

RESEARCH ARTICLE

Social Behavior in Fission–Fusion Groups of Red Uakari Monkeys
(*Cacajao calvus ucayalii*)

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Primates living in large groups that divide to forage must have social systems compatible with this mode of living. Uakari monkeys (*Cacajao* spp.) live in large groups and exhibit a form of fission–fusion grouping, but their social organization is poorly understood. We present some of the first data on social behavior for this genus based on a study on *Cacajao calvus ucayalii*. They traveled in multimale multifemale groups of highly variable sizes, with bachelor units on the periphery. Adult males were affiliative, and adult females associated with more than one adult male. Adult females typically traveled with their dependent offspring and an older juvenile within the group. In parties of two or more males, individuals engaged in previously unreported display behaviors and acted together to aggressively chase other males. Breeding was seasonal, and mating occurred away from other group members. We speculate on the social organization of *C. calvus ucayalii*, in which dispersal may be bisexual and peripheral males are affiliative with one another. Affiliated males appear to cooperate in fighting and displaying to other males for access to females during the breeding season. *Am. J. Primatol.* 71:1–12, 2009. © 2009 Wiley-Liss, Inc.

Key words: uakari monkeys; affiliative males; breeding systems; pitheciine

INTRODUCTION

While most primate species travel in cohesive groups that do not change in size in the short term, a few live in groups that frequently divide and reform [Robinson & Janson, 1987]. The term “fission–fusion” is generally used to describe these types of grouping patterns [Aureli et al., 2008; Chapman et al., 1993]. Common chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles* spp.) show a particular kind of fission–fusion in which all-male groups patrol territory borders, and females are frequently solitary [Goodall, 1986; McFarland, 1986; Nishida, 1968; Wrangham, 1977]. Woolly spider monkeys (*Brachyteles*) also show fission–fusion grouping patterns in some populations [de Moraes et al., 1998; Strier et al., 1993], and studies of some of the pitheciinae have revealed group fragmentation that could be described as fission–fusion [Kinzey & Cunningham, 1994].

Large group sizes are typical for the genus *Cacajao*; *Cacajao melanocephalus* occurs in groups of 100 or more individuals [Boubli, 1994; Barnett et al., 2005; Defler, 1999], *Cacajao calvus calvus* in groups of 45–50 [Ayres, 1986, 1989] and *Cacajao calvus ucayalii* has been observed in groups of 200 or more individuals [Aquino, 1988, 1998; Bowler, 2003]. Most populations of *Cacajao* that have been studied have demonstrated group fragmentation [Aquino, 1998; Ayres, 1986; Barnett et al., 2005; Bowler, 2003;

Defler, 1999], except for a group of 70 *Cacajao melanocephalus melanocephalus* in *caatinga* forests studied by Boubli [1999]. At that site, however, the group spread out widely during travel. Heymann [1992] hypothesized that the social organization of *C. calvus* comprised three levels; the “troop” (around 50 to over 100 individuals), which is composed of several “groups” (about 25–50 individuals), which in turn comprises several “foraging units” (up to about ten individuals).

The social systems of primates with fission–fusion grouping patterns must include behaviors that serve to reunite individuals and tolerance for frequent changes in the size and composition of associations. *Pan*, *Brachyteles* and *Ateles* spp. have multimale breeding systems in which females are the dispersing sex [see Di Fiore & Campbell, 2007; Stumpf, 2007; for reviews], but the social systems for the Pitheciines are less well known. A few studies

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have considered the social behavior of *Chiropotes* [Silva & Ferrari, 2009; Veiga & Silva, 2005; Veiga et al., 2006], but *Cacajao* has rarely been studied, and most studies have concentrated on the distribution, diet and ranging behavior of the genus [e.g. Aquino, 1988, 1998; Ayres, 1986, 1989; Barnett et al., 2005; Boubli, 1997, 1999; Hershkovitz, 1987]. The only previous study on the social behavior of *Cacajao* was on a semifree-ranging captive group of *C. calvus ucayalii* [Fontaine, 1981]. Ayres [1986, 1989] studied a group of 45–48 *C. calvus calvus* at Lago Tefé that regularly divided into smaller groups to forage. Ayres did not collect data on social behavior, but recorded a sociometric sex ratio of 1:1, temporary pair formation during the mating season and bachelor male groups of up to eight or nine individuals.

Zinner et al. [2001] noted that, in several species that forage in aggregations of hundreds of individuals, “one-male units” or harems form within the multimale group, and proposed that very large group sizes are incompatible with a typical multimale–multifemale group structure, because females “cannot maintain social relationships with most other group members.” Zinner et al. [2001] suggest that females of such species have stable relationships with single males to protect them from other unknown and infanticidal males. Applying this theory to *C. calvus*, Knogge et al. [2006] suggest that within the large troops, *C. calvus* are organized into small units composed of “around two adult females and offspring, two sub adults and always one guarding adult male.”

Here we examine the spatial distribution of age–sex classes within groups of *C. calvus ucayalii*, reporting on inter-male aggression, affiliation, display behavior, seasonal breeding and mating behavior. If *C. calvus* form a single-male or harem breeding system as predicted by Zinner et al. [2001] and Knogge et al. [2006], we would expect to see males in mixed social units associating with females more than other males, and females associating with only one male. In a multimale breeding system, males are expected to associate with each other more closely than with females, as found in *Ateles* and *Brachyteles*, in which females are the dispersing sex [e.g. Strier et al., 2002; Symington, 1990]. Alternatively, male–male special associations could be minimal, as in *Cebus* [Fragaszy et al., 2004], in which dispersal is male-biased [Strier, 1999], and *Lagothrix* in which dispersal is bisexual or female-biased [Di Fiore & Fleischer, 2005].

