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SOCIODEMOGRAPHY IN DIURNAL PRIMATES:
THE EFFECTS OF GROUP SIZE AND FEMALE DOMINANCE RANK
ON INTRA-GROUP SPATIAL DISTRIBUTION, FEEDING COMPETITION,
FEMALE REPRODUCTIVE SUCCESS, AND FEMALE DISPERSAL PATTERNS
IN WHITE SIFAKA, *PROTITHECUS VERREAUXI VERREAUXI*

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE BIOLOGICAL SCIENCES
AND THE PRITZKER SCHOOL OF MEDICINE
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
DEPARTMENT OF ECOLOGY AND EVOLUTION

BY
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ABSTRACT

The evolution of social living has been attributed to various factors. Predation pressure and intra-specific competition among groups have been hypothesized to favor larger groups, while competition within groups has been hypothesized to favor smaller groups. An important aspect of behavior that can influence this interplay of forces is spatial cohesion among groups members. However, maintaining spatial cohesion by members of larger groups can lead to overlap in their individual search fields during foraging, which would increase their intra-group feeding competition. If increased feeding competition (i.e. decreased feeding efficiency) consequently reduces female reproductive success, then the regulation of group size by behaviors such as dispersal should be affected by the factors that affect intra-group competition.

From June 1993 to January 1995, I studied the effects of group size and female dominance rank on individual behavior and demographic dynamics in 14 focal and 43 census groups of white sifakas, at Beza Mahafaly Special Reserve, in southwestern Madagascar.

Empirical data and spatial distribution models revealed that sifakas balanced the need to maximize group spatial cohesion with the need to minimize individual crowding by spacing themselves more closely and by changing the geometric spacing pattern of individuals in larger groups. At group sizes greater than 9 sifakas seemed to reach their threshold for maximum group spread and for maximum crowding, suggesting that they experienced a group size limitation somewhere between 11 and 13 members.

Furthermore, because members of larger groups experienced greater individual crowding, they traveled further per day and experienced lower feeding efficiency. Also, females in larger groups, where feeding efficiency was the lowest, gave fewer births per female, and were the only females to emigrate. Female emigration reduced the size of their groups.

As predicted for groups with female-female competition, sifaka females maintained dominance hierarchies within groups, and lower ranking females experienced lower feeding efficiency and consequently had fewer offspring per female than higher ranking females. The lowest ranking females in larger groups did not give births, and they were the females that emigrated. Emigrating females started their own new groups or joined existing single-female groups, thereby increasing their dominance ranks.

To
Stefania Gruca,
Wiktoria Kubzdela,
&
Esoahere

CHAPTER ONE

INTRODUCTION: SOCIO-DEMOGRAPHIC CONSEQUENCES OF GROUP SIZE IN WHITE SIFAKAS, *PROPITHECUS VERREAUXI VERREAUXI*

Primate social systems: identifying their causes and effects

Primates exhibit an unusually high diversity of social systems, posing the questions: (1) what caused such diversity and (2) what are the demographic consequences of different societies (Wrangham 1987). A social system portrays a complete set of social relationships within a group, where social relationships describe patterns of inter-individual interactions between and within age/sex classes represented by group members (Hinde 1976). In an effort to identify the causes of this social diversity, researchers have hypothesized that ecological pressures, such as food distribution or predation pressure, have over long periods of time imposed the primary selective force on patterns of primate sociality (e.g. Crook & Gartlan 1966; Clutton-Brock & Harvey 1977a; van Schaik and van Hoof 1983). Researchers also noted that demographic constraints, such as change in adult sex ratio or population density, could over short periods of time lead to evolutionary change in a social system (e.g. Altmann & Altmann 1979; Dunbar 1979, 1987; Kummer et al. 1985).

Based on the ecological hypothesis researchers predicted that species that are alike in aspects of their social systems experience similar ecological pressures (e.g. Crook

1970; Clutton-Brock & Harvey 1977a; Harvey et al. 1987) and, therefore, that certain aspects of social systems have corresponding ecological factors. After empirical research on primate behavior and ecology flourished in the past three decades, researchers began to try to identify which ecological factors correspond to which social parameters among different primate species and genera (e.g. Eisenberg et al. 1972; Hladik 1975; Clutton-Brock & Harvey 1977a; Harvey & Clutton-Brock 1985; Harvey et al. 1987; Isbell 1991). They mapped social systems onto arrays of ecological variables and these meta-analyses identified a few socioecological patterns (recent summaries in Wrangham 1987 and Janson 1992), for instance that nocturnal primates forage singly or in small groups. However, in the end these analyses did not explain the diversity of primate social systems. Once body size effects were controlled for almost no social factors were significantly correlated with ecological variables (Harvey et al. 1987). In these analyses, the authors were constrained to compare data between species and populations because the diversity within populations is still virtually unknown. Also the habitats of the compared taxa differed so widely, as to preclude extraction of any patterns from the number of confounding variables. Because of these problems and because large-scale comparisons usually cannot demonstrate causal relations between variables of interest, I decided to approach the study of the relationship between ecology and sociality by first trying to understand this relationship within populations and habitats.

With the aforementioned emphasis on how ecology affects primate behavior, the questions of how demography affects social systems and how in turn social systems affect demography remained largely unexamined. Only a few authors have explored the effect

of demography on social behavior (theoretical: Altmann & Altmann 1979; empirical: van Schaik et al. 1983a; Isbell 1991), and they each pointed to the pressing need for further research. A greater number of authors looked at the effects of social systems on group and population demography, but only a subset of possible relationships was explored. Authors primarily explored interdependence between: (a) dominance rank and reproduction (review in Fedigan 1983), (b) intra-sexual interaction patterns correlated with sex-specific dispersal and variance in reproductive success (reviews in Pusey & Packer 1987 and Smuts 1987), and (3) sex-specific dispersal and mortality patterns (review in Dunbar 1987).

Thus, in our attempt to unravel the causes and consequences of the unusual diversity in primate social systems, we must admit that we have not yet identified the causes of the diversity or how the different social systems affect primate population dynamics. This observation not only represents a gap in our knowledge but also a lack of basic information necessary to: (1) to accurately assess the extent to which different primate populations are endangered and (2) to design more reliable conservation plans in the face of habitat loss. If we want to understand primate population dynamics we must focus more attention on the understudied area of the relationship between social system and demography, and if we want to determine causes of primate social evolution we must focus on studies below the level of inter-population comparison. Because selection happens within populations, to understand selective forces and their outcomes we need to focus on within-population processes that involve reproductive success (Arnold 1983, 1988).

This observation suggests a number of sequential approaches to the study of primate social systems: (1) in order to study causes of the inter-specific diversity in primate social systems, we are likely to benefit by first understanding why and to what extent social systems vary within primate populations, (2) in order to identify which factors cause variation in group social systems within primate populations and how they do so, we would do well to begin by investigating how group size affects patterns of social interactions, and (3) in order to understand the selective forces regulating the relationship between social systems and primate demography we need to investigate how patterns of intra-group social interactions and patterns of population subdivision (i.e. sizes and composition of groups and the migration patterns among them) affect female and male reproductive success.

The need for intra-population studies to understand causes of social variation

Inter-population comparisons did not explain the diversity in primate social systems because most aspects of primate sociality lacked visible patterns corresponding to accompanying ecological factors and because causality could not be determined. A correlation might reflect a causal relationship between the correlated factors, or it might be detected because the correlated factors are caused by yet another factor or a set of factors perhaps not even included in the study. Even if we were to assume that a given correlation reflects a causal relationship, we cannot determine from a correlation alone the direction of causality.

Three other problems characterize inter-population comparisons of primate socioecology. (1) The levels of taxonomic division beyond that of species are somewhat arbitrary (i.e. criteria used to determine which species belong to a genus or a family are not consistent across taxa), yet authors have been forced to compare taxa at higher levels, such as genera or families, to avoid consequences of comparing unequally represented taxonomic levels (e.g. Harvey et al. 1987). (2) Variation among systems cannot be interpreted without taking into account variation within systems, yet data for the majority of species cover only a single group, occasionally a few, of each species or population (Harvey & Pagel 1991). Finally, (3) environmental conditions across species and populations are often so different from each other that confounding variables prevent extraction of patterns (Robinson 1988).

These problems can be largely avoided in studies of single populations where phylogenetic constraints are negligible, intra-specific variation can be determined, and variation in environmental conditions is often minimized. The last two features also increase our chances of determining causal relationships. Of course intra-specific studies cannot answer many questions about inter-specific variation, but they may provide the necessary background to extrapolate socioecological patterns at higher taxonomic levels that we have not been able to extract thus far.

The importance of group size effects for studies of social systems

Altmann & Altmann (1979) hypothesized that the number of group members constrains aspects of group social structure, demographic parameters, and feeding

ecology. Investigators of primate socioecology recognized group size as a key demographic parameter for socially living species and looked for behavioral variables that correlate with it (e.g. Crook & Gartlan 1966; Hladik 1975; Charles-Dominique 1977; Clutton-Brock & Harvey 1977a,b; Waser 1977; van Schaik et al. 1983a; Terborgh 1983; Andelman 1986; Janson 1988a; Janson & van Schaik 1988). However, because these authors usually had to compare groups from different populations and habitats, they were unable to distinguish confounding effects of habitat variables from those of group size on patterns of intra-group behaviors. Both group size and environment may affect social behavior simultaneously, but group size may be a more difficult variable to control for because it varies among groups and populations as well as within groups over time. Additionally, group size not only affects social behavior but it in turn is affected by behavior of individuals, such as by migrations. As a result, the effects of group size within habitats on primates' socio-demography should be determined before we can determine the effects of environmental variables, such as food distribution or predation pressure.

Intra-population studies should lend themselves best to investigations of the effects of group size on social behavior, because many environmental factors, such as climate and predation pressure, that are experienced by the studied groups would be controlled for if conducted simultaneously within a population rather than between populations. However, only a few parallel studies of multiple groups of a single population have been carried out (Waser 1977; Green 1978; van Schaik et al. 1983a,b; Janson 1986; Robinson 1988). Such studies are usually extremely difficult to realize

because groups of most species are too difficult to locate, view, or follow, or are simply too large in size to allow detailed observations of multiple groups. Thus examining a population that lends itself to the study of a large number of groups is highly desirable and the advantage of my study population is that it makes such research feasible.

Reasons for focusing on females' reproductive success

If one cannot simultaneously study the reproductive success of both sexes, one would benefit most by focusing on the reproductive success of individuals of the sex that most strongly determines reproductive success of the opposite sex (Wrangham 1980). Among primates, female reproductive success can be more readily determined in the field than male reproductive success because females give birth and nurse their offspring. Paternity of males is much more ambiguous in the absence of genetic tests. Also, in most primates, females tend to remain in their natal groups (Pusey & Packer 1987), maintain stable dominance relationships, and they constitute a more limiting reproductive resource for males than vice versa (Wrangham 1980; Smuts 1987). All females in estrus are usually sought out by males, but not all sexually able males get to mate with females.

Because evidence suggests a larger variance in the males' reproductive success in comparison to that of females, and because males seem to spend more effort to assure successful matings than do females, we can predict males' patterns of reproduction and behavior from those of females more reliably than we can predict females' reproduction and behavior based on those of males. Also, because females form more stable relationships than males in species with matrilocal females, we can investigate how

demography, social interactions, and reproductive success among females affect each other much more accurately than we can investigate them among the more frequently migrating males. Thus to determine the relationship between feeding competition and reproductive success, in this study I focused only on the reproduction of females.

General research approach

Many authors would insist on experimental manipulation with random assignment to show causality, but such experimental designs have their own problems and are usually not appropriate for studies of free-ranging primates. In this study, I test whether group size causes changes in other social and demographic factors by analyzing cross-sectional and longitudinal data. Cross-sectional analysis compares variables across groups of different sizes, and longitudinal analysis compares changes within a group as the group alters in size. Together, although the two types of analyses do not replace experimental approach, they constitute a reasonable first approximation to experimental design and remove or reduce many potential sources of confounding variability so common in observational research. In the absence of significant environmental variation, correlations between intra-group changes (for example in patterns of interactions and feeding competition) and group size cannot be easily explained by a third factor. Such correlations provide a strong evidence for a causal relationship between the intra-group changes and group size. For example, if group members do not change their territory as their group changes in size (longitudinal analysis), yet the patterns of social interactions or feeding competition change in the same manner as in groups of comparable sizes

(cross-sectional analysis), then we have strong evidence for group size causing the observed changes in patterns of social interactions or feeding competition.

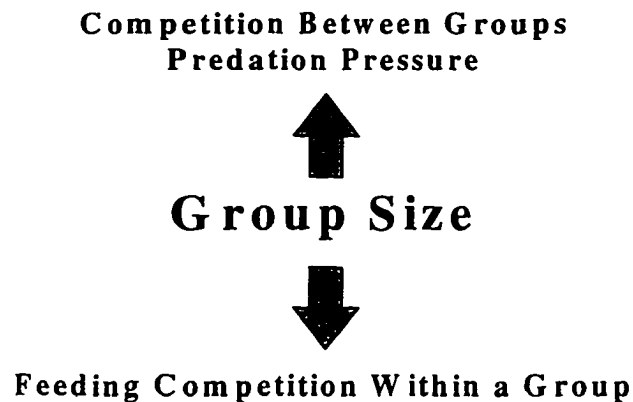
A population of white sifakas, *P. v. verreauxi*, at Beza Mahafaly Special Reserve, is particularly suitable for this type of study because: (1) groups contain multiple females and males, vary widely in size, and occupy a relatively uniform habitat, (2) group members are expected to experience considerable intra-group feeding competition, as suggested by severe annual energetic stress (Richard et al. in prep), and therefore to compensate behaviorally for the effects of competition, (3) numerous groups can be efficiently observed due to their relatively small size, short daily travel-path, small home ranges, presence of habituated individuals, good visibility in semi-arid forest canopy, and the fact that a large proportion of the population is marked, (4) the population resides in a protected Reserve, (5) the demography of the population has been followed since 1984 (Richard et al. 1993 and unpublished data), and, finally, (6) understanding forces driving the demography of sifakas can aid their conservation.

Model for social and reproductive consequences of group size

As the size of a group increases, some changes in the group's use of space and time must inevitably occur. Early socioecological models focused on the likely importance of group size in either hindering or enhancing an individual's food consumption (Crook & Gartlan 1966; Crook 1970; Eisenberg et al. 1972; Clutton-Brock & Harvey 1977a,b; Wrangham 1980,1987), such that food consumption of a group

member is hindered by intra-group feeding competition and enhanced by inter-group feeding competition.

Fig. 1.1. Schematic representation of inter-group competition and predation pressure driving group size up and intra-group competition driving it down.



To explain the effects of intra-group feeding competition Eisenberg et al. (1972) and S. Altmann (1974) postulated that group members overlap individual search fields, thereby reducing each other's rates of encountering food. This suggests that the intensity of intra-group feeding competition, in a given group, depends on how spread out the group members are in relation to the distribution of food in space. Eisenberg and Altmann further postulated that the size of social groups depends on the size of food patches, because if females have to expend more energy for foraging by traveling farther to obtain the same amount of food, they will be more likely to produce fewer offspring. Consequently, if females can increase their reproductive success by dispersing or causing other females to disperse from the group, then natural selection will favor females that do not tolerate groups too large for the size of available food patches, and intra-group

feeding competition will drive the size of a group down. Inter-group competition is viewed as the opposing selective force to intra-group competition because it is expected to favor larger groups (review in Wrangham 1980).

However, the outcome of inter-group competitive encounters might depend not only on group size but also on the distribution of group members in space. As groups have more members, individuals often spread themselves widely during foraging, and some group members end up relatively far from the rest of the group. These individuals or groups of individuals may find themselves far enough from the rest of the group that they may not be able to benefit from the advantage of the size of their large group when other groups challenge them over a resource or when they may be attacked by a predator. Thus when larger groups spread themselves over a large area they decrease their low spatial cohesion and therefore potentially their ability to detect and deter predators or displace smaller but more cohesive groups.

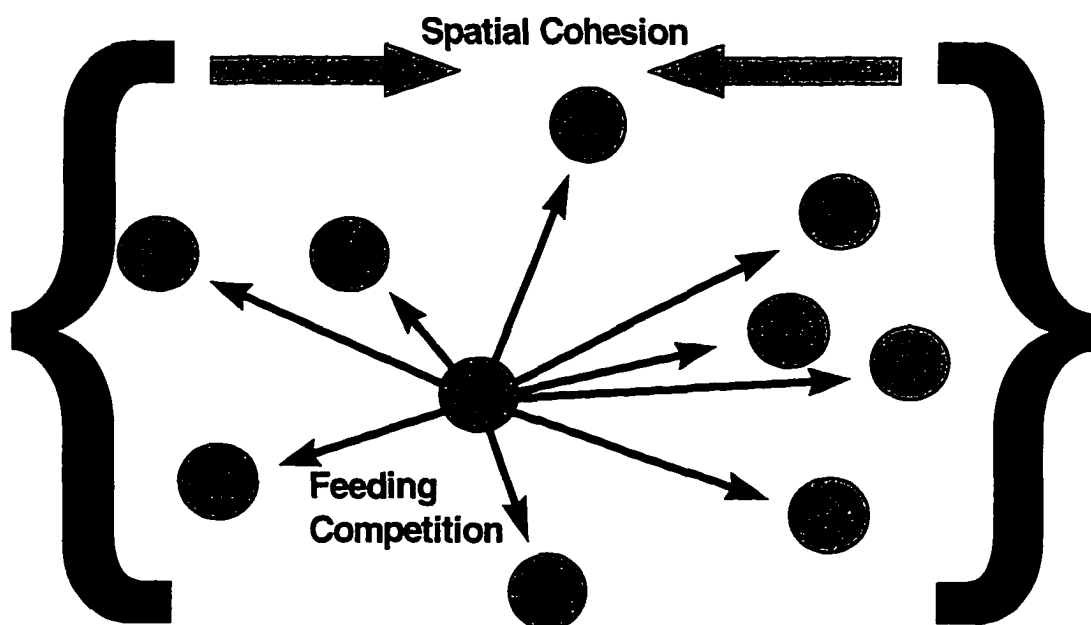
Increased group cohesion, in contrast, can increase a group's ability to compete with neighboring groups and to deter predators, but at the same time it may decrease the foraging efficiency of group members because closer spacing of individuals causes increased potential overlap in their search fields. Therefore, one would expect that the ability of individuals to maintain the cohesion of their group at distances far enough apart for group members to exploit separate food sources varies among species (Janson 1992) and habitats. Different species in the same habitat may vary in their ability to communicate over longer distances, or to converge rapidly in order to defend their resources or other group members, perhaps because they differ in body size or in the

ability to run fast. Similarly, groups of the same species may vary in these abilities because of differences in their habitats; for example, one might expect that denser forests hinder the ability of individuals to detect predators, and/or hinder intra-group communication and the group's ability to rapidly aggregate, because denser forest might obstruct visual communication, dampen sound, and impede fast movement. Therefore, the degree to which group members spread in space is likely to depend at least partially on the species-specific plasticity in maintaining group's cohesion at different inter-individual distances, the group's habitat (i.e. habitat architecture and the intensity and type of predation pressure), and the group's size.

If a group has to maintain a certain degree of spatial cohesion to benefit from group living, and if for a given species and a given habitat group cohesion is correlated with group size, then species- and habitat-specific maximum group size would be limited by the group's ability to maintain spatial cohesion. However, in some populations intra-group feeding competition might select strongly for groups that are smaller than the maximum imposed by group spatial cohesion, and therefore, in reality, groups might never even reach that maximum. Because arboreal primates experience lower visibility than many terrestrial primates, the maximum group size imposed by spatial cohesion is likely to be smaller for them than for the terrestrial primates. As a result, arboreal primates may be forced to forage closer together than terrestrial primates, thereby being subjected to greater intra-group feeding competition. If this is true, then one would also expect that the inter-individual distances change as a function of group size more in arboreal than terrestrial primates.

Therefore, with respect to space, if we assume that members of the smallest groups stay as close to each other as possible without having to overlap their search fields, then as group size increases, group members either space themselves more closely, and thereby overlap their search fields, or they maintain the original nearest-neighbor distance, and thereby spread themselves over a much greater area than originally, which compromises their group's spatial cohesion.

Fig. 1.2. Schematic representation of the opposing forces of maintaining spatial cohesion versus avoiding feeding competition on inter-individual spacing within a group.



Several empirical studies have found that larger groups travel farther and/or forage longer per day (Waser 1977, van Schaik et al. 1983a, Janson 1988b, McFarland

Symington 1988, Penning et al. 1993, Olupot et al. 1994), suggesting that members of larger groups experience higher feeding competition than members of smaller groups, which in turn implies that members of larger groups overlap their search fields to a greater degree. Because Alison Richard (pers. com.) observed even the largest groups at Beza Mahafaly move as spatially cohesive units during foraging, I predict that sifakas in larger groups space themselves more closely and overlap their search fields to a greater degree than members of smaller groups. This prediction is consistent with the fact that sifakas are highly arboreal, territorial, and give alarm calls in response to harrier hawks and fossas, which suggests that maintaining spatial cohesion by group members is necessary for intra-group communication, territory defense, and avoidance of predators. This leads to the first hypotheses:

Hypothesis 1: Members of larger groups experience a greater tradeoff between maintaining spatial cohesion and avoiding overlap in their foraging search fields resulting in larger groups simultaneously experiencing lower spatial cohesion and greater search field overlap than smaller groups.

Hypothesis 2: Greater overlap in group members' foraging search fields increases feeding competition among them.

The relationship between competition and differential reproduction is one of the most considered points in evolutionary theory. Many primate species exhibit agonistic

dominance relations, often with a clear dominance hierarchy among group members. Social dominance is defined as consistent asymmetries in the outcomes of agonistic conflicts between individuals or groups (Bernstein 1981). It has been most extensively studied in cercopithecines (e.g. Altmann 1962; Sade 1967; Hausfater 1975), for which asymmetries in submission rather than aggression have been defined as more relevant (Rowell 1974; Richard 1985). Dominance rank within primate groups is hypothesized to determine differential access to limiting resources, such as food, and as a result to correlate with reproductive success (Fedigan 1983). Yet evidence for a relationship between dominance and reproductive success, especially among primate females, remains scarce (Fedigan 1983; Silk 1984, 1987; Fedigan et al. 1986; Lee 1987; Altmann et al. 1988). In species whose females are matrilineal, females often aggressively compete for food and feeding sites (empirical studies by Hall 1965; Chalmers 1968; Klein 1974; Sussman & Richard 1974; Dittus 1977; Struhsaker & Leland 1979; Smuts 1985). Females of these species also maintain stable dominance hierarchy (Wrangham 1980), which suggests that lower-ranking females experience lower net food intake and lower fitness relative to higher ranking females (review in Lee 1987; Altmann 1998). Female fitness may be reduced by shorter life-span (Dittus 1977; Fedigan et al. 1986), delayed age of first reproduction (due to lower growth rate, poor nutrition, or behavioral suppression; Mori 1979), lower birth rate (Whitten 1983), and/or lower offspring survival rate (Fedigan et al. 1986).

Hypothesis 3: As intra-group feeding competition increases, the disadvantage of lower female dominance rank becomes greater with respect to foraging efficiency.

If within a group successful reproduction by one female limits the potential for successful reproduction by another female, then direct reproductive competition among females might arise in addition to competition for food (feeding competition might be viewed as indirect reproductive competition). Among primates, a number of callitrichids species exhibit the most severe form of reproductive competition in which one female prevents all other females within her group from reproduction. Reproductive suppression in female primates is behaviorally mediated, with dominant females actively suppressing subordinate females via high levels of aggression (Dunbar 1980; Harcourt 1987; Abbott 1987). Data collected from captive species show a continuum in consequences of reproductive suppression ranging from a total lack of reproduction to a slightly lower lifetime reproductive success (Abbott 1987). The benefits of high rank to female fertility in free-ranging primates, with the exception of marmosets and tamarins (callitrichids), have been difficult to quantify.

In sifakas, adult females are dominant over all adult males, especially in the context of feeding (Richard 1978b; Kubzdela et al. 1992), which is unusual among mammals. Female dominance over males has been hypothesized to result from an atypically high energetic stress experienced by females especially during reproduction (Hrdy 1981; Jolly 1984; Richard 1987), where females are believed to need to maintain a priority of access to food resources over males in order to successfully produce and wean

offspring. The advantages to females from exerting dominance over males are believed to be escalated in sifakas, because even with the feeding priority sifaka females maintain over males, they exhibit very low rates of successful reproduction (A. Richard unp. data). Obtaining enough food is of utmost importance to sifaka females, because their body mass is a very good predictor of their fertility in a given year (Richard et al. in prep.). Data from the Beza Mahafaly population collected between 1984 and 1992 is consistent with this hypothesis because, unlike in other primates with dispersing males, adult sifaka males do not experience greater mortality than adult females, suggesting that deaths due to dispersal among males are matched by deaths due to reproduction among females (Richard 1989 reports 1:0.74 adult sex ratio), i.e. that sifaka females have an unusually high mortality relative to that of males. The hypothesis that sifaka females experience high energetic stress during reproduction is additionally supported by the following hints of female-female reproductive competition: (1) more than three infants per year have never been observed in a group regardless of the number of adult females present (A. Richard pers. com.) and (2) adult females interrupt each other's copulations (Diane Brockman pers. com.). However, recently van Schaik and Kappeler (1996) proposed that female dominance over males did not result from high energetic stress on females, but rather is a leftover from a proposed pair-bonded and cathemeral (active during both day and night) history of currently diurnal prosimians. I address this new hypothesis in Chapter 4.

As evidence for female-female competition among female lemuriformes in general, data collected at the Duke University Primate Center suggest that females use

several modes of direct reproductive competition (Vick 1988): (1) elimination of potential competitors (expulsion of females has been observed in semi-free-ranging, long-term social groups of ring-tailed, brown, black, and ruffed lemurs - for example, in one brown lemur group 55% of females born over a 17-year period were "targeted" and ejected before they were able to breed), and (2) suppression of competitors' reproduction using pre- or post-copulatory tactics (only 33% of females giving birth in established, social groups of brown and ring-tailed lemurs delivered at age two, which is the earliest observed age of reproduction, in contrast, 60% of brown and 48% of ring-tailed mothers in pairs or small, newly established groups gave birth at two years of age).

Because in my study I was able to collect data only on spacing, feeding competition, births, infant survival, and emigration patterns, I only consider hypotheses linking these variables. In particular, if females have to expend more energy for foraging, their nutritional well being becomes compromised, which can reduce their reproductive success. Finally, if females with lowered reproduction can increase their reproductive success by dispersing or causing other females to disperse from their group, then natural selection will favor those females that do not tolerate groups too large for the available food resources. As a result, if females disperse from a larger group, intra-group feeding competition would have effectively driven the size of the group down.

Hypothesis 4: An increase in intra-group female-female competition, observed in larger as compared to smaller groups, results in lower mean reproductive success among

females in a group, and lower ranking females in larger groups are expected to have the lowest reproductive success.

Hypothesis 5: Females with a greater reproductive disadvantage should emigrate from their groups if by doing so they can increase their expected reproductive success.

All of the hypotheses tested in my study focus on the causes and effects of intra-group feeding competition, which selects for smaller group sizes. Due to insufficient data, the opposing selective force of inter-group feeding competition is not empirically addressed in this thesis. To understand selective forces determining acceptable and optimal group sizes for sifaka groups at Beza Mahafaly Reserve more completely, both inter- and intra-group competition need to be examined. I leave to future studies analyses of patterns and outcomes in inter-group encounters as well as of mortality rates as a function of group size, which will shed more light on the inter-group competition part of the story.

Summary of the Chapter

In an endeavor to understand evolution of social systems, particularly in primates, we cannot avoid grappling with causes and effects of group size. Group size is a key demographic parameter that is highly variable, between and within populations, and is hypothesized to constrain many aspects of social structure, demography, and feeding ecology. Among factors proposed to influence the size of groups, competition between

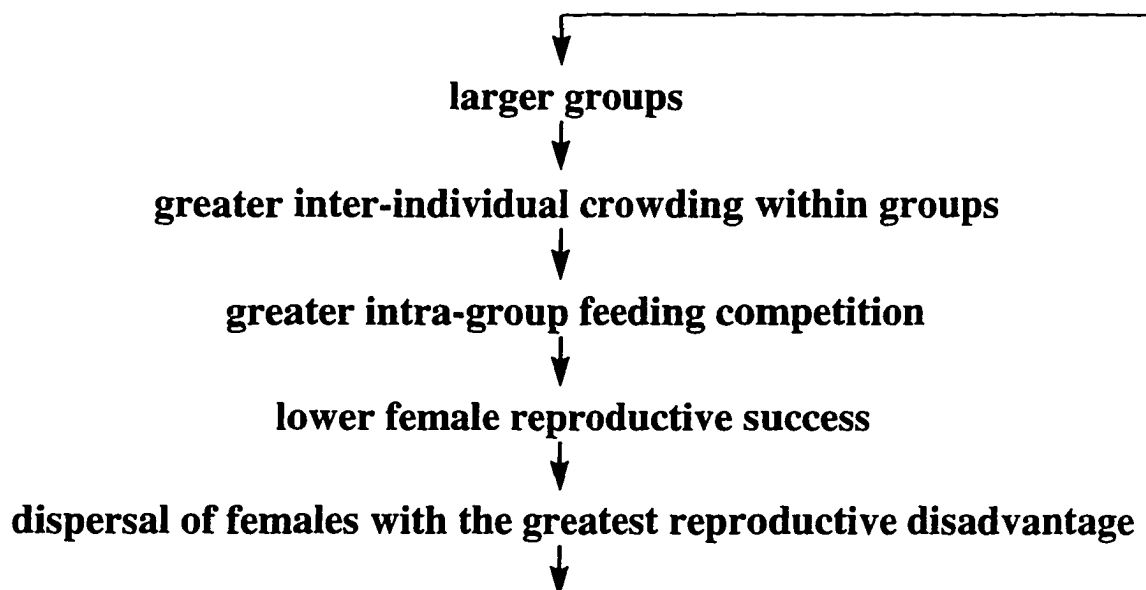
groups, such as for food or territories, is consistently thought to favor an increase in group size, while feeding competition within groups is thought to favor a decrease in group size. Regardless of the factor, for any selective pressure to drive the evolution of species-specific group size, the disadvantage of being in a group that is too small or too large must translate into a differential reproductive success and into heritable ability of individuals to disperse or cause other group members to disperse, if by doing so they can increase their own reproductive potential. Theoretical work on the causes and effects of group size has not yet been matched by empirical tests. This is especially true for primates, where following a large number of groups is extremely difficult.

The goal of the study presented here was to overcome this obstacle and to determine the relationship between group size, social structure, feeding competition, female reproductive success, and female dispersal in a diurnal primate. To avoid confounding ecological variables in the analyses I chose a population living in high density and in a relatively uniform habitat.

I predicted that all members of larger groups in the population would experience greater spatial trade-offs than members of smaller groups, and as a result, the overlap in their foraging search fields would be greater and they would experience greater intra-group feeding competition. For females in the larger groups, greater intra-group feeding competition would result in a lower mean reproductive success with lower ranking females experiencing the lowest reproductive success. Consequentially, if females that experience a reproductive disadvantage, due to their low rank and membership in larger groups, could increase their expected fitness by dispersing, they would try to disperse.

Summary of the Hypotheses:

Fig. 1.3. Schematic representation of hypotheses.



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CHAPTER TWO

GROUP SIZE AND SPATIAL STRUCTURE: ACCOMMODATING OPPOSING PRESSURES WITH IMPLICATIONS FOR INTRA-GROUP FEEDING COMPETITION

INTRODUCTION

Many mammals live and/or forage in spatially clumped aggregations such as herds or social groups. These aggregations are usually hypothesized to exist because they increase the ability of their members to spot or deter predators, guard mates, or find and defend patchy food sources (e.g. Crook and Gartlan 1966; Clutton-Brock and Harvey 1977a; Dunbar 1979, 1987; Kummer et al. 1985, van Schaik and van Hoof 1983, Stanford 1995). However, the increased clumping of individuals in space has a number of potential costs, the main being an increase in food competition among aggregation members (e.g. Crook 1970; Clutton-Brock & Harvey 1977a; Harvey et al. 1987).

Aggregations with unstable memberships, such as flocks or herds, have the opportunity to adjust their size to temporal food availability, but many species, such as most primates and many carnivores or rodents, live in well defined, relatively stable social groups, where the size of the group must accommodate seasonal fluctuations in food availability and distribution.

