

Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females

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Summary. The effect of variation in group size on age-specific survivorship and fecundity rates were examined in a population of wedge-capped capuchin monkeys *Cebus olivaceus* during a 10 year study. Life tables were constructed separately for four large (≥ 15 individuals) and four small groups (< 15 individuals). Female reproductive success, and its relative contribution to population growth, was much higher in large groups, primarily through higher age-specific fecundity. Age-specific survivorship was similar in groups of different sizes. The reproductive success of the single breeding male in a group was much higher in large than small groups. Compared to small groups, breeding males in large groups had a longer breeding tenure, and access to greater numbers of reproductive females with a higher average fecundity. Differences in female reproductive success apparently resulted from variation in access to monopolizable fruit trees. Large groups predictably displaced small groups during intergroup encounters. Group rank depended on the number of males resident in groups. The large number of non-breeding males in large groups results from their longer average residency time. I explain the longer residency of males in large groups by the higher average reproductive success of breeding males in these groups.

Introduction

Early attempts to account for variation in group size in primates relied on interspecific comparisons (Zuckerman 1932; Carpenter 1934; DeVore and Hall 1965; Crook and Gartlan 1966; Crook and Aldrich-Blake 1968; Eisenberg et al. 1972). These comparisons generated two general hypotheses: Group size varies with the spatial and temporal

distribution of resources and/or group size correlates with the absolute vulnerability of the species to predation. Testing these hypotheses requires comparison of the consequences of living in groups of different sizes within a species. Comparisons of the same species in different habitats or areas provided a first test (e.g. Hadow 1952; Sugiyama 1967; Gartlan and Brain 1968; Dunbar and Nathan 1972), but because habitat and group size covaried, conclusions remained inferential. Direct tests of the competing hypotheses are however possible by examining the consequences of variation in group size within a given habitat (Waser 1977; Green 1978; van Schaik et al. 1983a, b; Janson 1986).

Wrangham (1980) and van Schaik (1983) have recently derived specific predictions from these two general hypotheses. Both authors agree that as group size increases, there should be increased competition for food resources among group members. These authors differ in the relative importance they ascribe to between-group competition. Wrangham argues that individuals in large groups will be more efficient foragers because large groups can monopolize spatially clumped resources (the intergroup feeding competition theory or IGFC). Optimal group size is that at which the difference between the benefit of intergroup competition and the cost of intragroup competition is maximized. Van Schaik, on the other hand, suggests that living in large groups is advantageous because the individual's vulnerability to predators is reduced, and individual foraging efficiency will fall with increasing group size because of competition for resources within the group (the predation/intragroup feeding competition theory or PFC). Optimal group size is that at which the difference between the benefit of reduced predator vulnerability and the cost of intragroup competition is maximized.

Tests of these hypotheses might therefore compare individual foraging efficiencies in groups of different sizes. Van Schaik points out that with increasing group size, the PFC predicts a monotonic decline in foraging efficiency while the IGFC predicts an initial increase in foraging efficiency followed by a decline. However, this prediction is difficult to test directly because (a) different groups tend to eat different food items and comparisons among diets are difficult, and (b) the relationship between time budgets and feeding efficiency is exceedingly complicated (Clutton-Brock 1977; Robinson 1986; Stacey 1986). Even when using identical subjects and generating similar results, studies can yield diametrically opposite conclusions (see de Ruiter 1986; Srikosamatara 1987).

One might also compare female survivorship and fecundity in groups of different sizes. With increasing group size, van Schaik argues (a) the PFC predicts an increase in survivorship, particularly of juveniles, while the IGFC makes no prediction (b) the PFC predicts a decline in individual female fecundity in contrast to the IGFC which predicts an increase followed by a decline. Demographic information collected on a *Cebus olivaceus* population in central Venezuela between 1977 and 1986 can be used to test these two predictions.

Both of these formulations and the resulting tests, however, focus on females. For males, a general relationship between adult foraging efficiency and reproductive success has not been established (but see Clutton-Brock et al. 1982; Petrie 1983). The clearest correlate of reproductive success in males is generally the number of mates or matings an animal can secure, not his foraging efficiency (Bateman 1948; Alexander and Tinkle 1981). It is unclear therefore, how male reproductive success relates to group size in primates. In interspecific comparisons it is evident that the ratio of breeding females to breeding males is not a simple function of group size (Clutton-Brock and Harvey 1977). Both sexes need to be considered if we are to account for the variation in group size. At specified group sizes, the interests of the two sexes might be concordant or discordant. Accordingly, this study also examines the reproductive success of males in groups of different sizes.