METHODS

Study Area

Data were collected in the Lago Preto Conservation Concession (04°27.5'S 071°45.9'W) on the Yavarí River 175 km southeast of Iquitos, Peru. The concession is a 9,926.19 ha public–private reserve

granted to the Wildlife Conservation Society by the Peruvian government in 2006 to manage in collaboration with the Durrell Institute of Conservation and Ecology. The Lago Preto concession is bordered by the Yavarí and Yavarí–Mirín Rivers in the south and west, and by logging concessions in the north and east.

We collected data in a 2,200 ha study area on the west side of the concession, extending several kilometers outside the northern concession boundary. The area includes 1,400 ha of nonflooding *terra firme* forest, 500 ha of white-water *várzea* forest that floods with silt-laden water between November and May each year, and 300 ha of *aguajal* palm swamps; permanently waterlogged forest dominated by *Mauritia flexuosa* palms.

The Study Groups

There were more than 200 uakaris in the 2,200 ha study area that sometimes traveled together. Groups of at least 100 uakaris occurred throughout the study area and sometimes foraged together for several days. We could not regularly identify individuals, and therefore groups, during data collection. Smaller groups were not of a characteristic number, except in the short term, and did not occupy a particular area throughout the study. We therefore use the term “group” to refer to any aggregation of uakari monkeys, and not to imply a social group. The following terms are used in this study: *association*, the maximum group size at Lago Preto, effectively all the animals using the area; *group*, any aggregation of monkeys separated by more than 150 m from any other groups (150 m was the approximate range at which we could typically hear the monkeys); *unit*, hypothetical set of individuals within a group who maintain closer and more stable social ties and therefore closer physical proximity with one another.

Data Collection

Groups of *C. calvus ucayalii* were followed by Bowler, without assistants, for 945 hr and 10 min between April 2003 and July 2005. Data were collected in all months except February 2004, April 2005 and May 2005. Counts of infants were also made during additional visits to Lago Preto in April 2006 and November 2007. Monkeys were located each day by walking the trail system, or searching flooded *várzea* by canoe, and were followed until they settled into their sleeping trees at dusk, or the group was lost. When the group was followed to their sleeping trees, they were relocated before dawn the following day. Between December and June, when the *várzea* forest was flooded, the monkeys were sometimes lost when they entered flooded areas where no canoe was available. All data were collected under a permit from INRENA (Instituto Nacional

de Recursos Naturales) of the Peruvian government, and the methodology complies with their regulations.

Behavioral sampling

We collected point scan samples [Altmann, 1974] at 10-min intervals, allowing one minute to complete the scans. In each of the 5,671 scans obtained, we recorded the size of the group, and the age–sex class and behavior of each visible monkey. In addition to the categories “feed,” “search,” “rest” and “move,” we recorded social behaviors including displays, grooming, aggression and sexual behaviors. For relevant social interactions, we also scored whether the scanned animal was the performer or the recipient of the behavior (e.g. aggression and grooming). In addition to grooming recorded during scan sampling, between 14th May 2003 and 30th November 2003, we recorded *all* instances of grooming observed in which we could determine the age–sex classes of both animals. Throughout the research period we recorded all instances of sexual behavior, fighting and chasing behaviors ad libitum [Altmann, 1974], and described new display behaviors when they were observed.

Group size

There are a number of difficulties in determining primate group sizes in dense forest, and with large groups of uakari monkeys, spread over several hectares, these problems are exacerbated [Defler, 1999]. We estimated group sizes by walking the length or width of the group between scans, and listening for long calls and screams that were audible from 150 m or more under dry conditions. For many scan samples, few individuals were visible and the monkeys did not call. To avoid underestimating group sizes, and overestimating the frequency of fission–fusion behavior, estimates of group sizes were taken from repeat counts and calls heard throughout the 9-min period preceding the scan. If counting the monkeys took longer than 9 min, the resulting estimate was used for the scan following the completion of the count and group size was not recorded for scans that occurred during the count. Because large uakari groups sometimes split temporarily into smaller groups, they are roughly analogous to the “subgroups” discussed by Chapman et al. [1993] and these methods approximate their recommendations.

Because uakari groups spread out widely during foraging, a group was defined as distinct when the outermost individuals were >150 m from neighboring groups and was deemed to have fissioned when two parts of the group moved further than 150 m apart for the 10-min period during and preceding the scan. To further reduce the likelihood of underestimating group sizes during data analysis, the

largest counts from each hour were used to give hourly group size estimates.

