Subgrouping Patterns in a Group of Wild *Cebus apella nigritus*

Jessica W. Lynch Alfaro

Abstract Seasonal patterns of group fragmentation, including the size of subgroups and percentage of time spent in subgroups, may provide information on individual decision-making in response to resource distribution. Age-sex class composition of subgroup membership can offer insights into the social dynamics of the group as a whole. At most field sites, capuchins (*Cebus* spp.) form stable groups with no evidence of group fragmentation. Here I describe seasonal subgrouping patterns, including proportion of time spent in subgroups, subgroup size, age-sex membership, dyadic fidelity, stability of membership, and the effect of subgrouping on individual foraging efficiency, in a group of wild *Cebus apella nigritus*. From September 1996 to August 1997 the study group at the Estação Biológica de Caratinga, Brazil divided into 148 different subgroups, on 99 of 194 census days. In contrast to expectations for subgrouping patterns as a response to seasonal distribution of resources, the proportion of days spent in subgroups did not vary significantly by season. Subgroup composition was relatively fluid, with multimale multifemale subgroups the most common throughout the year. Unimale multifemale subgroups were restricted to the wet season; in contrast, all-male subgroups and unimale unifemale subgroups occurred in the dry season. For both males and females, low rank predicted membership in smaller subgroups. For males, but not females, subgrouping coincided with increased foraging efficiency, as measured by increased time spent ingesting food and decreased time spent traveling on days with subgrouping compared to days with the group in a cohesive unit.

Keywords capuchins · fission · group size · seasonality · subgroups

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Introduction

A subgroup is formed when any number of individuals, fewer than the total group, remains out of visual and vocal contact with all other members of the group, and travels, feeds, or rests together as a smaller unit. Subgrouping behavior appears obligate in a few primate species (chimpanzees, *Pan troglodytes*: Chapman *et al.* 1995; hamadryas baboons, *Papio hamadryas*: Kummer 1968) and facultative in many others (ruffed lemurs, *Variecia variegata*: Morland 1991; Rigamonti 1993; White 1991, mantled howlers, *Alouatta palliata*, Chapman 1988; Jones 1995; Japanese macaques, *Macaca fuscata*: Fukuda 1989; long-tailed macaques, *Macaca fascicularis*: van Schaik *et al.* 1983; van Noordwijk and van Schaik 1987; black-headed uakaris, *Cacajao melanocephalus*: Boubli 1999; Defler 1999; and muriquis, *Brachyteles arachnoides*, Milton 1984; Strier *et al.* 1993). One example of a taxon with facultative subgrouping is the capuchins (*Cebus* spp.). At most field sites, capuchin groups are stable in composition and do not divide into subgroups (*Cebus apella*: Di Bitetti and Janson 2000, 2001; Izawa 1990, 1992, 1997; Janson 1986; Robinson and Janson 1987; *C. olivaceus*: Miller 1996; Robinson 1988a, b; *C. capucinus*: Fedigan *et al.* 1996; Panger 1997; Perry 1996a, b). However, there is growing evidence that in some populations, capuchin groups may divide into subgroups either as a response to seasonal distribution of resources or as a precursor to group fission.

In particular, some censuses suggest that seasonal subgrouping may occur in *Cebus apella*. For example, Soini (1986) reported that at Pacaya-Samiria National Reserve, Perú, small groups of 2–4 *Cebus apella* seemed to be dispersed subgroups of larger groups. *Cebus apella* at Peneya River, Colombia, frequently formed temporary subgroups, as occurs in spider monkeys (Izawa 1976, 1980), but they never became habituated to the observer (Izawa 1980). In southeastern Brazil, Izar (2003) found that mean group size for *Cebus apella nigritus* censused at Carlos Botelho State Park was significantly lower in the dry than in the wet season, primarily owing to an increase in groups of: solitary males; 1 or 2 adult females with offspring; and 1 adult male, 1 adult female and offspring. Censusing capuchin groups and determining accurate group size and membership are difficult, in part because individuals within capuchin groups are often widely dispersed from one another while foraging or traveling (Izawa 1980; Kinzey and Cunningham 1994; Robinson and Janson 1987; Rímoli and Lynch, *unpubl. data*). However, Izar (2003) provided evidence that subgrouping in capuchins might be a dry season response to increased reliance on consumption of dispersed resources, as the capuchin diet shifted to mainly invertebrates and the foliar base of bromeliads during months with small group size.

Capuchin subgrouping can also occur during group fission and long-term division of home range. Izawa (1992, 1994a, b) reported group fission in a group of 22 *Cebus apella*, the largest group size reported in La Macarena during 5 yr of study. The split occurred after a severe male-male attack within the group, probably instigated by provisioning (Izawa 1994a). After the attack, 2 severely wounded males remained as solitaries, 3 adults disappeared, and the remaining individuals formed 2 new groups with 10 and 7 members (Izawa 1994a). The larger group included 3 adult males and females from the 3 highest-ranking matrilines, while the smaller group was composed of females from the lowest-ranking matriline along with 1 subadult and 1 juvenile male.

In southeastern Brazil, group fission in *Cebus apella nigritus* occurred after the disappearance of the α-male and female of the group, and the remaining group members subdivided evenly along matrilines (Izar 2003). Interestingly, 10 mo after group fission, several of the original group members reunited to reform a larger group (Izar 2003).

Robinson (1988b) reported group fission in wedge-capped capuchins (*Cebus olivaceus*). Before fission of a group with 37 individuals, 2 adult males and 2 low-ranking females and their offspring frequently foraged separately from the rest of the group during a 2-mo period (Robinson 1988a, b). When the others moved to another area of the home range, the subgroup remained behind, and eventually moved into a new area that capuchins had not occupied before (Robinson 1988a). One of the resulting groups was significantly larger than the other (28 vs. 9 individuals: Robinson 1988b), and the smaller group was composed of 2 low-ranking matrilines (Robinson 1988b). This budding off of low-ranking matrilines from large groups into smaller groups is similar to group fission in cercopithecine primates, particularly *Macaca* (*M. fuscata*: Koyama 1970; *M. mulatta*: Chepko-Sade and Sade 1979; Malik *et al.* 1985; *M. sinica*: Dittus 1988), and is probably a result of the similarity in social organization, with female kin forming the strongest affiliations, and rank an important mediator of relationship strength among females.