Methods

Study area

The population of wedge-capped capuchin monkeys (*Cebus olivaceus*) inhabits a gallery forest on a working cattle ranch, Hato Masaguaral, in central Venezuela. The region is a mosaic of grassland, palm savanna, shrub woodland, and gallery forest

Table 1. Characteristics of the study groups

Group	Inter-group displacement rank ^a	Average group size	Average number of subadult years and adult males	Complete census years
Cinnamon	1	> 30	> 6	—
Northern	2	> 30	> 6	—
Main	3	26.0	4.60	1977–1986
Grey	4	21.3	5.00	1978–1984
Orange	5	22.5	3.63	1978–1985
Cocoa	6	14.3	2.25	1979–1982
Red	7	20.5	3.63	1978–1985
White	8	8.2	1.60	1977–1986
Brown	9	13.0	3.50	1984–1985
Pale	10	13.2	3.80	1977–1979, 1984–1985

^a Intergroup displacement rank based on Table 2, averages based on group size and composition at annual census, most groups censused in most years but censuses are considered complete only when all resident individuals identified

bordering permanent water. In this area, the monkeys are restricted to gallery forest that borders two rivers, the Caño Caracol and the Rio Guarico. The forest has a canopy of from 14 to 22 m, with many species of trees losing their leaves during the dry season between December and April. A full description of the habitat can be found in Robinson (1986). A grid of trails, spaced 100 m apart and running N-S and E-W, allowed access to a 5 km² study area within the gallery forest.

Hato Masaguaral has been maintained as a wildlife refuge since 1944. On the ranch, human disturbance of the forest and its fauna has been negligible. Certain common tree species, such as palms *Copernicia tectorum* and quiebrahacho *Pithecellobium tortum* are occasionally cut from the forests for fenceposts, but this activity has little effect on the abundance and distribution of resources available to the monkeys. The forest has a full complement of terrestrial predators that potentially take monkeys: jaguar *Panthera onca*, puma *Puma concolor*, ocelot *Felis pardalis*, and tayra *Eira barbara*. Potential avian predators include the Ornate Hawk-Eagle *Spizaetus ornatus*. The constricting snake *Boa constrictor* is also abundant.

Study population

At least 12 groups ranged over at least 200 ha of the 500 ha study area. Group ranges covered 200–300 ha (Robinson 1986; Srikosamatara 1987), and overlapped completely, allowing comparisons among groups that are largely independent of habitat differences. Between 1977 and 1986, a census of groups was carried out annually between May and July, months when approximately 70% of births occur (Robinson 1988). Groups were also censused opportunistically at other times of the year. Of the 12 groups in the study area, eight were censused accurately and entirely on at least two consecutive years during the study period. The number of complete censused varied with the group (Table 1).

Reliable censuses require that individual capuchins be consistently identified by observers over time. Individual monkeys show considerable variation in pelage, facial characteristics, size, age, sex and behaviour, and could be reliably identified

and described (see Robinson 1981). During each group census, the presence, absence, and reproductive condition of each animal was recorded. Animals not recorded on three consecutive censuses were acknowledged to be absent. All births to each female were recorded, as were all disappearances, deaths, emigrations and immigrations (for details see Robinson 1988).

Life-table analysis

Construction of a life table for a population requires division of animals into age-sex categories, and calculation of mortality (q_x) and fecundity (m_x) rates for each category. Capuchin monkeys can be easily sexed in the field. Ages of animals born after June 1977 are known accurately. Ages of older animals were estimated by extrapolating from census data. For instance, census data over 10 years has revealed that small primiparous females are most probably six years of age, and therefore a small primiparous female recorded as present in 1977 is assigned an age of 16 in 1986.

Both sexes were defined as infants for the first year of life, and as juveniles from one to six years of age. Females can give birth at age six, so from this age they were defined as adults. Based on age extrapolations from census data, adulthood for females lasts at least 30 years. I divided adult females into three age categories: young adults (6–16 years), middle-aged adults (16–26 years), and old adults (26–36 years of age). Males were classed as subadults between the age of six, when males are similar in size to females, and 12, when they reach full adult size and pelage development. Based on age extrapolation, adulthood for males lasted at least 24 years, and I divided this period into three age categories: young adults (12–20 years), middle-aged adults (20–28 years), and old adults (28–36 years). Therefore for females, there were nine age categories, and for males there were 10. A full definition of aging methods and age categories can be found in Robinson (1988).