Group composition

It was sometimes possible to record the age–sex class of each individual during counts. Ages were defined following Fontaine [1981]. In the field, it is often difficult to distinguish subadult or even adult females from juvenile or subadult males; Defler [2003] describes the sexes of *C. melanocephalus* as indistinguishable up to 4 years old, and we found similar difficulties in *C. ucayalii*. We recorded the age–sex classes as: *infant one* (1–3 months), 10–25% length of the mother, face gray/brown with a trace of pink around the nose; *infant two* (3–12 months), 25–60% length of the mother, face pink/red, not as saturated as in adult females, thick gray scalp hair; *juvenile* (12 to 36 months including Fontaine’s [1981] “Juvenile one” and “Juvenile two”), face pink/red to red, thick gray scalp hair; *subadult male*, similar size or larger than an adult female, lacks the bulging cranial muscles of an adult male, scrotum usually visible, but superficially resembles adult female labia; *unsexed subadult*, for individuals the size of an adult female, but with thicker gray scalp hair and of undetermined sex; *adult male*, larger size, characteristic bulging cranial muscles, scrotum always visible, face usually a more intense scarlet than other classes; *adult female*, little or no gray scalp hair, lack the bulging cranial muscles of an adult male, smaller than an adult male. We recorded females carrying young as *adult female carrying dependent young*. Following Fontaine [1981], babies carried on bellies or with gray-brown or partially gray-brown faces were assumed to be *infant one* and under 3 months old. By recording the presence of these infants we gained an idea of the seasonality of births.

Nearest neighbor distances

During scan sampling, we randomly selected one “focal individual” for each scan by assigning each monkey in the scan a number and selecting the next matching number from a list of pregenerated random numbers. We recorded this individual’s age–sex class, and the age–sex class of its nearest neighbor. To control for the effects of visibility bias, only scans in which we could be absolutely sure we had seen the nearest neighbors were used. If the age–sex class of other nearest neighbors within 10 m of the focal individual could be determined, these were also recorded in order of proximity up until the first individual that could not be identified, or until we could not be sure we were detecting all individuals. We therefore obtained a *minimum* count for the numbers of each age–sex class within 10 m of the focal individual. When it was clear that a focal individual had no neighbors closer than 30 m, this

was recorded. We used 30 m because it was a distance that could be scanned reliably for monkeys, but was considered far enough to use as a measure for social isolation.

Data Analysis

Activity budgets were estimated using the percentage of each behavior recorded in scan samples. Frequencies of age–sex classes as nearest neighbors, proportions of scans that age–sex classes were >30 m from nearest neighbors and the frequencies that different age–sex classes were involved in aggressive encounters and social grooming were tested using the χ^2 test [BioEstat version 5.0; SPSS version 14.0]. Group size was correlated with the ratio of adult males to other age–sex classes in the group using the Pearson Correlation [BioEstat version 5.0]. $P=0.05$ was taken as the threshold for significance.

RESULTS

Group Size

Group size was variable and ranged from 1 to over 150 individuals (mean \pm SD: 43.5 ± 24.1 , $n = 759$; Fig. 1). The largest group sizes were estimated at 200 or more, but it was never possible to count them because they were spread over a large area. Both large and small groups sometimes foraged as a single unit persisting for several days, but would often fission and fuse during the day, generally forming larger groups at the end of the day. Additionally groups spread out widely during foraging. The spread of the group was difficult to measure in the rainforest environment, but larger groups often spread over areas of at least six hectares. This was confirmed by walking through the group to count the monkeys, and listening to their calls, which carried for around 150 m depending on conditions. Observations of single *C. calvus ucayalii* were rare, and were all of adult males ($n = 3$).

Group Composition

Age and sex classes were not evenly distributed within the groups. Males often grouped together. This is shown by the significant negative correlation between the number of *C. calvus ucayalii* sampled in partial or complete records of group composition and the ratio of adult and subadult males to other age–sex classes (Pearson Correlation, $n = 50$, $r = -0.382$, $P < 0.01$); more males are recorded in smaller records of group composition. For this reason, only complete or nearly complete records of group composition could be used to determine the average composition and age/sex ratios. It was never possible to determine the age–sex class of every individual in a group. Near-complete records of group composition in groups of 18, 23 and 26 monkeys contained minimum counts of 4, 6 and 4 adult males respectively. Frequently, groups were followed by what appeared to be associative units of up to 8 or more adult and subadult males, often traveling 50 to 100 m behind the main group. Occasionally, all-male groups appeared to be out of contact with other uakaris. From partial group composition records in which the main body of the group had an approximate composition of 1:2:2 for adult males:adult females:nonadults, and frequent observations of units of around 8 adult males on the periphery of a group of approximately 50 individuals, we crudely estimate that the composition of the troop and larger groups at Lago Preto approximates to one third adult males, one third adult females and one third nonadults. The proportion of adult males, adult females and nonadults in scan samples was 43.8, 18.4 and 37.8%, respectively. To control for visibility bias, these proportions were used to calculate expected values for the age–sex classes of nearest neighbors, and the performers and recipients in social interactions.

Nearest Neighbors

Of 5,671 scans, nearest neighbors could be identified in 426 cases, collected throughout the

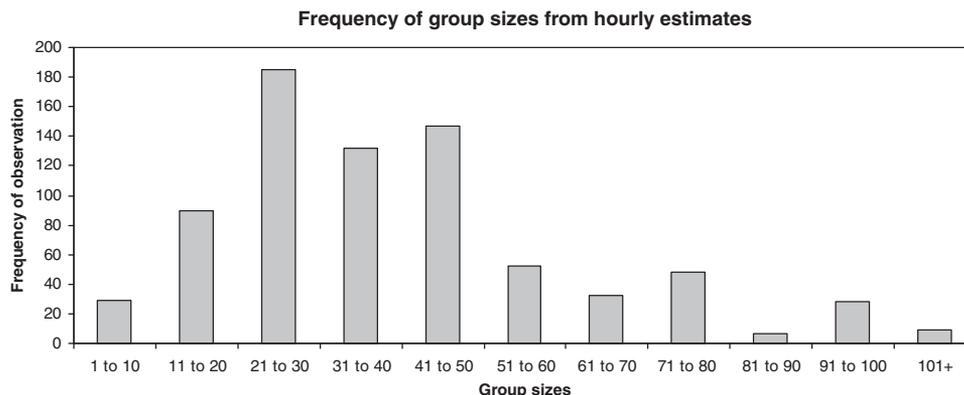


Fig. 1. Frequencies of group size categories of red uakari monkeys at Lago Preto from hourly estimates ($N = 759$).