As Chapman (1990) pointed out, ecological conditions may affect subgroup size, but it is not apparent how ecology directly affects subgroup composition. In other words, the sex-age class composition of smaller units may be more immediately dependent on social rather than environmental factors. For example, large multimale hamadryas baboon groups consistently break into smaller unimale subgroups, in which each male associates with adult females and their juveniles and infants (Kummer 1968). In contrast, the most frequent spider monkey subgroup is of adult females traveling with their young, not associated with any adult male (Chapman 1990). Ruffed lemur groups often divide into male-female pairs and associated offspring (Rigamonti 1993). In macaques, low-ranking adult females tend to form small subgroups away from the main group (Dittus 1988; van Noordwijk and van Schaik 1987). Subadult male ring-tailed lemurs (Jolly 1972) and squirrel monkeys (Soini 1986) will travel at a distance from the main group when resources are scarce. Subgrouping patterns reflect the strength of social bonds or associations within the group as a whole, so different mating, dominance, and dispersal patterns can determine different age-sex class compositions within subgroups.

I present a detailed description of the subgrouping patterns in a wild group of *Cebus apella nigritus* at the Estação Biológica de Caratinga (EBC), Brazil from September 1996 to August 1997. Rímoli (2001) studied foraging ecology in the same group for 14 mo (June 1995 to August 1996) immediately before my research. In that study, data collected on time spent feeding showed that fruits and seeds were the primary component of the group's diet in the wet season, and that invertebrates and vegetable matter—bark, stems, vines—became most important in the dry season (Rímoli 2001). Sugar cane and corn raided from fields and storehouses were relatively constant resources, making up ca. 20% of the group's feeding time in both wet and dry seasons (Rímoli 2001). In the feeding ecology study, researchers did not record data on subgrouping patterns (Rímoli, *pers. comm.*).

I compare the observed data on seasonality of subgroup size and percentage of time spent in subgroups, stability of subgroup membership, and effect of subgrouping on foraging efficency to expectations for subgroup patterns that result from 1) increased intragroup foraging competition, affecting lower-ranking individuals most strongly, and perhaps ultimately leading to their permanent separation from a group and 2) group-wide facultative responses to seasonal changes in resource distribution. Note that, in both scenarios, subgrouping behavior is ultimately driven by foraging decisions. Group fission may be the result of either direct intragroup feeding competition or of the cost of travel time, which increases with group size in capuchins, and differentially affects low-ranking individuals (Robinson 1988b). In contrast, in a group-wide response to seasonal distribution of resources, all group members might benefit from distributing themselves across the landscape to match resource distribution, breaking into subgroups when no large patches of fruit are available.

Regardless of the cause of subgrouping, subgroup age-sex class composition should be predictable based on the strength of social bonds among different age-sex classes in *Cebus apella* (Di Bitetti 1997; Izawa 1980, 1994a, b, 1997; Izar 2003; Janson 1984, 1986; Lynch 2001). I expect the α-male to form subgroups with high-ranking females and their offspring, lower-ranking females to form subgroups with their offspring, and subordinate adult males and subadult males to form subgroups together, or to be solitary. If groups of different sizes occur, lower-ranking females will be present more often in smaller subgroups, and higher-ranking females in the larger subgroups (Chepko-Sade and Sade 1979; Dittus 1988; Koyama 1970; Malik *et al.* 1985; Robinson 1988b). Subadult or juvenile males will have a higher frequency of membership in the smaller subgroups than adult males will (Dittus 1988).

If the subgroups at EBC represent incipient new groups, they may resolve themselves into stable subunits relatively quickly. There should be both an increasing stability of subgroup membership through time and an increasing proportion of time spent in subgroups, as the splinter group becomes more independent from the main group (Malik et al. 1985). Foraging efficiency will be lowest for low-ranking individuals when the group is cohesive, particularly in the dry season when resources are scarce (Izar 2003). Low-ranking individuals will benefit most from splitting off into subgroups, seen as a relative increase in foraging efficiency (ratio of time spent ingesting food to time spent traveling) when they are in subgroups.

In contrast, if subgrouping is a group-wide response to changing resource distribution, I predict fluid subgroup composition, with no expectation that subgroups become more stable in composition through time. In Izar's (2003) study, *Cebus apella nigritus* were present in smaller groups in the dry season, at which time they were feeding on dispersed resources, such as bromeliads and invertebrates. The capuchins at EBC also switch to invertebrates and vegetable matter during the dry season (Rímoli 2001), so I predict smaller mean subgroup size and an increase in the proportion of time spent in subgroups in the dry season in study. Rímoli (2001) reported no difference in either time spent ingesting food or time spent traveling from wet ($n=1$) to dry ($n=2$) seasons for the group, despite their change in diet. If capuchins manage their activity budget through fluid grouping in response to seasonal resource changes, I predict relatively small variance in foraging efficiency by rank, season, or group size.