Age and sex-specific mortality rates can be calculated from histories of individuals of known age and sex (for more details on procedures, see Robinson 1988). Individual histories in nine groups between 1977 and 1986 were used to calculate these rates. Age intervals began on June 23, the mean date of birth for this population. The mortality rate (q_x) was calculated for each age-sex category. This annual rate, the proportion of animals dying during the interval beginning at age x and ending one year later, can be calculated by including animals from all groups in all years,

$$q_x = f_x / N_x$$

where f_x is the number of deaths recorded in individual animals that entered the age interval x to $x+1$, and N_x is the total number of individual animals that entered this age interval during the study. These mortality rates were then used to calculate age-specific survivorship l_x which is defined as the probability that a liveborn animal will live to age x . I first calculated d_x , which is the probability of dying in each age interval x to $x+1$,

$$d_x = l_x \times q_x.$$

The survivorship at birth (l_0), by definition is 1.0. The entire survivorship schedule is then derived using

$$l_{x+1} = l_x - d_x$$

The probability of surviving to the end of the age interval, l_y , is the same as l_{x+1} for intervals that last one year. For intervals that last more than a year, l_y was estimated by assuming a constant annual q_x across the interval. The resulting age distribution is the proportion of the population surviving to each age, it is not the number of animals relative to newborns

in the population at a particular time. Robinson (1988) presents the resulting life table for the entire population. Approximately 60% of female infants survive to sexual maturity at age 6, and 40% of males survive to maturity at age 12.

The fecundity (m_x) of a females is the mean number of female offspring produced by a female during the interval beginning at age x and ending one year later. I counted the number of offspring produced by females in each adult age category, and divided by the number of females to generate this annual rate. Young adults on average give birth to 0.47 infants/year, middle aged adults to 0.45 infants/year, and old adults to 0.29 infants/year. Mean number of offspring was converted to mean number of female offspring by assuming a male: female birth sex ratio of 1:1.90 (calculated birth sex ratio between 1977 and 1986, see Robinson 1988).

The survival-fecundity rate of population increase r_s (Caughley 1977) was calculated from the survivorship and fecundity schedules. The calculated rate of increase, $r_s = 0.087$ indicates that the population was growing between 1977 and 1986.

Male residency

Residency of a male was the length of time he spent in a specified social category, and was estimated from census data. I considered three types of residency. The residency of a breeding male was the length of time that he occupied the breeding position in a group. The residency of a non-breeding adult male was the number of years that he was in the group as an adult male before he died, emigrated, or assumed the breeding position. The residency of a subadult was the number of years after he had immigrated into the group and before he died, emigrated, or became an adult.

Three methods were used to estimate male residency. The first simply counted the number of years that a male was recorded in the group during the annual census in June. Residency years did not need to be consecutive. Arrival and departure times could frequently not be dated more accurately than one year, so I assumed that the average time of arrival or departure is halfway through the year, and added half a year to each end of the residency time. An additional constraint is that the residency time of many individuals was censored. Of the 83 adult and subadult males recorded during censuses, 50 were present either on the first year the group was censused or on the last year. The total residency time was known for only 33 animals. Accordingly I used a survival analysis (SPSS 1986) which calculates residency times of all cases by assuming that censored (both arrival and departure times) and uncensored residencies have similar distributions. This analysis additionally allows statistical comparison of survival times. The second method divided the number of animals in each class in all years by the number of emigrations/deaths in all census years. The third method tabulates the duration of continuous censuses on a sample of groups, and divides by the total number of males recorded in that sample.

Results

Variation in group size

The size of groups in this population varied from 5 to more than 50 during the period 1977 to 1986. A two-way ANOVA without replication was used to examine the extent to which this variation was

Table 2. Outcome of intergroup encounters (1977–1986)

Winners	Losers										
	Cinnamon	Northern	Main	Grey	Orange	Cocoa	Red	White	Brown	Pale	Unknown
Cinnamon	–		1	1				1		2	
Northern		–	8				1	1			
Main			–	3	8	2	10	15	9		23
Grey			1	–	1			4	2	1	1
Orange			3		–			1	3		2
Cocoa						–	1				
Red							–	13			1
White								–	4		
Brown								2	–	1	
Pale										–	
Unknown			3				1	37	2		–

a consequence of within-group variation between years or of between-group variation within years. Cells contained group sizes of five groups (Main, White, Red, Orange, and Grey) that were censused annually from 1978 to 1984. The analysis revealed that both group identity ($F=25.85$, $df=4,24$, $P<0.001$) and census year ($F=5.15$, $df=6,24$, $P<0.005$) accounted for a significant proportion of the variance in group size. The population was growing throughout this period (see Robinson 1988), and the average group size of these five groups increased from 14.8 animals in 1978 to 23.0 in 1984.

In the following analysis, I define ‘small groups’ as those that averaged less than 15 individuals, and ‘large groups’ as those with averages of 15 or more individuals. Dividing the eight study groups into categories based on size is justified by the results of the ANOVA, which indicated a strong effect of the identity of the group. Individual groups were consistently either large or small. Dividing the groups at 15 animals followed from the observation that during the 10 year study, on only one census did a ‘small’ group reach 15 individuals, and during only one census did a ‘large’ group fall below 15. The small group category included White (mean group size=8.2, number of annual censuses=10), Cocoa ($\bar{x}=14.3$, $n=4$), Pale ($\bar{x}=13.2$, $n=5$), and Splinter ($\bar{x}=8.5$, $n=2$). The large group category included Main ($\bar{x}=26.0$, $n=10$), Red ($\bar{x}=20.5$, $n=8$), Orange ($\bar{x}=22.5$, $n=8$), and Grey ($\bar{x}=21.3$, $n=7$).