The evolution of group living and group size is thus subject to an inherent conflict in which some selective forces drive the group size up and others down. If there is an advantage to living in groups, then there must be a disadvantage for a group to spread over too large of a distance (i.e. to lose its spatial cohesion). In fact, at least among some primate species, the more group members are dispersed in space the less they seem able to outcompete smaller but more cohesive groups (baboons: Susan Alberts pers. com.; capucins: Charles Janson pers. com.), suggesting that groups may enjoy the benefits of their larger size only if they maintain spatial cohesion. Inter-group dominance is often a function of group size (Hausfater 1972; Cheney 1987). Hausfater (1972) also reported that in rhesus monkeys smaller groups characteristically grew extremely spatially compact when faced with a dominant group and/or withdrew from the area. He then pointed out that when subordinate groups came across pairs from dominant groups they often chased those pairs away. Musk oxen (*Ovibos moschatus*) routinely converge into tight herds when attacked by arctic wolves (Mech 1988) and groups of sifakas (*Propithecus verreauxi*) and ring-tailed lemurs (*Lemur catta*) converge at the base of tree crowns in response to aerial and ground predators (author's pers. obs.; Sauther 1989). All of these observations suggest that spatial cohesion of group members gives them an advantage in inter-group encounters and anti-predator responses. Group spatial cohesion is likely to determine the ability of group members to converge readily with one another for the purpose of joining forces in defense of a territory or a group member. Generally, cohesion may decrease when the dispersion of the group increases, because at larger distances communication among group members becomes impaired and/or the distance

becomes too large for group members to cover it in a time short enough to join forces in defense.

However, in order to avoid spreading over excessively large distances, members of large groups may have to pack more closely together than members of smaller groups. Yet the closer packing, which might give them a fitness advantage by decreasing the probability of being preyed upon or displaced from a resource by conspecifics, also increases the potential for overlap in their individual foraging search fields (Eisenberg et al. 1972, S. Altmann 1974). Individuals overlap in their search fields either because they are feeding within reach of one another or because the feeding path of one individual follows that of another and the group member that fed first on the path significantly depleted the food resource for the next group member.

Thus on the one hand larger groups might be able to displace smaller groups from food patches and territories, but on the other hand they might also experience greater intra-group food competition than smaller groups (Crook & Gartlan 1966; Crook 1970; Eisenberg et al. 1972; Clutton-Brock & Harvey 1977a,b; Wrangham 1980,1987). So as groups get larger, individuals within them face a more severe trade off between maximizing group spatial cohesion, by minimizing group spread, and minimizing intra-group food competition, by minimizing individual crowding (in this paper, group spread is the straight-line distance between two farthest group members, while individual crowding is an index that is proportional to the number of neighbors around an individual and inversely proportional to the distances to those neighbors).

Much theoretical consideration has been given to the evolution of group size in primates and carnivores (Wrangham 1987; Isbell 1991; Wrangham et al. 1993; Janson 1995). Species- and habitat-specific optimal group size is thought to be that which results in the greatest ratio of benefits (inter-group competition and predation avoidance) to costs (intra-group competition). Predation pressure is very difficult to measure for primates (van Schaik et al. 1983; Cheney & Wrangham 1987), and so is inter-group competition (Cheney 1987). The latter can be further complicated by great variability in group sizes within populations. A group usually comes into contact only with groups that are its immediate neighbors, especially among territorial species. As a result, the distribution of group sizes among the neighboring groups is likely to affect the benefits a group can draw from its size, thereby changing the optimal group size for that particular group. Benefits of living in larger groups are usually believed to be caused primarily by external factors, such as outcompeting groups of conspecifics or detecting and deterring predators, while costs are usually believed to be caused primarily by internal factors, such as intra-group competition. Because examining the benefits of living in large groups requires studies of inter-group interactions and/or of predation effects on groups of different sizes, while examining the costs requires studies of intra-group dynamics that are then compared between groups, studies of costs of living in large primate groups are logistically more feasible than studies of benefits. Studies of the costs are not however without problems either. For them the obstacle is the great difficulty of simultaneously studying enough groups of primates to in the end be able to demonstrate the effects of group size.

The tradeoff between maintaining a group's spatial cohesion and minimizing personal crowding may directly constraint group size for a primate species living in a given habitat.

In this paper I explore the relationship between group size and the distribution of group members in space in a natural population of a Malagasy primate, *Propithecus verreauxi verreauxi*. Using random distribution models, I examine whether group members arrange themselves in space so as to minimize their individual crowding and/or maximize their group's spatial cohesion. Additionally, because different geometry of individuals in space results in different spatial cohesion and/or different levels of personal crowding, I use spatial configuration models to examine whether the geometry of group members in space varies among groups of different sizes. In the end, I consider the potential effects of different levels of personal crowding on intra-group feeding competition.

If maintaining spatial cohesion and avoiding overlap in individual search fields are both crucial to the individual fitness of group members, then group spread and individual crowding should both be greater in larger groups, but each less so than expected if only the other was affecting the fitness of group members. Under the extreme scenario that minimizing individual crowding is the only concern, individuals probably would not live in groups in the first place. In contrast, if minimizing group spread was the only concern, then group members would move around as a tight clump of bodies. Because such extreme clumping has not been observed among primates or any mammals, I consider the less extreme alternative model for maximizing group spatial cohesion, one

in which group members move so as not to exceed a certain maximal distance from other group members. Within the constraining space defined by the maximal distance group members would move randomly, because no spatial constraint other than the space would be affecting their distribution. Alternatively, if group members were concerned only with minimizing group spread, then the distance to the nearest neighbor and the number of neighbors within various radii would be solely a function of group size and the constraining space.

Unfortunately, defining the space that may constrain groups is difficult, because no clear biological basis for choosing its size and shape is known. If the available space was the whole forest or a group territory, then we would merely test whether group members are indeed clumped in space at all. If, then we used the maximum observed group spread as the defining space, the question of shape remains unanswered. A sphere is the most symmetric of all shapes that allow distribution of group members in three dimensions. Its applicability is limited, however, because it contains the assumption that the habitat does not pose constraints in any direction within the distance of the maximal group spread. I address this limitation by assigning the shape of the space to be a one-dimensional line and a two-dimensional circle, in addition to the three-dimensional sphere (details in the Models section).

If, however, social groups do experience spatial tradeoffs, then the smallest groups should experience them the least. Even relatively large inter-individual distances do not result in an overly large group spread when only a few group members are involved. For this reason, groups of two can theoretically maintain optimal individual

crowding without losing their spatial cohesion, and thus experience the lowest intra-group feeding competition (Davies & Houston 1984). In order for larger groups to maintain the same minimal level of search field overlap as groups of two, they would have to maintain the same distance to their nearest neighbors as members of groups of two and would have to space themselves in a configuration that minimizes the potential for search field overlap, such as feeding in a line that is perpendicular to the direction of group's movement (Altmann 1974). In such a line-distribution, group spread would increase linearly with group size. Additionally, one may expect that the maximum viable group size would be relatively small because group spatial cohesion would diminish rapidly with group size.

In reality, group members are most likely to compromise between minimizing group spread and individual crowding. This can be best accomplished by changing the configuration of group members in space with increasing group size. Change in configuration in larger groups would still result in lower mean inter-individual distances and greater group spread in larger groups, but each of these changes could be kept to minimum. This suggests that a group could eventually become so large that both group spread and individual crowding would be pushed to the acceptable maximum for a given species in a given habitat. In such a case, group members would be expected to prevent their group from further increasing in size by preventing immigrations and/or emigrating themselves or causing other individuals to emigrate, thereby determining the maximum group size for the population.

FIELD METHODS

The Study Species and Site

The subject of this study, the white sifaka (*Propithecus verreauxi verreauxi*), is a 2.5-3.5 kg diurnal prosimian of Madagascar. The geographic range of the *P. verreauxi* species encompasses a rich, mixed deciduous forest in the northwest of the island and a tamarind-dominated gallery forest along with a semi-arid thorny forest in the south and the southwest. *P.v. verreauxi* is arboreal. At the study site, at Beza Mahafaly Reserve, the greatest proportion of the sifakas' diet is derived from leaves (76.4% of feeding time in the dry season and 66.1% in the wet), the rest mainly from flowers and fruits (Yamashita 1996). The sifaka groups occupy small, overlapping ranges with stable boundaries, which they often defend from neighboring groups (Jolly 1972, 1978; Jolly et al. 1982; Richard 1989). The females are matrilineal, and observations suggest a stable dominance hierarchy among the females and a less stable hierarchy among the males (Richard 1974, 1978b, 1987; Richard & Heimbuch 1975). *P.v. verreauxi* is well suited for the study of behavioral mediation of feeding competition because it is highly energetically stressed (Richard et al. in prep). Furthermore, sifaka groups defend their territories against neighboring groups and individuals are apparently subject to predation, as judged by their alarm calls in response to harrier hawks (*Polyboroides radiatus*) and fossas (*Cryptoprocta ferox*). Therefore, white sifakas are expected to maintain group spatial cohesion for defensive purposes, as is often observed in other mammals (Sherman 1977; Janson 1993; Wind 1993; Pacala et al. 1996).

The study site, Parcel 1 of Beza Mahafaly Special Reserve, is located in southwestern Madagascar and consists of 80 ha of protected land. To the north, west, and south of Parcel 1, the forest extends beyond the Reserve's boundaries, but there it is unprotected. Vegetation within and around the Reserve changes gradually from east to west. On the east side, the Reserve borders the seasonal Sakamena River, along which extends a thin strip of tall, tamarind-dominated gallery forest. Westwards, away from the river, the habitat turns into a less tall and more open semi-arid forest. The Reserve and its sifaka population are described in more detail in Richard et al. (1993).

A grid of trails running north-south and east-west at 100 meter intervals covers the Reserve. Prior to this study, since 1984, the history of 28 resident groups has been followed via annual censuses and marking of individuals (Richard et al. 1993). Group sizes range from 2 to 14 individuals (14 being the largest group of sifakas ever recorded), with the mean group size varying between populations and years from 4 to 7 individuals. In the subadult and adult classes the proportion of females in each group ranges from 0.3 to 0.8, with the group average equal to the population average of 0.42 (Richard et al. 1993).

Working Definition of a Group

A group was defined by, but not limited to, a core set of females or a single female that foraged and slept within a consistent area (territory) for at least a month. Study groups were generally stable in composition except for those in which the only existing female died, causing the group to go extinct. Rarely, however, a single female

(or at most two) from a multi-female group moved into a new area and either began to forage and sleep with another group, thus becoming a member of that group, or was joined by male(s) and established a new group. The other members of the migrating female's original group always remained together in the original area and thus continued to be identified as the original group. Groups were not identified by the male membership because males transferred at a high rate between groups.

Data Collection

Data were collected from June 1993 to March 1995 by the author and up to three assistants. Census data were recorded on all groups that had at least part of their territory within the 80 hectares of protected land in Parcel 1 of Beza Mahafaly Special Reserve. At any given time, the census population consisted of 175-195 juveniles, subadults, and adults, distributed among 36 to 37 social groups. Because some groups went extinct during the study and new groups formed, the total number of groups studied was 43. On average, we censused each group at least once every two weeks, and when groups were undergoing demographic change we censused them daily until their membership stabilized. All observed inter-group encounters were recorded.

Detailed behavioral observations, using focal and scan samples (Altmann 1974), were collected on 14 focal groups that ranged in the western part of the Reserve, a region chosen to minimize obvious differences in habitat among groups. During each focal sample a single female was followed, and scan samples were collected on all group members. Because two of the focal groups were newly formed and remained unstable

throughout the period of the study, they were excluded from the analyses in this paper. Similarly, all scan samples that did not include all group members or were recorded during a period of membership change were excluded. Furthermore, because 6 of the 12 included focal groups changed size during the course of the study, I was able to examine the effects of group size on four different spatial variables comparing data between groups as well as within groups as they changed their size (which is why Fig. 2.1 has 19 data points instead of 12, with some groups contributing to more than one size).

In order to record an equal number of focal samples per female, groups with six or more females (see Appendix 2.A) were usually observed for three consecutive days, groups with less than six but more than one female for two consecutive days, and groups with a single female were observed for a single day at a time. We tried to collect focal samples six days a week, and on those days we began to search for a focal group between 0730h and 0800h. If the scheduled group was not found within two hours, we began to search for the group next on the schedule. Between 1200h and 1230h the observation was terminated for lunch and resumed between 1330h and 1430h, depending on the temperature and difficulty in finding the group again. The group was then observed until it settled for sleep and the last focal sample was finished, usually between 1600h and 1730h.

Unless all group members were resting too high up in the tree to be identified, we recorded a scan sample for the group at the beginning of the observation period and then immediately after every 30-minute focal sample. Each scan consisted of a point sample

for every group member present with the recorded variables listed and defined in Table

2.1.

Table 2.1. Variables recorded during each scan sample (starting with the individual ID, the information was recorded for every group member present that was juvenile or older).

Variable	Description
date, time	
group name	Identified by the females present and the area
group spread	The distance in meters between two farthest individuals in the sample group at the moment of sampling
group size	Number of individuals in the sample group at the time of the sample
subject ID	Identification of the individual who is the subject of that point sample
activity	The activity of the ID animal at the point of the sample (affiliative, resting, sleeping, traveling, feeding); no activity was recorded if the animal was hidden by the canopy
number of neighbors within 2m number of neighbors within 5m	Number of group members within 2 or 5 meters, respectively, around the ID animal, in all directions; missing value was entered when the ID animal was traveling too fast to count its neighbors or if the nearest neighbors were hidden in the canopy
nearest neighbor distance	Distance to the closest group member, when the ID animal was within 5 meters of another identifiable group member, or when the ID animal was more than 5 meters from the closest group member but the second closest individual was at least another 3/4 of that distance away from the ID animal; missing value was entered at all other instances and when the ID animal and/or its closest neighbors were traveling too fast to estimate the distance, or if they were hidden by the canopy
nearest neighbor ID	If the nearest neighbor distance was recorded and the closest neighbor was identifiable, then its ID was recorded; otherwise missing value was entered. Sometimes up to 4 individuals were at the same closest distance of the ID animal, in which cases ID's of all of them were recorded

An individual was considered to be a part of the focal group if at the time of the sample: (a) it was not with another group, (b) it was within visible and/or audible distance from the group, and (c) it was within view of other group members for at least one hour and a half before and after the point sample. These criteria excluded the three or four instances when a wandering male was briefly visiting during a scan sample.

EMPIRICAL RESULTS

As predicted by the hypothesis of spatial compromise, both group spread and crowding increased with group size (Fig. 2.1). Crowding increased because nearest neighbor distance decreased (Fig. 2.1c) and numbers of neighbors within 2 and 5 meter radii increased (Fig. 2.1b,d). The effect of group size on all four measures of spatial distribution (i.e. the slope of change) was the greatest among smaller groups, with 2-5 members, and the weakest among the largest groups, with 9-13 members (Fig. 2.1). This asymptotic relationship between each spatial variable and group size suggests that larger groups approach some limit in each variable. In reality, only the nearest neighbor distance is limited by the distance of 0 meters, while group spread and number of neighbors could increase unbounded. We would expect group spread to be asymptotic in relation to group size if sifakas are moving in some constrained space, or if group members change their configuration in space so as to minimize the increase in group spread with increasing group size. In contrast, we would expect the number of neighbors to be asymptotic in relation to group size only if group members were spacing themselves in such a way as to minimize personal crowding.

At any one time (i.e. within a single group scan), group spread was negatively correlated with mean individual crowding: for every group size except group size 13, group spread was positively correlated with nearest neighbor distance averaged over group members present in a given scan sample, and negatively correlated with numbers of neighbors within 2 and 5 meter radii also averaged over all group members (Table 2.2).

Fig. 2.1. Mean Measures of Spacing for Each Social Group
numbers surrounded by standard error bars are means for a given group of a given size;
values for single groups that changed in size are connected by thin straight lines; thick curves
along the plots show quadratic fits to the data with the corresponding equations provided

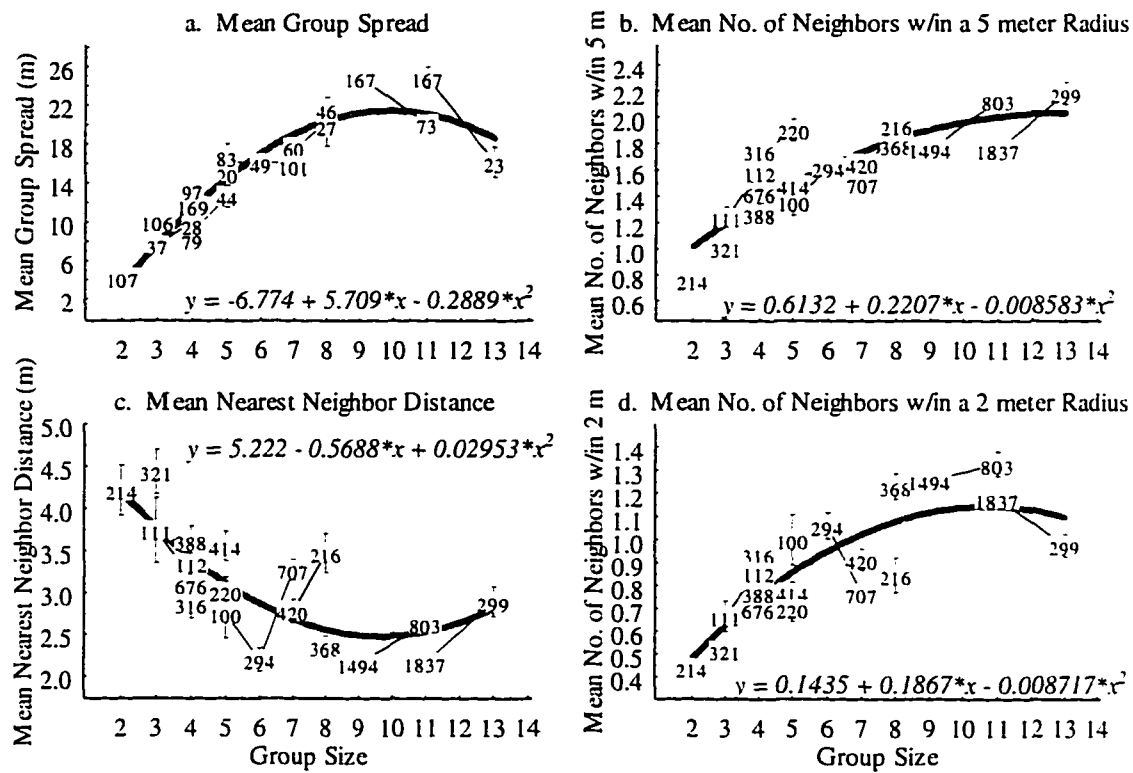


Table 2.2. The relationship between group spread and each measure of personal crowding (*Group Spread* = *a* + *b*[*given spatial variable*]). Fit of empirical data, from scan samples, into a linear regression model (*p_a* and *p_b* denote the probability that the constant *a* or coefficient *b* were accurately estimated).

Grp. Size	# Scan Smpls.	Nearest Neighbor Distance					# Neighbors within 2 m					# Neighbors within 5 m				
		<i>a</i>	<i>b</i>	<i>p_a</i>	<i>p_b</i>	adj <i>R</i> ²	<i>a</i>	<i>b</i>	<i>p_a</i>	<i>p_b</i>	adj <i>R</i> ²	<i>a</i>	<i>b</i>	<i>p_a</i>	<i>p_b</i>	adj <i>R</i> ²
2	105	0.0	1.0	0.95	***	1.00	6.5	-5.2	***	***	0.34	10.3	-7.8	***	***	0.63
3	173	1.1	2.0	*	***	0.74	12.6	-5.9	***	***	0.29	16.9	-6.9	***	***	0.51
4	382	2.8	2.6	***	***	0.63	15.3	-5.1	***	***	0.32	18.7	-5.2	***	***	0.44
5	168	5.2	3.3	***	***	0.51	20.8	-6.2	***	***	0.23	25.2	-5.9	***	***	0.39
6	72	5.9	4.8	***	***	0.62	25.8	-7.4	***	***	0.33	31.6	-8.2	***	***	0.35
7	179	7.6	3.2	***	***	0.25	22.1	-5.3	***	***	0.09	23.3	-3.5	***	***	0.13
8	71	9.8	4.0	***	***	0.28	25.4	-3.8	***	*	0.05	29.5	-4.5	***	***	0.13
9	162	9.8	7.0	***	***	0.55	37.5	-10.0	***	***	0.31	45.8	-11.9	***	***	0.38
11	237	7.1	7.2	***	***	0.35	31.9	-6.5	***	***	0.13	38.0	-7.5	***	***	0.18
13	23	2.7	4.7	0.68	*	0.15	21.4	-5.4	*	0.39	0.00	25.0	-4.0	***	0.07	0.11

*** *p*<<0.001 * *p*<0.05

Group size was a better predictor of spatial distribution of group members on the large scale, i.e. group spread and number of neighbors within a 5 meter radius (Fig. 2.1a,b), than on the small scale, i.e. nearest neighbor distance and number of neighbors within a 2 meter radius (Fig. 2.1c,d). This was consistent with changes in spatial distribution among members of groups that changed size (indicated by thin lines in Fig. 2.1), where changes in large scale measures could be predicted by group size (Fig. 2.1a,b), but changes in small scale measures could not (Fig. 2.1c,d).

Due to movements of males between groups and due to emigration of a few females, the groups that changed in size during my study happened to be smaller during the transitional (March, September, and October) and the wet (November through February) seasons than during the dry season (April through August; $\chi^2=15.1, p<0.0001$ when comparing dry to non-dry). Thus, if season plays a role in the spatial distribution of group members, seasonal effects might obscure the direction of change in mean crowding and mean group spread for groups that changed their size. Group size affected strongly all aspects of spatial distribution (Table 2.3), while season significantly affected only the small scale spatial measures (nearest neighbor distance and number of neighbors within a 2 m radius), but not the large scale (group spread and number of neighbors within a 5 m radius). Because the nearest neighbor distance was shorter and the number of neighbors within a 2 meter radius was greater in larger groups, and because groups were larger during the dry season than during the wet season, we would expect greater crowding during the dry season. However, the nearest neighbor distance was greater and the number of neighbors within a 2 meter radius was lower during the dry season, as

compared to the wet, suggesting that feeding competition is greater during the dry season than in the wet, and that the spacing of group members during the dry season was affected more by a pressure to avoid feeding competition than by group size. During the dry season as compared to the wet, the means for the small scale variables (nearest neighbor distance and number of neighbors within a 2 m radius) were being driven in the opposite direction than predicted by the effect of group size, which explains why the change in their means, within the 6 groups that changed size, could not be predicted by group size alone (Fig. 2.1c,d).

Dry season is traditionally equated with lower food availability and thus a potential for increased food competition. This is evidenced by weight loss during the dry season (Richard et al. in prep).

Table 2.3. The effect of group size and season on the four spatial variables (GLM^a probabilities).

The effect of:	Group Spread	# of Neighbors within a 5 m radius	Distance to the nearest neighbor	# of Neighbors within a 2 m radius
Group Size	0.000 ***	0.000 ***	0.017 **	0.000 ***
Season	0.166	0.182	0.000***	0.006 ***

^a general linear model was used to test the effects of group size and of season on each spatial measure; probability values are presented in the corresponding cells (Minitab Software for Windows Release 11.11, Minitab Inc. 1996)

*** p<<0.0005 ** p<0.05

Decrease in the small-scale individual crowding during feeding versus resting (Fig. 2.2 and Table 2.4) suggests once more that group members were attempting to spatially minimize feeding competition. Just as when food was more scarce (during the dry season), during feeding versus resting the distance to the nearest neighbor was greater and the number of neighbors within 2 meters of an individual was lower, while the number of neighbors within 5 meters did not change significantly (means and standard

deviations shown in Appendix 2.B). Instead, when individuals were feeding, the number of their neighbors within a 2-5 meter ring around each individual significantly increased (Fig. 2.2 and Table 2.4).

Fig. 2.2. Mean Measures of Personal Crowding During Feeding versus Resting Across Group Sizes

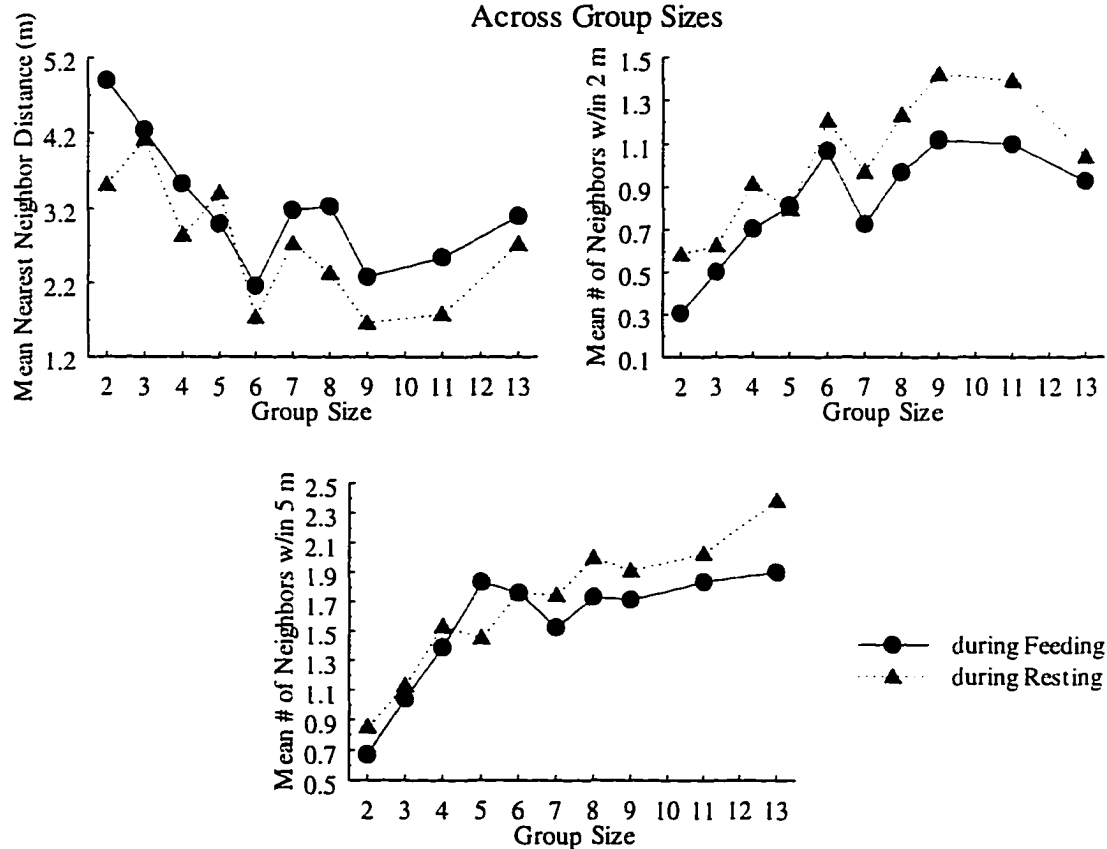


Table 2.4. Effects of activity (*feeding* vs. *resting*) on each measured spatial variable (t-test).

Dependent Variable	Direction of Change ^a	<i>p</i> Value	% of Change
nearest neighbor distance	increase	< 0.0005	7 %
packing within 2 meters	decrease	< 0.0005	10 %
packing within 2-5 meters	increase	< 0.0005	12 %
packing within 5 meters	no effect	0.78	0 %

^a "increase" means that the variable was greater during feeding than during resting.

SPATIAL MODELS AND RESULTS

In the observed groups, cohesion decreased with group size, and personal crowding increased. But how can we tell from these data whether group members were indeed actively trying to balance group cohesion against intra-group food competition?

To answer this question I developed three groups of spatial models. In the first group of models I examined how group members would be spaced if they moved randomly within a constrained space. In the second group of models I examined how group members would be spaced if they maintained the same inter-individual distances as members of groups of two. And, finally, in the third group of models I examined how group members would be spaced if they formed specific geometric configurations in space.

The first group of models (Models I) addresses the scenario in which group members behave so as to maintain spatial cohesion but are not concerned with personal crowding and avoiding intra-group feeding competition. This group of models determines how group members would space themselves if the only factor affecting their distribution in space was that of group spread, which, for groups of all sizes, was limited by some constant, specific maximum distance. This distance would be the maximum distance allowing groups to maintain their spatial cohesion in a given habitat.

The second group of models (Models II) addresses the scenario in which group members are concerned with inter-individual spacing, which affects intra-group feeding competition, but not with the spatial cohesion of their group or the number of neighbors.

In this group of models, the main assumption is that the inter-individual spacing in groups of two is optimal, and that the only spatial constraint across group sizes is that all dyads in larger groups maintain the same range and frequency distribution of inter-individual distances as pairs in groups of two. The consequence would be a constant average inter-individual distance across group sizes, but because each individual would have a greater potential numbers of neighbors in larger groups, the nearest neighbor distances would be smaller and the numbers of neighbors within specific radii would be greater in larger than in smaller groups.

Thus the first two groups of models examine what would the spacing patterns be if group members were mainly concerned with group's spatial cohesion (Models I) versus intra-group feeding competition (Models II), but where group members did not undertake specific geometric configurations in space. The last, the third group of models (Models III), examines the full spectrum of possibilities, ranging from group members being concerned exclusively with feeding competition to group members being concerned exclusively with minimizing their group's spread. The primary difference between this last set of models and the first two is that in this third set of models group members use specific geometric configurations in space to achieve these goals. It also allows us to examine what would the spacing of group members be if they were spacing themselves in such a way as to limit both the increase in personal crowding (i.e. increase in feeding competition) and increase in group spread (i.e. decrease in spatial cohesion).

As I present each group of models, I use their results to test whether sifaka in the observed study groups limited the decrease in their spatial cohesion and/or limited the increase in their personal crowding.

Models I. Maintaining spatial cohesion.

Models:

To determine whether group members distribute themselves randomly within a constrained space, as expected if they are only limited by a maximum space and feeding competition is absent, simulation models were created using a Borland compiled C++ program (© 1997 Borland International, Inc.). The constraining space in three different dimensions was considered: (a) a 3D sphere with $1S$ diameter, (b) a 2D circle with $1S$ diameter, and (c) a 1D line $1S$ in length. Each dimension implied different spatial constraints possibly imposed by the habitat and should have encompassed a full spectrum of possible shapes of the constraining space. For each dimension three different constraining diameters were chosen (Table 2.5). For each combination of dimension and diameter, simulations were run for group sizes of 2 to 13. Each of the 2 to 13 points, representing a group member, was placed randomly (i.e. had an equal probability of being placed on any set of coordinates) within the space defined by the dimension and the diameter but no points were allowed to be closer than 0.25 meters apart. For each combination of dimension, diameter, and group size, ten thousand simulations were run, and from them a mean and a coefficient of variation were calculated for group spread, nearest neighbor distance, number of neighbors within a 2m radius, and number of

neighbors within a 5m radius. The difference between the models and empirical data was evaluated graphically.

Table 2.5. Reasons for choosing the three different diameters that determine the range of possible group spreads, and the percent of group spreads observed in all focal groups that were equal to or smaller than the maximum group spreads allowed by each radius of the modeled constraining space.

Diameter r	Reasons for Choosing a Given Radius	% of Obs. Group Spreads \leq Diameter
12 m	the smallest possible size of the constraining space, adjusted so that the mean group spread expected in groups of two equals to that observed in groups of two	41.9 %
30 m	the largest likely size of the constraining space, adjusted so that the mean group spread expected in the larger groups equals to that observed in the larger groups	93.6 %
40 m	the largest possible size of the constraining space, chosen so that the maximum possible group spread encompasses over 95% of all observed group spreads	97.5 %

Results:

The mean expected group spreads and the mean expected nearest neighbor distances for groups of different sizes differed considerably between models with different diameters, but did not differ appreciably between models with different dimensions of the constraining space but the same diameters. Therefore, for the clarity of presentation, the expected mean group spreads and the expected mean nearest neighbor distances are only indicated for different diameters and not for different dimensions (Fig. 2.3a, 2.4a).

The coefficients of variation for group spread and nearest neighbor distance had the opposite pattern of differentiation than the means. They differed between dimensions but not diameters, and thus only dimensions and not diameters are indicated (Fig. 2.3b, 2.4b).