study period, which were considered free from visibility bias and used in the analysis. Excluding cases where nonadults were the nearest neighbors, adult males associated with adult males more than they associated with adult females (91.4% vs. 8.6%, $n = 139$); significantly more than expected if age–sex classes mixed randomly, based on the adult sex ratio appearing in scan samples ($\chi^2 = 29.3$, $df = 1$, $P < 0.01$; Fig. 2). Adult females associated with adult females more than they associated with adult males (59.6% vs. 40.3%, $n = 52$); significantly more than expected if age–sex classes mixed randomly, based on the adult sex ratio appearing in scan samples ($\chi^2 = 22.6$, $df = 1$, $P < 0.01$; Fig. 2).

When nonadults were included in the analysis, adult males associated with adults more than nonadults (75.1% of scans vs. 24.9%, $n = 185$) significantly more than expected, based on the proportion of adults to nonadults in scan samples ($\chi^2 = 13.1$, $df = 1$, $P < 0.01$). Overall, 52.2% of the nonadults that were nearest neighbors to adult males were subadult males.

Predictably, adult females associated with nonadults more than would be expected from their proportion in scan samples (55.2% of scans vs. 44.8%, $n = 116$, $\chi^2 = 15.0$, $df = 1$, $P < 0.01$). Excluding carried infants as nearest neighbors, females carrying infants also more commonly had nonadults than adults as their nearest neighbors (69.6% of scans vs. 30.4%, $n = 23$), associating with nonadults more than would be expected from their proportion in scan samples ($\chi^2 = 13.6$, $df = 1$, $P < 0.01$). This supports ad libitum observations that adult females typically travel in trios within groups consisting of one adult female, one infant and one juvenile. Subadult males were never recorded as the nearest neighbors of focal adult females in scan samples.

Uakaris were >30 m from their nearest neighbors in 10.9% of individual behavioral records,

including scans in which the age sex classes of nearest neighbors could not be identified ($n = 478$). Subadult males were >30 m away from their nearest neighbor in 31.8% of scan samples for this age–sex class ($n = 44$), compared with 15.9% for adult males ($n = 220$), 2.7% for juveniles ($n = 37$), 2.1% for adult females not carrying infants ($n = 95$) and 0% for adult females carrying infants ($n = 23$) (Fig. 3). Adult males were more often >30 m from other group members than adult females ($\chi^2 = 13.343$, $df = 1$, $P < 0.01$). Although subadult males were >30 m away from their nearest neighbors more often than adult males, this was not significant ($\chi^2 = 3.88$, $df = 1$, $P = 0.08$).

Adult Males Within 10 m of Adult Females

In 118 scans in which adult females were the focal individuals and the age–sex class of at least one individual within 10 m could be determined, 84 (71.2%) scans contained no adult or subadult males, 26 (22.0%) scans contained 1 male, 5 (4.2%) scans contained 2 males, 2 (1.7%) scans contained 3 males and 1 (0.8%) scan contained 4 males. As only the closest neighbors up to the limit of visibility were recorded, more males could have been within 10 m at each scan.

Agonistic and Display Behavior

Uakaris spent 39% of their time moving, 28% of their time feeding, 25% of their time resting, 5% of their time engaged in social behaviors and 3% searching branches and foliage (from scan samples, $n = 3,750$). Agonistic and display behaviors made up 41.8% of all social behavior. Actual fighting with physical contact was rarely observed, and did not appear in scans. Most agonistic behavior observed consisted of chasing accompanied by distinctive adult scream and alarm calls that were only heard during

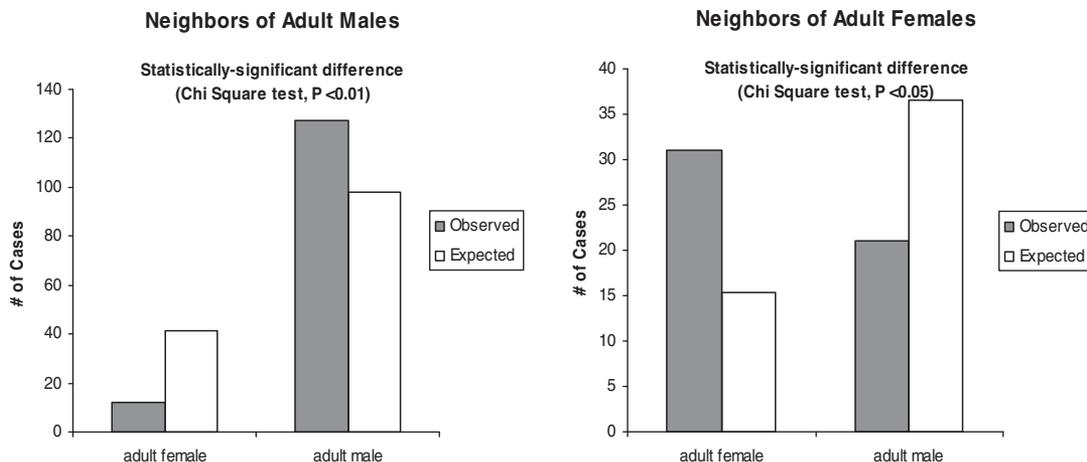


Fig. 2. Nearest neighbors of adult red uakari monkey males vs. females. Males had males as their nearest neighbors more often than expected by chance, based on the adult sex ratio appearing in scan samples. Females had females as their nearest neighbors more often than expected by chance, based on the adult sex ratio appearing in scan samples.