Group size and intergroup interactions

Ranges of different groups overlap completely. No group in the study area had access to an exclusive area, and there apparently was no relationship between the activity and isolation fields (Waser and

Wiley 1979) of groups (Robinson 1986). Many groups were using the same area, and thus groups interacted with a large number of other groups (see Robinson 1986; Srikosamatara 1987).

Animals frequently detected other groups when they were separated by 100 to 200 m. Following countercalling, adult and subadult males, and very occasionally some of the high ranking adult females, would then move towards the other group, frequently on the ground. Close range interactions were almost always restricted to males, and involved chases and threats. Physical contact was rare. One group would eventually retreat rapidly. Interactions were more prolonged if the groups contained equal numbers of adult and subadult males. If one group was smaller and contained fewer males, there was a tendency for that group to move quickly away.

The outcome of interactions were largely independent of the location of the interaction. Dyadic relationships between groups were generally stable wherever in the range they interacted; one group reliably displaced the other. Table 2 ranks groups according to the overall directionality of spatial displacements. This rank correlates with the average group size (Table 1) during the study period ($r_s=0.92$, $P<0.01$). Large groups displaced small groups.

The nature of the intergroup interaction suggests that outcomes depended less on group size *per se*, and more on the number and identity of adult and subadult males in the group. Many males would generally overwhelm a few. Large groups generally contained many subadult males. Figure 1 plots the number of males, both adult and subadult, against group size during annual censuses. A regression line is plotted to illustrate the trend, but no statistics are presented because neither axes nor annual censuses on a specific group are statisti-

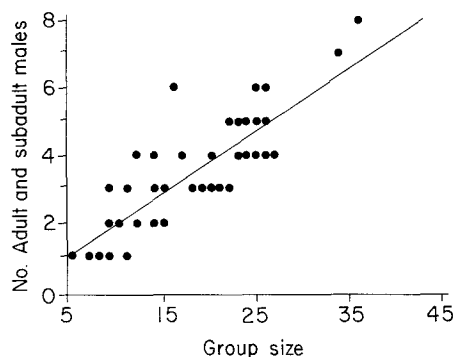


Fig. 1. Number of adult and subadult males in groups of different sizes. Each point is an annual census of one group. Line illustrates trend

cally independent. As larger groups tended to have more males, there is a strong correlation between group size and the ability of the group to displace others. The rank of groups based on spatial displacements correlated with the average number of adult and subadult males in a group ($r_s = 0.73$, $P < 0.05$). Outcomes were also influenced by the identity of the interacting males. Cocoa group outranked the larger Red group, for instance, apparently because the large breeding male in Cocoa was able to drive off the adult and subadult males of Red.

Group size and female reproductive success

Following Lotka's (1907) demonstration that the intrinsic rate of increase of a genotype depends on the schedule of births and expected mortality, a standard measure of reproductive success has been the contribution an animal makes to population growth. Contribution to population growth can be calculated from age-specific survivorship and fecundity schedules, which vary with the size of the group in this population. Therefore the relative contribution that the average female in a large group makes to population growth can be compared to the relative contribution made by the average female in a small group.

Female survivorship. If the vulnerability of animals to predation decreases with the size of the social group, then survivorship of animals in larger groups should be greater. In other studies of primates, young animals, especially infants, are more vulnerable to predators (Cheney and Wrangham 1987), so any effect of group size on survivorship should be more pronounced in these age classes.

Life tables were constructed separately for the four large groups and the four small groups (Table 3). I calculated mortality rates (q_x) for all nine female age categories (for details see Robinson

Table 3. Life tables for *Cebus olivaceus* in large and small groups (based on data collected 1977–1986)

	Age interval (x, y) in years	l_x	l_y	m_x	q_x	N_x
Large group age classes						
Infants	(0,1)	1.000	0.795	0	0.205	70.5
	(1,2)	0.795	0.719	0	0.095	47.5
	(2,3)	0.719	0.701	0	0.025	40
Juveniles	(3,4)	0.701	0.662	0	0.057	35
	(4,5)	0.662	0.640	0	0.032	31
	(5,6)	0.640	0.640	0	0	26
Young adults	(6,16)	0.640	0.497	0.313	0.025	118
Middle-aged adults	(16,26)	0.497	0.497	0.309	0	65
Old adults	(26,36)	0.497	0.107	0.210	0.157	49
Small group age classes						
Infants	(0,1)	1.000	0.923	0	0.077	15.5
	(1,2)	0.923	0.835	0	0.095	10.5
	(2,3)	0.835	0.596	0	0.286	9
Juveniles	(3,4)	0.596	0.596	0	0	9
	(4,5)	0.596	0.596	0	0	7
	(5,6)	0.596	0.596	0	0	7
Young adults	(6,16)	0.596	0.449	0.284	0.028	36
Middle-aged adults	(16,26)	0.449	0.449	0.197	0	23
Old adults	(26,36)	0.449	0.087	0.142	0.167	24