Methods

Field Site and Study Group

I collected data from September 1996 through August 1997 at EBC, a 890-ha fragment (Rímoli 2001) of Atlantic forest in Minas Gerais, Brazil, known as a long-term field site for muriquis (*Brachyteles arachnoides hypoxanthus*: Strier 1992), buffy-headed marmosets (*Callithrix flaviceps*: Ferrari 1988; Guimarães 1998), and brown howlers (*Alouatta fusca*: Mendes 1989; Strier *et al.* 2001). Researchers have also studied black-horned capuchins (*Cebus apella nigritus*) at EBC (Lynch Alfaro 2005; Lynch and Rímoli 2000; Rímoli and Ferrari 1997), and the main study group was well habituated to observers at the onset of the project (Rímoli 2001). Individuals were recognizable via pelage patterns and facial characteristics. The group was the largest censused in the EBC forest (Lynch and Rímoli 2000), with group size ranging from 24 to 28 individuals during the study period, as a result of 4 births and the loss of 2 infants and 1 juvenile (Lynch and Rímoli 2000). All of the adults and juveniles had been in the group for ≥1 yr at the beginning of this study, and their membership remained constant throughout the year, so that excluding infants, group membership did not change from 24 individuals.

Observation Methods

I recorded a census of group members daily on a checklist with the names of all individuals in the group. I considered the group a cohesive unit when I ticked all individuals for a given day, while the observer remained with that group. I considered the census incomplete on days that the group was lost before the observer was able to identify all individuals, or when the viewing conditions were so poor that the observer could not identify all individuals seen.

I used stringent guidelines to distinguish true subgroups from a widely dispersed group that was traveling as a single unit. I considered observed individuals to be a distinct subgroup only when I had 1) censused all individuals present, 2) recounted all the individuals at least twice, and 3) traveled with the group of individuals for ≥1 h with no change in group membership. Various lines of evidence confirmed the existence of discrete subgroups, which traveled and foraged separately in the forest out of visual and vocal contact from one another. For example, in 11 cases, identical subgroup membership was repeated on consecutive days. I frequently identified subgroups with reciprocal memberships on the same or subsequent days. When subgroups reunited, traveling from different directions, individuals performed reunion displays, hugging, mounting, or screaming (Lynch Alfaro, in prep.), which occurs in captive *Cebus apella* when an individual is reintroduced to the cage after being isolated completely from the group (Matheson *et al.* 1996; Philips and Shauver Goodchild 2005). From February through June 1997, a field assistant traveled separately with subgroups other than the one that I was following, which allowed for the simultaneous observation of the different locations and different direction of movement of different subgroups, confirming that 2 subgroups were out of the range of communication with one another (except perhaps olfactory cues from urine washing

or scent marking on trees). I included only subgroups for which I was confident of entire membership in the analyses.

I took a scan sample (Altmann 1974a) on each individual's activity—ingesting food, handling food, searching for food, traveling, resting, social behavior, or other-once every hour for all observed individuals. Owing to the dense vegetation throughout much of the study group's home range, and the dispersed nature of the group, I allotted 5 min to complete each scan sample (Altmann 1974a).

To determine rank of individuals within the group, I recorded data on both approach-retreat interactions and dyadic aggressive interactions, noting the individuals involved and the direction of signals (Lynch 2001). I entered approach-avoid interactions into a matrix to construct a dominance hierarchy (modified from Perry 1995). I produced an alternate dominance hierarchy on the basis of the actors and recipients in dyadic aggressive interactions (Di Bitetti 1997). As both methods of constructing the hierarchy produced similar and corroborative results, I pooled the 2 data sets. I analyzed the combined data set in Peck Order 2.03 (Hailman and Hailman) to test for linearity of the dominance hierarchy. Because the data set does not have interactions for all dyads, and there are some reversals, the data do not define a unique linear hierarchy. However, there are few reversals, and dominance appears transitive across individuals. When the rank relationships are ambiguous because of reversals or because of no datum across particular dyads, I gave ≥2 individuals the same rank.

Analyses of seasonal variation in subgroup size and composition use wet and dry seasons per Strier et al. (1999) for the same year and location. For more detailed analyses of temporal changes in subgroup patterns, I divided the data into 15-d periods.

Statistical Analyses

I counted each day in which I encountered and followed a new subgroup as 1 observation of that subgroup. If a subgroup retained the same composition over multiple days, I counted it as 1 observation for the length of the days. If a subgroup changed membership while the observer followed it, I counted the resultant subgroup as a new observation. I excluded dependent infants from all statistical analyses. Thus operative group size remained at 24 individuals throughout the year, allowing parallel comparison of subgroup size from season to season.

I utilized an association index (Chapman 1990; Symington 1990; also called familiarity index in Nishida and Hiraiwa-Hasegawa 1987), which controlled for unequal number of observations of each individual, via the following equation: $100c/(a + b + c)$, which contains 2 individuals, A and B; a=the number of subgroups that contain A but not B, b=the number of subgroups that contain B but not A, and c=the number of subgroups containing both A and B. I performed hierarchical cluster analysis on the results for each dyad, to construct a phenogram of degree of association between individuals in their membership of all subgroups.

To test whether individuals of all ranks were equally likely to be present in subgroups of the same size, I first calculated the mean subgroup size per individual per 15-d observation period throughout the study, then from the period means calculated a yearly mean subgroup size per individual, and performed a regression analysis of mean subgroup size by individual rank.

To determine how subgrouping affected activity budget, I compared percentage time spent traveling, searching for food, handling food, ingesting food, resting, and socializing, for each individual, based on scan sample data, for days with subgrouping compared to days with the group intact. To test the effect of subgrouping on foraging efficiency further, I took the ratio of time spent traveling to time spent ingesting food, and tested the directional change in the ratio by pairwise comparisons of each individual across whole group and subgroup conditions.

Results

Subgroup Size Distribution and Seasonality

The main capuchin group fragmented into smaller subgroups on more than half ($n=99$ of 194) of the observation days in which a census was completed. Across the study period, I recorded 148 different subgroups of the main group. Subgroups were relatively stable during a given day. On 66 d, I observed only 1 subgroup, without change in composition. On the remaining 33 days, I recorded 2–4 subgroups, either because the observed subgroup changed composition, or because I located >1 subgroup independently during that day.