Fig. 2.3. Observed and Expected Group Spread (Models I)

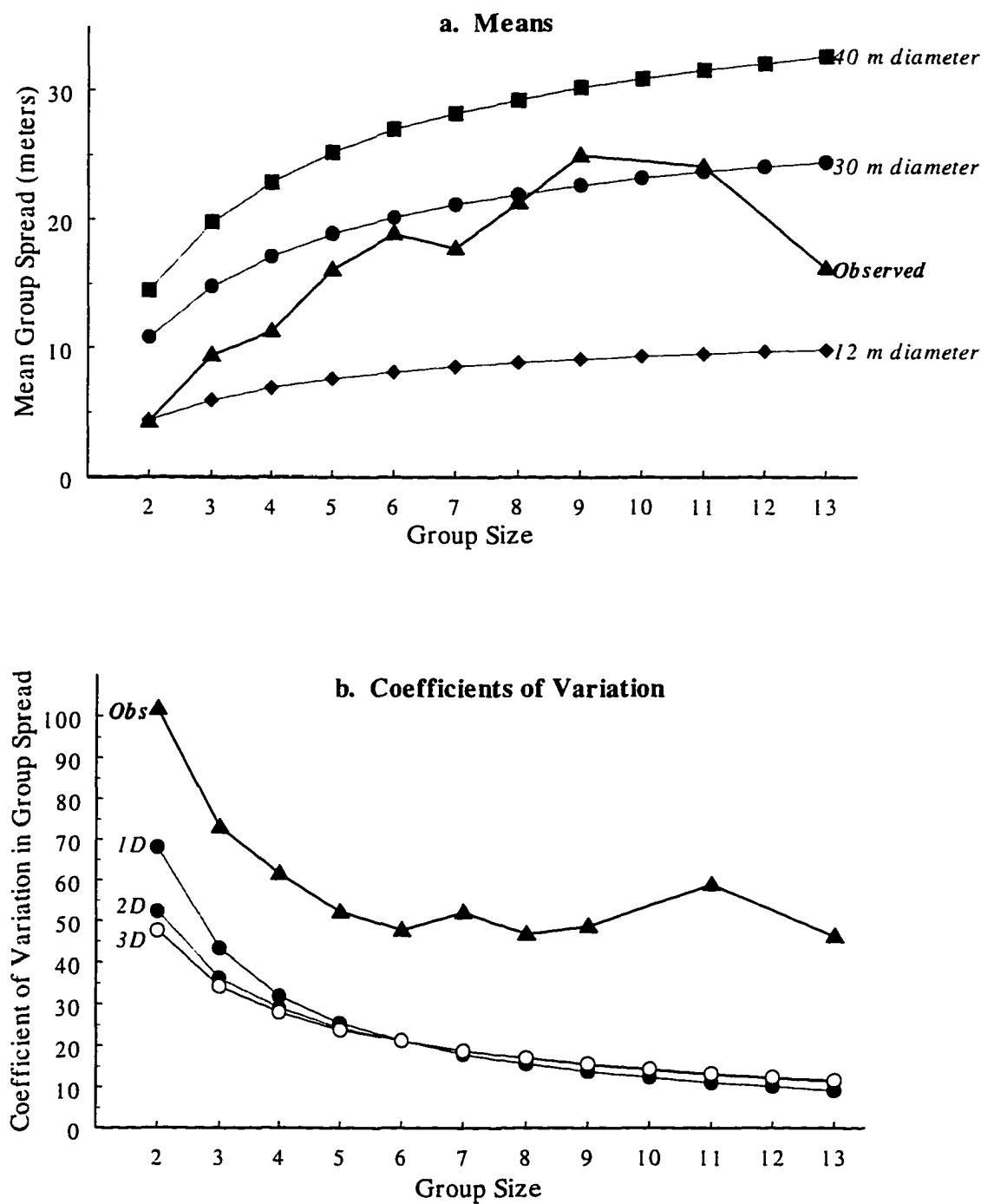


Fig. 2.4. Observed and Expected Nearest Neighbor Distance (Models I)

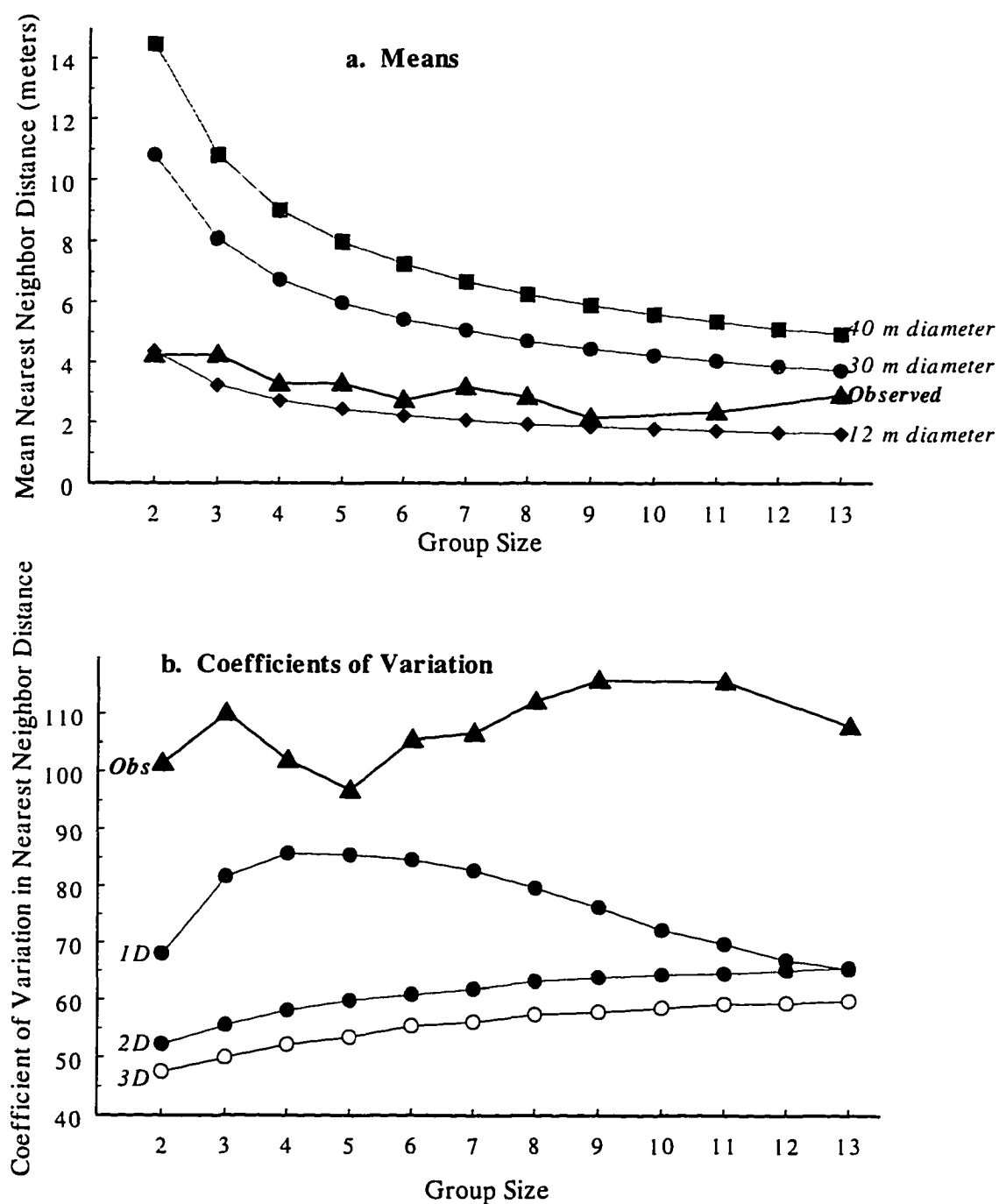
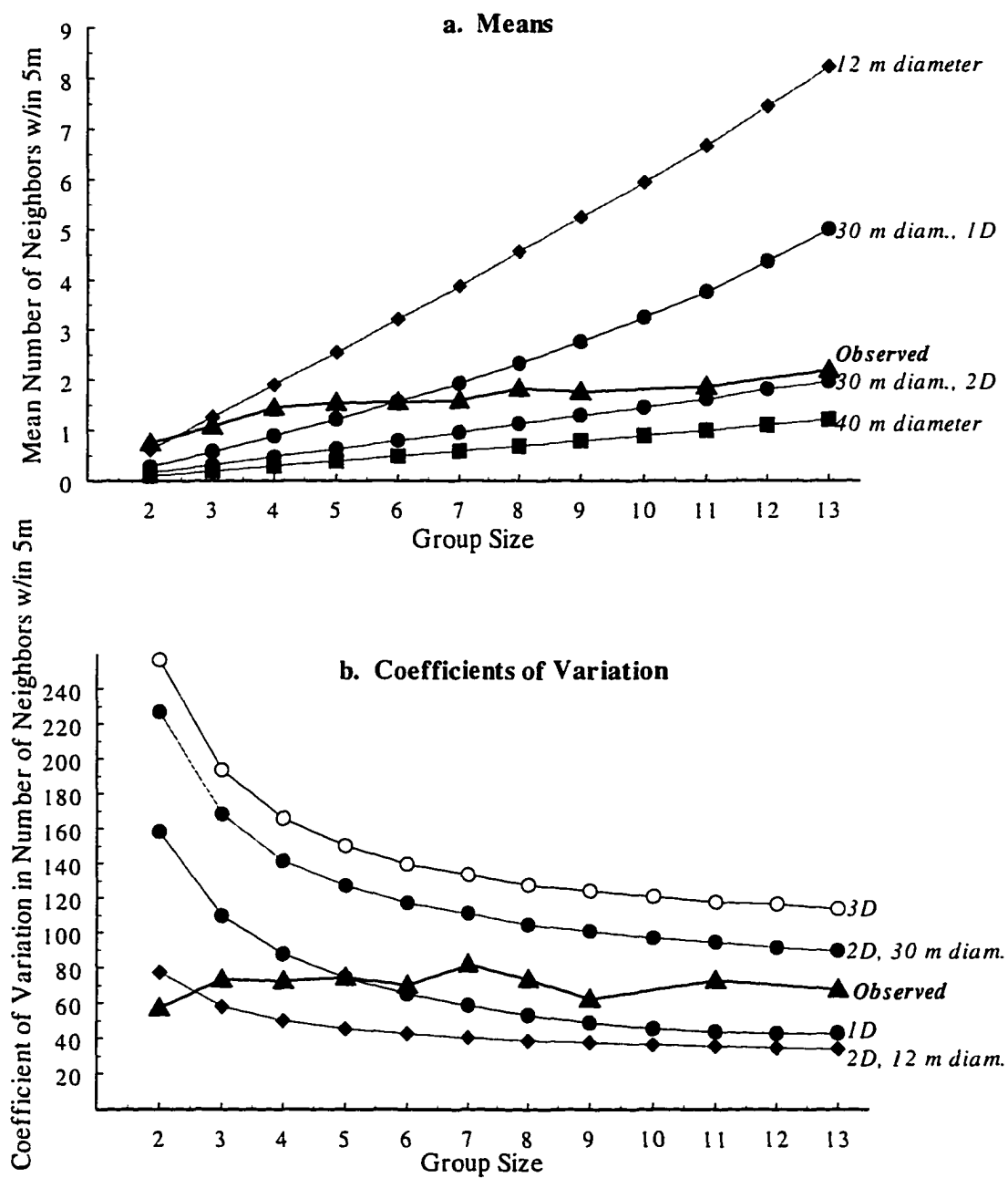


Fig. 2.5. Observed and Expected Number of Neighbors Within a 5m Radius
(Models I)



The relative patterns of observed versus expected means and coefficients of variation for number of neighbors within a 2m radius were nearly identical to those within a 5 meter radius, and thus only the results for the number of neighbors within a 5 meter radius are shown. The means and coefficients of variation for the number of neighbors varied significantly with both the dimensions and the diameters. For graphical clarity, only some of the dimension/diameter combinations are shown, but they represent fully the differences between observed and expected results (Fig. 2.5a,b).

The observed mean group spread increased with group size much more rapidly than predicted by any of the models (Fig. 2.3a), and its coefficients of variation (pooled for all point samples for a given group size) were approximately twice as large as predicted (Fig. 2.3b).

The observed mean nearest neighbor distance decreased considerably less with increasing group size than predicted by the models, but it did approximate the means predicted by the 12 meter diameter models (Fig. 2.4a). The observed coefficients of variation did not visibly change with group size and, similarly to group spread, were much higher than predicted (Fig. 2.4b).

The observed mean number of neighbors within a 5 meter radius increased considerably less than predicted by the models (Fig. 2.5a), and the observed coefficients of variation did not change with group size at all, again not as predicted (Fig. 2.5b).

Similarly to the empirical data (Table 2.2), group spread predicted by the model was positively correlated with nearest neighbor distance and negatively correlated with numbers of neighbors within 2 and 5 meter radii, across group sizes.

Models II. Limiting an increase in personal crowding by controlling inter-individual distances only.

Model:

In this model, members of large groups try to buffer the increased crowding they experience by controlling only inter-individual distances and not the spatial configuration of the group, while no constraint is imposed on group spread. The most efficient way of minimizing personal crowding under these conditions is to maintain constant nearest neighbor distances across group sizes. However, group members do not space themselves in this way (Fig. 2.1c). Another possibility is to maintain the same distribution of inter-individual distances within each dyad, in a group, as is maintained in groups of two. Under this scenario, if

N = group size

r = specified radius in meters

k = the number of neighbors within r -meter radius

i = distance to the nearest neighbor

v = the probability that members of a group of two are within a distance r from each other

v_i = probability of having a neighbor within distance i in group size of 2

l_i = prob. of having at least 1 neighbor within distance i in group size of N

p_k = the probability of having k neighbors within r meters in a group size of N

then p_n follows the binomial distribution:

$$p_k = \binom{N}{k} v^k (1-v)^{N-k-1} \quad (\text{Equation 4})$$

and:

$$l_i = 1 - (1 - v_i)^{N-1} \quad (\text{Equation 5})$$

Equation 4 allowed me to calculate for every group size: (1) the expected mean number of neighbors within r meters around an individual and (2) the expected frequency with which an individual has a given number of neighbors within r meters. From *Equation 5* the cumulative frequency of nearest neighbor distances for each group size were calculated.

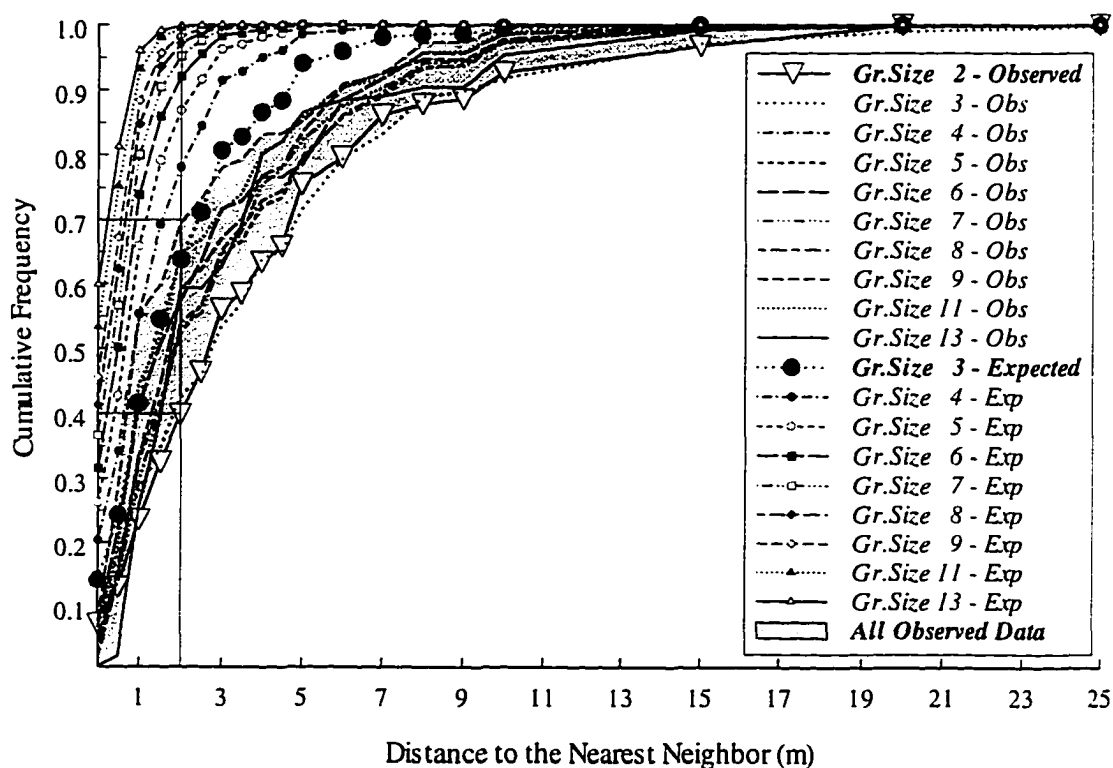
This model assumes independence among the neighbors of the focal individual. Independence of neighbors is not a problem for group sizes smaller than fourteen in 3D, and for group sizes smaller than eight in 2D, because as many as twelve identical spheres can be packed tightly around a single sphere in 3D, and as many as six identical circles can be packed tightly around one circle in 2D. If the central sphere or circle represents the focal individual and the surrounding spheres or circles its neighbors, then under the tight packing scenario all neighbors can maintain the same frequency distribution to their adjacent neighbors as they do to the focal individual. Because the focal groups I studied did not exceed the size of thirteen, this model can be applied to their system. Under a 3D scenario we can compare the expected to the observed values for all sifaka group sizes, while under a 2D scenario we can make the same comparison including only group sizes smaller than eight.

Results:

The cumulative frequencies of nearest neighbor distances predicted by the model change with group size more than the observed frequencies (Fig. 2.6). The observed

cumulative frequencies for all group sizes (the shaded area in Fig. 2.6) range only between those expected for group size of 2 and 3.

Fig. 2.6. Observed and Expected Cumulative Nearest Neighbor Distance Frequencies for Each Group Size (Models II)



The predicted numbers of neighbors within 2 and 5 meter radii increase with group size at a rate many times higher than the slow increase in the observed data (Fig. 2.7a,b). Similarly, frequencies predicted by the model of having a certain number of neighbors (anywhere between zero and groups size minus one) within a 2 and a 5 meter radii change significantly with group size (Fig. 2.8b,d), while the observed frequencies did not (Fig. 2.8a,c).

Fig. 2.7. Observed and Expected Mean Number of Neighbors within a Given Radius Based on Values for Groups of Two (Models II)

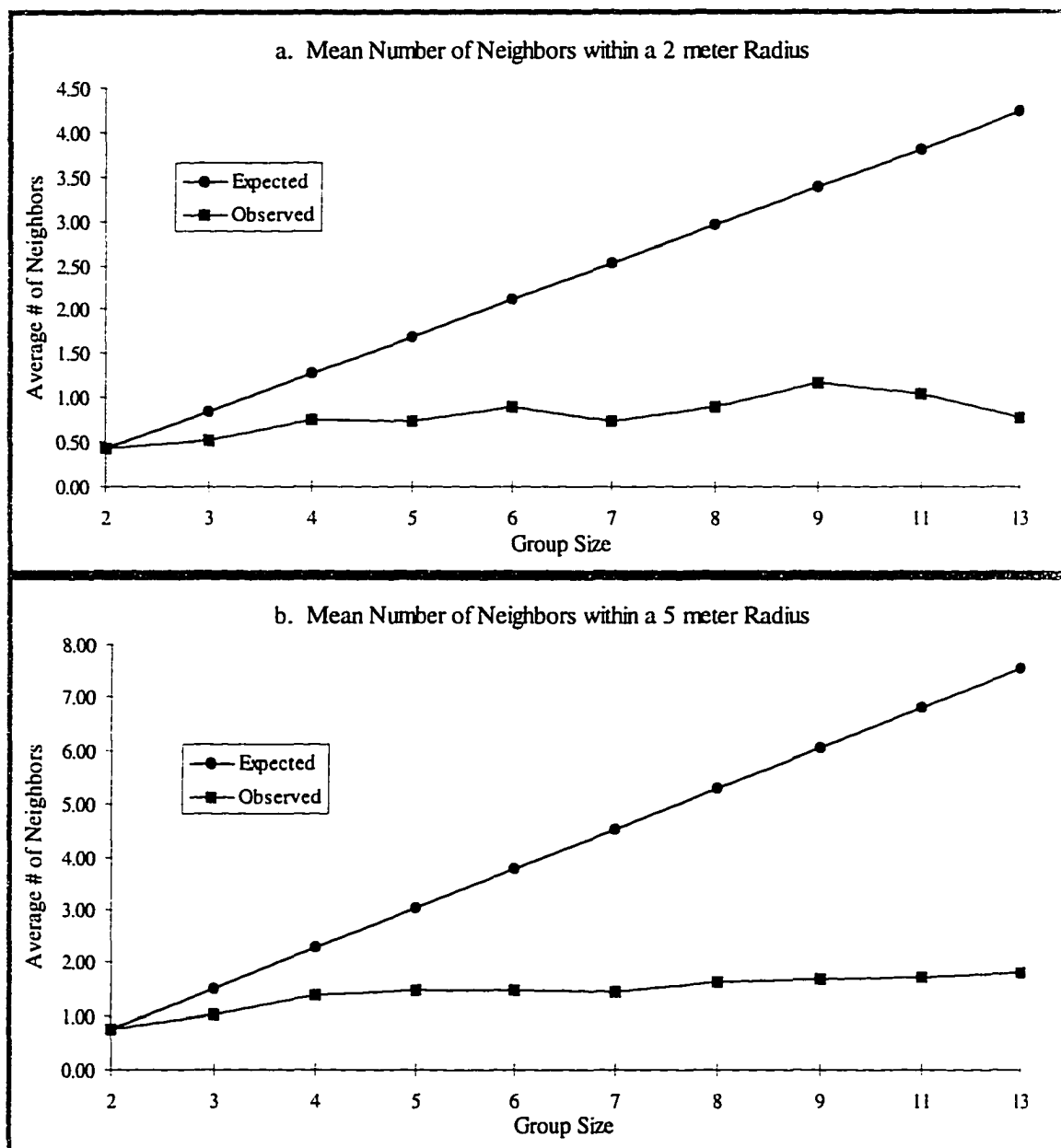
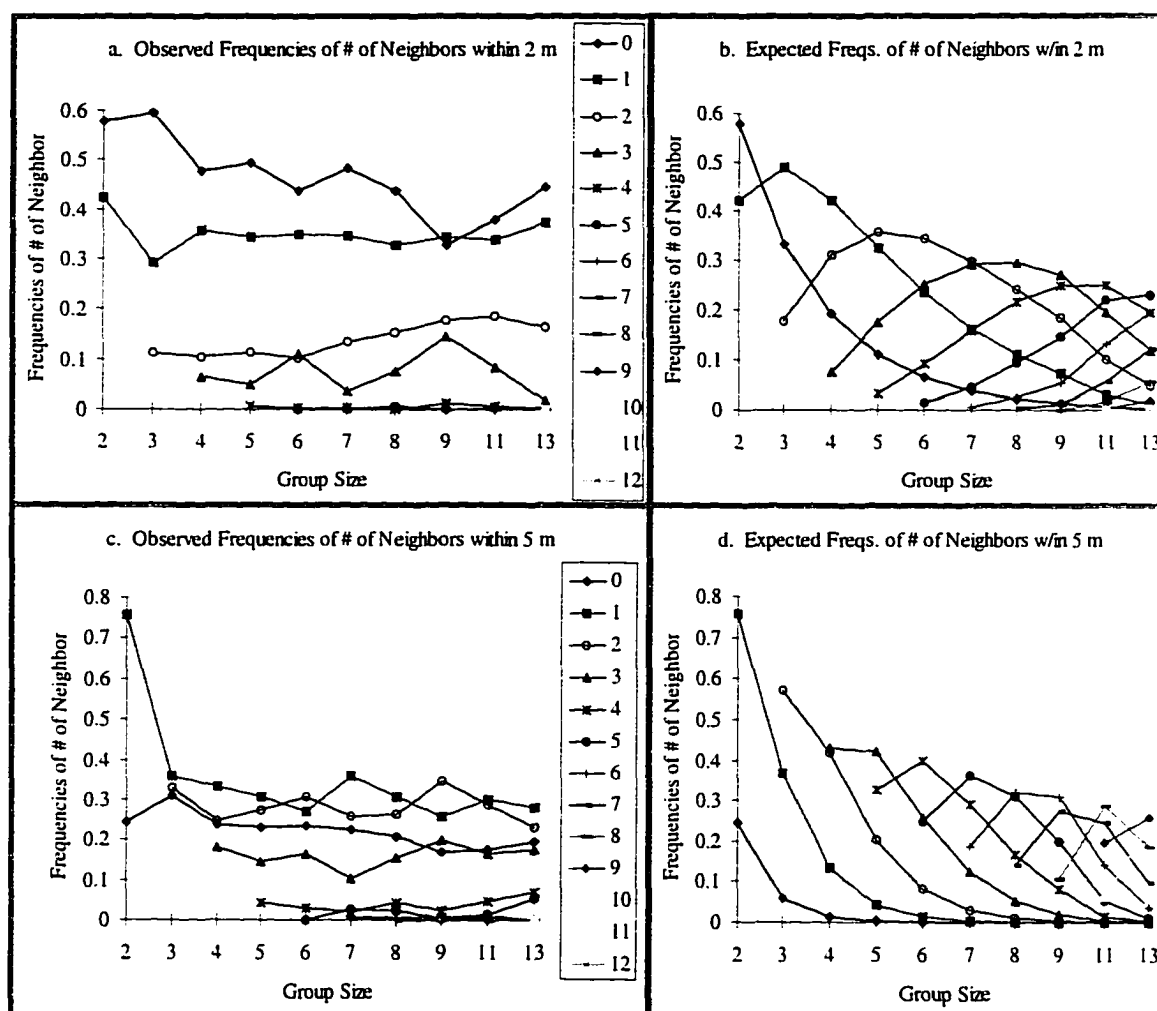


Fig. 2.8. Observed and Expected Frequencies of Numbers of Neighbors within a Given Radius (Models II)



Models III. Using specific geometric configurations of group members in space to control group's spatial cohesion and/or individual crowding.

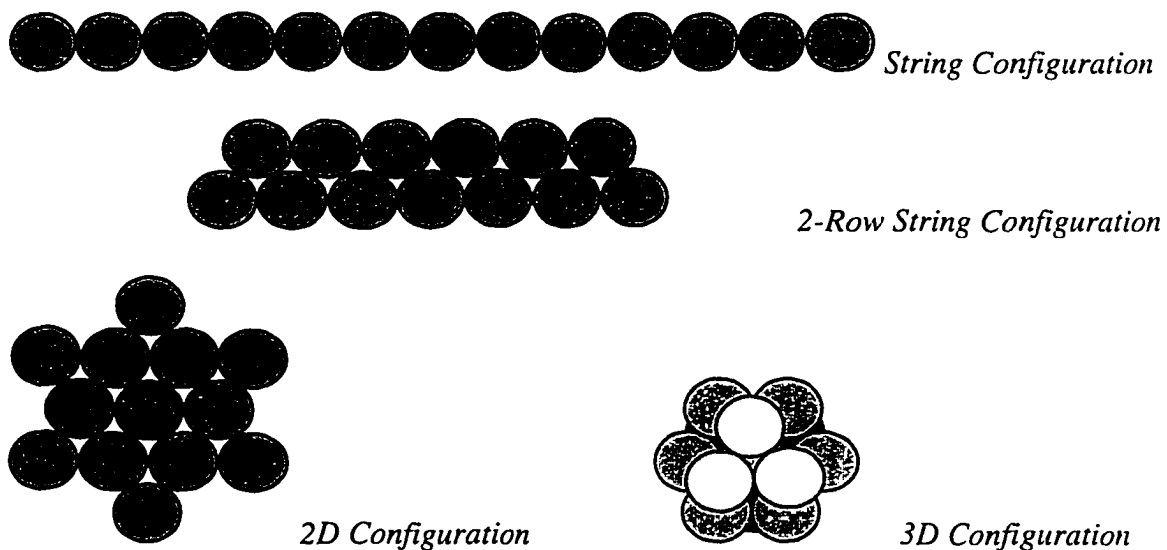
Models:

In a three dimensional habitat, one can imagine that as an individual moves unconstrained through space while foraging, its search field forms a tunnel. A cross-section of the tunnel is a circle with the individual at its center, and the circle has a radius

r . Now, if the food is distributed uniformly throughout the space, the next adjacent individual can forage in a parallel tunnel with the same radius r and be as little as $2r$ distances away from the first individual. If we assume uniform food distribution, we could envision that regardless of group size, group members forage in parallel tunnels and thus avoid intra-group food competition by not overlapping their search fields.

If minimizing personal crowding is the only factor affecting intra-group spatial distribution, then r would not change with group size. If minimizing both group spatial cohesion and personal crowding affects the distribution of group members, then r would be expected to decrease with group size.

Fig. 2.9. Spatial Configuration Models for Group Size of 13.



Being arranged in a row (*string configuration*) results in the least crowding because for a given inter-individual distance each group member has the least number of neighbors within some specified radius. However, the string configuration has a drawback, in that it also results in the greatest increase in group spread with each

additional group member. Thus foraging in a string configuration is problematic. We might expect it to be maintained in small groups, provided that it is not selected against by the local predators' hunting tactics, but in larger groups the resulting large group spreads would likely diminish the advantages of living in a group.

Three other configurations are considered here, which cover a range of tradeoffs between minimizing group spread and minimizing personal crowding (because in the configuration models, nearest neighbor distance is held constant, personal crowding is redefined as only the number of neighbors within a given radius) (Fig. 2.9): (1) a 2-row string model consists of two rows stacked on top of each other in a manner that minimizes group spread for a given group size, (2) a two dimensional (2D) model, where group members follow the closest circle packing in two dimensions, which can be envisioned as a wall moving in the direction perpendicular to its plane, and (3) a three dimensional (3D) model, where group members follow the closest packing of spheres in three dimensions, which can be envisioned as a ball. The string model is on one end of the spectrum with the lowest potential search field overlap and the greatest group spread. The 2D model still permits group members their unique search tunnels. These are, however, packed tightly against each other, resulting in an intermediate potential overlap in search fields and an intermediate group spread. Lastly, the 3D model is on the opposite end of the spectrum from the string model with the greatest potential and actual overlap in search fields and the smallest possible group spread. All of these models make the same predictions for group size of two and begin to differ for groups larger than two. Table 2.6 shows equations for calculating the expected group spread and number of

neighbors for each of the four models, where:

N = group size

G = group spread for group size of N

d = average inter-individual distance in group size of 2

s = number of neighbors at distance d for a given group member

X_s = average number of neighbors at distance d for group size of N

Table 2.6. Four models of group member configuration in space, with equations for the expected group spread, G , number of neighbors, X_s , and the resulting expected values for groups of 13.

Model	G	X_s	G for $N=13$	X_s for $N=13$
string	$d(N-1)$ for all N	1 for $N = 2$ $[2+2(N-2)]/N$ for $N > 2$	12	1.85
2-row string	$(N-1)/2$ for N odd $[(N-1)^2+3]/2$ for N even	1 for $N = 2$ 2 for $N = 3$ $[10+4(N-4)]/4$ for $N > 3$	6	3.54
2D	1 for $N = 2$ $(N-2)^{1/2} *$ for $N > 2$	1 for $N = 2$ 2 for $N = 3$ $[8+3(4\sqrt{N}-8)+4(N-4\sqrt{N}+4)]/N$ for $N > 3$	3.3 (3.5)	2.89 (3.23)
3D	1 for $N < 3$ $(N-3)^{1/3} *$ for $N > 3$	1 for $N = 2$ 2 for $N = 3$	2.2 (2.0)	5.54

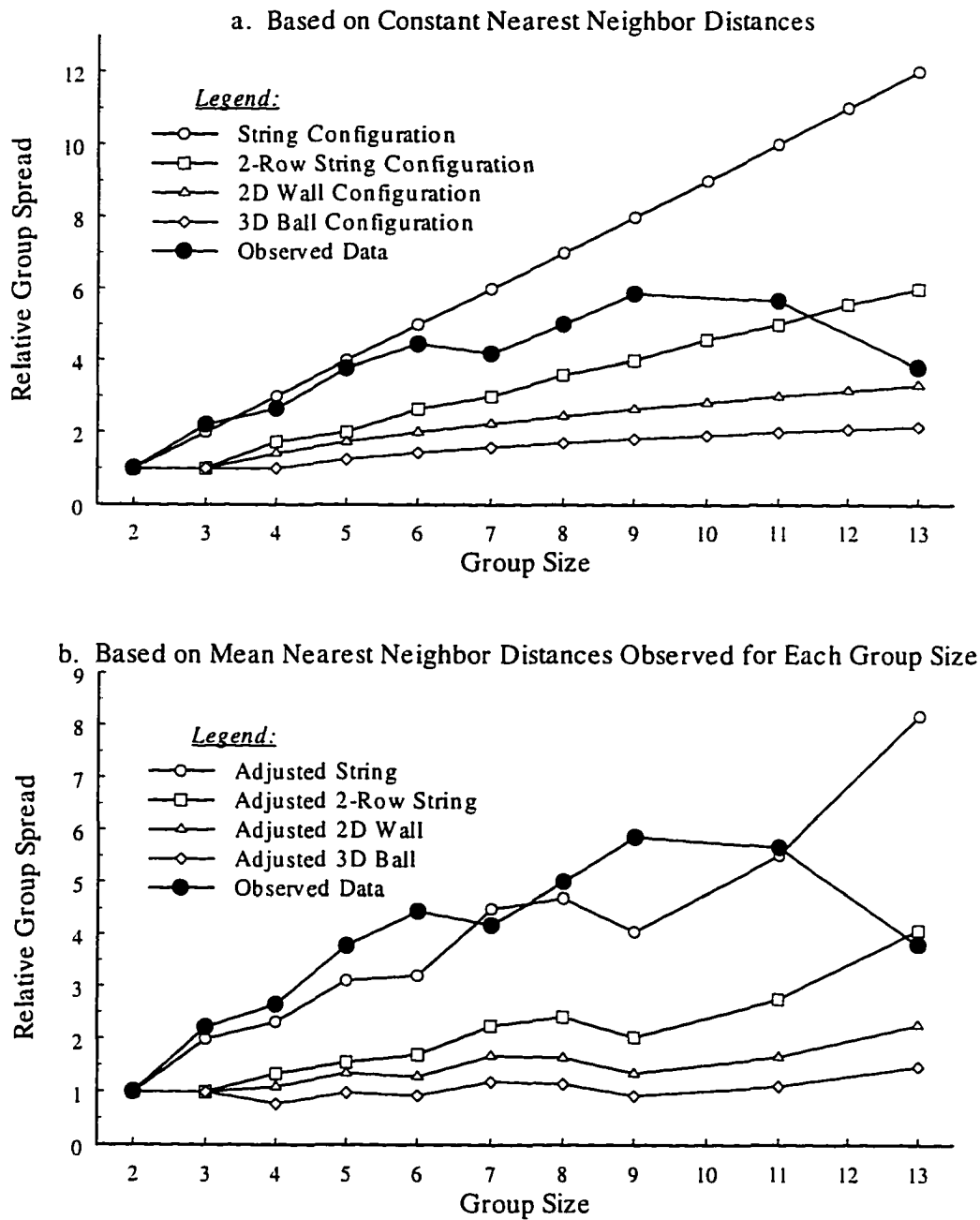
* for small group sizes, such as those of sifakas, group spread resulting from 2D and 3D closest packing configurations can be approximated by equations. G and X_s for $N=13$ are calculated from the approximation equations; in parentheses G and X_s obtained from true closest packing models are shown for comparison.

