a range of habitats and group sizes.