Subgroup size was variable, reflecting relatively fluid membership. Subgroup size ranged from 1 to 23 individuals, and a frequency histogram of subgroup size approximated a bimodal distribution (Fig. 1, modes=2 and 20, median=14). To test
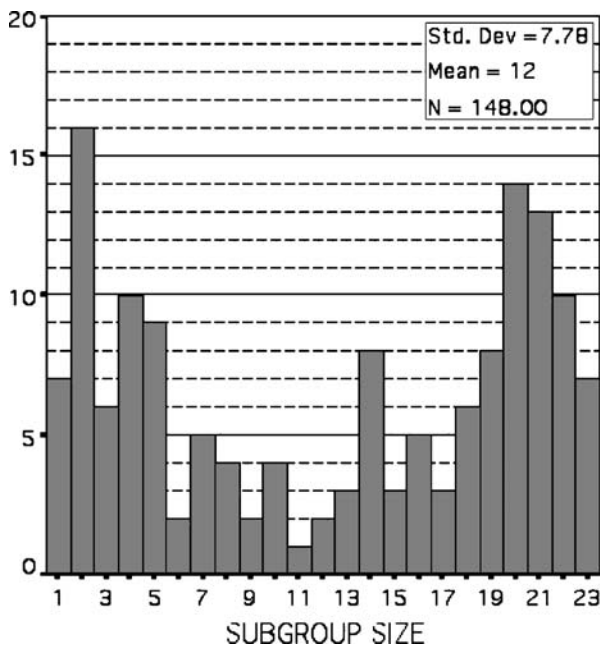

Fig. 1 Frequency histogram of the size of capuchin subgroups during the study year ($n=148$ subgroups).

for seasonality of subgroup size distribution, I compared frequency histograms between the wet and dry season (Fig. 2). In the wet season, subgroup size was trimodal, with peaks at 5, 14, and 21 individuals/subgroup ($n=88$, median=13). In contrast, in the dry season, subgroup size showed a bimodal distribution, with peaks
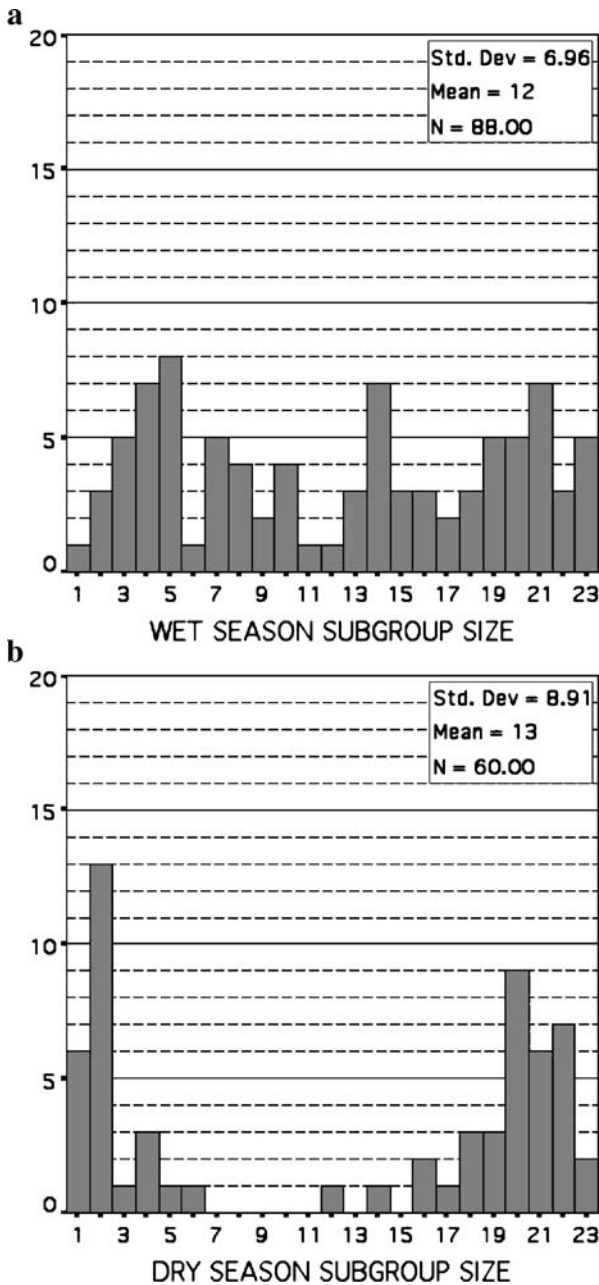

Fig. 2 Frequency histograms of the size of capuchin subgroups observed in the (**a**) wet and (**b**) dry seasons.

Table I Proportion of observation days with completed census that included subgroups, across 15-day periods throughout the study