Results:

In groups up to 6 members in size, the observed group spread approximated most closely the string configuration model, and as group size increased above 6, the observed group spread approximated progressively more the 2-row string configuration model, and for group size 13, it approximated the wall configuration model (Fig. 2.10a). When instead of using the mean nearest neighbor distance in groups of two for all group sizes (as in Fig. 2.10a), I used the observed mean nearest neighbor distance for each respective group size, the observed data followed that of the string configuration model for all but

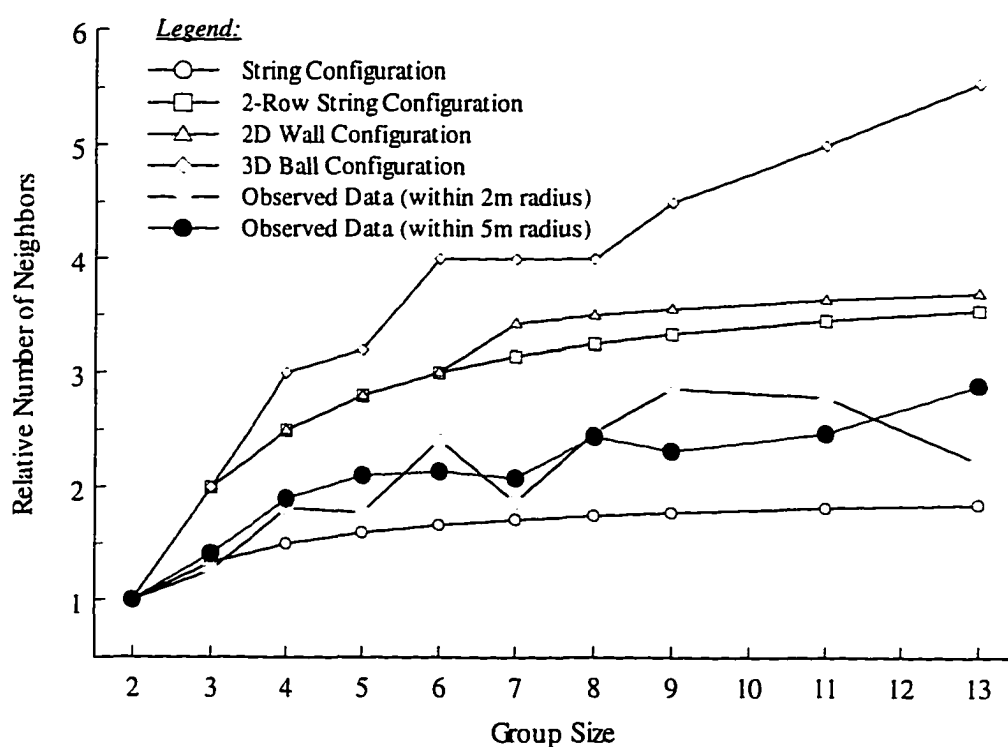
the largest group size of 13 where it approximated the 2-row string configuration (Fig. 2.10b).

Fig. 2.10. Observed and Expected Group Spread Predicted by Configuration Models (Models III)



The observed numbers of neighbors within 2 and 5 meter radii fall between values expected by a string and a 2- row string models (Fig. 2.11).

Fig. 2.11. Observed and Expected Number of Neighbors as Predicted by Spatial Configuration Models (Models III)



DISCUSSION

Non-random spacing

Not surprisingly, none of the random distribution models accounted for the spatial distribution of sifakas within groups (Models I). In every case the results differed from the empirical data (Fig. 2.3-2.5). Only the mean nearest neighbor distance approximated

the model with a 12 meter diameter limit, but because sifakas had group spreads much greater than 12 meters over 58% of the time, the 12 meter diameter limit could not be considered realistic. The seeming fit must have resulted from group members arranging themselves spatially so as to not decrease their nearest neighbor distance any more than necessary. Group spread increased much more rapidly with group size than predicted by the hypothesis of only maintaining spatial cohesion (Fig. 2.3), and crowding variables increased much less than expected (Fig. 2.4, 2.5). This shows that although sifakas in larger groups were more crowded and more dispersed than sifakas in smaller groups, they spaced themselves very carefully so as to buffer the changes in their spatial distribution. Group members behaved in ways that limited an increase in personal crowding and, at the same time, limited a decrease in group's spatial cohesion.

The observed frequencies of nearest neighbor distances for different group sizes were much more conservative than predicted by the hypothesis that group members try to only minimize personal crowding by maintaining the same inter-individual distances within dyads as pairs in groups of two (Fig. 2.6) . This suggests, that even though nearest neighbor distances of sifakas decrease with group size (Fig. 2.1c), group members must be buffering the degree of this decrease by measures other than maintaining conservative inter-individual distances. The fact that their nearest neighbor distances and neighbor numbers change so little in the face of up to six and a half-fold increase in group size (Fig. 2.6-2.8), suggests that group members arrange themselves in space in a structured configuration that limits the potential number of neighbors around an individual.

String configuration

The frequency distribution of neighbor numbers across group sizes (i.e. the frequency with which individuals had one, two, or three neighbors around themselves), did not change with increasing group size (Fig. 2.8). The fact that at almost all times individuals had zero to two neighbors suggests that, on average, group members may have spaced themselves in some form of a string configuration. However, these data do not suggest whether the string configuration would have been in a straight line or folded in some fashion.

The frequency distribution of nearest neighbor distances was skewed towards the smallest distances: 24-55 % of time group members had a neighbor within 1 meter, and 40-70 % of time they had a neighbor within 2 meters (Fig. 2.6 and Appendix 2.C). Therefore, even if individuals were arranged in a string configuration, with the mean inter-individual distance equal to the mean nearest neighbor distance observed, the expected mean number of neighbors within a given distance would be somewhat greater than the calculated $[2+2(N-2)]/N$. Thus the expected mean numbers of neighbors in Fig. 2.11 are underestimated and the real difference between the observed values and those expected under string configurations is even smaller.

The final measure, mean group spread across all different group sizes, matched almost perfectly the group spread expected in a straight-line string configuration among groups with up to 6 members. Then it began to deviate, suggesting that groups with 7 members or larger formed a more clumped configuration, with the largest group size of 13 approximating the very clumped wall configuration (Fig. 2.10a).

Thus, contrary to the constant frequencies of specific numbers of neighbors (Fig. 2.8), the mean group spread for larger group sizes suggests that sifakas alter their spatial configuration to a more clumped one (such as the two-string or the wall models in Fig. 2.9).

Existence of personal space

Individuals compromised the distance to their nearest neighbor as group size increased, but only to a point. Among smaller groups the mean nearest neighbor distance decreased rapidly with increasing group size (Fig. 2.1). This means that group members were increasing personal crowding, presumably thereby buffering against more rapid increase in group spread. Among larger groups the mean nearest neighbor distance did not decrease very much with group size and it stopped decreasing all together past group size of 9. This, in turn, suggests that individuals had a fixed space buffer around themselves (referred to from here on as *personal space*), and that in groups greater than 9 they packed themselves at the smallest tolerable inter-individual distance. The increase in mean group spread also leveled off past group size of 9 (Fig. 2.1), suggesting that groups of 9 individuals spread themselves at the maximum acceptable distance. The successful buffering against further rapid increase in personal crowding and a simultaneous successful buffering against further increase in group spread were presumably achieved by altering the spatial geometry of the group from a string configuration to a more two-row string configuration (Fig. 2.9).

The lowest mean nearest neighbor distances were just above 2 meters (Fig. 2.1c) and during feeding, versus resting, sifakas decreased the number of neighbors within a 2 meter radius, but increased the number of neighbors within a 2-5 meter ring around themselves (Table 2.4). This seems to suggest that their personal space was approximately 2 meters from the nearest neighbor.

Sifakas show no body length sexual dimorphism, and their mean body length (torso + upper limb length + lower limb length) is 0.854 meters (Alison Richard unp. data). Thus the suggested personal space of sifakas is only slightly larger than twice their mean body length. One can imagine that as neighboring sifakas stretch towards each other to obtain food within their own reach, each could easily utilize the distance of its body length. This would predict that nearest neighbors would maintain a distance of approximately 2-body lengths between themselves, as was observed. If the minimum acceptable distance to the nearest neighbor is 2 meters, then the minimum acceptable radius around each individual is 1 meter, suggesting that each individual maintains a 1 meter buffer around itself which, as suspected, corresponds to a personal space equal to 1.17 sifaka body length.

Possibility of group spatial subdivision

The unusually high coefficients of variation in the observed group spread and nearest neighbor distance, relative to those expected under random distribution (Fig. 2.2-2.3; frequency distributions of group spread for each group size are shown in Appendix 2.C), suggest a spatial subdivision, or sub-clumping, within groups. It remains difficult.

however, to explain the high observed coefficients of variation for the smallest groups (i.e. with 2 or 3 members), where sub-clumping would not be expected.

Feeding competition

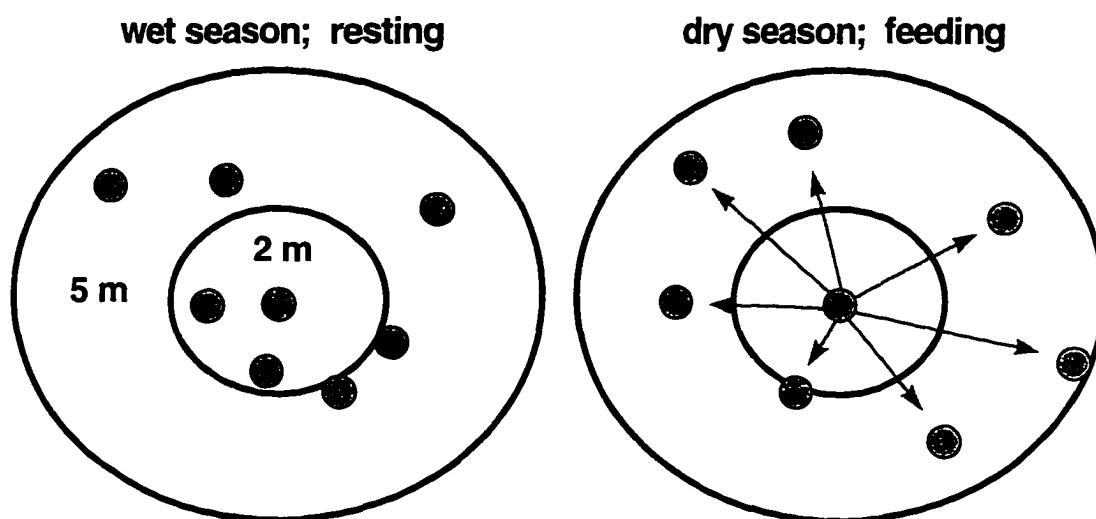
With regards to implications for intra-group feeding competition, the conclusion is that members of larger groups experience shorter nearest neighbor distances and have more neighbors around themselves within different radii than members of smaller groups (Fig. 2.1). Thus regardless of how group members compromised between overlapping their search fields and maintaining group spatial cohesion, larger groups experienced greater crowding and therefore their members were likely to experience greater intra-group food competition.

Empirical data also showed that during periods of high food scarcity, the dry season (Table 2.3), and during feeding as opposed to resting (Table 2.4), individuals spaced themselves more distantly within their immediate vicinity, but did so in such a way as to not decrease their group's spatial cohesion. They decreased the number of their neighbors within 2 meters, but did not change the number of their neighbors within 5 meters (Fig. 2.12). They behaved as mutually repelling magnets constrained by a finite space around them. This further shows, that even when food was scarce, group members walked the fine line between keeping the feeding competition as low as possible without losing their group's spatial cohesion.

As sifakas balanced opposing selective pressures on their inter-individual spacing, members of larger groups experienced greater personal crowding than members of

smaller groups. And although sifakas seemed to exercise a limit on the extend of personal crowding they experienced, all measures of personal crowding in the larger groups were approximately double as those in the smallest groups.

Fig. 2.12. Schematic representation of changes in patterns of personal crowding when food is scarce, during the dry versus the wet season, and during feeding versus resting.



Group size constraints

The severity of the tradeoff, or the ability of individuals to maintain group spatial cohesion at distances far enough apart for group members to avoid feeding competition and exploit separate food sources, is likely to vary among species (Janson 1992) and habitats (e.g. Eisenberg et al. 1972; Hladik 1975; Clutton-Brock & Harvey 1977a; Harvey & Clutton-Brock 1985; Harvey et al. 1987; Isbell 1991; Chapman et al. 1995; Rasa 1995). In the same habitat, different species may vary in their ability to communicate over the same distances or to converge rapidly due to differences in their vocal or locomotory

abilities. In different habitats, groups of the same species may differ in their cohesiveness due to differences in their predators' tactics and/or differences in vegetation cover, which might obstruct to a varying degree their visual and vocal communication or fast movement. The role of vegetation suggests that among large species those that live in open habitats, such as savannas, may be able to spread out more without compromising their group's spatial cohesion than can forest-living species (members of groups of yellow baboons, for example, routinely spread themselves over large areas: Stuart Altmann pers. com.). Also, an ability to maintain cohesion at greater distances should allow for greater group size, and extremely large group sizes are most common among open habitat species (Clutton-Brock and Harvey 1977a).

Similarly, the severity of food competition, given certain crowding, depends on the species-specific body size, nutrient requirements, rates of digestion, and the distribution of food. Body size is likely to correlate with the size of an individual's search field, thereby determining at what distance these fields begin to overlap, while stomach size, the rate of digestion, food type, nutrient density, and daily nutrient requirements determine how much food per unit time satiates an individual. Together, body size and satiation rates determine the severity of food competition given a certain level of crowding. If food is distributed in patches, then crowding increases with the number of individuals foraging in a patch and decreases with the patch size. A number of empirical studies have shown that in a given patch size members of larger groups obtain less food per distance traveled than members of smaller groups (Robinson 1981; Janson 1988, 1990; Chapman 1988; White & Wrangham 1988). Moreover, Eisenberg et al.

(1972) and S. Altmann (1974) postulated that, in general, the size of social groups within a species depends on the size of their food patches.

In this study, the slopes of all four measured spatial variables level off past group size of 9. This suggests that in groups greater than 9 sifakas reach their limits in all four variables. Consistent with this hypothesis is the fact that groups have never been seen to exceed the size of 14, and that the only observed group of 14 decreased in size after less than a month (Kubzdela pers. obs.). Also, the only group of 13 in this study population showed an unusual spatial distribution and after one season it decreased in size to 11, at which point its spatial distribution became more appropriate for its size (see Fig. 2.1).

The species- and habitat-specific tradeoff between minimizing food competition and maximizing group's spatial cohesion defines the shape of cost/benefit curves for different group sizes, thereby designating the optimal and the largest reasonable group size for a given species in a given habitat. Data from this study suggest that the need to stay as a cohesive group and the need to minimize intra-group feeding competition, via spatial variables, both strongly impose an upper limit on group size and that for the focal groups in this study that maximum size was between 11 and 13 group members.

Conclusion

Sifakas balance the need to minimize group spread versus crowding, which they accomplish by packing more closely up to a point and by apparently changing the geometric configuration of group members in space. At group sizes greater than 9 they seem to reach their threshold for maximum group spread and for maximum crowding,

suggesting that they experience a group size limitation somewhere between 11 and 13 members. Furthermore, because individual crowding does increase with group size, intra-group feeding competition probably also increases.

APPENDIX 2.A: Focal Groups

Table 2.7. Focal groups used in the analyses.

Group	Usual # of Females	Average Group Size	Range in Size	Sample Size
Nify	1	2.00	2	107
Emelia2	1	3.00	3	107
TsyEmelia	1	3.43	3 - 4	65
Chocolat	<5	4.00	4	169
Felix	<5	4.00	4	97
PapozyR	<5	4.36	4 - 5	123
Kashka	<5	5.00	5	83
Fotaka	<5	6.48	5 - 7	170
Emelia	<5	7.31	7 - 8	87
Fanondrovery	<5	8.00	8	46
Zavmad	>5	9.61	9 - 11	239
Sary	>5	11.20	11 - 13	190

APPENDIX 2.B: Personal Crowding During Feeding Versus Resting

Table 2.8. Means and Sample Sizes for Spatial Variables During Feeding versus Resting.

Means	Mean Nearest Neighbor Distance		Mean Number of Neighbors within 2m		Mean Number of Neighbors within 5m		Sample Sizes	
Size	fd	re	fd	re	fd	re	fd	re
2	4.895604	3.521782	0.307692	0.584158	0.67033	0.851485	91	101
3	4.238378	4.129469	0.502703	0.628019	1.043243	1.130435	185	207
4	3.535225	2.844965	0.706177	0.915395	1.390651	1.533981	599	721
5	2.997465	3.409343	0.814085	0.799308	1.833803	1.453287	355	289
6	2.157746	1.732787	1.070423	1.20765	1.760563	1.759563	71	183
7	3.183054	2.732031	0.728033	0.971264	1.525105	1.745211	478	522
8	3.236047	2.332955	0.97093	1.232955	1.732558	1.997159	172	352
9	2.279404	1.65875	1.119107	1.420833	1.712159	1.910417	403	960
11	2.546202	1.779404	1.102117	1.392269	1.835616	2.024715	803	1578
13	3.101408	2.725895	0.929577	1.042105	1.901408	2.384211	71	190

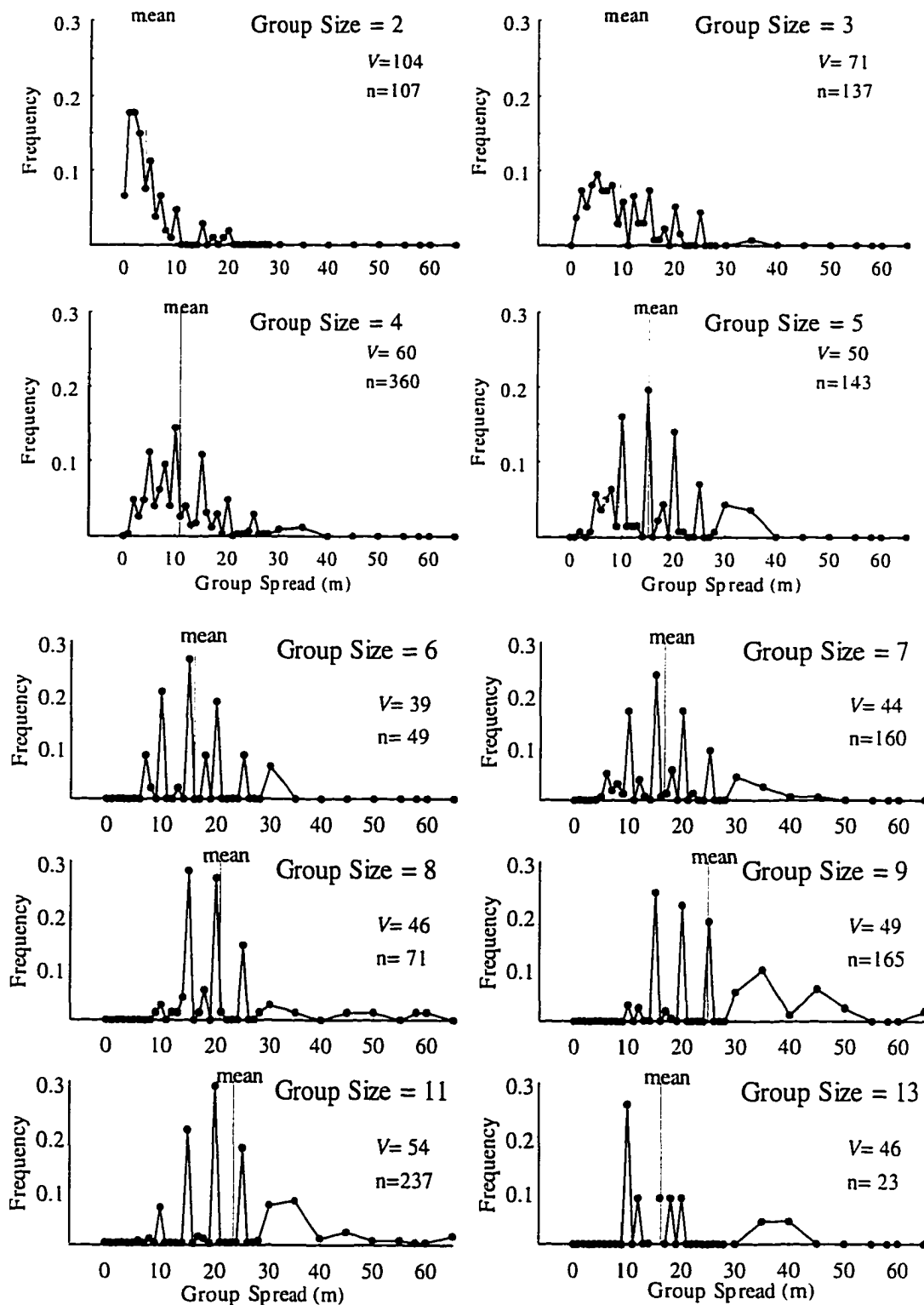
Table 2.9. Standard Deviations for Spatial Variables During Feeding versus Resting.

Standard Deviations	Nearest Neighbor Distance		# of Neighbors within 2m		# of Neighbors within 5m	
Size	fd	re	fd	re	fd	re
2	3.912115	4.746043	0.464095	0.495325	0.472698	0.357383
3	3.832241	4.845111	0.684648	0.718539	0.778984	0.804955
4	3.303562	2.953135	0.846286	0.948566	1.034996	1.051069
5	3.025825	3.394667	0.90468	0.954448	1.133958	1.232685
6	2.463775	2.076561	0.915329	0.978082	1.061869	0.912131
7	3.075879	2.978703	0.772489	0.966392	1.191513	1.310751
8	3.486831	2.436216	1.161907	1.089836	1.417719	1.266484
9	2.332764	2.035531	1.015162	1.101702	0.985732	1.052479
11	2.54203	2.022618	1.085857	1.27365	1.283067	1.35421
13	3.37082	3.061741	0.850612	0.847228	1.353883	1.530903

APPENDIX 2C: Fig. 13. Frequency Distribution of Group Spreads for Each Group Size

mean vertical line denotes the mean group spread for a given group size;

V =coefficient of variation ($100 \times \text{St.Dev.}/\text{Mean}$); n =number of scan samples



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CHAPTER THREE

THE EFFECT OF GROUP SIZE, NUMBER OF FEMALES IN A GROUP, AND FEMALE DOMINANCE RANK ON INTRA-GROUP FEEDING COMPETITION

INTRODUCTION

Early socioecological models focused on the likely importance of group size in either hindering or enhancing an individual's food consumption (Crook & Gartlan 1966; Crook 1970; Eisenberg et al. 1972; Clutton-Brock & Harvey 1977a,b; Wrangham 1980,1987). Food consumption of a group member is believed to be hindered by intra-group feeding competition and enhanced by inter-group feeding competition. To explain the effects of intra-group feeding competition, Eisenberg et al. (1972) and S. Altmann (1974) postulated that group members overlap individual search fields, thereby reducing each other's rates of encountering food. In the previous chapter I showed that individual crowding increases with group size among white sifakas, and in this chapter I examine whether, as a result, members of larger groups experience greater intra-group feeding competition.

By definition, increased intra-group feeding competition is a reduction in feeding efficiency of group members. Feeding efficiency is the ratio between energy obtained

from food (I_d) and the energy used to acquire this food (E_f ; Equation 1). The energy obtained from food eaten is proportional to the energetic value of each food item (F_v) multiplied by the number of items eaten. The number of items eaten can be calculated from the rate of ingesting the items (F_r) multiplied by time spent feeding (F_t). Thus daily energy intake (I_d) can be estimated from the product of energetic value of food, ingestion rate, and feeding time (Equation 2). The energy spent on foraging (E_f), also referred to as foraging effort, is the energy expended on collecting and processing food (C_f) plus the energy expended on travel to acquire this food (C_t ; Equation 3). Foraging effort (E_f) increases when feeding rate, daily time spent feeding, and/or daily distance traveled increase.

$feeding\ efficiency = I_d / E_f$	(Equation 1) [†]
$I_d = F_v * F_r * F_t$	(Equation 2) [†]
$E_f = C_f + C_t$	(Equation 3)
where:	
I_d = daily energy intake (J/day)	E_f = daily energy expended on foraging (J/day)
F_v = energetic value per food (J/g)	C_f = energy expended on feeding (J/day)
F_r = ingestion rate (g/seconds feeding)	C_t = energy expended on travel (J/day)
F_t = feeding time (seconds feeding/day)	
[†] assuming independence among the factors (Welsh et al. 1988)	

Daily energy intake (I_d) is proportional to time spent feeding (F_t ; Equation 2). If energetic value of food (F_v) and ingestion rate (F_r) do not differ among individuals, then individual differences in daily energy intake (I_d) can be evaluated by individual differences in time spent feeding (F_t). An increase in daily time spent feeding would reduce the daily time available for other activities, such as socializing or resting (Janson 1988).

Daily energy expended on foraging (E_f), increases with energy expended on travel (C_t ; Equation 3). If ingestion rate and food types eaten do not differ between individuals, then energy expended on feeding (C_f) also does not differ among individuals. In such case, individual differences in energy expended on foraging (E_f) can be evaluated by individual differences in energy expended on travel (C_t). The energy expended on travel (C_t), in turn, is proportional to the distance traveled, and if individuals have on average similar gaits, then individual differences in energy expended on travel (C_t) can be evaluated by individual differences in travel distance.

As a result, an index of relative differences in feeding efficiency of individuals can be calculated from the time these individuals spent feeding divided by the distance they traveled. In this case, food intake is estimated by feeding time, and foraging effort by travel distance.

Primates that feed largely on leaves, such as sifakas, probably are not able to increase adequately their feeding rate or daily time spent feeding, because they are constrained by digestion rate more than other primates and require prolonged digestion periods between feedings (Milton 1984). Additionally, despite the abundance of leaves and their distribution, which appears to be less patchy than that of fruits, not all leaves are equally digestible or have the same nutritional value (Goodall 1977, Richard 1985). Consequently, valuable leaf sources are more patchily distributed than they appear. Monkeys choose leaves high in protein and low in fiber and secondary compounds (Harkin 1973, Milton 1979, Glander 1981, Gaulin and Gaulin 1982). Leaves also provide vitamins and minerals, and they differ in content by plant species and age. Most

primates prefer younger leaves and shoots rather than mature ones (Richard 1985).

Because leaf species differ in their nutrients and digestibility, primates tend to feed on a large variety of species throughout the day and year. White sifakas, for example, have been observed to feed on 65-77 plant species throughout the year, and the majority of their food comes from rare tree species (Richard 1978a), which by the virtue of their scarcity are patchily distributed.

As discussed in the previous chapter, the patterns of spatial distribution among group members can have profound effects on the potential intensity of feeding competition. However, what matters to any given individual is not just the average degree of crowding in a group, as demonstrated in Chapter 2, but also that individual's relative spatial position within the group. Depending on the way group members distribute themselves, at any given moment some are at more central and others at more peripheral positions in relation to the whole group. Central individuals typically have more nearby neighbors than do peripheral ones. From the perspective of individuals' strategies, being on the periphery of the group minimizes their crowding, but it also minimizes their ability to benefit from the presence of other group members (selfish-herd theory, Hamilton 1971) because many group members might be too far away to communicate with or quickly join for defense against predators or aggression from neighboring groups (Pulliam 1973, Altmann 1979, Robinson 1981). Thus, one may expect that when feeding competition is severe, individuals might benefit by feeding on the peripheries, but when safety is a greater concern, they might benefit by being in a more central position. If both or either of these strategies provided significant benefits to

group members of a given species or a population, and if individuals could use their dominance ranks to choose their relative spatial positions in a group, then we would expect the dominant group members to attain the preferred positions.

Many primate species exhibit agonistic dominance relations, often with a clear dominance hierarchy among group members. Social dominance is defined as consistent asymmetries in the outcomes of agonistic conflicts between individuals or groups (Bernstein 1981). Among primates, it has been most extensively studied in cercopithecines (e.g. Altmann 1962; Sade 1967; Hausfater 1975), for which asymmetries in submission rather than aggression have been identified as more consistent and revealing (Rowell 1974; Richard 1985). Dominance rank within primate groups is hypothesized to determine differential access to limiting resources, such as food, and consequently to correlate with reproductive success (Fedigan 1983). Yet evidence for a relationship between dominance and reproductive success, especially among primate females, comes only from a few species and is often equivocal (Fedigan 1983; Silk 1984, 1987; Fedigan et al. 1986; Lee 1987; Altmann et al. 1988). In species whose females are matrilocal, females often aggressively compete for food and feeding sites (empirical studies by Hall 1965; Chalmers 1968; Klein 1974; Sussman & Richard 1974; Dittus 1977; Struhsaker & Leland 1979; Smuts 1985). Females of these species also maintain a stable dominance hierarchy (Wrangham 1980), which suggests that lower-ranking females experience lower net energy intake (I_d) and lower fitness relative to higher ranking females (review in Lee 1987). Female fitness may be reduced by: (1) shorter life-span (Dittus 1977; Fedigan et al. 1986), (2) delayed age at first reproduction, due to

slower growth, poor nutrition, or behavioral suppression (Mori 1979), (3) lower birth rate (Whitten 1983), and/or (4) lower offspring survival rate (Fedigan et al. 1986).

In this chapter, I examine the effects of group size and female dominance rank on intra-group feeding competition or, more precisely, on relative feeding efficiency, in *Propithecus verreauxi verreauxi*.

THE STUDY SPECIES AND SITE

The subject of this study, the white sifaka (*Propithecus verreauxi verreauxi*), is a 2.5-3.5 kg diurnal prosimian of Madagascar. The geographic range of *P. verreauxi* species encompasses a rich, mixed deciduous forest in the northwest of the island and a tamarind-dominated gallery forest along with a semi-arid thorny forest in the south and the southwest. *P.v. verreauxi* is arboreal. At the study site, at Beza Mahafaly Reserve, the greatest proportion of the sifakas' diet is derived from leaves (76.4% of feeding time in the dry season and 66.1% in the wet), the rest mainly from flowers and fruits (Table 3.1). The sifaka groups occupy small, overlapping ranges with stable boundaries, which they often defend from neighboring groups (Jolly 1972, 1978; Jolly et al. 1982; Richard 1989). The females are matrilineal, and observations suggest a stable dominance hierarchy among the females and a less stable hierarchy among the males (Richard 1974, 1978b, 1987; Richard & Heimbuch 1975). *P.v. verreauxi* is well suited for the study of feeding competition because it is highly energetically stressed (Richard et al. in prep) and is therefore especially likely to experience consequences of intra-group food competition.

Table 3.1. Percent of time spent feeding on different plant parts by *Propithecus v. verreauxi* in Parcel 1 of Beza Mahafaly Special Reserve (from Yamashita 1996).