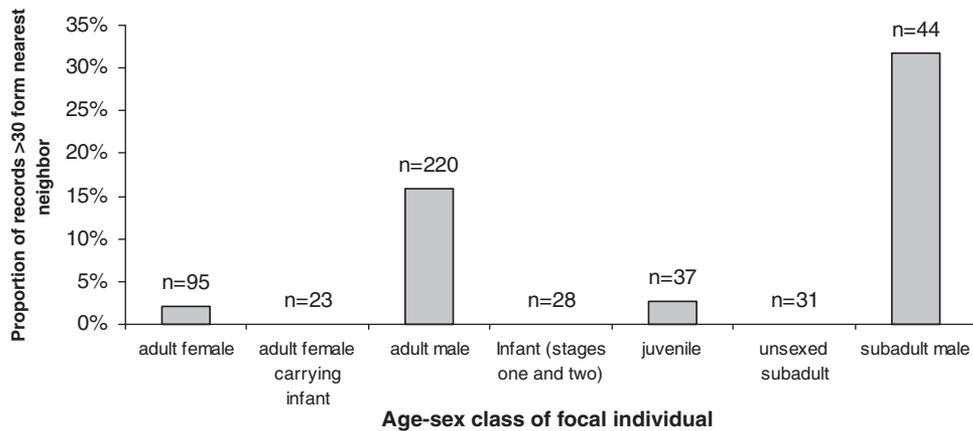


Fig. 3. Proportion of observations in which red uakari focal individuals of each age-sex class were >30 m from their nearest neighbor.

aggressive encounters. Aggressive chasing was conspicuous and made up of 0.48% of scan samples, but due to low visibility, many more aggressive interactions were heard than seen. Additionally, more subtle, less visible aggression may have been more frequent.

In 23 records of aggressive chasing appearing in scan samples, the age-sex class of the aggressors could be identified in 19 records, and the recipients in 17 records. In 18 (94.7%) scans the aggressor or aggressors were adult males; significantly more than would be expected based on the ratio of adult males to adult females and nonadults in scan samples ($\chi^2 = 20.0$, $df = 2$, $P < 0.01$). In 1 (5.3%) of the scans, the aggressor was an adult female. No nonadults were the aggressors in aggressive chasing observed in scan sampling. The age-sex classes of the recipients of aggressive chasing could be identified in 17 of the 23 records. Recipients of aggression included multiple adult or subadult males (4 records), single adult males (4 records), single subadult males (3), juveniles (3), an unsexed subadult (1) and an adult female carrying an infant (1).

In 5 (21.7%) of the 23 records of aggressive chasing recorded in scans, more than one adult male was involved in chasing one or more adult or subadult male. Aggressive encounters often lasted several minutes and included up to eight or more males. On ten occasions, including observations outside scan samples, we clearly observed pairs or small groups of adult males working together to chase other individuals or small groups. In three of these incidents, an adult male appeared to wait for support from other adult males before resuming a chase, and on one occasion adult males being chased faced up to a single male, only to flee when a second male arrived.

Aggressive chasing was often accompanied by display behaviors that included hindquarters bounce, lateral and inverted swing, branch shake, branch sway, straight-leg strut, urine washing, or penis display (Table I). These were highly visible and made up of 0.77% of the activity budget. Display

behaviors recorded in scan samples included branch sway (0.18%), inverted swing (0.18%), branch shake (0.11%), straight-legged strut (0.11%), hindquarters bounce (0.08%), lateral swing (0.08%) and urine wash (0.03%), whereas others were recorded outside the scan samples. Only adult males were recorded performing display behaviors in scan samples, but some display behaviors were performed by other age-sex classes outside the scan samples. Display behaviors were sometimes performed simultaneously by pairs or small groups of males.

Grooming

Social grooming made up 1.8% of the activity budget, and usually occurred during bouts of resting, often in dense cover. The few grooming bouts that were recorded in their entirety ($n = 65$) were short and involved frequent changes between “groomers” and “recipients” of all age-sex classes (Table II). Adult females groomed other individuals more often (59% of records), and adult males groomed less often (9% of records), than expected by chance based on the ratio of adult females, adult males and nonadults in the population ($\chi^2 = 74.9$, $df = 2$, $P < 0.01$). Nonadults were more likely to be the recipients of grooming compared with adult males and females, based on their estimated proportional representation in the population ($\chi^2 = 11.6$, $df = 2$, $P < 0.01$). Adult males were not observed grooming juveniles or infants, but did groom adult females, adult males and subadult males.

Mating

Mating, identified by mounting and rhythmical thrusting, was observed on six occasions during the study period, but in no case was intromission confirmed. All occurrences were between late April and mid June. Mating made up less than 0.1% of the activity budget, and was conducted away from other group members.