Period(15-day intervals)	Subgroup days/ census days	% Days	No. of groups	Mean	Median	Range	Modes
9/12/96	0/12	0	–	–	–	–	–
9/27/96	0/13	0	–	–	–	–	–
10/12/96	9/11	81.8	12	14.3	19	2–23	4
10/27/96	13/14	92.9	30	10.7	10	3–21	3, 5, 10, 14
11/11/96	0/11	0	–	–	–	–	–
11/26/96	2/6	33.3	2	12.5	12.5	4–21	4, 21
12/11/96	8/13	61.5	12	9.3	7.5	1–23	3, 7, 8
12/26/96	1/2	50	1	21	21	21	21
1/10/97	4/4	100	5	10.4	5	2–22	5
1/25/97	3/4	75	3	13	15	7–17	7, 15, 17
2/9/97Δ	2/4	50	2	17.5	17.5	14–21	14, 21
2/24/97Δ	4/6	66.7	5	15	14	9–23	9, 10, 14, 19, 23
3/11/97	–	–	–	–	–	–	–
3/26/97Δ	4/7	57.1	6	13.5	17	4–20	18
4/10/97Δ	7/11	63.6	10	15.3	18	4–23	5, 23
WET TOTAL:	57/118	48.3%	88	12.3	13	1–23	5, 14, 21
4/25/97Δ	*5/15*	*33.3*	*5*	*15.6*	*21*	*1–23*	*21*
5/10/97Δ	*2/12*	*16.7*	*3*	*14.7*	*20*	*1–23*	*1, 20, 23*
5/25/97Δ	*2/9*	*22.2*	*3*	*15.7*	*20*	*5–22*	*5, 20, 22*
6/9/97Δ	*4/10*	*40*	*5*	*12.8*	*14*	*2–21*	*21*
6/24/97	*11/11*	*100*	*16*	*10.1*	*4*	*1–22*	*2*
7/9/97	*13/14*	*92.9*	*22*	*12.5*	*17.5*	*1–22*	*2*
7/24/97	*5/5*	*100*	*6*	*13.3*	*18*	*1–22*	*18*
DRY TOTAL:	*42/76*	*55.3%*	*60*	*12.5*	*17.5*	*1–23*	*2, 20*
YEAR TOTAL:	99/194	51.0%	148	12.4	14	1–23	2, 20

Dates indicate first day of each 15-d interval. Percentage of days with subgroups, number of subgroups observed, mean subgroup size, median subgroup size, range in subgroup size, and modes of subgroup size are also calculated per 15-d period and by wet and dry season. Dry season data are indicated by italics. Δ indicates periods in which 2 observers followed the subgroups.

at 2 and 20 individuals ($n=60$, median$=17.5$). While there is no difference in mean subgroup size for the wet and dry season (wet season mean$=12.33$, $n=88$, dry season mean$=12.5$, $n=60$; Mann-Whitney U, $z=.149$, $p=.882$), the reason was primarily that the group rarely broke into >2 subgroups at a given time, in either season. Testing for homogeneity of variance between seasonal means, group size showed significantly more variation during the dry season compared to the wet season ($F=23.2$, $p<.001$). The reason for the difference was that the group divided into 1 very large and 1 very small subgroup in much of the dry season.

Proportion of Days with Subgroups

I compared the proportion of days of observation with subgrouping present across 15-d periods (Table I). The range was 0-100%. The percentage of observation days with subgrouping present was 51.2% for the wet season and 57.8% for the dry season. There was no seasonal difference in the proportion of days with subgrouping when comparing means based on percentage of days of observation with subgrouping present per 15-d period within each season ($n_1=14$, $n_2=7$, Mann-Whitney $U=43.5$, $p=.68$).

Table II Subgroup type by age-sex class composition, for the wet and dry seasons, including frequency of observations of each subgroup type, percentage of observations of each type, and the range of number of individuals found in subgroups of each type

Subgroup type	Wet season			Dry season			Total		
	Frequency	%	Range	Frequency	%	Range	Frequency	%	Range
MM-MF (J)	64	72.7	5–23	36	60	6–23	100	67.6	5–23
UM-MF (J)	15	17.0	3–13	0	0	–	15	10.1	3–13
UM-UF (J)	2	2.3	3	5	8.3	2	7	4.7	2–3
MM-UF (J)	1	1.1	7	4	6.7	4–5	5	3.4	4–7
MM	2	2.3	2–4	8	13.3	2	8	6.8	2–4
SM	1	1.1	1	3	5.0	1	4	2.7	1
MF (J)	1	1.1	3	1	1.7	4	2	1.4	3–4
UF (J)	2	2.3	2	0	0	–	2	1.4	2
SF	0	0	–	3	5.0	1	3	2.0	1
TOTAL	88	100	1–23	60	100	1–23	148	100	1–23

MM=multimale, UM=unimale, MF=multifemale, UF=unifemale, SM=solitary male, SF=solitary female. Only adults and subadults are counted in determining the MM, UM, MF, UF, SM, and SF categories. Subgroup types with (J) indicate that juveniles and infants may also be present in these subgroups. No subgroups were composed of juveniles and infants only.

Age-Class Composition and Individual Membership

Multimale-multifemale subgroups, with or without associated juveniles, were the most common subgroup type, accounting for 100 of 148 (67.6%) subgroups observed (Table II). Multimale-multifemale subgroups accounted for all subgroups of >13 individuals. Unimale-multifemale subgroups (with or without associated juveniles) are the second most common subgroup type (10.1% of observations; $n=15$ groups). All-male subgroups occured 10 times (6.8% of subgroups). I observed solitary individuals on 7 occasions only (4.7%). Subgroups also included 7 male-female pairs (4.7%) and 5 cases of multiple males with a single female (3.4%). I never observed multiple adult females, either with or without juveniles, in subgroups without males. The number of adult females in a subgroup correlated positively with the number of adult males ($r_s=.783$, $p<.001$), the number of subadult females ($r_s=.871$, $p<.001$), and the number of juveniles ($r_s=.894$, $p<.001$) in a subgroup.

I compared frequency of subgroup types across seasons (Table II). The multimale-multifemale subgroup is the most common in both seasons. The unimale-multifemale subgroup type is the second most common type in the wet season ($n=15$), but it never occurred during the dry season. In contrast, 8 all-male subgroups, 6 solitary individuals, and 5 male-female pairs occurred in the dry season and were rare or absent throughout the wet season.