Plant Part	Percent of Time Spent Feeding on Different Plant Parts	
	Dry Season	Wet Season
immature leaves	48.3 %	38.2 %
mature leaves	14.3 %	24.1 %
immature and mature leaves	13.8 %	3.8 %
stalks	11.6 %	5.3 %
fruit pulp	6.7 %	0.4 %
flowers	0 %	26.8 %
other	5.3 %	1.4 %

The study site, Parcel 1 of Beza Mahafaly Special Reserve, is located in southwestern Madagascar and consists of 80 ha of protected land. To the north, west, and south of Parcel 1, the forest extends beyond the Reserve's boundaries, but there it is unprotected. Vegetation within and around the Reserve changes gradually from east to west. On the east side, the Reserve borders the seasonal Sakamena River, along which extends a thin strip of tall, tamarind-dominated gallery forest. Westwards, away from the river, the habitat turns into a less tall and more open semi-arid forest. The Reserve and its sifaka population are described in more detail in Richard et al. 1993.

A grid of trails running north-south and east-west at 100 meter intervals covers the Reserve. Prior to this study, since 1984, the history of 28 resident groups has been followed via annual censuses and marking of individuals (Richard et al. 1993). Group sizes range from 2 to 14 individuals (14 being the largest group of sifakas ever recorded), with the mean varying between populations and years from 4 to 7 individuals. In the subadult and adult classes the proportion of females in each group ranges from 0.3 to 0.8, with the group average equal to the population average of 0.42 (Richard et al. 1993).

HYPOTHESES

If *Propithecus v. verreauxi* is typically energetically stressed, as has been strongly suggested in the literature (Jolly 1994, Richard 1987, Richard et al. in prep), then group members should increase their foraging effort (i.e. distance traveled or feeding time) in response to increased feeding competition. Because sifakas at Beza feed primarily on leaves, each time after ingesting a certain amount of foliage they are probably forced to spend a certain amount of time digesting the leaf matter before they can feed again (Milton 1984). If the sifakas are also severely energetically stressed, then they most likely already spend as much time feeding per day as they can. Therefore, most likely, the sifakas are not able to increase their foraging effort by increasing their daily feeding time, but instead may be able to travel farther distances per day and thereby increase their foraging effort by visiting food sources that may provide a greater food density and/or food quality (since despite appearances the distribution of leaves of different quality is patchy).

Further, because among sifakas, females in particular experience severe energetic stress during the dry season (Richard et al. in prep), and because females are believed to maintain stable, linear dominance relationships year around (Richard 1987), dominant females should benefit from their rank and therefore be relatively less affected by intra-group feeding competition than subordinate females. Also, if feeding efficiency experienced by an individual increases with dominance rank, the difference in feeding

efficiency between the highest and the lowest ranking females should be greater in groups with more females.

Hypothesis 1: Because personal crowding is greater in larger groups, intra-group feeding competition is also greater.

Prediction: The average daily distance traveled by group members will increase with group size and thereby their feeding efficiency will decrease.

Hypothesis 2: Within groups, lower ranking females experience lower feeding efficiency, and if intra-group feeding competition is greater in larger groups, then low ranking females in the largest groups will experience the lowest feeding efficiency of all females.

Prediction: As intra-group feeding competition increases with group size, the variance in the average daily distance traveled and in feeding efficiency among female group members will also be greater. Additionally, lower-ranking females will travel farther per day and experience lower feeding efficiency than higher-ranking females.

FIELD METHODS

Working Definition of a Group

A group was defined by, but not limited to, a core set of females or a single female that foraged and slept within a consistent area (territory) for at least a month. Study groups were generally stable in composition except for those in which the only existing female died, causing the group to go extinct. Rarely, however, a single female (or at most two) from a multi-female group moved into a new area and either began to

forage and sleep with another group, thus becoming a member of that group, or was joined by male(s) and established a new group. The other members of the migrating female's original group always remained together in the original area and thus continued to be identified as the original group. Groups were not identified by the male membership because males transferred at a high rate between groups.

Data Collection

Data were collected from June 1993 to March 1995 by the author and up to three assistants. Detailed behavioral observations, using focal and scan samples (Altmann 1974), were collected on 14 focal groups that ranged in the western part of the Reserve, a region chosen to minimize obvious differences in habitat among groups. Because two of the focal groups were newly formed and remained unstable throughout the period of the study, they were excluded from the analyses in this paper. Similarly, all scan samples that did not include all group members or were recorded during a period of membership change were excluded.

In order to record an equal number of focal samples per female, groups with six or more females (see Appendix 3.A) were usually observed for three consecutive days, groups with less than six but more than one female for two consecutive days, and groups with a single female were observed for a single day at a time. We tried to collect focal samples six days a week, and on those days we began to search for a focal group between 0730h and 0800h. If the scheduled group was not found within two hours, we began to search for the group next on the schedule. Between 1200h and 1230h the observation

was terminated for lunch and resumed between 1330h and 1430h, depending on the temperature and difficulty in finding the group again. The group was then observed until it settled for sleep and the last focal sample was finished, usually between 1600h and 1730h.

We collected thirty-minute focal samples on each female in each group, including: (1) all approaches and departures within or across an imaginary 3 meter radius around the focal female, (2) the duration (in seconds) of her sleeping, resting, feeding, traveling, or interacting, (3) the distance (in meters) that she covered every time she traveled, and (4) all aggressive or affiliative interactions that involved her. Additionally, we recorded *ad lib.* social interactions (Altmann 1974) involving only non-focal group members.

Unless all group members were resting too high up in the tree to be identified, we recorded a scan sample for the group at the beginning of the observation period and then immediately after every 30-minute focal sample. Each scan consisted of a point sample for every group member present with the recorded variables listed and defined in Table 3.2.

An individual was considered to be a part of the focal group if at the time of the sample: (a) it was not with another group, (b) it was within visible and/or audible distance from the group, and (c) it was within view of other group members for at least one hour and a half before and after the point sample. These criteria excluded the three or four instances when a wandering male was briefly visiting during a scan sample.

Table 3.2. Variables recorded during each scan sample (starting with the individual ID, the information was recorded for every group member present).

Variable	Description
date, time	
group name	Identified by the females present and the area
group spread	The distance in meters between two farthest individuals in the sample group at the moment of sampling
group size	Number of individuals in the sample group at the time of the sample
subject ID	Identification of the individual who is the subject of that point sample
activity	The activity of the ID animal at the point of the sample (affiliative, resting, sleeping, traveling, feeding); no activity was recorded if the animal was hidden by the canopy
number of neighbors within 2m number of neighbors within 5m	Number of group members within 2 or 5 meters, respectively, around the ID animal, in all directions; missing value was entered when the ID animal was traveling too fast to count its neighbors or if the nearest neighbors were hidden in the canopy
nearest neighbor distance	Distance to the closest group member, when the ID animal was within 5 meters of another identifiable group member, or when the ID animal was more than 5 meters from the closest group member but the second closest individual was at least another 3/4 of that distance away from the ID animal; missing value was entered at all other instances and when the ID animal and/or its closest neighbors were traveling too fast to estimate the distance, or if they were hidden by the canopy
nearest neighbor ID	If the nearest neighbor distance was recorded and the closest neighbor was identifiable, then its ID was recorded; otherwise missing value was entered. Sometimes up to 4 individuals were at the same closest distance of the ID animal. in which cases ID's of all of them were recorded

Data Analyses

Matrices of agonistic behaviors extracted from focal data were used to establish dominance hierarchies among group members. Differences in levels of personal crowding among age/sex classes were determined from scan sample data. The effects of group size and female dominance rank on female's activity budget and travel distance were determined from focal data. Data from all months of observations were used to establish dominance hierarchies.

The ratio of feeding time (in seconds) to distance traveled (meters) by females in focal groups was used to calculate the index of relative feeding efficiency among these females. From here on, all references to measures of feeding efficiency refer to this index.

The effects of group size and female rank on feeding efficiency were based only on data from the month of August, for which, of all dry season months, I had the greatest sample sizes for both large and small groups. Because, due to time constraints, the present analyses are limited to data from one month, I chose a month from the period of highest food scarcity, the dry season, when I expected intra-group feeding competition to be highest.

Because individual crowding in general was lower during feeding than during resting (Chapter 2), I wanted to determine whether individual sifakas changed the degree of their personal crowding more in larger versus smaller groups, and whether within groups higher ranking individuals changed the degree of their crowding more than lower ranking individuals. To determine these amounts of change, I calculated an index of spatial change by subtracting the mean distance to the nearest neighbor when feeding from the distance when resting. Similarly, I subtracted the mean number of neighbors within 2 and 5 meter radii when feeding from the number of such neighbors when resting. I then looked for the effects of group size and of age/sex classes on this index of spatial change.

I used regression analyses to determine the effects of group size and sex on measures of personal crowding, and the effects of group size, female age, female

dominance rank, and number of females in a group on distance traveled by females and on females' feeding efficiency. To determine which predictors or which sets of predictors gave the best fit, I used best subsets regression (Minitab Software for Windows Release 11.11, Minitab Inc. 1996). Best subsets regression uses the maximum $R^2(\text{adj})$ criterion to determine the set of predictors that result in a relatively most precise model, which is equivalent to choosing the model with the smallest mean square error. $R^2(\text{adj})$ is an approximately unbiased estimate of the population R^2 .

$R^2(\text{adj}) = 1 - \{[\text{sum of squares error} / \text{total sum of squares}] * [(n - 1) / (n - p)]\}$ <p>where</p> <p style="margin-left: 40px;">n = sample size</p> <p style="margin-left: 40px;">p = number of coefficients fit in the regression equation</p> <p>Best subsets regression also uses the minimum C_p criterion, which is another indicator that a model is relatively precise, i.e. has small sampling variance:</p> $C_p = (SSE_p / MSE_m) - (n - 2p)$ <p>where</p> <p style="margin-left: 40px;">SSE_p = sum of squares error for the best model with p parameters</p> <p style="margin-left: 40px;">MSE_m = mean square error for the model with all m predictors</p>
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RESULTS

Female-Male and Female-Female Dominance:

Females, adult and sub-adult, were dominant to males (Table 3.3: H1), both when considering the direction of aggressive behaviors and when considering the outcome of agonistic encounters (the direction of submissive behaviors). Nine incidents inconsistent with the hypothesis that females are dominant to males involved only vocalizations (8 aggressive vocalizations and 1 submissive chatter), and in the remaining two incidents, when a male exhibited aggression towards a female, the young males involved were still

in their natal groups, where the females towards whom they vocalized aggressively were most likely their mothers.

White sifakas at Beza Mahafaly Reserve exhibit very low rates of agonistic behaviors as compared to other diurnal primates, including sympatric ringtailed lemurs (Sauther 1992). As a result, agonistic encounters were observed among only 17 out of 66 possible dyads of sifaka females in the focal groups. However, in 16 of these 17 dyads older females were dominant to younger females ($\chi^2=13.24$, $p<0.0003$) regardless of the number of females in the group (Table 3.3: H2). The only occasion when a younger female threatened to bite an older female (i.e. she made a biting gesture near the skin of the older female but without actually making contact) was in the group Emelia, where the only two females in the group were both over 10 years old (11 and 23). This was also the only agonistic encounter between them.

Because among all of the female-female dyads with observed agonistic encounters over 94% exhibited dominance of older females over younger females, I extrapolated that in the remaining 49 dyads within which agonistic encounters were not observed, older females were also dominant to younger females. Thus, within groups, I assigned dominance rank according to the relative age of female group members, with the oldest female being the most dominant (1st in rank) and the youngest female being the least dominant (last in rank). Of all 14 focal groups, only one group (Fotaka) had two females of the same age, and an agonistic encounter observed among them was used to assign their dominance ranks. Consequently, from here on, dominance rank reflects the relative age of females within a group, and analyses of the effects of rank on any variables are in

fact analyses of the effects of relative female age from which dominance ranks were inferred. These analyses of the effects of inferred dominance ranks differ from the analyses of the effects of absolute female age on the same variables, because 1st ranking females in the focal groups ranged in age from 7 to 24 years, which represents 75% of the entire observed range of female ages.

Table 3.3. Direction of intra-group aggressive and submissive behaviors between males and females (*H1*) and between females of different ages (*H2*).

Type of Activity	Activity	Proportion of instances that support each hypothesis ^a :		Total Sample Size
		<i>H1</i> : Females are Dominant to Males within a Group	<i>H2</i> : Older Females are Dominant to Younger Females within a Group	
aggr	bit	15 / 16	6 / 6	22
	displaced	13 / 13	-	13
	grabbed	6 / 6	-	6
	hit	8 / 8	2 / 2	10
	threatened-to-bite	5 / 5	1 / 2	7
	threatened-to-hit	1 / 2	1 / 1	3
agg-voc	yelled-at	20 / 28	7 / 7	35
subm	chattered	4 / 5	1 / 1	6
	ran-away	9 / 9	1 / 1	10
<i>Summary for each behavior type:</i>				
aggression		48 / 50	10 / 11	61
aggressive-vocalization		20 / 28	7 / 7	35
submission		13 / 14	2 / 2	16
Pooled for all agonistic behaviors		81 / 92	19 / 20	112

χ^2 test	<i>H1</i>	<i>H2</i>
	<i>df</i> = 1	
aggression	$\chi^2 = 192.36, p < 0.0001$	$\chi^2 = 7.36, p = 0.007$
aggressive-vocalization	$\chi^2 = 13.09, p = 0.02$	$\chi^2 = 4.45, p = 0.008$
submission	$\chi^2 = 13.09, p = 0.001$	$\chi^2 = 0.36, p = 0.157$
Pooled	$\chi^2 = 445.45, p < 0.0001$	$\chi^2 = 29.45, p < 0.0001$

^a In case of aggressive behaviors, the ratios indicate how many aggressive behaviors were directed by an individual in a class hypothesized to be dominant (all females in *H1*) towards an individual in a class hypothesized to be subordinate (all males in *H2*) out total number of aggressive behaviors observed between the two classes of individuals. In case of submissive behaviors, the ratios indicate how many submissive behaviors were directed by an individual in a class hypothesized to be subordinate towards an individual in a class hypothesized to be dominant.

Age/Sex Class Differences in Personal Crowding:

In principle, personal crowding increases as the distance to the nearest neighbor decreases and the number of neighbors within 2 and 5 meter radii increases. In this study, adult females, in groups of almost every size, experienced greater mean personal crowding than all other age/sex classes (Fig. 3.1-3.3). Among females, mean crowding increased with age class in a more pronounced and consistent fashion than among males.

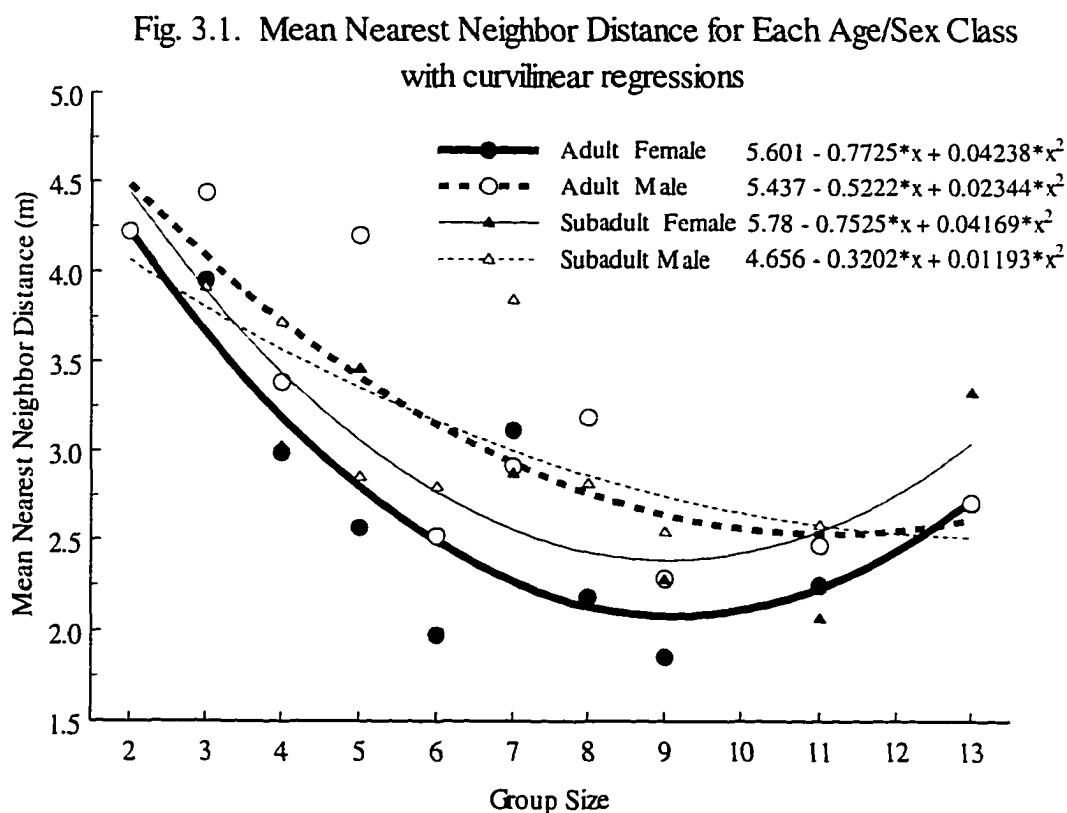


Fig. 3.2. Mean Number of Neighbors within 2 meters for Each Age/Sex Class with curvilinear regressions

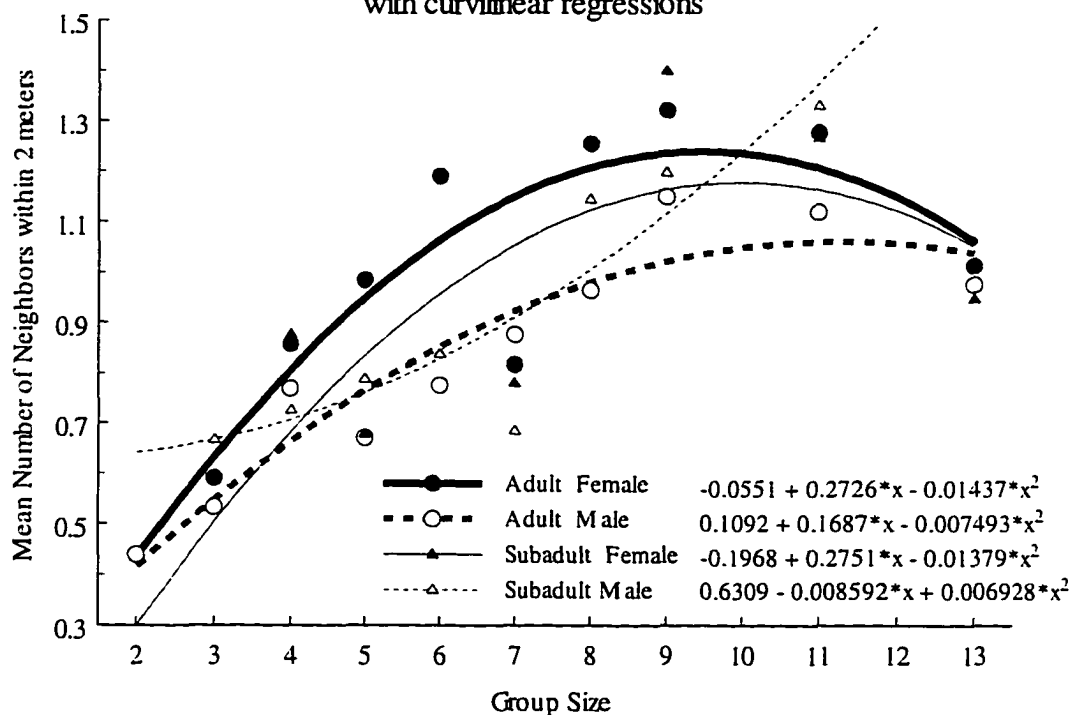
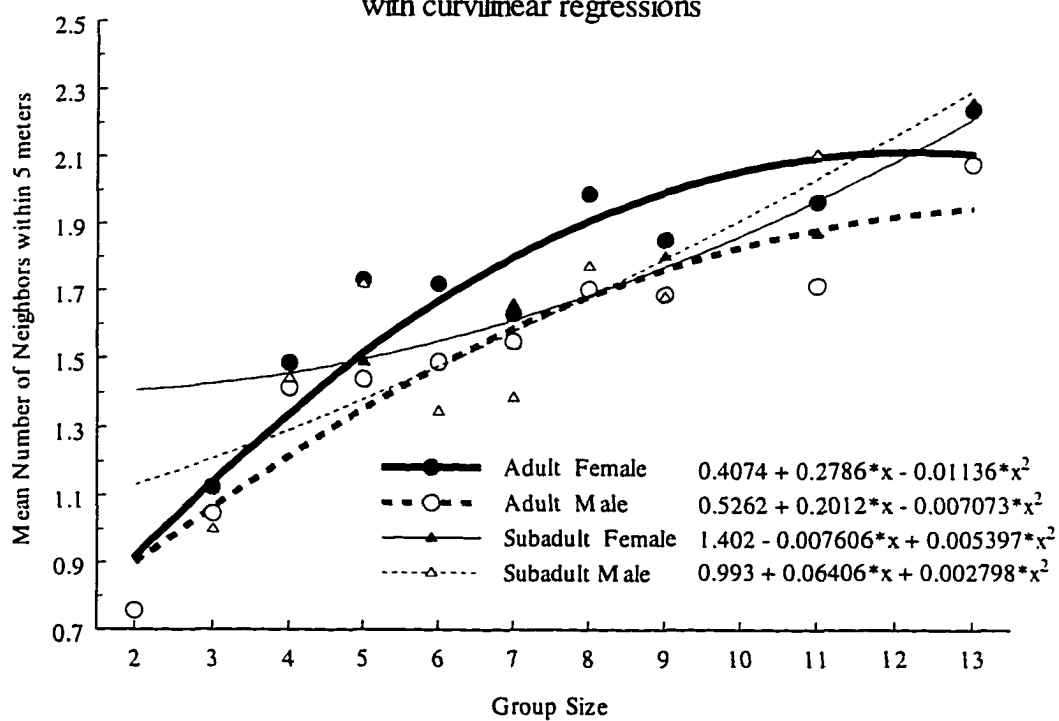


Fig. 3.3. Mean Number of Neighbors within 5 meters for Each Age/Sex Class with curvilinear regressions



A different pattern of crowding emerged when data for feeding and resting were considered separately. During feeding, mean personal crowding increased significantly with group size (Table 3.4), but within groups, there was no significant difference between males and females. During resting, on the other hand, mean personal crowding increased significantly with group size and within groups it was significantly greater for females than for males (Table 3.4). The index of change in mean personal crowding, from resting to feeding states, did not change with group size (except for the number of neighbors within a 5 meter radius, discussed below), but for females, mean personal crowding decreased more between resting versus feeding than it did for males (Table 3.4).

Table 3.4. Regression analysis of the effect of group size and sex (females were assigned the value of 1, and males of 2) on the three different measures of personal crowding when feeding, resting, and for the index of change in crowding. Best subsets regression was used to choose the best set of predictors for each independent variable (see Appendix 3.B: Table 3.11).

Regression Equations	n	R ² (adj)	p
<u>While Feeding</u>			
Distance to the Nearest Neighbor = $3.66 - 0.08 \text{ group size}$	130	0.064	0.002
No. of Neighbors w/in 2m radius = $0.58 + 0.04 \text{ group size}$	130	0.127	< 0.0005
No. of Neighbors w/in 5m radius = $1.21 + 0.06 \text{ group size}$	130	0.152	< 0.0005
<u>While Resting</u>			
Distance to the Nearest Neighbor = $2.65 + 0.53 \text{ sex} - 0.11 \text{ group size}$	127	0.167	< 0.0005
No. of Neighbors w/in 2m radius = $0.95 - 0.17 \text{ sex} + 0.05 \text{ group size}$	127	0.234	< 0.0005
No. of Neighbors w/in 5m radius = $1.31 - 0.21 \text{ sex} + 0.11 \text{ group size}$	127	0.507	< 0.0005
<u>While Feeding minus While Resting</u>			
Change in Distance to the Nearest Neighbor = $0.93 - 0.38 \text{ sex}$	127	0.025	0.042
Change in No. of Neighbors w/in 2m radius = $-0.38 + 0.13 \text{ sex}$	127	0.021	0.055
Change in No. of Neighbors w/in 5m radius = $-0.21 + 0.27 \text{ sex} - 0.04 \text{ group size}$	127	0.132	< 0.0005

As mentioned above, during the transition from resting to feeding, members of both large and small groups experienced a decrease in their personal crowding on the large spatial scale (number of neighbors within a 5 meter radius) but not on the small spatial scale (nearest neighbor distance and number of neighbors within a 2 meter radius). This decrease was significantly greater for larger groups than for smaller groups, implying that, when changing from feeding to resting, large groups altered their large-scale geometric configuration of group members in space significantly more than did small groups.

In order to determine whether females in larger groups experienced greater personal crowding during feeding and resting, I analyzed the effect of group size on mean crowding using only data for females as the focal individuals (Table 3.5). Females' distance to their nearest neighbor did not differ with group size, during feeding or resting (thus the highly significant effect of group size on mean nearest neighbor distance shown in Table 3.4 must have resulted entirely from the effects of group size on mean crowding in males). However, the mean number of neighbors females had within 2 and 5 meter radii increased significantly with group size, both during feeding and resting (Table 3.5). Thus, by these two measures, mean personal crowding experienced by females was significantly greater in larger groups than in smaller groups.

Change in mean personal crowding differed only for mean number of neighbors within a 5 meter radius, but not for mean nearest neighbor distance or mean number of neighbors within a 2 meter radius (Table 3.5), as with both sexes pooled (Table 3.4).

This implies that females were subject to the same large-scale changes in group spatial configuration as were males.

Table 3.5. Regression analysis of the effect of group size on the three different measures of females' individual personal crowding when feeding, resting, and for the index of change in crowding.

Regression Equations	n	R ² (adj)	p
<u>While Feeding</u>			
Distance to the Nearest Neighbor = $3.17 - 0.03$ group size	62	0.000	0.382
No. of Neighbors w/in 2m radius = $0.72 + 0.03$ group size	62	0.058	0.033
No. of Neighbors w/in 5m radius = $1.33 + 0.04$ group size	62	0.082	0.014
<u>While Resting</u>			
Distance to the Nearest Neighbor = $2.84 - 0.07$ group size	62	0.032	0.088
No. of Neighbors w/in 2m radius = $0.86 + 0.04$ group size	62	0.106	0.006
No. of Neighbors w/in 5m radius = $1.06 + 0.11$ group size	62	0.491	< 0.0005
<u>While Feeding minus While Resting</u>			
Change in Distance to the Nearest Neighbor = $0.33 + 0.03$ group size	62	0.000	0.403
Change in No. of Neighbors w/in 2m radius = $-0.14 - 0.01$ group size	62	0.005	0.255
Change in No. of Neighbors w/in 5m radius = $-0.27 - 0.07$ group size	62	0.169	0.001

Table 3.6. The effect of female dominance rank (as inferred from relative ages) on the three different measures of females' individual crowding when feeding, resting, and for the index of change in crowding, as measured by a paired two-sample t-test for means. Positive *t* values indicate that the mean for higher ranking females was greater than the mean for lower ranking females, and negative values indicate the reverse.

Measure of Crowding being Correlated with Female Dominance Rank	Pearson Correlation Coefficient	n	t	p
<u>While Feeding</u>				
Distance to the Nearest Neighbor	0.24	43	0.44	0.33
No. of Neighbors w/in 2m radius	0.45	43	-0.29	0.39
No. of Neighbors w/in 5m radius	0.12	43	-0.43	0.33
<u>While Resting</u>				
Distance to the Nearest Neighbor	0.49	43	-1.84	0.04
No. of Neighbors w/in 2m radius	0.54	43	1.28	0.10
No. of Neighbors w/in 5m radius	0.46	43	1.66	0.05
<u>While Feeding minus While Resting</u>				
Change in Distance to the Nearest Neighbor	0.13	43	1.80	0.04
Change in No. of Neighbors w/in 2m radius	0.19	43	-1.48	0.07
Change in No. of Neighbors w/in 5m radius	0.15	43	-1.51	0.07

During feeding, the degree of personal crowding did not differ for females of different dominance rank (as inferred from relative ages of females within groups), but during resting higher ranking females were significantly more crowded than lower ranking females (Table 3.6). Also, during feeding as compared to resting, the degree of mean personal crowding of higher ranking females decreased more so than that of lower ranking females, but significantly only through an increase in mean nearest neighbor distance (Table 3.6).

The index of change in mean personal crowding when feeding versus resting revealed that the age/sex classes that were the most crowded during resting (females and higher ranking females in particular) experienced the greatest decrease in their mean personal crowding, so that during feeding they had the same degree of mean personal crowding as did other members of their group (Table 3.4, 3.6). However, the degree to which their mean personal crowding decreased did not change with group size, except for the large-scale spatial measure of the mean number of neighbors within a 5 meter radius (Table 3.4, 3.5).

The Effect of Group Size and Female Age on Females' Activity Budgets:

The percent of time individuals spent feeding or resting did not differ with group size, the number of females in the group, focal female's age, or female's dominance rank (Table 3.7). The length of feeding bouts and resting bouts also did not differ with these four predictors. Similarly, the proportion of feeding bouts during which the focal female was approached by another group member, and the difference in average duration of the

feeding bouts during which the focal female was approached versus those during which she was not approached did not differ with the four predictors (Table 3.7). Thus neither group size nor female dominance rank significantly affected daily time spent feeding or the likelihood that female's feeding bouts would be disrupted.

Table 3.7. The effect of group size, number of females in a group, female age, and females dominance rank on different measures of activities and activity budget. Linear regression R^2 and p values are given only where the effect was significant or nearly significant ($p < 0.10$).

Different Measures of Activities	Group Size	Number of Females in a Group	Female Age	Female Dominance Rank
percent time spent feeding	ns	ns	ns	ns
percent time spent resting	ns	ns	ns	ns
mean feeding bout length	ns	ns	ns	ns
mean resting bout length	ns	ns	ns	ns
proportion of feeding bouts during which the focal female was approached by another group member	ns	ns	ns	ns
difference in average duration of feeding bouts during which the focal female was approached vs. not approached	ns	ns	ns	ns
percent time spent traveling	$R^2=0.128$ $p=0.023$	$R^2=0.169$ $p=0.010$	$R^2=0.081$ $p=0.060$	$R^2=0.102$ $p=0.039$
travel speed (meters/second)	$R^2=0.160$ $p=0.012$	ns	ns	ns
daily travel distance (meters)	$R^2=0.277$ $p=0.001$	$R^2=0.254$ $p=0.002$	ns	$R^2=0.104$ $p=0.038$
feeding efficiency (seconds spent feeding / meters traveled)	$R^2=0.121$ $p=0.027$	$R^2=0.107$ $p=0.036$	$R^2=0.067$ $p=0.080$	ns

However, the percent time spent traveling and the mean distance traveled per unit time did increase significantly with group size and the number of females in a group. Additionally, within groups, they increased significantly with lower female dominance

rank (as inferred from relative ages) and percent time spent traveling also increased with younger absolute age of females (Table 3.7). The speed with which females traveled increased significantly with group size and did not change with any of the other three predictors (Table 3.7). Feeding efficiency, as estimated by the ratio of time spent feeding to distance traveled, increased significantly with group size and the number of females in a group. It also decreased significantly with younger female age, but did not change significantly with female rank alone (Table 3.7).

Table 3.8. The effect of group size, female age, and/or female dominance rank on time spent traveling (minutes spent traveling per an hour of observations), travel speed (meters traveled per second), distance traveled (meters traveled per an hour of observations), and on the estimate of feeding efficiency (seconds feeding per meters traveled). Best subsets regression was used to choose the best set of up to two predictors for each independent variable (see Appendix 3.B: Table 3.12, 3.13, 3.14, 3.15).

Regression Equations	R ²	p
travel time = $0.3 + 0.02\text{size} - 0.01\text{age}$	0.178	0.020
distance traveled = $32.8 + 5.66\text{size} - 1.12\text{age}$	0.291	0.002
travel speed = $2.2 + 0.07\text{size}$	0.160	0.012
feeding efficiency = $51.4 - 2.37\text{size} + 0.93\text{age}$	0.201	0.023

Best subsets regressions revealed that time spent traveling and daily distance traveled by females were both best predicted by group size and female age (Appendix 3.B: Table 3.12, 3.14), where each increased with group size and decreased with female age (Table 3.8). Female feeding efficiency was also best predicted by group size and female age (Appendix 3.B: Table 3.13), but it decreased with group size and increased with female age (Table 3.8). Travel speed was best predicted by group size alone (Appendix 3.B: Table 3.15), with which it increased (Table 3.8).

Table 3.9. The mean and variance in distance traveled by females (meters traveled per an hour of observations), an estimate of feeding efficiency in females (seconds feeding per meters traveled), travel speed (meters traveled per second), feeding time (minutes spent feeding per an hour of observations), and travel time (minutes spent traveling per an hour of observations) in groups of different sizes. The mean and the variance for each variable were calculated from data on each female.