TABLE I. Display Behaviors in *Cacajao calvus ucayalii* Recorded at Lago Preto

Behavior	Description	Perceived context at Lago Preto
Arm raising [Fontaine, 1981]	Raising a straight forelimb, out in front of the body	Mild annoyance or disturbance. Occasionally observed in response to researchers
Branch slapping [Fontaine, 1981]	An arm raise that is brought down sharply onto the substrate	Annoyance or mild aggression. Only recorded in adult males. Occasionally observed in response to researchers
Tattoo	Both arms are slapped on the substrate alternately in a short rapid sequence	Annoyance or mild aggression. Only recorded in adult males. Rarely observed
Piloerection [Fontaine, 1981]	Piloerection of the dorsal pelage	Often observed in combination with other display behaviors
Arched back [Fontaine, 1981]	Arching of the back, usually in combination with piloerection	In response to aggression. Occasionally observed in response to researchers
Branch shaking [Fontaine, 1981]	Brief, vigorous shaking of branches	Aggression. Often during, before or after male-male aggression. Often accompanied by contact and alarm calls from other group members. Occasionally observed in response to researchers
Branch breaking and dropping [Fontaine, 1981]	Breaking and dropping of branches	Aggression. Often accompanied by contact and alarm calls from other group members. Occasionally observed in response to researchers
Branch swaying [Fontaine, 1981]	Rocking rhythmically back and forth on branches to make the limb of the tree sway. Often for several minutes	Only recorded in adult males. Often during, before or after male-male aggression. Usually performed in the tops of canopies in very conspicuous locations. Sometimes performed in pairs, apparently directed at other more distant males
Hindquarters bounce [Fontaine, 1981]	Bilateral, abrupt leg extension and flexion resulting in a rapid bobbing motion	Annoyance or mild aggression. Often during, before or after male-male aggression. Occasionally observed in response to researchers
Strut [Fontaine, 1981]	Running or bounding across supports with locked knees and elbows. Often with piloerection, and a raised tail	Aggression. Often during, before or after male-male aggression. Only recorded in adult males
Inverted swinging	Suspended by the hind legs below a branch, swinging backwards and forwards and with his arms hanging outstretched beyond the head. Usually with piloerection, often with penis exposed, and often for several seconds	Only observed in adult males. Often during, before or after male-male aggression. Sometimes done in pairs or small groups in the tops of trees during male-male conflicts. Often before or after bouts of branch rocking, hindquarters bounce, urine washing or branch shaking behaviors. Occasionally observed in response to researchers
Lateral swinging	Similar to the inverted swing, but suspended below a branch by one hind leg and one arm	Often during, before or after male-male aggression. Sometimes done in pairs or small groups in the tops of trees during male-male conflicts. Often before or after bouts of branch rocking, hindquarters bounce, urine washing or branch shaking behaviors. Occasionally observed in response to researchers
Penis display	Erect penis exposed. The penis is pink in color	Adult males often displayed erect penises during other display behaviors, sometimes hanging with the rear legs apart. Occasionally observed in response to researchers
Urine washing [visual component; Fontaine, 1981]	Vigorous movements with the forearm from the groin forwards, whilst urinating onto the fur of the stomach and chest. Rear limbs also occasionally used	Often during, before or after male-male aggression. Only observed in <i>adult males</i> . Occasionally observed in response to researchers

On 11th June 2003 mating occurred three times in the same group within 47 min and involved at least two different males. The number of females involved was unclear. At 15:47 an adult male

copulated with an adult female for 57 sec. The pair was a minimum of 10 m from other members of the group. At 16:03 a small adult male or subadult male copulated with an adult female at least 10 m from

TABLE II. Percent Distribution of 65 Grooming Bouts Noted During Scan and All-Occurrence Sampling According to the Age-Sex Class of the Groomer and Recipient

Recipient	Groomer							Total
	Adult male	Subadult male	Adult female	Unsexed subadult	Juvenile	Infant (one and two)	Unknown	
Adult male	3.1	0.0	13.8	3.1	1.5	0.0	1.5	23.1
Subadult male	1.5	0.0	1.5	1.5	1.5	0.0	0.0	6.2
Adult female	4.6	0.0	10.8	1.5	0.0	6.2	0.0	23.1
Unsexed subadult	0.0	0.0	6.2	6.2	0.0	0.0	0.0	12.3
Juvenile	0.0	0.0	7.7	1.5	0.0	1.5	0.0	10.8
Infant (one and two)	0.0	0.0	15.4	0.0	0.0	0.0	0.0	15.4
Unknown	0.0	0.0	3.1	0.0	0.0	0.0	6.2	9.2
Total	9.2	0.0	58.5	13.8	3.1	7.7	7.7	100.0

TABLE III. Temporal Distribution of the Presence of Infant Ones (0–3 months old) in the Population at Lago Preto

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2003	No data	No data	N	N	N	N	N	Y ^a	Y ^a	Y ^a	Y ^a	N
2004	N	No data	N	Y ^b	N	N	N	N	N	N	N	Y ^b
2005	N	N	N	No data	No data	No data	No data	Y ^c	Y ^c	Y ^c	Y ^c	No data
2006	No data	No data	No data	N	No data	No data	No data	No data	No data	No data	No data	No data
2007	No data	No data	No data	No data	No data	No data	No data	No data	No data	No data	Y ^d	No data

Note. Y: Infant ones present, N: Infant ones absent.

^aMinimum and maximum counts not obtained, but infant ones were regularly observed.

^bSingle observation of an infant one.

^cNo data collected in these months, but presence of infant ones inferred from observations of 5- to 7-month-old infant two young in April 2006.

^dMinimum count of 6 infant one young obtained in a group of approximately 40 uakaris.

other members of the group. Mating lasted 30 sec after which the male mounted again for a further 30 sec. The pair then moved off together. At 16:34 an adult male was observed mating with an adult female at least 20 m from the rest of the group.