When restricting the analysis of individual partitioning into subgroups to the 6 adult females only, there were clear differences in female associations from the wet season to the dry season (Fig. 3). In the wet season, the modes of adult females present in subgroups a 1 female and 5 females, but there were subgroups containing each number of adult females across the entire range of 0–6, thus adult females were most often divided across subgroups. In contrast, in the dry season, the modes for subgroups a 0 and 6 adult females, thus the adult females were traveling together most of the time.
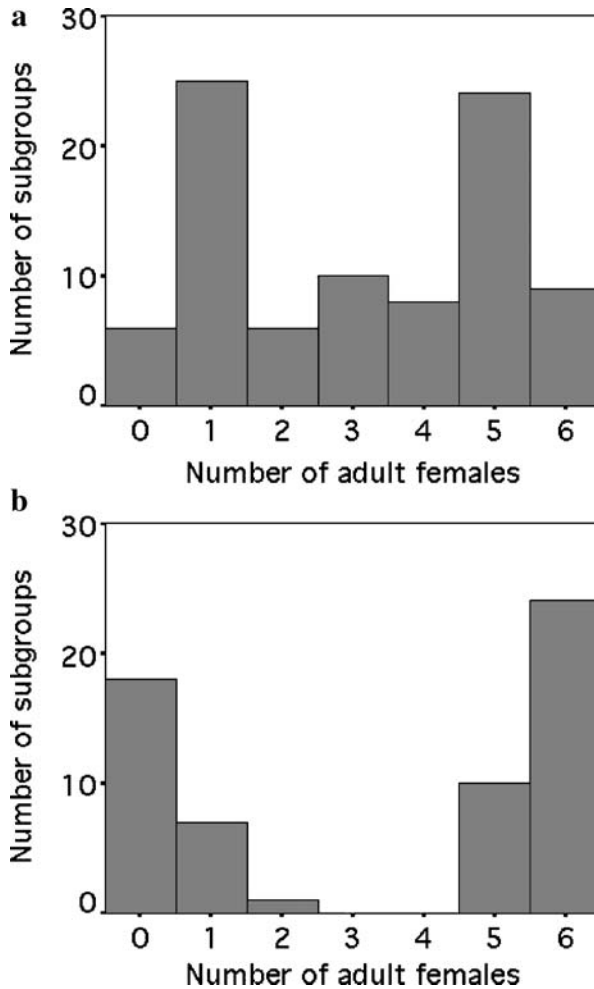
Fig. 3 Frequency histograms of the number of adult females in subgroups in the (**a**) wet ($n=88$ subgroups) and (**b**) dry ($n=60$ subgroups) seasons.

I calculated an association index value for each dyad to represent the likelihood that I would find a given pair within the same subgroup as one another. I performed hierarchical cluster analysis on the values (Fig. 4). Two high-ranking males and 4 high-ranking females formed the adult core of the main cluster; they associated strongly with subadult females, juveniles, and infants. The remaining adult and subadult males ($n=4$) more closely associated with each other and the lower-ranking adult and subadult females in the group.

For adult and subadult males, higher dominance rank was a strong predictor of larger mean size of subgroup membership (Fig. 5: $r_s=-.883$, $p=.02$, $n=6$). Similarly, high-ranked adult females were members of larger subgroups on average compared to lower-ranking adult females (Fig. 5: $r_s=-.829$, $p=.042$, $n=6$), and higher-ranking
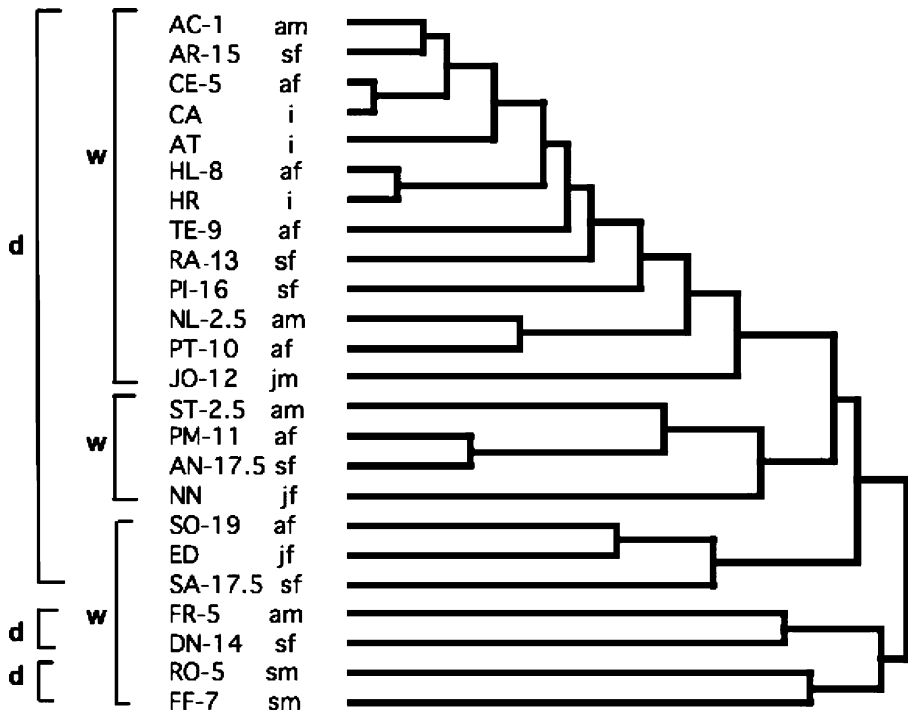
Fig. 4 Phenogram based on hierarchical cluster analysis of the association patterns of adult and immature capuchins, based on subgroup membership in 148 subgroups from September 1996 to August 1997. Two-letter codes in capital letters represent names of individuals, and numbers in parentheses indicate individual rank in dyadic interactions, based on the dominance matrix (see Methods). After dominance rank, am=adult males, sm=subadult males, af=adult females, sf=subadult females, jm=juvenile males, jf=juvenile females, and i=independent infants. W=wet season core subgroups; D=dry season core subgroups.
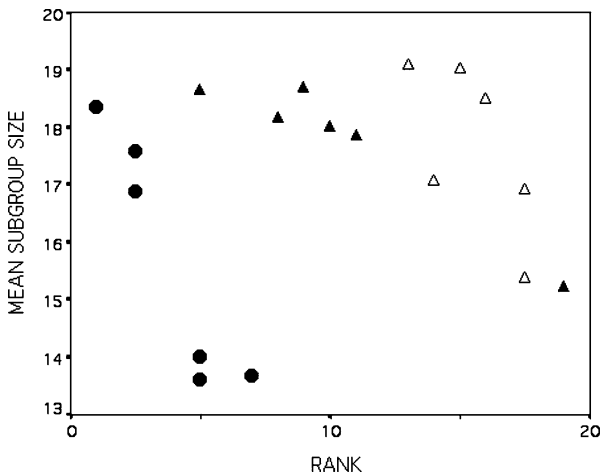
Fig. 5 Individual dominance rank and mean subgroup size participation, by sex. Closed circles=adult and subadult males; closed triangles=adult females; open triangles=subadult females.
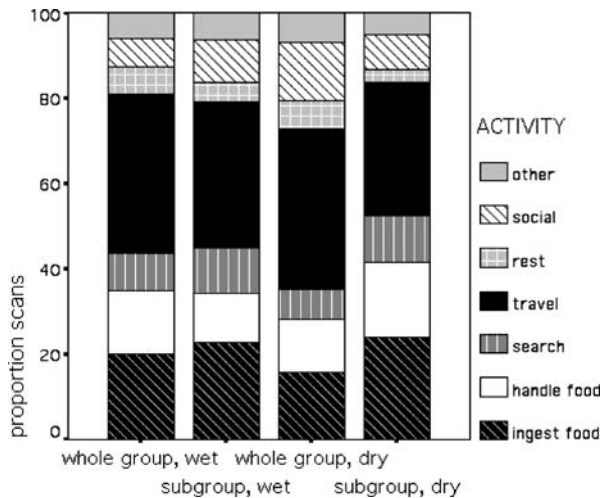
Fig. 6 Activity budgets for the capuchin group based on proportion of individual scan samples for ingesting food, handling food, searching for food, traveling, resting, social behavior, and other behaviors. Activity budgets are displayed for the following conditions: wet season, when group is traveling as a unit ($n=2134$ scans); wet season, when group is divided into subgroups ($n=1287$ scans); dry season, when group is traveling as a unit ($n=912$ scans); and dry season, when group is divided into subgroups ($n=983$ scans).