Grp. Size	# of Fems.	Female Hours of Obs.	Distance Traveled		Feeding Efficiency		Travel Speed		Feeding Time		Travel Time	
			Mean	Var.	Mean	Var.	Mean	Var.	Mean	Var.	Mean	Var.
2	2	16	28.9	3	57.9	17.2	2.32	0.09	28.0	14.2	0.21	0.0002
4	5	52	46.1	209	50.3	569.3	2.45	0.08	34.2	84.8	0.31	0.0104
5	2	8	75.1	728	35.7	105.5	2.67	0.07	42.3	10.3	0.46	0.0153
7	7	38	61.5	404	42.6	219.7	2.41	0.32	39.5	8.7	0.46	0.0575
8	4	30	42.7	368	57.5	581.2	2.99	0.27	35.7	25.3	0.24	0.0094
11	13	57	89.8	1289	30.5	397.9	2.91	0.17	36.4	69.2	0.52	0.0479

Means and variances for distance traveled by females, their feeding efficiency, travel speed, as well as time spent feeding and traveling in groups of different sizes are shown in Table 3.9. The variance in distance traveled, feeding efficiency, travel speed, and time spent traveling were greater in larger groups than smaller groups. The variance in time spent feeding showed no increase with group size.

DISCUSSION

In Chapter 2, I showed that members of larger groups experienced greater personal crowding than members of smaller groups, as measured by decreasing nearest neighbor distance and increasing number of neighbors within 2 and 5 meter radii with increasing group size. I further showed that although during feeding, as compared to resting, and during lower food availability, during the dry season, as compared to the wet, individuals did not increase the overall group dispersion and did not change their number

of neighbors within a 5 meter radius, they increased the distance to their nearest neighbors and decreased the number of neighbors within a 2m radius (by increasing the number of neighbors within a 2-5 meter ring around themselves). These changes in spacing strongly suggested that, especially during periods of highest potential energetic stress, group members rearranged their relative spatial positions in ways that reduced the potential for intra-group feeding competition. However, in the end, sifakas in larger groups still experienced significantly greater personal crowding than sifakas in smaller groups, and therefore had a greater potential for overlap in their individual foraging search fields.

Thus, the results of Chapter 2 strongly suggested that members of larger groups experienced lower feeding efficiency, in which case, they would be expected to compensate behaviorally for lower rate of nutrient intake. In the current chapter, the results demonstrate that, as expected for primarily folivorous primates constrained by their digestion rates (Milton 1984), sifaka group members did not increase their feeding or resting time in larger groups (Table 3.7). They did, however, significantly increase their foraging effort by traveling longer distances in larger groups, and their estimated feeding efficiency significantly decreased (Table 3.7, 3.8). Also, the variance in both distance traveled and feeding efficiency increased with group size (Table 3.9), reflecting a greater variance in foraging effort and feeding efficiency among females of larger groups.

Because I could not measure directly sifakas' daily energy intake (I_d , Equation 2), the possibility exists that members of larger groups compensated for greater energy spent on travel by increasing their rate of food intake and/or by increasing the energetic value of

the food they ingested. This is unlikely, however, because the focal data analyzed in this chapter was collected during the dry season, during which white sifakas have the greatest difficulty meeting their energetic needs in general, as evidenced by a significant weight loss among both sexes during the dry season as compared to the wet (Richard et al. in prep). Although data on the degree of weight loss in groups of different sizes is not yet available, we now know that sifaka females lose significantly more weight than males, and that female's body mass predicts very closely whether she will have an offspring that year (Richard et al. in prep.). In order to reduce weight loss during the dry season, all females should maximize their net energy intake regardless of group size, and because females in all groups seem to have difficulty maintaining their weight, females in larger groups are unlikely to be able to increase their rate of nutrient intake above that of females in smaller groups. Thus, if females in larger groups are not gaining more energy during foraging than females in smaller groups, but, as observed, travel farther per day, then they should experience lower net energy gain per day and are expected to lose proportionally more weight during the dry season than females in smaller groups, a test for which data are not yet available.

The emerging picture of increased negative effects of intra-group feeding competition in larger groups is further supported by the relationship between female dominance, personal crowding, and feeding efficiency. As suggested for different populations of various subspecies of *Propithecus verreauxi* (Richard 1974, 1978b, 1987; Richard & Heimbuch 1975, Kubzdela et al. 1992), all females in this study were dominant to all males, and within groups older females were dominant to younger

females (Table 3.3). Personal crowding increased significantly for females, as compared to males, and with female rank (as inferred from their relative ages) during resting. This suggests that females (Table 3.4), and higher ranking females in particular (Table 3.6), were the most centrally positioned during resting, which is predicted as the safest position by the selfish-herd theory (Hamilton 1971). During feeding, however, personal crowding did not differ with age and sex classes (Table 3.4, 3.6).

Thus although females may have been enjoying a greater protection from predators or aggressive encounters with neighboring groups due to their central position during resting (Hamilton 1971, Pulliam 1973, Robinson 1981), during feeding they were not subjected to greater crowding and therefore were not subjected to greater potential overlap of their foraging search fields (Eisenberg et al. 1972, Altmann 1974). This provides another piece of evidence in support of the hypothesis that by increasing spatial dispersion individuals reduce their intra-group feeding competition.

Females, and higher ranking females in particular (i.e. older females in a group), experienced the greatest decrease in their personal crowding when comparing feeding to resting (Table 3.4, 3.6). Therefore, within groups, females, and higher ranking females in particular, traveled the shortest distances per day and experienced the highest feeding efficiency. As mentioned earlier, the results suggest that higher ranking females benefited from central positions during resting. In addition, they appeared also to have benefited during the transition to feeding; because males and low ranking females expended more effort, by traveling greater distances, as all group members decreased their personal crowding from resting to feeding. This allowed for the observed decrease

in personal crowding of higher ranking females to the level enjoyed by other group members during feeding.

I have noted in the introduction that without a complete knowledge of group size effects on individual energy budgets it is difficult to estimate the effects and interpret the precise meaning of the observed decrease in feeding efficiency as a function of group size. However, the fact that travel distance increased and feeding efficiency decreased among younger, and therefore lower ranking female group members, provided a proximate currency for the costs of lower dominance rank. It thus also provided additional evidence for the hypothesis that intra-group feeding competition plays a significant role in sifaka groups, and that among dominance ranks, both within groups and between groups of different sizes, the difference in feeding efficiency reflects real differences in individual energetic gains.

Because the number of females giving birth in any given year has never exceeded three at Beza Mahafaly Reserve, regardless of the number of females in a group (author's pers. obs. and A. Richard pers. com.), and because sex ratios varied between groups (Chapter 4), I tried to determine whether it was the number of females in a group or group size that had the strongest effect on females' feeding efficiency. Although group size and the number of females in a group were highly correlated (Pearson correlation coefficient = 0.93), best subsets regression analysis suggests that the linear combination of group size and female age had a slightly stronger effect on travel distance and feeding efficiency than the linear combination of number of females in a group and female age (Appendix 3.B: Table 3.12, 3.13). The result is not surprising considering that all members of a

group are likely to contribute to each other's degree of personal crowding, regardless of the group's sex ratio.

The proposed hypotheses 1 and 2 were confirmed. The results of this chapter strongly suggest that, among white sifakas, intra-group feeding competition is greater in larger groups than in smaller groups, and that, within groups, the disadvantageous consequences of intra-group feeding competition increase with lower dominance rank, both between sexes and among females.

APPENDIX 3.A: Focal Groups

Table 3.10. Focal Groups.

Group	Usual # of Females	Average Group Size	Range in Size	Sample Size
Nify	1	2.00	2	107
Emelia2	1	3.00	3	107
TsyEmelia	1	3.43	3 - 4	65
Chocolat	6	4.00	4	169
Felix	6	4.00	4	97
PapozyR	6	4.36	4 - 5	123
Kashka	6	5.00	5	83
Fotaka	6	6.48	5 - 7	170
Emelia	6	7.31	7 - 8	87
Fanondrovery	6	8.00	8	46
Zavmad	>5	9.61	9 - 11	239
Sary	>5	11.20	11 - 13	190

APPENDIX 3.B: Best Subsets Regressions

Table 3.11. Best subsets regressions for three measures of personal crowding (distance to the nearest neighbor and numbers of neighbors within 2 and 5 meter radii) with group size and sex as predictors. Each set calculated separately for when individuals were feeding, resting, and for the index of change in crowding (feeding - resting).

activity	measure of crowding	# of predictors	R ² (adj)	C _p	group size	sex
Feeding	Distance to the Nearest Neighbor	1	0.064	1.6	X	
		2	0.061	3	X	X
		1	0.004	9.7		X
	# of Neighbors within 2m radius	1	0.127	1.5	X	
		2	0.123	3	X	X
		1	0.006	19.1		X
	# of Neighbors within 5m radius	1	0.152	1.5	X	
		2	0.149	3	X	X
		1	0.000	25.6		X
Resting	Distance to the Nearest Neighbor	2	0.167	3	X	X
		1	0.115	9.8	X	
		1	0.079	15.1		X
	# of Neighbors within 2m radius	2	0.234	3	X	X
		1	0.194	8.5	X	
		1	0.073	28.1		X
	# of Neighbors within 5m radius	2	0.507	3	X	X
		1	0.469	11.6	X	
		1	0.091	107.4		X
Feeding - Resting	Distance to the Nearest Neighbor	1	0.025	1.8		X
		2	0.024	3	X	X
		1	0.004	4.5	X	
	# of Neighbors within 2m radius	1	0.021	1.9		X
		2	0.021	3	X	X
		1	0.004	4.1	X	
	# of Neighbors within 5m radius	2	0.132	3	X	X
		1	0.079	9.6	X	
		1	0.076	10.1		X

Table 3.12. Best subsets regression for distance traveled by females (meters traveled per an hour of observations) with group size, female age, female dominance rank, and number of females in a group as predictors.

# of predictors	R ² (adj)	C _p	group size	female age	dominance rank	# of females
3	0.303	3.0	X	X	X	
2	0.291	2.5	X	X		
1	0.277	2.1	X			
1	0.254	3.1				X
2	0.253	4.1	X		X	
2	0.253	4.1	X			X
2	0.252	4.1		X		X
3	0.241	5.5		X	X	X
2	0.230	5.1			X	X
1	0.104	9.5			X	
1	0.045	12.1		X		

Table 3.13. Best subsets regression for feeding efficiency in females (seconds feeding per meters traveled) with group size, female age, female dominance rank, and number of females in a group as predictors.

# of predictors	R ² (adj)	C _p	group size	female age	dominance rank	# of females
3	0.201	3.2	X	X	X	
2	0.159	3.7	X	X		
3	0.140	5.4		X	X	X
2	0.131	4.8		X		X
1	0.121	4.2	X			
1	0.107	4.7				X
2	0.092	6.2	X		X	
2	0.092	6.2	X			X
2	0.078	6.7			X	X
1	0.067	6.2		X		
1	0.037	7.4			X	

Table 3.14. Best subsets regression for travel time of females (minutes spent traveling per an hour of observations) with group size, female age, female dominance rank, and number of females in a group as predictors.

# of predictors	R ² (adj)	C _p	group size	female age	dominance rank	# of females
2	0.196	1.3		X		X
2	0.178	2.0	X	X		
3	0.178	3.0		X	X	X
1	0.169	1.3				X
3	0.158	3.7	X	X	X	
2	0.150	3.0			X	X
2	0.148	3.0	X			X
1	0.128	2.8	X			
2	0.121	4.0	X		X	
1	0.102	3.7			X	
1	0.081	4.5		X		

Table 3.15. Best subsets regression for travel speed of females (meters traveled per second) with group size, female age, female dominance rank, and number of females in a group as predictors.

# of predictors	R ² (adj)	C _p	group size	female age	dominance rank	# of females
2	0.404	1.5	X			X
1	0.160	12.5	X			
2	0.143	14.0	X		X	
2	0.140	14.1	X	X		
3	0.114	15.9	X	X	X	
1	0.031	18.9				X
1	0.007	20.1			X	
2	0.006	20.5		X		X
3	0.000	21.6		X	X	X
2	0.000	21.8			X	X
1	0.000	22.0		X		

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CHAPTER FOUR

THE EFFECTS OF GROUP SIZE, FEMALE AGE, AND FEMALE DOMINANCE RANK ON FEMALE REPRODUCTIVE SUCCESS AND DISPERSAL PATTERNS

INTRODUCTION

To determine the impact of demographic factors and social status on female reproductive success in female-bonded species, I examine in this chapter the effects of group size, number of females in a group, female age, and female dominance rank on female reproductive success and on female dispersal patterns in white sifakas, *Propithecus verreauxi verreauxi*.

Wrangham (1980) defined female-bonded species as those in which “females maintain affiliative bonds with other females in their group and normally spend their lives in the group where they were born” (p.264). His first demographic criterion is that females typically breed in their natal groups, and his second criterion is that males systematically move between groups while female movements are restricted. Recently, Kappeler (1997) proposed that diurnal prosimians are not female-bonded, however, because both Wrangham’s definition and his criteria for recognizing female-bonded

species are met by *Propithecus verreauxi verreauxi*, I consider sifakas to be female-bonded.

Most primate species with multiple females per group are female-bonded, and food is believed to be the key resource affecting their reproductive success (reviews in Wrangham 1980, Silk 1987). When comparing food-provisioned with non-provisioned free-ranging primates, increased nutritional accessibility has been associated with lower age at first reproduction, shorter inter-birth intervals, and/or longer life span of females (*Macaca fuscata*: Mori 1979, Takahata 1980, Sugiyama and Ohsawa 1982; *Macaca mulatta*: Drickamer 1974; review for *M. fuscata* and *M. mulatta*: Loy 1988). One would therefore expect individuals of female-bonded species to focus on maximizing their net nutrient intake, yet group living, in itself, has long been hypothesized to hinder individual food consumption as a result of intra-group feeding competition (Crook & Gartlan 1966; Crook 1970; Eisenberg et al. 1972; Clutton-Brock & Harvey 1977a,b; Wrangham 1980, 1987).

The relationship between feeding competition and reproductive success plays a central role in evolutionary theory (for primates: Altmann 1962, Goss-Custard et al. 1972, Chapais and Schulman 1980, Wrangham 1980, Robinson 1988). One may expect that if individuals in larger groups have a lower feeding efficiency, based on intra-group competition, then females, who are already highly energetically stressed during reproduction (Portman 1970, Buss and Voss 1971, Prentice and Prentice 1988), will experience lower reproductive success than females in smaller groups. Of course, the benefits of living in larger groups may negate and even outweigh the costs. Infants may

be better protected from infanticide or predation (van Schaik 1983), the larger group may gain access to a high energy resource over a smaller group, or be better able to locate rich food sources (Wrangham 1980). However, beyond a certain group size, specific for a given species in a given habitat, the costs of living in large groups, incurred from increased intra-group competition, are likely to outweigh the benefits. Consequently, if females in overly large groups can increase their reproductive success by dispersing or causing other females to disperse from their groups, then natural selection will favor those females that do not tolerate groups too large for a given environment, and will thereby select for a species-specific optimal group size with a range of acceptable group sizes around it.

Models relating competition to reproductive success invariably propose that dominance hierarchies among group members determine the outcome of competition for limiting resources that are necessary for reproduction (theory and review: Fedigan 1983, Silk 1987, Wrangham 1980; empirical studies: Dittus 1977, Post et al. 1980, Wrangham 1981, Wrangham and Waterman 1981, Whitten 1983, Fairbanks and McGuire 1984, Mitchell et al. 1991). Fedigan (1983) pointed out in her review that, for both males and females, some studies but not others detected effects of dominance rank on reproductive success. She suggested that only in populations with chronically scarce food, or during periods of unusually low food availability in other populations, would females of higher dominance rank have a detectable nutritional advantage over lower ranking females. This advantage would be caused by dominant females' priority of access to food, and it would result in their higher reproductive success. Fedigan (1983) cited two studies in which

groups were believed to be under particular nutritional stress: (1) a population of toque macaques showed higher mortality among lower ranking females during periods of drought, and it showed higher survival to reproductive age among offspring of higher ranking females, and (2) a population of vervet monkeys (Cheney et al. 1981) showed no overall difference in reproductive success among females of different ranks, but offspring of lower ranking females tended to die of illness, which may have resulted from restricted access to food and water in dry seasons, whereas offspring of higher ranking females tended to die of predation.

In addition to patterns of dominance among females, dominance between sexes may also shed light on underlying energetic constraints imposed on a population. Female dominance over males is prevalent among prosimians, but unusual among mammals. Female dominance has long been hypothesized to result from unusual energetic stress caused by marked seasonality in Madagascar (Jolly 1984, Richard 1987, Meyers and Wright 1993, Sauther 1993) and/or from low energetic efficiency of prosimians during reproduction (Richard and Nicoll 1987, Young et al. 1990; hypometabolism of lemurs: Ross 1992). More specifically, the unusually low probability of sifaka females to reproduce successfully (A. Richard and the author unp. data), presumably resulting from the hypothesized unusual difficulty to meet the energetic demands of their reproduction, escalates the stakes for females to assert their feeding priority over males so as to provide those females with a chance to reproduce. The proposed unusually high energetic constraints on sifaka female reproduction are supported by the observation that all sifaka species breed seasonally, once a year, and among the southwest populations, including the

study population, weaning occurs towards the beginning of the wet season, but almost the entire period of gestation and lactation falls within period of food scarcity, the dry season (Richard 1985). In the subject population of the present study, Richard et al. (in prep) have found that both males and females lost weight during the dry season, but females lost significantly more weight than males. In drought years the drop in weight during the dry season was significantly higher than in other years. Richard et al. (in prep) also showed that female fertility in any given year was significantly correlated with female's body mass, and that this effect was independent of female age. These authors thus provided evidence strongly suggesting that (1) sifakas are more energetically stressed during dry seasons and drought years than during wet season and non-drought years, that (2) the seasonal energetic stress is more acute among females than among males, and that (3) female body mass is a good predictor of female fertility. In concordance, sifaka females at the Duke University Primate Center, in North Carolina, which are provisioned with food year around, begin to reproduce at a much earlier age than their wild counterparts, at two and a half years of age, and the distribution of their births lacks seasonality (Diane Brockman pers. com.). Therefore the unusual pattern of female dominance over males seems to reflect a behavioral strategy of sifaka females in response to their difficulty to reach a threshold body mass necessary to reproduce.

In contrast to the energetic stress hypothesis, van Schaik and Kappeler (1996) recently proposed that female dominance over males is a leftover from a potential pair-bonded and cathemeral (active during both day and night) ancestry. However, the authors based their arguments on a number of hypotheses which have not yet been tested on

diurnal prosimian species. Considering that empirical evidence, as presented above, supports the hypothesis that energetic stress among sifakas, and especially among females, is very high (Richard et al. in prep.), while no data support the hypothesis that this species is or has been pair-bonded, the most plausible explanation for female feeding priority in sifakas is unusually high energetic stress.

Sifaka females in larger groups experienced lower feeding efficiency than females in smaller groups, and, within groups, the younger females (which proved to be subordinate to older females in dyads for which agonistic interactions were observed) experienced lower feeding efficiency than the older females (Chapter 3). Consequently, higher ranking females in this population are expected to experience greater reproductive success than lower ranking females, and this differential reproductive success may be greater in larger groups where disadvantages of lower dominance rank are the greatest. Further, if the nutritional state of females is the primary factor limiting their reproductive success, then females in smaller groups may have a higher reproductive success than those in larger groups. Finally, if lower ranking females in larger groups experience especially low reproductive success and can increase their chances for successful reproduction elsewhere, they are expected to disperse. In short, the constraints imposed on feeding efficiency by group living (Chapter 2) might explain much of the variation in reproductive and dispersal patterns of individual female sifakas.

METHODS

The Study Species and Site

The subject of this study, the white sifaka (*Propithecus verreauxi verreauxi*), is a 2.5-3.5 kg diurnal prosimian of Madagascar. The geographic range of *P. verreauxi* species encompasses a rich, mixed deciduous forest in the northwest of the island and a tamarind-dominated gallery forest along with a semi-arid thorny forest in the south and the southwest. *P.v. verreauxi* is arboreal. At the study site, at Beza Mahafaly Reserve, the greatest proportion of the sifakas' diet is derived from leaves (76.4% of feeding time in the dry season and 66.1% in the wet), the rest mainly from flowers and fruits (Yamashita 1996). The sifaka groups occupy small, overlapping ranges with stable boundaries, which they often defend from neighboring groups (Jolly 1972, 1978; Jolly et al. 1982; Richard 1989). The females are matrilineal, and observations suggest a stable dominance hierarchy among the females and a less stable hierarchy among the males (Richard 1974, 1978b, 1987; Richard & Heimbuch 1975). *P.v. verreauxi* is well suited for the study of reproductive effects of food competition because it is highly energetically stressed (Richard et al. in prep).

The study site, Parcel 1 of Beza Mahafaly Special Reserve, is located in southwestern Madagascar and consists of 80 ha of protected land. To the north, west, and south of Parcel 1, the forest extends beyond the Reserve's boundaries, but there it is unprotected. Vegetation within and around the Reserve changes gradually from east to west. On the east side, the Reserve borders the seasonal Sakamena River, along which extends a thin strip of tall, tamarind-dominated gallery forest. Westwards, away from the

river, the habitat turns into a less tall and more open semi-arid forest. The Reserve and its sifaka population are described in more detail in Richard et al. 1993.

A grid of trails running north-south and east-west at 100 meter intervals covers the Reserve. Prior to this study, since 1984, the history of 28 resident groups has been followed via annual censuses and marking of individuals (Richard et al. 1993). Group sizes range from 2 to 14 individuals (14 being the largest group of sifakas ever recorded), with the mean varying between populations and years from 4 to 7 individuals. In the subadult and adult classes the proportion of females in each group ranges from 0.3 to 0.8, with the group average equal to the population average of 0.42 (Richard et al. 1993).

Working Definition of a Group

A group was defined by, but not limited to, a core set of females or a single female that foraged and slept within a consistent area (territory) for at least a month. Study groups were generally stable in composition except for those in which the only existing female died, causing the group to go extinct. Rarely, however, a single female (or at most two) from a multi-female group moved into a new area and either began to forage and sleep with another group, thus becoming a member of that group, or was joined by male(s) and established a new group. The other members of the migrating female's original group always remained together in the original area and thus continued to be identified as the original group. Groups were not identified by the male membership because males transferred at a high rate between groups.

Data Collection

Data were collected from June 1993 to March 1995 by the author and up to three assistants. Census data were recorded on all groups that had at least part of their territory within the 80 hectares of protected land in Parcel 1 of Beza Mahafaly Special Reserve. At any given time, the census population consisted of 175-195 juveniles, subadults, and adults, distributed among 36 to 37 social groups. Because some groups went extinct during the study and new groups formed, the total number of groups studied was 43. On average, we censused each group at least once every two weeks, and when groups were undergoing demographic change we censused them daily until their membership stabilized. All observed inter-group encounters were recorded.

In 1993 I arrived at the field site at the beginning of the birth season. Because it took time to locate all the groups and to learn to recognize all of the individuals, groups were censused less frequently during the 1993 birth season than during the 1994. As a result, I was much more likely to miss a short-lived infant in 1993 than in 1994. For this reason I did not pool data pertaining to reproduction for these two years, but analyzed them separately. I expect that all estimates of the effects of any variables on the likelihood of giving birth or on the proportion of infants surviving are more accurate for 1994 than 1993.

Inclusion of Females in the Analyses by Age

Age at reproductive maturity has not yet been determined for *Propithecus verreauxi*. When white sifakas reach their second year of age, it becomes difficult, and

sometimes impossible, to distinguish them from older individuals without knowing their history or seeing their tooth-wear. At two years of age, ranges of body mass for females of adjacent ages begin to overlap. The youngest females seen mating in the Beza Mahafaly population, during the last fourteen years, were three years of age, and, in the last two years (1995, 1996), three year-old females gave birth. Long-bone, and thus body length growth is completed in females by fifth year of age (A. Richard personal communication). The youngest age at which females were seen giving birth during this study period (1993 and 1994 birth seasons) was seven years. Female body mass increases rapidly with age until they become ten years old, at which point the rate of annual weight gain slows down significantly but continues to increase (A. Richard pers. com.).

Consequently, for analyses of female reproduction and dispersal patterns in this chapter I divided females into four age categories: (1) females 1-2 years of age, before the earliest age at first reproduction, (2) females 3-6 years of age, encompassing the earliest observed age at first reproduction and the end of long-bone growth, (3) females 7-9 years of age, encompassing the earliest age at first reproduction during this study period and the remaining years of rapid body weight gain, and (4) females above 10 years of age, encompassing adult females above the age of rapid body mass gain (this includes females up to 24 years of age, which was the oldest known female age during this study period; Alison Richard unp. data).

Dominance Ranks

As discussed in Chapter 3, because among all of the female-female dyads in focal groups with observed agonistic encounters over 94% exhibited dominance of older females over younger females, I assigned dominance ranks according to the relative ages of female group members, with the oldest female being the most dominant (1st in rank) and the youngest female being the least dominant (last in rank). Consequently, from here on, dominance rank reflects the relative age of females within a group, and analyses of the effects of rank on any variables are in fact analyses of the effects of relative female age from which dominance ranks were inferred. These analyses of the effects of inferred dominance ranks differ from the analyses of the effects of absolute female age on the same variables, because 1st ranking females in the focal groups ranged in age from 7 to 24 years, which represents 75% of the entire observed range of female ages.

RESULTS

Group Size and Composition

In 1993, I routinely censused 36 groups, which included 175 sifakas above infant age. Of the 175 individuals, 84 were females and 91 males (Appendix 4.A). In 1994, I censused 37 groups, which included 195 sifakas with 91 females and 104 males. The distribution of group sizes, number of females per group, or number of males per group did not differ between 1993 and 1994 (Fig. 4.1-4.3). The median group size was 5, and the median number of females as well as of males per group was 2.

Fig. 4.1. Number of Groups with Different Group Sizes in 1993 and 1994.

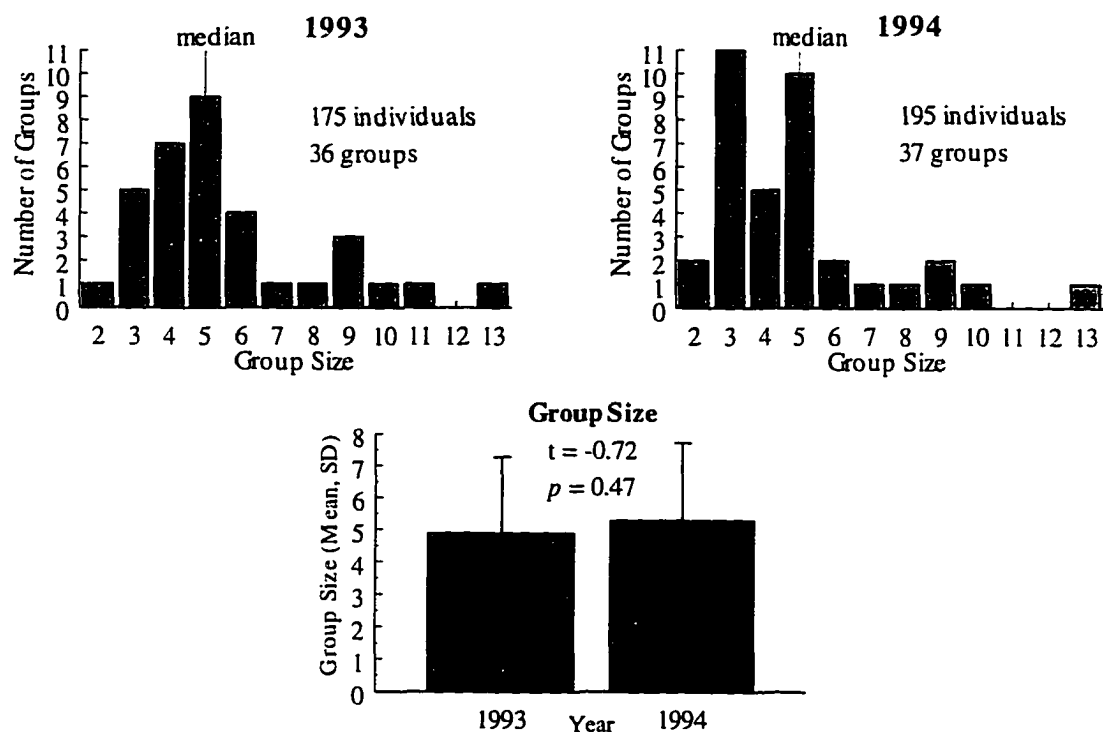


Fig. 4.2. Number of Groups with Different Numbers of Females per Group (juveniles to adults) in 1993 and 1994.

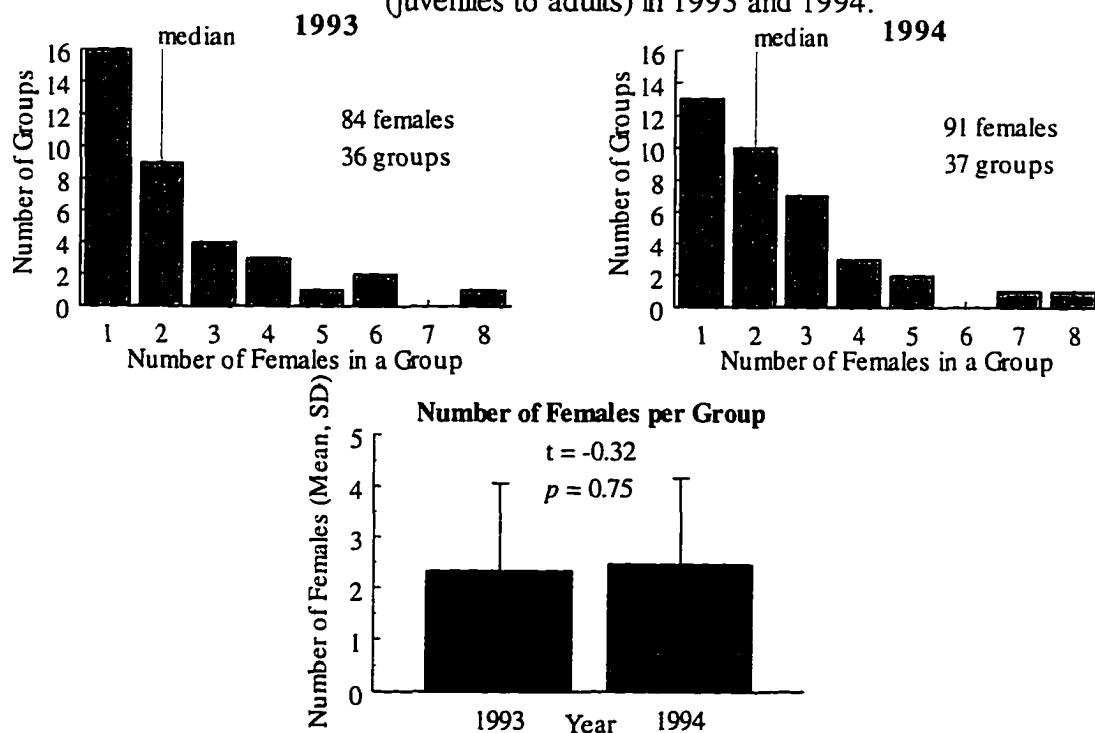
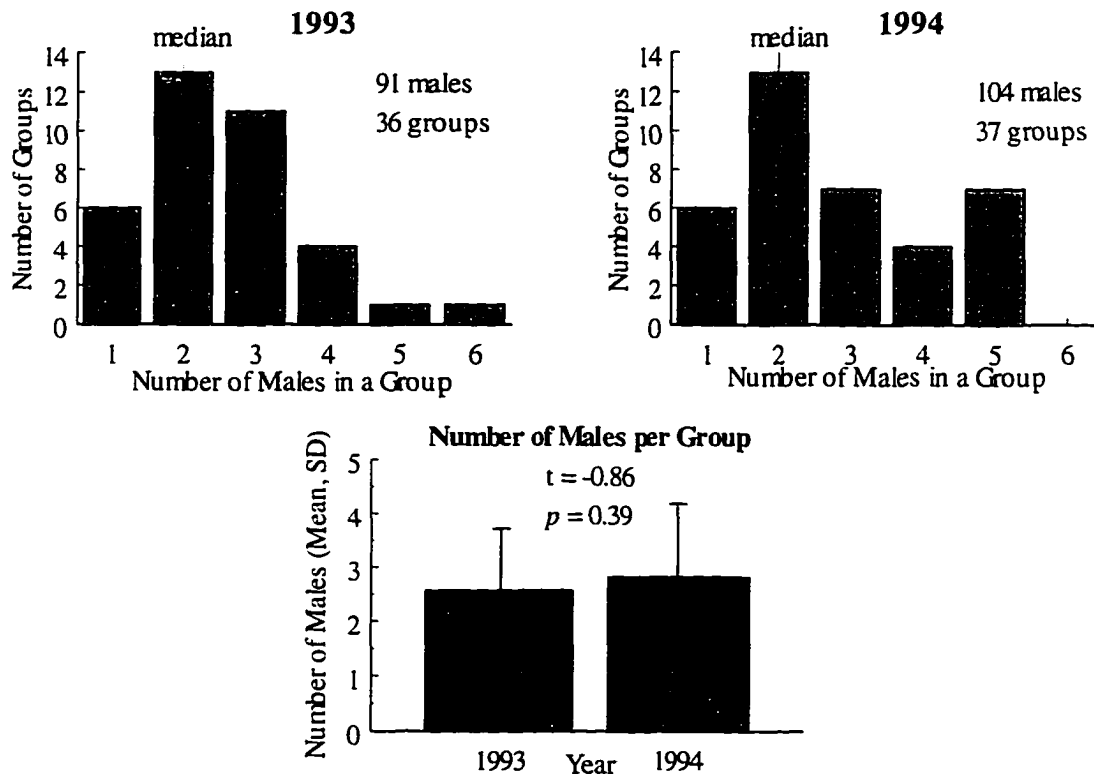


Fig. 4.3. Number of Groups with Different Numbers of Males per Group (juveniles to adults) in 1993 and 1994.