l_x = Survivorship, probability of surviving to age x; l_y = Probability of surviving to age y (end of age interval); m_x = Fecundity rate, mean number of female offspring produced per year by a female of age x (assuming birth sex ratio of 1:1.90); q_x = Mortality rate, proportion of animals alive at age x that die by age x + 1 year; N_x = Sample size used to calculate q_x

1988). I then calculated the survivorship schedules (l_x) for animals in large and small groups.

Survivorship schedules for animals in large groups are remarkably similar to those in small groups (Fig. 2). There are differences in observed mortality rates in infants and juveniles, but these are probably the result of the small sample size in each age category of the small group category. The survivorship schedules of large and small groups were not significantly different ($\chi^2 = 0.054$, $df = 1$, Log rank test, Mantel 1966). Survivorship to maturity is very similar (Large = 0.640, Small = 0.596). Mortality rates of the adult classes in large and small groups are virtually identical.

Female fecundity. Fecundity is clearly related to access to resources in primates (Dunbar 1987). If the ability of larger groups to supplant smaller groups affects the access of the latter to resources, then individual females in larger groups should be more fecund than those in smaller groups.

I first compared overall fecundity of females in each age class between large and small groups (Table 4). Overall fecundity was defined as the total number of infants born divided by the product of the number of adult females in each category and the number of census years. In all three age classes, overall fecundity of females in large groups was higher than in small groups. Within each group size category, fecundity drops with age. However, in large groups, fecundity does not drop dramatically until the old age class, while in small groups it drops throughout life.

I then examined the relationship between average group size of a group and overall fecundity of that group (Fig. 3). Average group size was measured as a simple average of the total number of animals in the group during June of each census year. Average group size accounted for 56% of the variance in overall fecundity, and the positive regression between the two variables was statistically significant ($P < 0.05$).

If survivorship of juveniles in large and small groups is similar, as suggested above, then a higher fecundity in large groups should translate into more juveniles per female in large groups. Figure 4 plots the number of juveniles per female in annual censuses of the study groups. A line is plotted to illustrate the positive trend. Because censuses of the same group in different years are not independent of one another, no statistics are presented.

Female contribution to population growth. The greater fecundity and similar survivorship of females in large groups means that these females

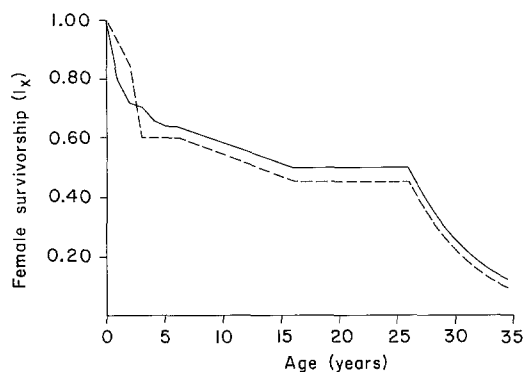


Fig. 2. Age-specific survivorship for females in large groups (—) and small groups (----).

Table 4. Variation in fecundity (offspring/female/year) with group size and age

	Small groups	Large groups	Overall
Young females	0.433	0.477	0.469
Middle aged females	0.300	0.471	0.450
Old females	0.217	0.320	0.288

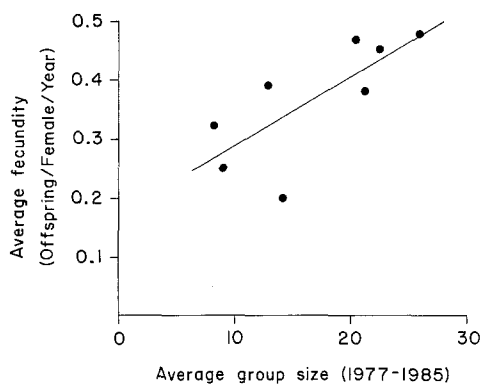


Fig. 3. Effect of group size of female fecundity. Each point is the average size of each group and the average female fecundity throughout the census period. The calculated regression line is plotted ($y = 0.012x + 0.17$, $r^2 = 0.56$).