On 12th June 2003 at 08:50 an adult male was observed mating with an adult female. It was unclear how far away from other group members the pair were. It was not clear whether or not this was the same group under observation on 11th June 2003.

On 30th April 2004 at 13:58 a mature adult male was observed mating with an adult female in the lower canopy at least 15 m away from the next nearest neighbor. Mating lasted at least 40 sec, after which the male spent 10–20 sec rubbing his ano-genital region on a branch before moving in the opposite direction to the female.

On 16th May 2004 at 8:56 an adult male was observed mating with an adult female 25 m away from rest of group. Mating lasted 30 sec, after which the male spent about 10 sec rubbing his ano-genital region on a branch. Ten minutes later the same male was seen following the same female.

Births

Infant ones (0–3 months) were observed on multiple occasions in August, September, October and November

2003; minimum and maximum counts were not obtained. In April 2004 we made a single observation of a very small infant carried low on the belly, estimating that the birth occurred in February or March 2004. In December 2004 we recorded infant one uakaris only once. In April 2006 we counted a minimum of five infant two monkeys in a group of 50–80 individuals, which we estimated to be around 5–7 months old, indicating births between August and November 2005. In November 2007, *all* adult females ($n = 6$) that were inspected by tracking them with binoculars until the presence or absence of infant one young was determined were found to be carrying infant one young. Individual females could not be recognized, so while a minimum of six different adult females were inspected, more females were probably carrying young. From these observations it can be seen that breeding was seasonal, with most births between August and October (Table III), although the single observation in April 2004 suggests one birth several months after the normal season. It was also clear that far fewer births occurred at Lago Preto in 2004 than in 2003, 2005 and 2007.

DISCUSSION

Group Structure

Uakaris at Lago Preto foraged in groups of widely variable sizes, occasionally forming groups of

more than 200 individuals that appeared to forage together for long periods without conflict. More frequently observed were groups of 20–50 individuals. Group size, however, was highly flexible and did not appear consistent at any level, particularly over the long term. We suggest that uakari social “groups” in fact represent aggregations of smaller, more stable social units of up to 10 or so individuals that regularly associate with other such units on a flexible short-term basis, forming the group sizes encountered. We furthermore suggest that uakari social units may not have fixed home ranges, but rather may range semi-nomadically over vast areas. This view is consistent with observations made during censuses on the Yavari–Mirín River where uakaris often disappear from an area for several months.

One-Male Units or a Multimale Breeding System

There are two theories on how the social groups are organized. Garber and Kowalewski [2009] hypothesize that *Cacajao* has a multimale breeding system in which males are likely to be tolerant of each other’s sexual activity, and females are likely to be promiscuous. They suggest that kinship might play an important role in this male–male tolerance. Alternatively, Ayres [1986] posited that pair formation and observations of bachelor groups were evidence for a single-male breeding system in *C. calvus*. This equates to the “one-male unit” organization suggested by Knogge et al. [2006].

At Lago Preto, adult and subadult male *C. calvus ucayalii* were most often closest to other males, but no distinction was made in the data between males in bachelor units and males associating with adult females. However, the frequency of scans in which adult females were within 10 m of more than one adult male supports the hypothesis that social units were multimale, and it was clear from ad libitum observations that males traveling with adult females also associated closely with other males. Adult males were observed grooming each other and some display behaviors were conducted by pairs or small groups of adult males. This combined with observations of adult male *C. calvus ucayalii* engaging in aggressive chasing behaviors in cooperating units within groups leads us to conclude that *C. calvus ucayalii* does not form one-male units, and that foraging units containing females were accompanied by multiple males.

Affiliative Males, Bachelor Male Units and Dispersal

The strength of male–male relationships vs. female–female relationships at Lago Preto hints at a social system akin to that of the atelines and *Chiropotes* in which males are affiliative, and females

tend to be the dispersing sex [Garber & Kowalewski, 2009]. However, all lone *C. calvus* observed at Lago Preto were adult males, and the formation of bachelor units of up to 8 or more adult males at Lago Preto and in *C. calvus calvus* [Ayres, 1986] might suggest male dispersal. Di Fiore and Fleischer [2005] also observed solitary adult and subadult males, and a bachelor group of five males, in *Lagothrix poeppigii* in which dispersal is thought to be predominantly female, but may also be bisexual [Di Fiore, 2002, 2009; Di Fiore & Fleischer, 2005; Di Fiore et al., 2009]. Dispersal patterns in *Cacajao* may therefore resemble those of *Lagothrix* to some extent.

One possible explanation for the formation of bachelor units is that young male *C. calvus ucayalii* disperse from their mother units to join bachelor units. Young males may then form affiliative bonds with other males and eventually attempt to usurp males that control or associate with females. Thus males could be dispersing from their natal groups. Alternatively, bachelor male units could be explained by a dominance hierarchy, in which weaker males, including subadults, are forced to the periphery of groups by dominant males. Here they are close to other similar males. In this scenario, marginalized males might not disperse, and may eventually rise up the dominance hierarchy and secure access to females. Under such conditions, female-biased dispersal might be expected. A third possible explanation for the existence of bachelor units is that they are units of males that *do* have access to females, but on occasion forage away from the rest of the group. Seasonal breeding might allow males to form bachelor foraging units during most of the year without the risk of losing mating opportunities.