immature females were members of larger subgroups than lower-ranking immature females were (Fig. 5: $r_s=-.812$, $p=.05$, $n=6$).

Effect of Subgrouping on Activity Budget and Foraging Efficiency

In comparisons of group-wide activity budgets for the length of the study, across the whole group and subgroup conditions, time spent ingesting food increased by 4.5% (from 18.8% to 23.3%) when the group was in subgroups. In contrast, time spent traveling decreased by 5.2% (from 37.3% to 33.1%) when in subgroups. Time spent resting decreased by 2.6% in subgroups (from 6.4% to 3.8%), and time spent searching for food increased by 2.5% when in subgroups (from 8.2% to 10.7%). Time spent in social activities and time spent handling food changed less than 1% across conditions.

The effect of subgrouping on group activity budgets within seasons had the same general pattern (Fig. 6). In the wet season, time spent ingesting food and searching for food increased, and time spent traveling, handling food, and resting decreased in the subgroup condition. In the dry season, time spent ingesting food, handling food, and searching for food all increased, and time spent traveling, socializing, and resting decreased in the subgroup condition.

Paired comparisons of individual activity budgets on days with subgroups to days with the cohesive group reveal significant increases in time spent ingesting food (Wilcoxon signed ranks, $z=2.4$, $p=.016$) and searching for food ($z=3.43$, $p=.001$), no difference in time spent handling food, and a decrease in time spent traveling ($z=-2.03$, $p=.043$) and resting ($z=-3.143$, $p=.002$) on days when the group was in subgroups.

Re changes in foraging efficiency by sex, males showed a significant increase in time spent ingesting food (Wilcoxon signed ranks, $z=2.429$, $p=.015$) and a significant decrease in time spent traveling ($z=-2.429$, $p=.015$), when in subgroups vs. days when the group was cohesive. In fact, all adult, subadult, and juvenile males show the same directionality for the changes in activity budget. Conversely, the only significant differences for females were an increase in time spent searching for food (Wilcoxon signed ranks, $z=2.668$, $p=.008$) and a decrease in time spent resting ($z=-2.605$, $p=.009$) on days with subgrouping vs. days when the group was a cohesive unit. Re time spent ingesting food vs. time spent traveling, there is no evidence for lower rank conferring decreased feeding efficiency when the group was together as a whole. Rank effects also did not help to explain changes in activity budget from the whole group to subgroup conditions for males, females, or for all group members.

Discussion

Contrary to expectations, there is no significant seasonal difference in the proportion of days in which the group subdivided, nor any trend toward increasing frequency of time spent in subgroups. In fact, for adult females there was a trend toward greater group cohesion in the dry season, at the end of the study (Fig. 3). In contrast, a pair of subadult males became increasingly independent from the group and began to shadow another capuchin group in the last months of the study. A low-ranking adult male and a subadult female also traveled for days at a time away from the main group in the dry season, and on ≥3 different days, formed a subgroup with the 2 subadult males away from the rest of the group. Thus the subgrouping patterns in the study encompass ≥2 distinct phenomena. Low-ranking females, associated with low-ranking males as well as juveniles, frequently separated from the main group during the wet season. During the dry season, 3 low-ranking males and a subadult female grew increasingly independent from the group, but were usually present together in pairs or as a group of 4 when away from the main group. It seemed likely that they were in the process of group transfer. Parallel dispersal is common in *Cebus capucinus*, both for natal males and older males (Jack and Fedigan 2004a, b), and these data suggest parallel dispersal may occur in *Cebus apella nigritus* also, and that females may disperse alongside males in this subspecies.