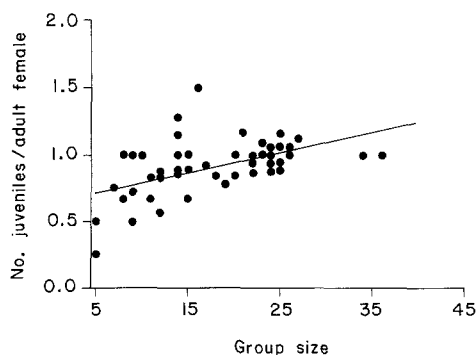


Fig. 4. Number of juveniles per adult female in groups of different sizes. Each point is an annual census of one group. Line illustrates trend.

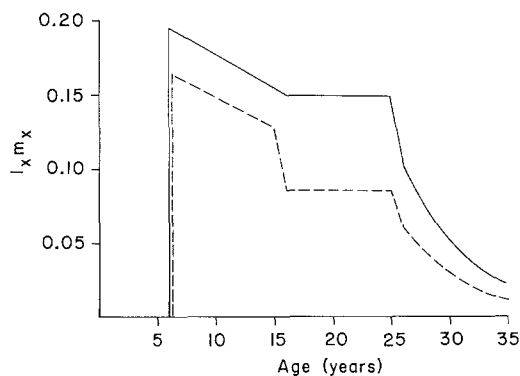


Fig. 5. Comparison of the reproductive rates of the average female in large groups (—) and small groups (----). $l_x m_x$ curves calculated from observed survivorship and fecundity schedules

Table 5. Variation in sex of offspring produced in small and large groups

	Small groups	Large groups	Overall
Males	8	21	29
Females	10	45	55
Totals	18	66	84

have a higher reproductive rate than females in small groups. The reproductive rate, which is the multiplication rate per generation, is calculated as the sum of the product of age-specific survivorship and fecundity rates ($\sum l_x m_x$). Figure 5 compares the reproductive rates of females in large and small groups. The areas under the two curves measures the relative contribution to population growth of the average female in a large group and in a small group. A female in a large group contributes more to population growth, and to the ancestry of future generations than a female in a small group.

Another way to illustrate the disproportionate contribution of females in large groups to population growth is to extrapolate out the percentage of the female population in large and small groups through time, based on the two sets of life tables. At the present time, 42% of the adult females in the study population live in small groups. Using the calculated rates of increase for females in large and small groups, this will fall to 26% in 25 years. This extrapolation assumes that large groups remain large and small groups remain small, and females do not emigrate from small groups into large groups.

A female's contribution to population growth can also vary with the sex of the offspring she produces. Table 5 suggests that the birth sex ratio of large and small groups differs. During the

10 years of this study, the birth sex ratio of the entire population was 1:1.9, and Robinson (1988) suggested that female-biased sex ratios might characterize *Cebus* populations when resources are not limited. If females in large groups have greater access to fruit resources, the prediction follows that the female bias should be more pronounced in the four large groups. The birth sex ratio in large groups of 1:2.1 was significantly different from unity ($z_c = 2.83$, $P < 0.005$, one-tailed test of binomial proportions, Snedecor and Cochran 1974). In small groups, the birth sex ratio of 1:1.25 was not significantly different from unity, but it was significantly different from the sex ratio observed in large groups ($z_c = 1.94$, $P < 0.05$, one-tailed test). Females in small groups appear to produce a higher percentage of sons than females in large groups.

Group size and male reproductive success

Male reproductive success depends primarily on the length of breeding tenure obtained by a male and the number of reproductive females in that group. Breeding tenure is the length of time that an animal is the breeding male in a group (Hrdy 1974; Chapman and Hausfater 1979). *Cebus olivaceus* groups typically contain a single full-sized adult male. Even in groups containing more than one male, only a single male apparently breeds. Other adult males, if present, are found at the periphery of the group. Adult females rarely groom or engage in affiliative interactions with these peripheral males, and frequently are aggressive towards them. This contrasts with the social role of the breeding male. He is usually found at the front-center of the foraging group, and he is groomed frequently by adult females. When females are in oestrus, they follow and solicit him for copulation. The breeding male was the only male observed to copulate during months of the year when females generally conceive (Robinson 1981; Robinson and Janson 1987).

The breeding residency of a male in a large group, based on the survival analysis, is at least nine years, while the tenure of a male in a small group is about half as long (Table 6). Sample sizes were small and all but two residencies were censored, so this difference is not statistically significant ($\chi^2 = 0.439$, $df = 1$, $P = 0.51$). The two other methods of computing residencies give comparable results. In addition to the length of breeding tenure, the process of male changeover differs between large and small groups. When breeding males were replaced in large groups, it was always by males

Table 6. Residency in years of males in groups. Method 1 gives the median value, Method 2 and 3 give means. Sample sizes in brackets (Method 1 = number of individuals, Method 2 = number of individual-years, Method 3 = number of group-years)

	Method 1		Method 2		Method 3	
	Large groups	Small groups	Large groups	Small groups	Large groups	Small groups
Breeding males	9.0+ (8)	4.5+(10)	9.0 (36)	6.2 (31)	8.3 (33)	5.2 (26)
Other adult males	2.8 (6)	1.4 (4)	3.5 (14)	2.3 (7)		
Subadult males	5.4 (37)	3.6 (26)	7.3 (110)	2.5 (37)		

who had already been present in the group for a number of years ($n=4$). In contrast, male changeovers in small groups always involved takeovers by extragroup adult males ($n=5$). Adult males were only observed to immigrate into small groups. This high permeability of small groups to immigration and takeover may be due to the absence of large numbers of subadult males in these groups.