Not surprisingly, the number of females per group that were in the two oldest reproductive age categories (7-24 years of age) increased significantly with group size in both years (Fig. 4.4), and so did the number of males of all ages (Fig. 4.5). However, within groups, the number of males of all ages was not correlated with the number of females over six years of age in 1993. In 1994, although the variance around regression was large ($R^2=0.11$), the number of males increased significantly with the number of females (Fig. 4.6).

Fig. 4.4. Number of Females over 6 Years of Age that were in Groups of Different Sizes.

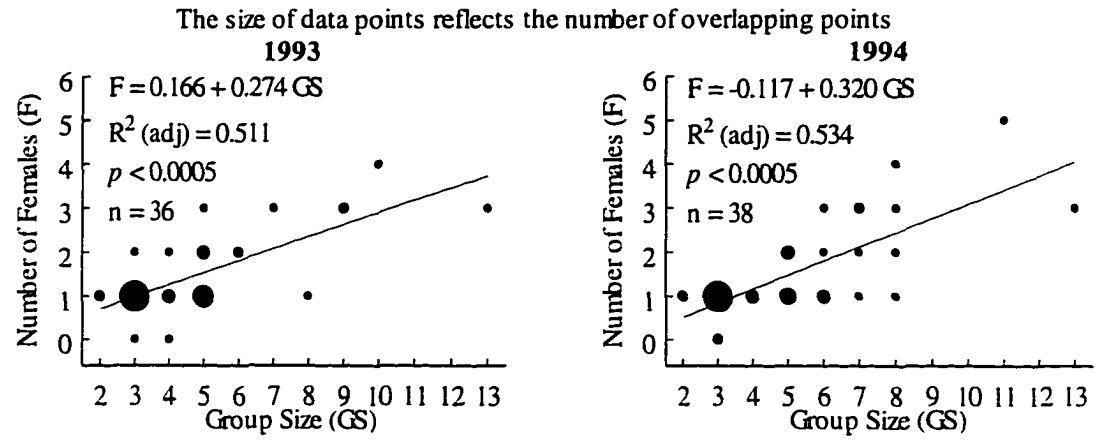


Fig. 4.5. Number of Males of all Ages in Groups of Different Sizes.

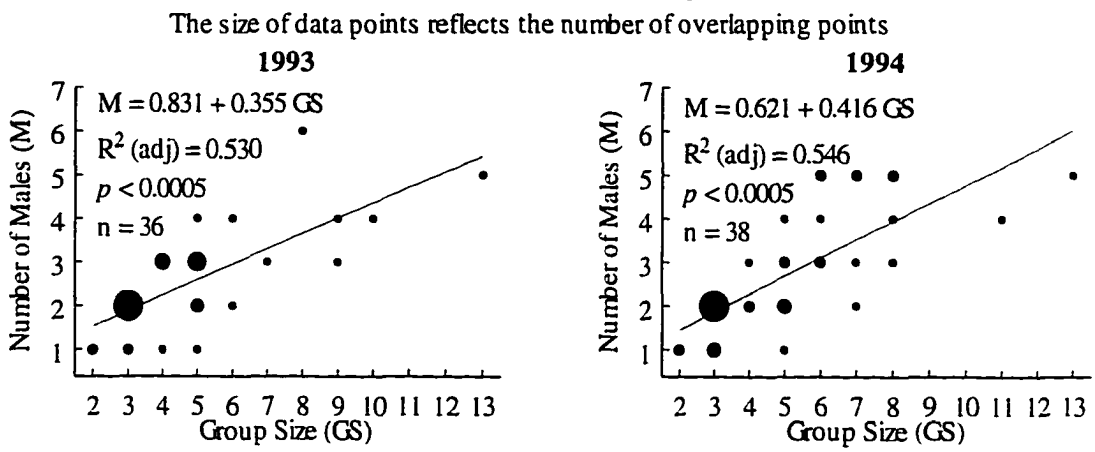
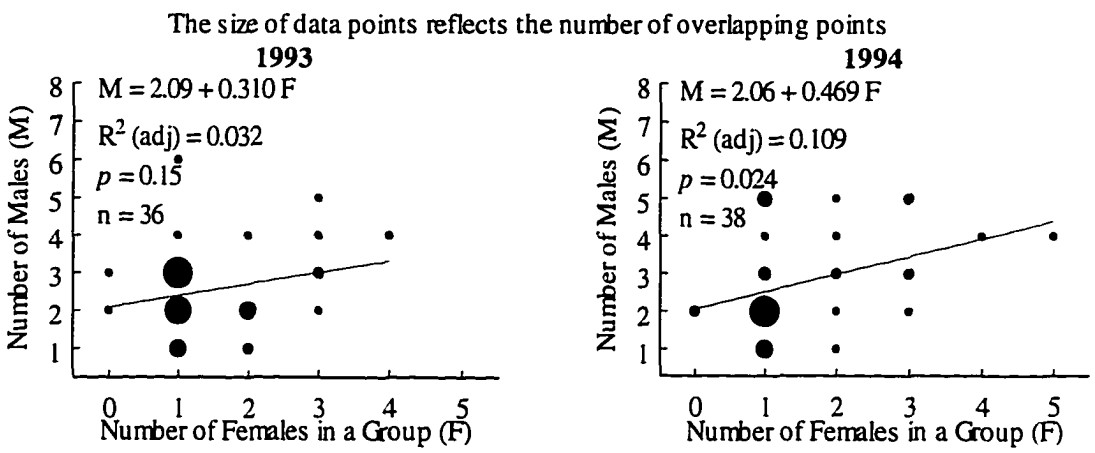


Fig. 4.6. Number of Males of All Ages in Groups with Different Numbers of Females over 6 Years of Age.



Reproductive Patterns as a Function of Group Size

as measured per group:

Not surprisingly, the total number of infants born per group increased significantly with group size (Kruskal-Wallis Test: $h_{(adj)}=16.56$ $df=9$ $p=0.056$ in 1993, $h_{(adj)}=16.62$ $df=8$ $p=0.034$ in 1994) and with the number of females in a group that were over six years of age ($h_{(adj)}=12.86$ $df=4$ $p=0.012$ in 1993, $h_{(adj)}=28.93$ $df=5$ $p<0.0005$ in 1994).

The total number of infants that survived to one year of age in a group did not change significantly with group size in either year, nor with the number of females over six years old in a group in 1993. It did, however increase with the number of females in 1994 (Kruskal-Wallis Test: $h_{(adj)}=14.78$ $df=5$ $p=0.011$).

as measured per female:

In the two oldest reproducing age classes (7-9 and 10-24 years of age), the number of infants born per female was greater in groups of median size or smaller than in groups larger than the median (Appendix 4.B: Table 4.9), but the difference was not statistically significant in either 1993 or 1994.

The number of infants that survived to one year of age per female did not change significantly with either group size or number of females per group in either year. However, in 1993, there was a tendency among the reproducing age classes (7-9 and 10-24 years old) for more infants to survive per female in groups of median size or smaller, than in groups larger than the median (Appendix 4.B: Table 4.10).

as measured per infant born:

In 1993, in the two oldest reproducing age classes (7-9 and 10-24 years old), the proportion of infants that survived in a group was greater in groups of median size or smaller than it was in groups larger than the median (Appendix 4.B: Table 4.11), but this difference was not significant in 1993, and in 1994 there was no difference.

Intra-group Variability in Reproductive Patterns

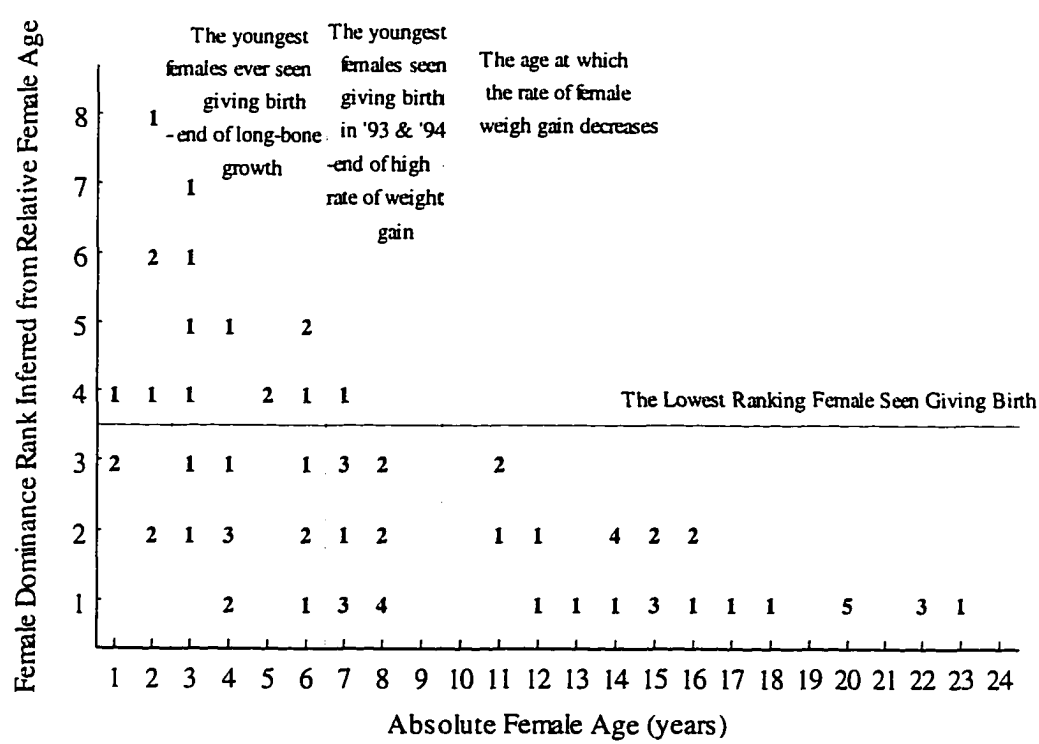
In 1993 and in 1994, none of the females in 3-6 years-old age class gave birth, and females in 10-24 years-old class gave proportionally more births than females in 7-9 years-old class (Appendix 4.B: Table 4.9). The difference was significant when, for each group size, the proportion of females 7-9 years of age that gave birth was compared to the proportion of females 10-24 years of age that gave birth (Wilcoxon's matched pairs sign-rank test: $n=7$ $p<0.025$ in 1993, $n=7$ $p<0.05$ in 1994).

In 1993, females in the 10-24 years-old class had more surviving infants than females in the 7-9 years-old class (Wilcoxon's matched pairs sign-rank test: $n=7$ $p<0.05$), but in 1994 females in the two age classes did not differ (Appendix 4.B: Table 4.10). In 1993, groups of only three sizes had females of both age classes that gave birth, thus providing too small a sample size to analyze the proportion of infants surviving to each female age class. In 1994, the proportion of infants surviving to females did not differ in either age class (Appendix 4.B: Table 4.11).

During eleven years of observations in the population (1984-1994), no females known to be younger than the third oldest female in a group (which corresponds to fourth

in dominance rank or lower: Chapter 3) were ever seen giving birth (A. Richard unp. data). This was also true in 1993 and 1994. When we compare females in different age classes, we find that in either year the number of females under seven years of age that were in first to third dominance ranks and in fourth to eighth dominance ranks (as inferred from relative ages; see results on dominance in Chapter 3) were approximately equal, but that almost all females seven years of age or older were in first to third dominance rank (Table 4.1).

Fig. 4.7a. The Number of Females of Different Ages and Dominance Ranks in 1993 Census Population



In 1993, one female seven years-old was fourth in dominance rank (Fig. 4.7a), and in 1994, one seven years-old was fourth and one fifth in dominance rank, and one eight years-old was fourth in dominance rank (Fig. 4.7b). The lack of older females in low dominance ranks could be a side effect of older females residing predominantly in groups with at most 3 females, where the lowest possible dominance rank is three, but females of all age categories were approximately equally distributed between groups with 1-3 females versus 4-8 females (Table 4.2).

Fig. 4.7b. The Number of Females of Different Ages and Dominance Ranks in 1994 Census Population

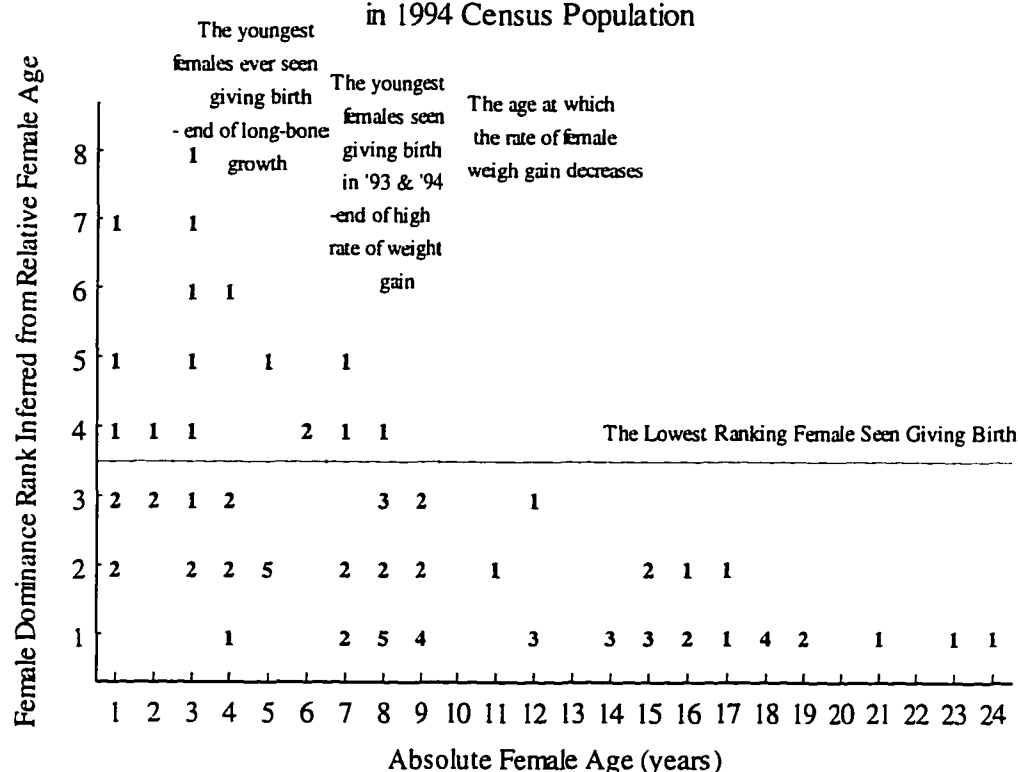


Table 4.1. The number of females of different age classes that were first-third versus fourth-eighth in dominance rank (as inferred from relative ages), in 1993 and 1994. The χ^2 test shows whether the proportion of females in each rank range differed significantly between age classes.

Age Class (years)	Dominance Rank			
	1993		1994	
	1 st - 3 rd	4 th - 8 th	1 st - 3 rd	4 th - 8 th
1 - 2	4	5	6	4
3 - 6	11	10	13	9
7 - 9	15	1	22	3
10 - 24	33	0	27	0
significance	$\chi^2=27.05$, $df=3$, $p<0.0005$		$\chi^2=16.82$, $df=3$, $p=0.001$	

Table 4.2. The number of females of different age classes that were in groups with 1-3 versus 4-8 females (as inferred from relative ages), in 1993 and 1994. The χ^2 test shows whether the proportion of females in each females-per-group category differed significantly between age classes.

Age Class (years)	Number of Females in a Group			
	1993		1994	
	1 - 3	4 - 8	1 - 3	4 - 8
1 - 2	4	5	5	5
3 - 6	9	12	12	10
7 - 9	8	8	15	10
10 - 24	21	12	16	11
significance	$\chi^2=2.69$, $df=3$, $p=0.442$		$\chi^2=0.402$, $df=3$, $p=0.940$	

In 1993, 30 females were known to be less than seven years of age, and 48 to be seven years or older. Of these 48 older females, 47 were first to third in dominance rank (as inferred from relative ages), and of these 47, 30 (63.8%) gave birth. In 1994, 33 females were known to be less than seven years of age, and 52 to be seven years or older. Of these 52 older females, 49 were first to third in dominance rank, and of these 49, 42

(89.4%) gave birth. Of the remaining four lower ranking females in these two years, none gave birth.

Of the 7 females seven years of age or older and first to third in dominance rank, 5 were seven to eight years of age and were never before seen giving birth (additionally, 2 of these 5 emigrated from their groups and joined other females establishing new groups before the 1994 birth season), and one was seen by a villager with an infant still wet from delivery. However, when I located that one female two days later, she did not have an infant and since I could not verify the villager's observation, I did not record her as having given birth that year. In short, almost all females that were seven years of age or older and first to third in dominance rank gave birth in 1994.

Female Emigration and Transfer Patterns

Because the earliest age at reproduction observed in this study population was three years of age, I consider only females three years of age or older in the following analyses. Females labeled as those that emigrated were females that left the group in which they were found at the onset of the study and after emigration started their own group or joined an existing group, and did not return to the group in which they were originally found by the end of the study (incidentally, as of August 1996, none of these females has yet returned to her original group). Females labeled as those that attempted to emigrate were females that left the group in which they were found at the onset of the study and tried to start a group of their own, but within three weeks of their leaving the

group in which they were originally found, returned to that group and stayed in it until the end of this study.

The proportion of females that emigrated from groups of median size or smaller (1-5) was significantly less than the proportion of females that emigrated from groups larger than the median and so was the proportion of females that emigrated and/or attempted to emigrate (Table 4.3). It is also worth pointing out, that all females that emigrated from their groups, emigrated from large groups.

Table 4.3. The number of females that emigrated from groups that had equal or less number of group members than the median 5 versus more (only females that were three years of age or older are considered here). The χ^2 test shows whether the proportion of females in each group size category is significantly different from the proportion of females that emigrated or attempted to emigrate in each group size category.

Group Size	Number of Marked Females	Number of Females that Emigrated	Number of Females that Emigrated or attempted to Emigrate
2 - 5	25 (38%)	0 (0%)	0 (0%)
6 - 13	41 (62%)	6 (15%)	9 (22%)
significance		$\chi^2=4.02$, $p=0.045^a$	$\chi^2=6.35$, $p=0.012^a$

^a χ^2 values were calculated using 4x4 tables, where the number of females marked minus the number of females that emigrated or attempted to emigrate was compared to the number of females that emigrated or attempted to emigrate.

The proportion of females that emigrated was significantly greater in groups with more than 3 females three years of age or older than in groups with 3 females or less (Table 4.4), and the proportion of females that emigrated and/or attempted to emigrate was significantly greater in groups with more than 3 females three years of age or older than in groups with 3 females or less (Table 4.4).

Table 4.4. The number of females that emigrated from groups with different numbers of females (only females that were three years of age or older are considered here). The χ^2 test shows whether the proportion of females in each females-per-group category is significantly different from the proportion of females that emigrated or attempted to emigrate in each females-per-group category.

Females per Group	Number of Marked Females	Number of Females that Emigrated	Number of Females that Emigrated or attempted to Emigrate
1 - 3	37 (56%)	0 (0%)	0 (0%)
4 - 8	29 (44%)	6 (21%)	9 (31%)
significance		$\chi^2=8.42$, $p=0.004^a$	$\chi^2=13.30$, $p<0.0005^a$

^a χ^2 values were calculated using 4x4 tables, where the number of females marked minus the number of females that emigrated or attempted to emigrate was compared to the number of females that emigrated or attempted to emigrate.

During the study period, in the census population, 14 females were both fourth in dominance rank or lower and three years of age or older (Table 4.5). Of these 14 females 5 emigrated, 3 tried to emigrate, and 1 vanished. Thus only 5 of these females (38%) did not attempt to emigrate.

Table 4.5. Group membership history of all marked females in the census population that were older than two years of age and were fourth in dominance rank or lower during June 1993 - March 1995 study period. Group size, number of females in the group, and female dominance rank, all refer to the group the female left or attempted to leave.

Group	ID	Group Membership History	Age	# of Females	Group Size	Rank	Infants born
VavyGoa	233	stayed	3	5	8	4	0
Sary	188	stayed	3	8	13	8	0
Sary	238	stayed	4	8	13	6	0
Fotaka	124	stayed	6	5	7	4	0
Sary	215	stayed	6	8	13	4	0
Fotaka	122	emigrated -> joined	3	5	7	6	0
Fotaka	202	emigrated -> new	4	6	9	5	0
MasiakaBe	175	emigrated -> new with group mate	4	4	6	4	0
Sary	115	emigrated -> joined	5	8	13	5	0
Fanondrovery	220	emigrated -> new	7	4	8	5	0
Zavmad	224	attempted to emigrate with group mate	3	7	11	6	0
Zavmad	225	attempted to emigrate with group mate	7	7	11	5	0
Zavmad	209	attempted to emigrate with group mate	8	7	11	4	0
Sary	131	vanished	4	8	13	7	0

The proportion of females that emigrated that were fourth or lower in dominance rank and were three years of age or older was significantly greater than the proportion of females that were first to third in dominance rank and three years of age or older (Table 4.6). Similarly, the proportion of females that emigrated and/or attempted to emigrate that were fourth or lower in dominance rank and were three years of age or older was significantly greater than the proportion of females that were first to third in dominance rank and three years of age or older (Table 4.6).

Table 4.6. The number of females that were fourth in dominance rank or lower and were three years of age or older that emigrated from their groups. The χ^2 test shows whether the proportion of females in each rank/age category is significantly different from the proportion of females that emigrated or attempted to emigrate in each rank/age category.

Rank; Age	Number of Marked Females	Number of Females that Emigrated	Number of Females that Emigrated or attempted to Emigrate
1 - 3; 3 - 24	53 (80%)	1 (2%)	1 (2%)
4 - 8; 3 - 24	13 (20%)	5 (38%)	8 (62%)
significance		$\chi^2=16.90$, $p<0.0005^a$	$\chi^2=31.54$, $p<0.0005^a$

^a χ^2 values were calculated using 4x4 tables, where the number of females marked minus the number of females that emigrated or attempted to emigrate was compared to the number of females that emigrated or attempted to emigrate.

All females that attempted to emigrate were between three and eight years old, which is during the first five years of potential reproductive maturity. All of them were also among the youngest females in their initial groups, they were from groups with many females, and none of these females were seen to give birth prior to their emigration, regardless of their age.

Furthermore, the only female three years of age that emigrated, left her group to join a female that left the same group 2 months earlier to establish a new adjacent group.

Also the only female three years of age that attempted to emigrate was trying to emigrate together with an older female from her group.

Group Extinctions and Formations

During the course of this study 5 groups went extinct (Appendix 4.C). They were all single-female groups and were all adjacent to each other along a thin strip of land in the western part of the reserve. The strip extended from southwest to northeast. All of these groups went extinct between February and April of 1994, which is the earliest part of the gestation period. Since 4 of these 5 females were the only females known to have died during the entire study period (they were seen dying or their dead bodies were found), and since at least 3 of them appeared to have died of illness, this suggests that females might be particularly vulnerable to diseases during gestation. Only long-term, high-frequency census data could shed more light on this possible pattern.

When females from single-female groups died, the males of those groups dispersed and tried to transfer into neighboring groups (case histories in Appendix 4.D). In each case, a territory that was vacated by a group extinction was immediately occupied by either a shift of a territory by an existing, neighboring group that was previously largely overlapped with other groups, or by a young female emigrating from her large natal group and attempting to start a new group of her own.

Even when a female moved into a new vacancy, holding on to the territory was difficult for this new, unestablished, single-female group, and such new groups were often harassed by more established, neighboring groups.

DISCUSSION

Group Reproductive Patterns

The number of infants born per group increased significantly with group size and with the number of females over six years of age residing in a group. This is not surprising because the number of older females was greater in larger groups, and in both years the majority of older females were known to have given birth (63.8 % in 1993, 89.4% in 1994). Thus, as expected, the number of older females in a group was the best predictor of the number of infants born.

However, the number of infants surviving per group did not change significantly with group size. It increased significantly with the number of females that were over six years of age only in 1994, but not in 1993. The observation that the number of infants surviving per group per year does not increase with group size, suggests that larger groups as a whole do not have a greater reproductive value and thus, from the point of view of male reproductive success, they might not be any more attractive than smaller groups. Consistent with this hypothesis is the result, that even though the number of males increased significantly with group size (Fig. 4.5), as did the number of females (Fig. 4.4), the number of males did not increase with the number of females in a group (Fig. 4.6).

However, the number of infants born or surviving per group are not likely to reveal potential effects of feeding competition on reproductive success, because they are so strongly confounded by the number of females in a group, and therefore by group size. The effects of feeding competition are most likely to be reflected in the proportion of infants surviving in different groups, and in the proportion of potentially reproductive

females that gave birth or had surviving offspring in groups of different sizes. Although the proportion of infants that survived to one year of age did indeed tend to decrease with group size in each year of observations and with the number of females in 1993, the decreases were not statistically significant (group size: $R^2=0.06$ $p=0.11$ in 1993, $R^2=0.00$ $p=0.50$ in 1994; number of females: $R^2=0.04$ $p=0.30$ in 1993, $R^2=0.00$ $p=0.71$ in 1994). Because 36-37 groups were analyzed each year, and they were further divided into 11 group size categories, or 5 categories of the number of females of six years or older per group, and since there were disproportionately fewer groups with large number of any group members or of females (Fig. 4.1-4.2), the sample sizes might have been too small to detect a weaker effect.

In the face of greater intra-group feeding competition in larger groups, one might expect females of larger groups to be in worse nutritional state than females of smaller groups, and thus to be more likely to not ovulate, undergo spontaneous abortion, or be less successful at rearing their offspring. The number of infants born and the number of infants surviving per female decreased with group size, but, again, the difference was not significant. Thus even though the results hint at a weak effect of group size on the reproductive success of females of seven years of age or older, in 1993 and 1994, the effect cannot be fully determined given data from only two birth seasons.

Individual Reproductive Patterns

In 1993 and 1994 no females from the 3-6 years-old age class were known to have given birth, despite the fact that females of that age have reproduced prior to and after this

study. Additionally, in both years, females in the 7-9 years-old age class had proportionally fewer births than females in the 10-24 years-old age class and, in 1993, 7-9 year old females had proportionally fewer surviving infants than 10-24 years-old females. The effects of female age on the proportion of infants surviving could not be tested for 1993, and it was not affected by female age in 1994. As a result, we cannot conclude that the fully grown, 10-24 year-old females, were more successful at rearing offspring, but we can conclude that the probability of giving birth increased with female age.

I used relative female age to infer female's dominance rank within groups, based on the highly consistent patterns of relative age and directions of agonistic encounters (Chapter 3), with older females being dominant to younger females. However, determining whether female absolute age or female dominance rank (i.e. relative age) were better predictors of female annual reproductive success was very difficult, because there were almost no females that were seven years of age or older that were also lower than third in dominance rank, and almost no females ten years of age or older that were lower than second in dominance rank (Fig. 4.7a,b; Table 4.1). This pattern could be caused by either increased mortality of low ranking females between seven and ten years of age, or by age- and rank-specific female emigration to start their own groups or to join existing single-female groups.

To depict the effects of age versus dominance rank, and to determine whether females second or third in dominance rank had lower reproductive success in larger groups than in smaller groups, one would need data of equal depth as presented here from more than two birth seasons.

In 1994, when I gathered the most precise data on infant births, almost all females that were seven years or older and first to third in dominance rank gave birth. What proximate mechanism may cause age and rank effects on female sifaka reproduction? Female body mass has been shown to be a strong indicator of the likelihood that the female will give birth that year, regardless of her age (Richard et al. in prep.). At the same time, higher ranking females expended significantly less effort on foraging than lower ranking females, within the same groups, but females of all ranks experienced greater intra-group feeding competition in larger groups than in smaller groups (Chapter 3). No data yet exist on relative female weights in groups of different sizes or female weights between different ranks within the same group. However, if female body mass is the key predictor of female's ability to give birth, then one might expect that in energetically stressed populations lower ranking females, who presumably do not have priority access to food, may not be able to build up their body mass to the species-specific reproductive threshold. One may also expect that in years with especially low food availability younger females, such as those 3-6 years old, who on average have lower body mass than older females, may also not be able to gain enough weight to reach the reproductive threshold.

The preceding hypothesis of energetic constraint on reproduction does not exclude the possibility of additional social and/or hormonal reproductive suppression of lower ranking females. A strong, linear dominance hierarchy among females lends itself to socially mediated reproductive suppression (Dunbar 1980; Harcourt 1987; Abbott 1987) and the existence of reproductive suppression has been suggested for diurnal prosimians

(Vick 1988). Based on data collected at the Duke University Primate Center, Vick (1988) suggested several modes of direct reproductive competition among female lemuriformes: (1) elimination of potential competitors (expulsion of females has been observed in semi-free-ranging, long-term social groups of ring-tailed, brown, black, and ruffed lemurs - for example, in one brown lemur group 55% of females born over a seventeen year period were "targeted" and ejected before they were able to breed), and (2) suppression of competitors' reproduction using pre- or post-copulatory tactics (only 33% of females giving birth in established, social groups of brown and ring-tailed lemurs delivered at age two, which is the earliest observed age of reproduction, in contrast, 60% of brown and 48% of ring-tailed mothers in pairs or small, newly established groups gave birth at two years of age). However, even though hints of the existence of reproductive suppression among prosimians exist, there are no empirical data testing the possibility of reproductive suppression among sifakas or diurnal prosimians in general.

Female Emigration and Transfer Patterns

In both 1993 and 1994, only the oldest 2 to 3 females in each group gave birth and, consistent with my hypothesis, it was the non-reproducing, younger females in large groups that attempted to emigrate. Both group size and number of females in a group were good predictors of the likelihood that a female would attempt to emigrate, 22% if in groups greater than 5 and 31% if in groups with more than 3 females (Table 4.3, 4.4). However, the best predictor was the combination of the female's rank and age, 62% if three years or older and fourth or lower in dominance rank (Table 4.6).

The very well defined pattern of female emigration suggests that the reason that initially an equal number of females younger than seven years-old hold high and low dominance ranks but then, suddenly, females seven years of age or older hold only high ranks (Table 4.1) is that females try to emigrate from groups with large number of females before they reach seven or eight years of age. The pattern of sifaka emigration further supports the hypothesis that low ranking females suffer a significant disadvantage with respect to their reproduction.

Three of the five females that were expected to attempt to emigrate but did not (Table 4.5) were from group Sary, which has historically been the largest group in the Beza population, with 11-14 members (A. Richard pers. com.). This group has an unusually large home-range territory that extends mostly outside of the reserve, and is the only group with a large number of females (8) into which an outside female was seen immigrating (female 198, Appendix 4.C). It is possible that, perhaps due to the size and/or quality of its home-range, Sary can accommodate a greater number of members without a considerable increase in intra-group feeding competition. However, it is also possible that the location of Sary provides less opportunities for female dispersal, since much of its range is in the heavily grazed forest outside of the Reserve. Among marked females, at least two females did emigrate from Sary, and they did so into the neighboring territories within the boundaries of the Reserve (female 86 in 1991 and female 115 in 1994).

The next largest group with the next greatest number of females in the census population was Zavmad (Appendix 4.A). Three low ranking females, fourth to fifth in

rank, attempted to emigrate from Zavmad after an extinction of a neighboring group, but females from another neighboring group ended up in the newly vacated territory (forming group Kashka, Appendix 4.D). Thus the three Zavmad females returned to their original group, where they have remained. Zavmad was also a group with a large territory that extended considerably into the grazed forest outside of the Reserve.

After emigration, a female either moved into a smaller group with fewer females than her original group, or she started a new group and tried to defend a territory with up to three males. However, all females, at some point after their emigration, tried to join an existing group, suggesting that females preferred to join other females rather than start or maintain a new single female group.