Five mo after the study, in January 1998 (Lynch and Rímoli 2000), I spent 4 d with the study group. Of the 4 individuals that had been increasingly independent from the group, 1 of the subadult males (FF) and the low-ranking adult male FR were back among group members, but the other subadult male (RO) and the subadult female DN were not with the group. During a population census of primates at EBC, in July and August 1998 (Strier *et al.* 1999), I again encountered group members, but now RO and FF were traveling as integrated members of a different group, and FR was traveling in a subgroup or now independent group with the lowest-ranking adult female (SO), lowest-ranking subadult female (SA), a juvenile (ED), the dependent infant of SO, and an unknown subadult male. Group transfer or group fission can be an extended process in *Cebus apella nigritus*; Izar (2003) found that a *C. a. nigritus* divided into 2 groups and reunited 10 mo later. The observation contrasts with *Cebus*

olivaceus (Robinson 1988a, b), *C. capucinus* (Jack and Fedigan 2004a, b), and even *C. apella* in Colombia (Izawa 1994a), in which emigration or group division occurs over a brief period of time.

For the capuchins at EBC throughout the year, subgrouping was most commonly a result of a small number of individuals splintering off from the main group, as in ring-tailed lemurs (Jolly 1972), macaques (Dittus 1988; Fukuda 1989; van Noordwijk and van Schaik 1987), and some squirrel monkeys (Baldwin and Baldwin 1981), leading to a bimodal subgrouping pattern, with most subgroups either quite large or quite small. In groups with linear dominance hierarchies, and both intra- and intergroup feeding competition, the lowest-ranking individuals, disproportionately affected by intragroup competition, may be expected to opt out and forage or travel away from the rest of the group. This was true in both seasons, but in the wet season the lower-ranking adult females were more likely to be present in the smaller splinter groups. Conversely, in the dry season there was greater cohesion among adult females, and most subgroups splintering off from the main group contained only subordinate adult males, subadult males, subadult females, or all 3. The conception season coincided with the dry season (Lynch Alfaro 2005; Lynch *et al.* 2002), and the males that frequently separated from the group then had the lowest mating success within the group (Lynch 2001; Lynch Alfaro 2005). It is possible that these males were separating from the group in order to search for mates, rather than due to ecological circumstances. In fact, during the conception season FR interacted sexually with an extragroup female, out of visual and vocal contact with either group (Lynch Alfaro 2005).

Unlike the many primate taxa in which subgrouping occurs in 1 season only, capuchins at EBC showed subgrouping behavior on approximately half of observation days throughout the year, with no change in proportion of days in subgroups from the wet to the dry season. Apparently, they were responding, not to broad seasonal trends in resource distribution, but to distribution of particular food items, and possibly nonecological circumstances, i.e. mating opportunities, so that decision making about group membership occurred on a much finer time scale. This led to a dynamic pattern in subgroup size and proportion of time spent in subgroups throughout the year (Table I).

The variability in capuchin subgroup membership is manifest in the spread in the histograms for subgroup size (Figs. 1 and 2) and differs from subgroup membership for mouse lemurs, geladas, and hamadryas baboons, in which subgroup membership is predictable and constant through time (*Microcebus marinus* and *M. rufus*: Martin 1972, 1973; Tattersall 1982; *Theropithecus gelada*: Altmann 1974b; *Papio hamadryas*: Kummer 1968), and is more like the fluid membership in spider monkey, chimpanzee, and bonobo subgroups (*Ateles geoffroyi*: Chapman 1988; Symington 1990; *Pan troglodytes:* Matsumoto-Oda *et al.* 1998; Wrangham and Smuts 1980; *Pan paniscus*: White and Wrangham 1988).

Though capuchin subgroups fluctuated in size, particular dyadic associations remained strong throughout the year. In black-horned capuchins at EBC, most subgroups were multimale-multifemale. The pattern mirrors the age-sex composition of subgroups in *Cebus olivaceus* (Robinson 1988b) and macaque subgroups (Dittus 1988), and contrasts with the subgroups in *Cebus apella*

nigritus at Carlos Botelho, where they were frequently solitary males, or females and offspring unaccompanied by males (Izar 2003). In fact, from the cluster analysis on dyadic association within subgroups (Fig. 4), it is apparent that particular individuals show relatively high fidelity to one another, and that the associations are strongly associated with rank, so that low-ranking females cluster together and with low-ranking or subadult males, and high-ranking females cluster together and with the α-male. For the EBC capuchins, the ubiquity of multimale-multifemale subgroups, and the lack of any multifemale groups traveling unaccompanied by males, may reflect strong individual male-female associations within the group.

One unexpected finding that merits more research is the possibility that subgrouping may benefit males, but not females, in terms of foraging efficiency, as measured by increased time spent ingesting food and decreased time spent traveling, on days with subgroups vs. days when the group was intact. The finding may indicate that it is the males, not the females, that are choosing to bud away from the group to form subgroups, and that females may be following preferred males into the smaller subgroups, which is counter to Wrangham's (1980) expectation that male distribution follows female distribution. It is also interesting in light of Boinski's (2000) observations that females are responsible for the direction of group movement in *Cebus apella* in Suriname.

The combination of facultative, fluid subgrouping and hierarchical rules about subgroup composition may allow capuchin groups to break apart in certain seasons without a permanent division in the group. Like squirrel monkeys (Soini 1986) and ring-tailed lemurs (Jolly 1972), lower-ranking members of the group may become peripheral or form a separate subgroup during part of the year. Capuchins also show highly variable interindividual distance even when the group is traveling as a whole (Kinzey and Cunningham 1994; Robinson and Janson 1987: Lynch Alfaro and Rímoli, *unpubl. data*). These diverse strategies for managing feeding competition while simultaneously retaining group membership and high indices of dyadic affiliation may be a mechanism that has allowed capuchins to exploit far more diverse habitat types than any other neotropical primate.

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