The large number of subadult males, and occasionally other adult males, in large groups is not a consequence of more immigration into these groups. The immigration rate into large groups (1.0 immigrations/group-year, $n=30$) is similar to that into small groups (0.94 immigrations/group-year, $n=16$). Instead, the residency times of both subadults and non-breeding adults is much longer in large groups (Table 6). For subadults, the survival analysis comparison between large and small groups is statistically significant ($\chi^2=5.48$, $df=1$, $P=0.019$, number of censored residencies = 24,15). For other adult males it is not ($\chi^2=1.36$, $df=1$, $P=0.24$, number of censored residencies = 3,2). The calculated residency of subadult males suggests that once a subadult has immigrated into a large group, on average he remains there at least until he reaches adulthood.

The larger number of reproductive females in large groups, and the higher reproductive success of these females, further enhances the reproductive success of the breeding male. To illustrate, a breeding male in a large group of 25 individuals with eight adult females will, on average, produce 31.2 offspring during his tenure. This calculation assumes that females produce 0.47 offspring per year (from equation in Fig. 3), and the average breeding male tenure of 8.3 years. A breeding male in a small group of 10 individuals with three adult females will, on average, produce 4.5 offspring during his tenure. This assumes that females produce 0.29 offspring per year, and an average breeding male tenure of 5.2 years. This production of offspring is equivalent to the reproductive success of a male if males do not assume the breeding position in more than one group. This seems to be

generally true. In seven of the 10 changeovers observed, the original male was not found again. In one case, he migrated into another group as a non-breeding adult and then disappeared. However, in one case, the breeding male in a small group became the breeding male in another small group. In another case, the original breeding male in a large group did not emigrate and resumed his breeding role by the census of the subsequent year. A second opportunity therefore is rare but possible.

Discussion

Primates might benefit from living in large groups by reducing their vulnerability to predators (DeVore and Hall 1965; Eisenberg et al. 1972; Altmann 1974; Alexander 1974; Terborgh 1983; van Schaik 1983). If there are no other influences on survivorship, the probability of surviving should be higher in larger groups of a species. Any difference in survivorship between animals in larger and smaller groups should be more pronounced in the immature age classes who presumably are more vulnerable to predators (van Schaik 1983). In this study of *Cebus olivaceus*, a full complement of predators was present, yet survivorship schedules of females in large and small groups were very similar. This result does not conclusively reject a relationship between group size and vulnerability to predators. It could be argued that the survivorship of animals living in large groups is enhanced through protection from predators, but decreased through high intragroup food competition. One way to address this question is to compare the survivorship of groups of similar sizes living in habitats which differ only by the presence of predators (van Schaik 1983).

Primates might benefit from living in large groups by increasing their foraging efficiency (Eisenberg et al. 1972; Altmann 1974; Wrangham 1980, 1987). Although there are numerous mechanisms by which individuals might enhance their foraging efficiency when living in a group,

Wrangham's postulate that larger groups gain by their ability to displace smaller groups from patchily distributed food resources, has a number of pre-requisites that apply to *Cebus olivaceus*. In this population, (a) group ranges are large and overlap one another completely (Robinson 1986), (b) animals feed at fruit trees which are themselves resource patches, and are frequently patchily distributed through the area (Robinson 1986), (c) groups are composed of matrilineal females and associated non-related males (Robinson 1981), and (d) the ability of a group to displace other groups is site-independent but is related to the size of the interacting groups.

Under these circumstances, Wrangham predicted that the foraging efficiency of females in large groups should be greater. De Ruiter (1986) in a preliminary study, and Srikosamatara (1987) compared the foraging of two groups of *Cebus olivaceus* in this population. Main group was composed of between 25 and 36 individuals during their studies, while White group was composed of between 5 and 9 individuals. Both studies described significant differences in the diet and average time budgets of animals in the two groups. Srikosamatara demonstrated that the small group both interacted with and was displaced by other groups more frequently. These intergroup interactions increased the day range of the small group, and frequently reversed their ongoing movement patterns. As a consequence, animals in the small group were denied access to fruiting species that were patchily distributed in space and relatively uncommon.