Tolerance and Aggression

While spectators occurred during mating in *Brachyteles* [Strier et al., 2002], and *Lagothrix* [Di Fiore & Fleischer, 2005], in *C. calvus ucayalii* mating was conducted away from other individuals. Additionally, Ayres’ [1986] observed bachelor groups harassing pairs of *C. calvus calvus* at Lago Tefé. Tolerance of mating between male *C. calvus ucayalii* may therefore be lower than in other ateline genera.

Although male *Chiropotes satanas* at Tucuruí, Brazil were affiliative, Veiga and Silva [2005] and Silva and Ferrari [2009] did not report the formation of discrete bachelor groups or sequences of aggression between groups of males. Although levels of aggression were not compared statistically, adult male *C. calvus ucayalii* often have scars and injuries [personal observation] that are presumably caused by fights and levels of aggression in *C. calvus ucayalii* may prove higher than in *Chiropotes*. *Chiropotes* engage in a number of male-specific affiliative behaviors, in which physical contact is made, including

lining up, synchronous tail wagging and body rubbing [Veiga & Silva, 2005]. These behaviors were not observed in *C. calvus ucayalii*, although adult males occasionally groomed each other or presented their rears to other adult males. Groups of *C. calvus ucayalii* males did, however, sometimes perform very conspicuous display behaviors such as inverted swinging, urine washing and branch swaying synchronously. These behaviors appear to be associated with aggression between units of *C. calvus* males.

At Lago Preto, aggression from adult males was usually directed at adult males, subadult males and juveniles. It is possible that young males are targeted by adult males. Sexual crypsis has been noted in *C. melanocephalus* [Defler, 2003], and was noted in *C. calvus ucayalii* in this study. Captive juvenile male *C. calvus ucayalii* entered a subadult male phase lasting 2–3 years, in which they displayed physical characteristics typical of adult females, including pendulous scrotal alae resembling female labia [Fontaine, 1981]. The function of this sexual crypsis is unknown, but if young males are likely to receive aggression from adult males, sexual crypsis could reduce attacks.

Kinship, Cooperation and Sex in Large Fission–Fusion Groups

Adult females typically appeared to travel with one infant and one juvenile or subadult; several of these units and a number of adult males making up groups of varying sizes. The degree of cohesion between female–juvenile–infant units is unclear, but flexible group sizes may be indicative of a loose social system in which smaller units are the most stable social groups within larger aggregations.

Groups containing multiple males may offer females the advantage of increased infant survivorship [Altmann, 1990; Garber, 1997]. Female promiscuity and sexual receptivity during nonfertile periods would reduce the likelihood of infanticide by maintaining multiple male–female bonds [Garber & Kowalewski, 2009]. The advantages for males living in groups containing multiple males are less clear, and the cost of tolerance of another male’s sexual activity must be offset by the benefit of cooperation. In the atelines, one important benefit appears to be in cooperative defense from extra group males that are potential competitors for receptive females. Invading males may also be infanticidal [Garber & Kowalewski, 2009; Gibson et al., 2008]. The cost of male–male tolerance is lower when males are kin, and for this reason Garber and Kowalewski [2009] predict that dispersal in *Chiropotes* and *Cacajao* is female biased. This is supported in *Chiropotes* by observations of lone females [Peetz, 2001; Veiga & Silva, 2005], but not in *Cacajao*.

The fission–fusion grouping patterns, very large group sizes, promiscuity of females and particularly

the large numbers of adult males in groups may make it less likely that affiliated male *C. calvus ucayalii* are close kin. This would mean that the cost of affiliation and shared mating opportunities in *C. calvus ucayalii* are not offset by strong genetic relationships and must instead be matched by the benefits of cooperation. While affiliative behavior is often explained in terms of kinship [Gouzoules & Gouzoules, 1987], several studies have shown that affiliative behavior can occur between unrelated male common chimpanzees [Gagneux et al., 1999; Mitani et al., 2000; Vigilant et al., 2001], and “coalitions” of unrelated males that cooperatively invade groups and evict resident males occur in red howler monkeys [Pope, 1990], golden lion tamarins [Baker & Dietz, 1996] and saddleback tamarins [Goldizen et al., 1996]. We speculate that the male coalitions that seem to cooperate in aggressive encounters with other males are defending or obtaining access to females. The short breeding season, large group sizes and fission–fusion behavior of *C. calvus ucayalii* may make defense of females more difficult and require cooperative effort between unrelated males.

Predictions on the Social Organization of *C. calvus ucayalii*

While our results are largely preliminary, we speculate that the large groups that form in *C. calvus ucayalii* may be made up of smaller units. Males may be forming affiliative male units within the larger group after dispersing from their natal units. Units of affiliated males, who may not be related, fight and display to other units of males for access to females during the breeding season. We predict that females are promiscuous, and mating is conducted discreetly to avoid harassment from other males. Dispersal in *C. calvus ucayalii* is most likely bisexual, with social units moving freely between foraging groups during fission–fusion behavior. The distinction between “dispersal” and “fission–fusion” could thus be blurred in this species.

Dispersal patterns in *C. calvus ucayalii* could be tested using molecular methods to determine the genetic structure of the population. If dispersal is male biased or bisexual, then we would expect adult males to have equal numbers or fewer same-sex kin in their social units than adult females, and average pairwise relatedness among adult females within social units should be equal to or greater than among adult males. Additionally, if both sexes disperse, but one sex tends to disperse farther than the other, then we would expect the sex that disperses farther to have fewer same-sex kin in their local population than the sex that tends to disperse over shorter distances.

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