Almost all female emigrations seemed to happen in response to an extinction of a neighboring group (Appendix 4.D). Some females joined or attempted to join other single females, and among females with known group histories, they tried to join females that originated in the same groups as themselves. However, more data on emigrating females with known group histories are needed to confirm this pattern. The important point, however, is that female transfers seem beneficial, because if a female can join an established group, she can emigrate from her large group and yet avoid harassment that new groups attract.

Therefore, the likelihood of a given female dispersing seemed to depend not only on her age and dominance rank, but also on other females' claims to the territory. Sometimes, after a vacancy occurred, neighboring, well established groups expanded their ranges into the vacated territory, and sometimes recently formed but more

established single-female groups moved into the vacancy (Appendix 4.D). Neighboring groups often aggressively chased one another, and new, single-female groups were harassed frequently by larger groups. Also, almost all of the youngest females, among those attempting to emigrate, tried to do so with other females from their group or tried to join existing groups, suggesting that the difficulties of establishing a new group might be especially greater for younger, and therefore usually smaller females. This suggests that smaller body size poses a disadvantage in aggressive encounters.

Summary

The results suggest that, as predicted by the hypothesis that increased feeding competition results in lowered female reproductive success, greater group sizes correspond to lower reproduction per female, however the data were too few to allow strong conclusions. The results also show that female age is an important factor influencing a female's probability of reproducing, and rank seems to determine whether a female will give birth at all. Unfortunately, the distribution of age classes between dominance ranks, coupled with the relatively late earliest age of reproduction seen during the study period, did not allow for a conclusion of the exact effects of rank. However, because the emigration patterns of females were closely tied to their age and dominance rank, they suggested that rank is indeed an important determinant of white sifaka reproduction. In addition to age and rank, female emigration seemed also to be constrained by available space and the size and relatedness history of neighboring groups.

The results imply that females that did not emigrate from their groups despite their low rank and three to eight years of age will experienced a selective disadvantage compared to females of the same age that lived in or emigrated into smaller groups. Only analysis of birth data past 1994 can determine whether this prediction holds.

Therefore, although final conclusions on the effects of feeding competition on reproductive success are prevented by sample sizes that are too small, the data strongly suggest trends in the predicted directions.

APPENDIX 4.A: Census Groups

Table 4.7. All 43 census groups with their group size, number of males and females (juvenile - adult), total number of infants born that year and surviving to one year of age, and percent of infants that survived to one year of age.

Group	1993						1994					
	Grp. Size	# of Males	# of Fem.	# of Infants Born	# of Infants Surv.	% of Infants Surv.	Grp. Size	# of Males	# of Fem.	# of Infants Born	# of Infants Surv.	% of Infants Surv.
Andafy	5	2	3	2	0	0	5	2	3	2	1	50
Andrefana	5	4	1	1	0	0	-	-	-	-	-	-
Andrefana2	5	3	2	1	1	100	5	2	3	0	0	-
BoryBory	4	3	1	1	1	100	4	3	1	1	1	100
Celeste-R	-	-	-	-	-	-	5	3	2	0	0	-
Chocolat	3	1	2	1	1	100	3	1	2	1	1	100
Disoraty	3	2	1	1	1	100	3	2	1	1	1	100
Emelia	6	4	2	2	1	50	6	4	2	2	2	100
Emelia2	3	2	1	0	0	-	3	2	1	1	1	100
Enafa	5	3	2	1	1	100	6	3	3	1	0	0
Fanondrovery	9	4	5	2	0	0	8	4	4	3	0	0
Felix	5	2	3	2	0	0	4	2	2	1	0	0
Fety	5	3	2	1	0	0	4	2	2	1	1	100
Fotaka	9	3	6	1	0	0	7	2	5	2	2	100
Gobera	-	-	-	-	-	-	8	5	3	1	1	100
Kashka	-	-	-	-	-	-	5	2	3	0	0	-
Lahavelo	-	-	-	-	-	-	2	1	1	0	0	-
Lavaka	4	3	1	0	0	-	-	-	-	-	-	-
Lolo2	3	2	1	1	1	100	3	2	1	1	0	0
Maka	3	2	1	1	1	100	3	1	2	1	1	100
MangaKely	3	2	1	1	0	0	3	2	1	1	0	0
MasiakaBe	6	2	4	1	1	100	6	5	1	1	1	100
Nenibe	4	3	1	1	1	100	3	2	1	1	1	100
Nify	3	1	2	0	0	-	2	1	1	1	1	100
Papozy-R	5	3	2	1	0	0	5	4	1	1	0	0
Raiki-Pitia	2	1	1	0	0	-	6	5	1	1	0	0
Rebel	-	-	-	-	-	-	3	2	1	-	-	-
Rivotse	5	2	3	1	0	0	6	3	3	2	2	100
Saba	5	3	2	0	0	-	5	3	2	2	0	0
Saksud	3	1	2	0	0	-	3	1	2	0	0	-
Sambeto	-	-	-	-	-	-	8	5	3	3	3	100
Sary	13	5	8	3	0	0	13	5	8	3	1	33
TsyEmelia	3	2	1	1	0	0	3	2	1	1	1	100
TsyGoa	3	2	1	1	1	100	-	-	-	-	-	-
Vahiny	4	1	3	1	1	100	5	1	4	2	2	100
Vamba	-	-	-	-	-	-	3	2	1	0	0	-
Vaovao	7	3	4	1	1	100	7	3	4	2	1	50
VasaDiso	4	3	1	0	0	-	-	-	-	-	-	-
VavyGoa	5	1	4	2	2	100	8	3	5	2	2	100
VavyGoa2	8	6	2	0	0	-	7	5	2	1	0	0
VavyMasiaka	3	2	1	1	1	100	7	5	2	1	1	100
VavyMasiaka2	2	1	1	0	0	-	-	-	-	-	-	-
Zavmad	10	4	6	1	1	100	11	4	7	3	2	67
Total	175	91	84	34	17	50	195	104	91	47	30	63.8

APPENDIX 4.B: Reproductive Tables

Table 4.8. Number of females of different ages in groups of different sizes. At the bottom the data are pooled for groups equal to and below the median group size (1-5) and for groups above the median group size (6-13).

Group Size	Female Age (in years)									
	in 1993					in 1994				
	1-2	3-6	7-9	10-24	unknown	1-2	3-6	7-9	10-24	unknown
2	0	0	1	1	0	0	0	0	1	1
3	1	2	3	7	1	1	3	4	5	0
4	1	1	0	3	2	0	2	0	2	1
5	3	6	4	9	2	4	4	6	2	2
6	0	2	0	3	1	1	1	2	4	2
7	1	0	1	2	0	2	2	4	5	0
8	0	1	0	1	0	1	4	4	5	1
9	1	4	3	3	0	0	0	0	0	0
10	1	1	2	2	0	1	1	3	2	0
13	1	4	2	1	0	0	5	2	1	0
<i>pooled</i>										
1-5	5	9	8	20	5	5	9	10	10	4
6-13	4	12	8	12	1	5	13	15	17	3

Table 4.9. Proportion of females of different ages, in groups of different sizes, that gave birth ("-" indicates that there were no females of that age in groups of that size). At the bottom the data are pooled for groups equal to and below the median group size (1-5) and for groups above the median group size (6-13).

Group Size	Female Age (in years)							
	in 1993				in 1994			
	3-6	7-9	10-24	unknown	3-6	7-9	10-24	unknown
2	-	0	0	-	-	-	1.00	0
3	0	0.67	0.71	1.00	0	0.75	1.00	-
4	0	-	0.67	0.50	0	-	1.00	1.00
5	0	0.75	0.89	0.50	0	0.67	1.00	0.50
6	0	-	0.67	1.00	0	1.00	0.75	1.00
7	-	0	0.50	-	0	0.50	0.80	-
8	0	-	0	-	0	0.75	1.00	1.00
9	0	0	1.00	-	-	-	-	-
10	0	0.50	0	-	0	0.33	1.00	-
13	0	1.00	1.00	-	0	1.00	1.00	-
<i>pooled</i>								
1-5	0	0.63	0.75	0.60	0	0.70	1.00	0.50
6-13	0	0.38	0.58	1.00	0	0.67	0.88	1.00

Table 4.10. Proportion of females of different ages, in groups of different sizes, that had infants surviving to one year of age ("-" indicates that there were no females of that age in groups of that size). At the bottom the data are pooled for groups equal to and below the median group size (1-5) and for groups above the median group size (6-13).

Group Size	Female Age (in years)							
	in 1993				in 1994			
	3-6	7-9	10-24	unknown	3-6	7-9	10-24	unknown
2	-	0	0	-	-	-	1.00	0
3	0	0.33	0.57	1.00	0	0.75	0.60	-
4	0	-	0.67	0.50	0	-	0.50	1.00
5	0	0.25	0.22	0.50	0	0.17	0.50	0.50
6	0	-	0.33	1.00	0	0	0.75	1.00
7	-	0	0.50	-	0	0.50	0.40	-
8	0	-	0	-	0	0.50	0.60	1.00
9	0	0	0	-	-	-	-	-
10	0	0.50	0	-	0	0.33	0.50	-
13	0	0	0	-	0	0.50	0	-
<i>pooled</i>								
1-5	0	0.25	0.40	0.60	0	0.40	0.60	0.50
6-13	0	0.13	0.17	1.00	0	0.40	0.53	1.00

Table 4.11. Proportion of infants surviving to one year of age to females of different ages, in groups of different sizes ("-" indicates that there were no females of that age in groups of that size that gave birth in that year). At the bottom the data are pooled for groups equal to and below the median group size (1-5) and for groups above the median group size (6-13).

Group Size	Female Age (in years)					
	in 1993			in 1994		
	7-9	10-24	unknown	7-9	10-24	unknown
2	-	-	-	-	1.00	-
3	0.50	0.80	1.00	1.00	0.60	-
4	-	1.00	1.00	-	0.50	1.00
5	0.33	0.25	1.00	0.25	0.50	1.00
6	-	0.50	1.00	0	1.00	1.00
7	-	1.00	-	1.00	0.50	-
8	-	-	-	0.67	0.60	1.00
9	-	0	-	-	-	-
10	1.00	-	-	1.00	0.50	-
13	0	0	-	0.50	0	-
<i>pooled</i>						
1-5	0.40	0.53	1.00	0.57	0.60	1.00
6-13	0.33	0.29	1.00	0.60	0.60	1.00

APPENDIX 4.C: Group Extinctions And Formations And Female Transfers

Table 4.12. Group extinctions (via female death), formations (started by emigrating females), female emigrations and transfers observed during June 1993 - March 1995 study period. Group size, number of females in the group, and female dominance rank, all refer to the group the female left or attempted to leave, except when the female joined a group or immigrated into a group, in which case data for the group into which the female transferred are given. Females 129, 201, and 198 appeared as unmarked females and were later marked, but their origins are unknown.

Date	Event	Female ID	Female Age	Dominance Rank	Group	Group Size	# of Females in a group
Feb 1994	extinct	F	^a	^b	TsyGoa	3	1
Mar 1994	extinct	96	^a	^b	VasaDiso	4	1
Mar 1994	extinct	F	^a	^b	VavyMasiaka2	2	1
Apr 1994	extinct	119	^a	^b	Andrefana	5	1
Apr 1994	extinct	204	13	^b	Lavaka	4	1
Sep 1993	emigrated	202	3	5	Fotaka	9	6
May 1994	emigrated	9016	7	3	MasiakaBe	6	4
May 1994	emigrated	175	4	4	MasiakaBe	6	4
Aug 1994	emigrated	220	7	4	Fanondrovery	8	4
Aug 1994	emigrated	115	5	5	Sary	13	8
Oct 1994	emigrated	122	3	5	Fotaka	7	5
Nov 1993	started	202	3	^b	Vamba	^c	^c
Mar 1994	started	129	8	^b	Celeste-R	^c	^c
Mar 1994	started	227	5	^b	Celeste-R	^c	^c
Apr 1994	started	9001	5	^b	Kashka	^c	^c
May 1994	started	9016	7	^b	Kashka	^c	^c
May 1994	started	175	4	^b	Kashka	^c	^c
Aug 1994	started	220	7	^b	Rebel	^c	^c
Aug 1994	started	201	4	^b	aaGroup-B	^c	^c
Apr 1994	attempted to start	209	8	4	Zavmad	11	7
Apr 1994	attempted to start	225	7	5	Zavmad	11	7
Apr 1994	attempted to start	224	3	6	Zavmad	11	7
Jul 95	joined	122	4	2	Rebel	2	1
Aug 1994	joined	115	5	2	Papozy-R	5	1
Nov 1993	joined	170	7	2	VasaDiso	4	1
Mar 1994	immigrated	198	3	8	Sary	13	7
Feb 1994	visited	196	19	1	Fotaka	7	5

^a these females were not aged

^b female rank has no relevance to groups that went extinct (they were single-female groups) or to newly formed groups

^c group size or the number of females have no relevance to newly formed groups

APPENDIX 4.D: Case Histories Of Group Extinctions And Formation

General:

Three of the five groups that went extinct had marked females which were found dead (VasaDiso, Andrefana, Lavaka). The unmarked female of TsyGoa (TG) disappeared, but at the same time both males of this group along with her six and half month-old infant began to try to enter an adjacent group, suggesting that the TsyGoa female died. The unmarked female of VavyMasiaka2 (VM2) was last seen on March 11th, 1994. On April 8th, 1994, her only male partner was seen with another female with whom he remained. At the same time, on April 1st, 1994, an unmarked female joined female 227's territory that had little overlap with other groups (PC), and was adjacent to the VavyMasiaka2's territory which was almost entirely overlapped when the group existed. The unmarked female that joined 227 on Celeste-R (CER) territory was later captured (ID 129) and aged to have been 8 years old at the time of her transfer. This female may have been the VavyMasiaka2 female.

TsyGoa and Lavaka:

After the onset of this study, I saw female 227 for the first time on July 18th, 1994, at which time she was with female 86. In 1992, 227 was with another marked female in group Celeste, but the other female died between the 1992 census and the onset of this study. A few years ago, female 86 was a member of group Sary, and in 1991, at the age of six, she started her own group, Papozy, just east of Sary's territory. In 1992, female 86 was in a single-female group Papozy, that was adjacent to Celeste. Presumably, after the

older Celeste female died, 227 and 86 joined together and formed group Papcel (PC). which persisted until March 1994. Sometime between March 17th and March 28th, of 1994, female 86 left female 227 and moved south, with a new set of males, to an adjacent territory newly vacated by the extinction of groups TsyGoa and Lavaka (LV). At this point she reestablished her own group, which I named Papozy-R (PAR). In August of 1994, she was joined by female 115, which came straight from 86's old group Sary. Female 115 remained with 86 until 115 disappeared in October of 1994.

Andrefana:

Shortly after group VavyMasiaka2 disappeared, an adjacent group with a large territory, Andrefana (AF), went extinct. Only two groups that were adjacent to Andrefana had more than 3 females, MasiakaBe (MB) and Zavmad (ZM). An unknown unmarked female, female 175 of MasiakaBe, and female 209 of Zavmad, were attempting to join together and establish a new group on Andrefana's territory as soon as the Andrefana female begin to die (she was alone and dying for 3 days). At the same time group MasiakaBe begin to shifting its territory south onto Andrefana's territory. For the next two weeks female 175 went back to MasiakaBe and females 224 and 225 of Zavmad joined 209 and the unmarked female in attempting to start the new group. The youngest of them, 224 was the first to return to Zavmad, and a week later 209 and 225 also returned to Zavmad. At this point 175 and 9016 of MasiakaBe joined the unmarked female and they established a new group Kashka (KK) on Andrefana's and VavyMasiaka2's territories.

VasaDiso:

In 1992, female 170 was with female 204 in group Lavaka. When we saw 170 for the first during this study, on July 8th, 1993, she was alone with a male trying to establish a territory, adjacent to Lavaka. In September 1993, her male began to leave her for female 202, who was trying to establish a new group Vamba in the same territory. Being left alone, 107 joined female 96 of VasaDiso (VD). She remained in VasaDiso until 96's death between March 7th and March 15th, 1994, two weeks after group TsyGoa went extinct. At this point, 170 established her own territory with a new male in the southern range of TsyGoa and eastern range of VasaDiso. At the same time, groups east of VasaDiso's range immediately shifted west, and a recently established group Vamba expanded its territory north and east onto the southern portion of VasaDiso's territory.

Group Vamba was formed during a break in censuses in October 1993, and the exact circumstances of 202's emigration from Fotaka and of Vamba formation are not known. In October 1994, the youngest female in group Fotaka, 122, emigrated from her group and joined 202 in Vamba.

In August 1994, no new territories were vacated, but five males were suddenly trying to immigrate into group Fanondrovery, which at the time had four males and four females. This began a period of constant fights between the males and a lot of aggression from the three oldest females with infants to males. As the group membership instability and male-male fighting increased with time, the three oldest females began to extend their aggression toward the youngest female 220. By the mid August 1994, 220 left her group

and established a new group, partially on Fanondrovery's territory, with a couple of new males.

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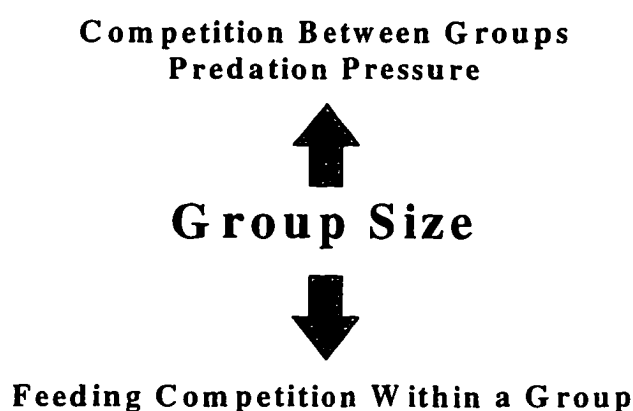
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CHAPTER FIVE

SUMMARY AND CONCLUSIONS

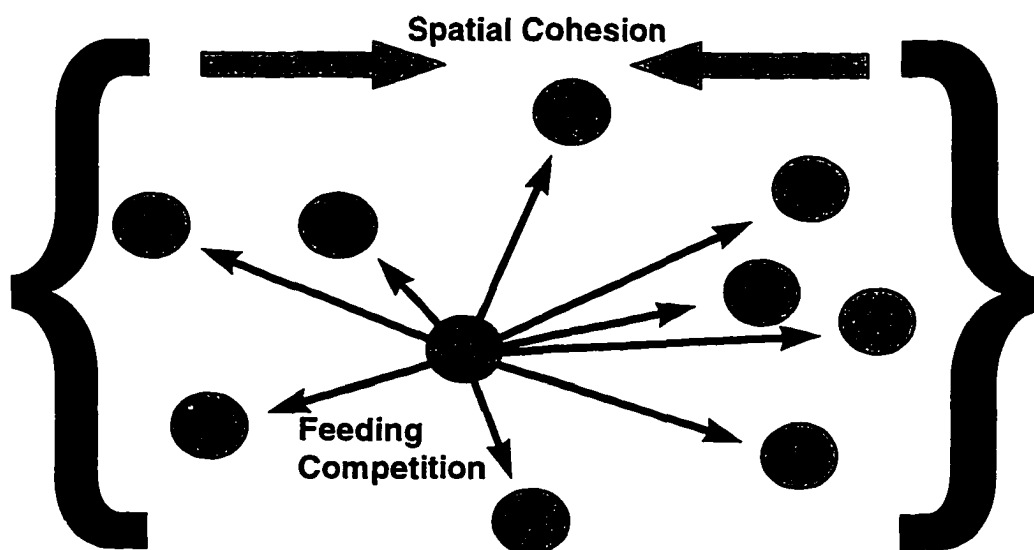
The evolution of living in social groups has been attributed to a number of factors. For diurnal primates, most often the need to detect and deter predators and to compete for food and territories with other groups of conspecifics are hypothesized to favor an increase in group size (Fig. 5.1). Social groups may benefit from a larger size if they maintain spatial cohesion, but close spacing among group members increases overlap in their individual search fields during foraging. An overlap in search fields results in competition, and intra-group feeding competition is hypothesized to favor a decrease in group size.

Fig. 5.1. Schematic representation of inter-group competition and predation pressure driving group size up and intra-group competition driving it down.



However, if group members decrease their foraging field overlap to minimize intra-group feeding competition, they also decrease their group's spatial cohesion which can significantly reduce their group's ability to deter predators or defend food patches and territories from neighbors. Thus when a group gets larger, its members, by regulating distances between themselves, must compromise between the degree of intra-group feeding competition and the group's spatial cohesion. The consequences of both, severe feeding competition and low spatial cohesion, can significantly affect individual survival and reproductive success. The tradeoff between minimizing food competition (minimizing personal crowding) and maximizing group cohesion (minimizing group spread) defines a cost/benefit curve for different group sizes, thereby designating the optimal and maximum group size for a given species and habitat.

Fig. 5.2. Schematic representation of the opposing forces of maintaining spatial cohesion versus avoiding feeding competition on inter-individual spacing within a group.



In order to determine the relationship between primate group size, intra-group feeding competition, dispersal patterns, and female reproductive success, I studied a sub-population of white sifakas, *Propithecus verreauxi verreauxi*, from June 1993 to January 1995. I conducted my research on this diurnal, matrilineal primate at Beza Mahafaly Special Reserve, in southwestern Madagascar, where sifaka group territories partially overlap and are fiercely defended from neighbors.

My results showed that members of sifaka groups did not distribute themselves randomly in space, but acted so as to minimize the degree of individual crowding they experienced while maximizing their group's spatial cohesion (i.e. minimizing its overall spread). Group members seemed to accomplish this by maintaining the spatial configuration that minimizes the potential for overlap in individual foraging search fields, altering this configuration to a more clumped one as groups reached the maximum observed size. Also, during periods of high food scarcity, individuals spaced themselves more distantly within the short-scale space of 2 meters, but did not alter their large-scale spacing at a 5 meters distance. This suggests that they behaved in a manner similar to mutually repelling magnets that are constrained in the total space they can occupy, thereby strictly minimizing their personal crowding without increasing the group's spread. During feeding, as compared to resting, members of smaller groups decreased their personal crowding significantly more than members of larger groups, indicating that the spread of larger groups was near the acceptable threshold and could not be increased further.

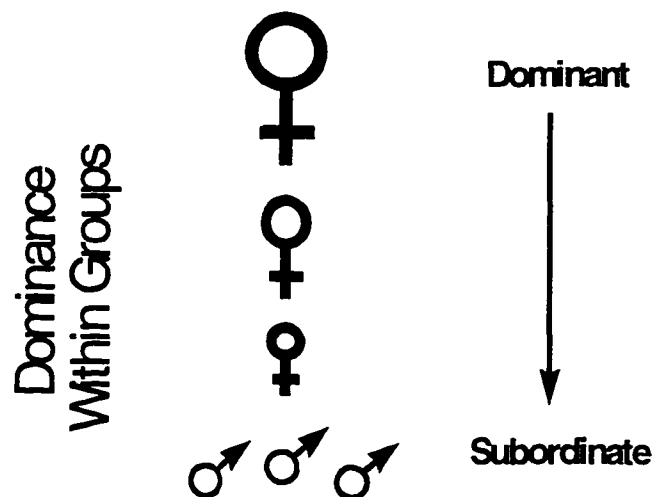
All measures of spatial distribution changed rapidly with group size among groups below the median size, but groups larger than the median seemed to reach a threshold, beyond which spacing changed at a much lower rate. The compromise between the disadvantages of being too close versus too far seemed to be more difficult to meet within the largest groups, implying that the spatial constraints imposed an upper limit on viable group size. Presumably, beyond this upper limit, group members begin to pay too great of a cost, by having a lower than sustainable feeding efficiency and/or by lacking adequate protection from other group members.

Because sifakas balance opposing selective pressures on their inter-individual spacing, members of larger groups experienced greater personal crowding than members of smaller groups. And although sifakas seemed to exercise a limit on the extent of personal crowding they experienced, all measures of personal crowding approximately doubled in the largest groups as compared to the smallest. Within groups, dominant individuals (i.e. females -- older females in particular) enjoyed a preferable (i.e. safer -- according to the selfish herd theory) central position while resting, but during feeding all group members experienced the same degree of personal crowding. Thus all members of larger groups equally experienced greater potential overlap in their foraging search fields.

The advantage of dominance within groups played itself out in the energetic effort extended daily on travel. All members of larger groups traveled further per day than members of smaller groups, but within groups, low ranking females traveled the furthest. My estimate of individual feeding efficiency (time spent feeding divided by distance traveled) also decreased significantly with group size and lower female dominance rank.

Because lower ranking females spent the same time feeding and resting as higher ranking females, but they expended significantly greater energy on travel, they were likely to experience lower net energy gain. Thus the lowest ranking females in the largest groups were most likely to experience the greatest cost of intra-group feeding competition among females and, consequently, to lose the greatest proportion of their body mass during periods of food scarcity, such as the dry season.

Fig. 5.3. Schematic representation of dominance among females and of females over males.



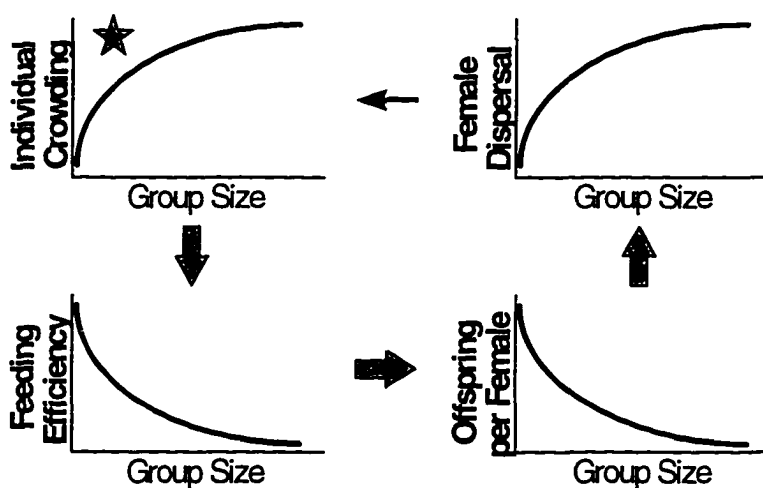
Richard et al. (in prep) found that both males and females lose weight during the dry season as compared to the wet, and that females lose significantly more weight than males. Furthermore, they found that among females old enough to reproduce, a female's body mass predicted whether she gave birth that year. Since intra-group feeding competition increases with group size and with lower dominance rank, females in larger

groups are expected to experience lower reproductive success, and low ranking females in those groups are expected to have the lowest reproductive success. In both years, fewer infants were born per female and infant survival was lower in larger groups, though the effect was not significant. Also, a maximum of only three of the highest ranking females reproduced in any group, and low ranking females of reproductive age did not reproduce at all in both years. Unfortunately, the number of low ranking females of reproductive age was too small to analyze the data statistically. In short, the trends of all data were in the predicted directions, but, perhaps due to sample sizes, not significantly so.

If low ranking females in large groups are in a worse nutritional state than other females, as suggested by my data on feeding efficiency, and if the level of their nutritional well-being is below a threshold for successful reproduction, as suggested by Richard et al. data on body mass and reproduction, then among female group members, the difference between costs and benefits of living in large groups are the greatest for the low ranking females. As a result, the potential net advantage of emigrating from a group is also the greatest for low ranking females. This is consistent with the result that, almost exclusively, low ranking females at or beyond the earliest age of first reproduction that were from groups larger than the median left or tried to leave their groups. Further, probably as a result of this emigration pattern, no females at their full reproductive potential (10 years of age or older) resided in groups where they would be 4th in rank or lower. Thus by the empirically suggested criterion that only females 3rd in rank or higher reproduce, during the period of this study, all fully reproductively mature females were in a position to reproduce and almost all of them did.

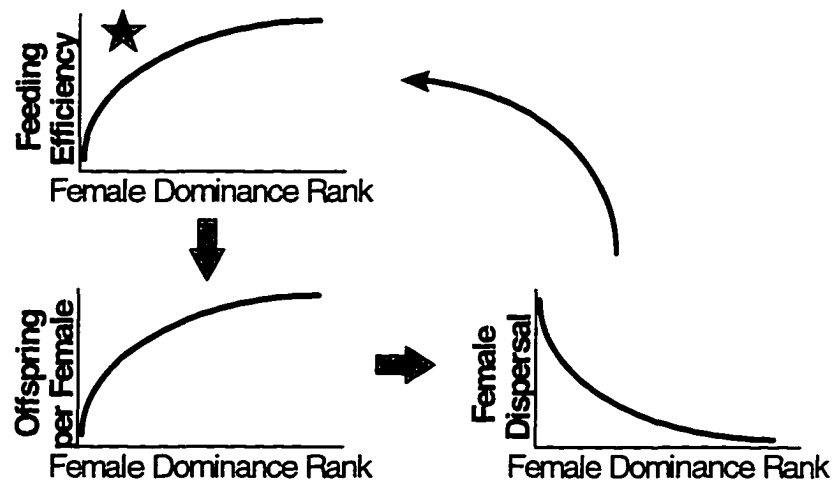
In summary, the original set of hypotheses was confirmed. With regards to group size, individual crowding increased in larger groups and feeding efficiency decreased. In large groups with low feeding efficiency, females gave fewer births per female, and it was females from those larger groups that emigrated or attempted to emigrate, thereby reducing the size of their group.

Fig. 5.4. Summary of The Effects of Group Size.



With regards to female dominance rank, lower ranking females experienced lower feeding efficiency and had fewer offspring per female. It was the low ranking females that did not give birth at all, that were the females that emigrated or attempted to emigrate to start their own new group or join an existing single-female group, thereby increasing their dominance rank. group.

Fig. 5.5. Summary of The Effects of Female Rank.



The results strongly suggest that sifakas experience real costs of living in large groups, but two important links in the proposed chain of hypotheses require more data to verify whether the observed trends are significant: 1) questions of the final energetic consequences of group size and dominance rank could be answered by body weights of females of different dominance ranks in groups of different sizes, and 2) questions of annual and life-long advantages and disadvantages of group size, female dominance rank, and different dispersal strategies on female reproductive success could be answered by long-term detailed reproductive data on females with different group membership histories.

As we begin to understand the effects of group size and dominance rank on intra-group feeding competition, and consequently on individual reproductive success, by

studying groups of a single population in a relatively uniform habitat, we gain the necessary knowledge base on which we can begin to examine consequences of different habitats. My census population encompassed groups living in a tall, gallery forest dominated by *Tamarindus indica* as well as groups living in a lower and more open semi-dry forest with xerophytic vegetation. Many demographic parameters differ in a consistent direction between these forest types. This provides an opportunity to test further hypotheses relating food, group size, dispersal, and reproductive patterns to each other. Also, because the reserve is surrounded by unprotected forest, heavily utilized by humans and livestock, and because in this region of Madagascar *sifakas* are not subject to direct pressure from humans, such as hunting, the study site provides an opportunity to quantify the indirect impact forest utilization has on primates. Because many conservation programs are trying today to create sustainable zones of wildlife and human coexistence, such study would have both scientific and conservation merits.

The influence of males on female reproductive success, as well as the story of male group membership, relative dominance, dispersal patterns, and reproductive success, such as that presented here on females, has been almost entirely omitted in these chapters. Yet, our understanding of both male and female strategies, the selective pressures that shape them, are necessary for understanding primate societies.

Finally, in order to advance our understanding of group size evolution as influenced by feeding competition, the presented here study of the patterns of *intra*-group competition needs now to be matched by a study of *inter*-group competition. The costs of group living are generally believed to result from internal factors in the group, such intra-

group feeding or reproductive competition. The benefits of group living, on the other hand, are generally believed to result from external factors, such as advantage of larger groups over smaller groups in inter-group encounters, or advantages of larger groups in detecting and deterring predators. Thus studies of costs of group living would necessarily focus on differences between groups of different size and differences between individuals within groups, while studies of the benefits of group living, would necessarily focus on differences between groups. I collected some data on inter-group interactions, which I plan to analyze in the future. However, more such data are needed, along with an analysis of small-scale vegetation patterns, to relate inter- and intra-group effects. An analysis of mortality rates in groups of different size might also reveal potential disadvantages of living in groups of different sizes. One might imagine that predation may cause greater mortality among members of smaller groups, while poorer nutrition may cause greater mortality among members of larger groups.

Achieving a better understanding of the precise selective forces operating within and between groups in different populations and species, would allow us in the end to conduct inter-species comparisons with a greater control over how we subdivide and match different ecological factors with aspects of social structure. In the absence of understanding how selection ties ecology with sociality within populations, we cannot hope to understand the evolution of diversity in primate and carnivore social systems.

The wonderful aspect of the sifaka population at Beza is that all of the projects mentioned above, however ambitious, are indeed feasible. With more empirical research conducted, species of diurnal lemuriformes living in semi-dry habitats are increasingly

proving to provide unique and great opportunities for studies intra- and inter-group dynamics in primates.

REFERENCES

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