A relationship between foraging efficiency and a female's reproductive success is a central justification for many foraging studies. A number of studies have demonstrated a relationship between a female's nutritional condition and the rate at which she produces offspring (Sadleir 1969; Harpending 1976; Mori 1979). Because it appears that females in large groups have greater access to resources (Srikosamatara 1987), I expected that they would show higher fecundity than females in small groups. The observed relationship between group size and fecundity, and between group size and number of juveniles per adult female accords with this expectation, and indicates that the reproductive success of females in large groups is greater than in small groups. These results do not support the predictions outlined by van Schaik for the PFC theory. There is a suggestion however that intragroup feeding competition might lower fecundity in the very largest groups. During two years when there was over 30 animals in Main group and just before the group fissioned, the number of juveniles

per female fell below the general trend (see Fig. 4). This pattern is similar to that reported for *Alouatta palliata* by Calhoun (1963).

The *Cebus olivaceus* results accord with the predictions of the IFGC model, and indicate that it is advantageous for females to live in large groups. As females grow up and breed in their natal groups, the chance of birth strongly affects their relative contribution to population growth. Females should attempt to remain in large groups and produce offspring that do likewise. Indeed, large groups remained large, and never dwindled to produced small groups. When large groups fissioned (see Robinson 1988), at least one of the resulting groups remained large. Large groups, in effect, bud off small groups, and do not fission to produce only small groups. In the closely followed fission of Main group in 1984, the resulting groups were composed of 28 and 9 animals. The small group that budded off was composed of two low ranking matrilineal females. When Cinammon group fissioned in 1981, one of the resulting groups included about 30 animals.

Females in small groups might gain membership in a large group if females are able to emigrate out of small groups into large groups, if small groups are able to fuse into large groups or if they grow into large groups. There are no records of females emigrating out of small groups into large groups. Female dispersal, while rare, does occur, but in all cases, adult females have moved into small groups, not into large groups. A fusion of a small group with part of another small group has been recorded (Robinson 1988), but even this did not produce a large group. Small groups rarely grow into large groups. With the exception of Red group which included only 11 animals in 1978, not one of the other five small groups followed during the study period broke the "15-animal barrier". Females in small groups apparently alleviate their relative disadvantage by producing a greater proportion of male offspring than females in large groups, males which might be able to migrate into large groups and ultimately assume a breeding position.

A focus on females is however misleading. The IFGC model was derived from the scenario that "female-bonded" social groups evolved as alliances among females in the competition for patchily distributed food resources (Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Wrangham 1980). The model suggests that it is the number of related females that determine a group's ability to displace other groups. In *Cebus olivaceus* however, like many other primate species

(Cheney 1987), it is the males, not the females, that are most active during intergroup encounters. And it is the number of males that determine the outcome of encounters, and the group's subsequent access to resources.

The large number of males in large groups can be explained by their longer residency. The longer residency in turn can be explained if male feeding efficiency, like that of females, is enhanced. However, the longer residency in large groups more probably is related to a male's expected reproductive success at the time when he enters a large or a small group. Expected reproductive success is the product of the probability that an animal will achieve breeding status and his average reproductive success if he does. The probability that an animal will achieve breeding status depends on the number of competing males resident in a group. The average reproductive success of a breeding male depends on the number of reproductive females in the group and the length of his breeding tenure. Young males should therefore enter and remain in groups with the greatest numbers of females and the fewest number of competing males. This will eventually result in an equilibrium situation in which the expected reproductive success of a male is the same whether he resides in a large or a small group, but there will be more males in groups with more females.

In addition to enhancing the foraging success of the females, these males directly affect the reproductive success of both the adult females and the breeding males. The presence of these males reduces the possibility of immigration and breeding takeover by extragroup adult males. Breeding male changeovers in large groups have always been through inheritance within the group, in contrast to changeovers in small groups, which have always involved extragroup male takeover. This social stability might augment the reproductive success of females and presumably is responsible for the longer breeding male tenure in large groups. The long breeding tenure and the high reproductive success of adult females, together with the large number of females, further enhances the reproductive success of the breeding male in a large group. In addition, the female offspring produced in a large group have a much higher reproductive value than female offspring produced in a small group. I have no data concerning variation in the reproductive value of male offspring produced in groups of different sizes.

In summary, the reproductive success of females in large groups is greater than that of females in small groups. This apparently results from their

greater access to resources. The greater access to resources of large groups is a consequence of the large number of resident subadult and adult males. There are more resident males in large groups because the value of the breeding position is higher than in small groups. The resident males further enhance the reproductive success of both males and females by increasing breeding male tenure and social stability. Reproductive success of both males and females therefore depends on the size of the group in which the animal lives. The age-sex composition of groups, the probability of dispersal and residency times, the sex ratio of produced offspring, all reflect this situation.

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