Behavioral and Endocrine Responses in Male Marmosets to the Establishment of Multimale Breeding Groups: Evidence for Non-monopolizing Facultative Polyandry

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Studies of wild callitrichids provide conflicting evidence regarding polyandrous groups. One perspective supports a monopolizing breeding strategy on the part of one male, while the alternative perspective suggests that polyandry does not lead to a breeding monopoly. We tested the hypotheses in male marmosets (Callithrix kuhlii) *with 5 polyandrous groups composed of related/familiar males as our attempts to establish polyandrous groups of unrelated/familiar males failed. We monitored male social and sexual behavior and urinary testosterone (T) and cortisol (CORT) across the first 80 days of group formation and contrasted them with similar measures in males housed in monogamous groups. We also examined the same measures across the females' ovulatory cycles for polyandrous males. We found little evidence that males in polyandrous groups exercised a mating monopoly over the female and no evidence for overt competition between polyandrous males. We found 2 behavioral differences: polyandrous males were less often in proximity and copulated more often with the female than monogamous males did. Our findings suggest that the males in newly-formed groups of marmosets do not monopolize breeding and social behavior with the female. This appears to be the case for 3 reasons. First, males may use sperm competition rather than overt competition. Secondly, it may take longer for relationships to develop between the female and the males in polyandrous groups versus in monogamous groups. Thirdly, the cost of infant care is sufficiently high to demand that*

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*group members get along when groups are small and reproductive benefits
are shared.*

INTRODUCTION

Trivers's (1972) theory of parental investment predicts that male mammals will maximize their reproductive success if they mate with ≥1 female, because the production of sperm is relatively inexpensive. Conversely, females have costly gametes and maximize their reproductive success when they restrict mating to a single male and devote considerable time and energy to produce and to rear the offspring. Polygyny, where one male mates with ≥2 females follows readily from Trivers's theory and is the typical mating system in mammals. Only rarely (5%, Clutton-Brock, 1989), mammals form long-term social and sexual bonds with a single mate that persists for one or several breeding seasons. The rarest mating system identified in mammals is polyandry, which arises when males maximize their investment by foregoing mating opportunities with other females and multiple males copulate and remain with a single female. In order for polyandry to arise, the cost of rearing offspring should be considerable and offset by the presence of several parents (Emlen and Oring, 1977).

Polyandry in mammals likely arose from cooperative breeding because polyandry has only been reported in mammalian species that cooperatively breed. In mammals, polyandry occurs in dwarf mongooses (*Helogale parvula*: Keane *et al.*, 1994), African wild dogs (*Lyocaon pictus*: Creel and Creel, 2002) and in the Callitrichidae (pygmy marmosets: *Cebuella pygmaea*, Soini, 1987; tassel-ear marmoset: *Callithrix humeralifer*, Rylands, 1986, as cited by Rylands, 1996; Ferrari and Digby, 1996; buffy-headed marmoset: *C. flaviceps*, Ferrari, 1992; saddle-back tamarins: *Saguinus fuscicollis*, Goldizen, 1987; moustached tamarins: *S. mystax*, Garber *et al.*, 1993; golden lion tamarins, *Leontopithecus rosalia*: Baker *et al.*, 1993). Dwarf mongooses, African wild dogs, marmosets and tamarins are all characterized as cooperative breeders in which long-term social and sexual bonds exist between the breeding adults, usually the parents, and offspring postpone or forgo entirely independent breeding to aid the parents in rearing offspring (Solomon and French, 1997).

Polyandry in dwarf mongoose and African wild dog packs is well-understood and verified with genetic testing. Subordinate males breed with the dominant female groups, albeit at a much lower rate than dominant males do (Creel *et al.*, 1992; Creel and Creel, 2002). In dwarf mongoose packs, subordinate males accrued direct fitness benefits by siring nearly a quarter of the offspring (Keane *et al.*, 1994) and dominant males actively deterred the

mating by subordinate males during the breeding season (Creel *et al.*, 1992). In African wild dogs, dominant males mated more frequently than subordinate males did (5–10 times higher), depending on the rank of the subordinate; however beta males beta were responsible for siring 10% of the offspring of the dominant female in the groups (Creel and Creel, 2002). The intensity, but not the frequency, of aggression also increased among males during the breeding season. In spite of the increased risk of aggression between males in dwarf mongoose and African wild dog packs, dominants likely tolerate subordinate mating rather than lose the benefits provided by having helpers (Keller and Reeve, 1994).

The origin of polyandry in marmosets and tamarins is not as clear as in the cases of dwarf mongooses and African wild dogs. The cooperatively breeding social system of callitrichids is characterized by delayed dispersal of adult offspring that assist their parents in the care of young (French, 1997) and high rates of paternal care (Santos *et al.*, 1997; Tardif *et al.*, 1986). Group demography for callitrichids is highly variable, including instances of polygyny, monogamy, and polyandry often within the same species (Baker *et al.*, 1993; Dietz and Baker, 1993; Digby, 1995; Garber *et al.*, 1993). Evidence for polyandrous groups stems primarily from field studies, which reveal that some groups contain multiple adult males, that some or all of the males mate with the breeding female, and that all males engage in infant care (*Leontopithecus rosalia*: Baker *et al.*, 1993; *Saguinus mystax*: Garber *et al.*, 1984; *S. fuscicollis*: Goldizen, 1987; *Cebuella pygmaea*: Soini, 1987). Reports from captivity also reveal that groups consisting of ≥1 mating adult male can be stable (Kleiman, 1978; Price and McGrew, 1991; Rothe and Koenig, 1991). However, confirmation of paternity in captive and wild groups of tamarins and marmosets remains to be achieved.

The most complete data on social organization and polyandry in callitrichids stems from 2 long-term studies on wild groups of golden lion tamarins (Baker *et al.,* 1993) and saddle-back tamarins (Goldizen, 1987). Although the provided evidence that polyandry is a facultative strategy used by tamarins, they yielded different patterns of behavioral data that led to different characterizations of the social dynamics within the different species in which polyandrous groups were observed. One account supported a view that demographically polyandrous groups occurred, but that a genetic monopoly existed within them (monopolizing strategy), whereas the second view provided evidence for true polyandry in which paternity was likely shared by males (non-monopolizing). The non-monopolizing account for polyandry in tamarins was derived from evidence that small, newly-established groups of saddle-back tamarins were composed of multiple breeding males and that all males copulated with the female at very similar rates throughout the breeding cycle. Goldizen (1987) found no evidence

for a preferential relationship between one male and the female, and overt male-male competition was absent. As group size increased and alloparental assistance was available in the form of maturing young, monogamous groups appeared to be the rule. The non-monopolizing view of polyandry was argued to arise from reproductive demands on females. Females typically give birth to twins (French, 1997) and undergo a postpartum ovulation within 1–2 weeks following parturition (French *et al.*, 1996). Consequently, females require help from ≥2 individuals to rear offspring successfully (Creel and Creel, 1991; Goldizen, 1987): additional males can provide such services especially when groups are small. Since female callitrichids produce dizygotic twins (Dixson, 1993), it is possible that ≥1 male could sire both offspring and thus additional males can acquire direct fitness benefits. Further, in cases where in only a single male sired offspring, the second male could acquire indirect fitness benefits if he is related to the male that sired the offspring.

Baker *et al.* (1993) characterized polyandry in lion tamarins as monopolizing, because multiple males within a group competed for access to the female and a single male monopolized mating that led to the conception of young. In addition, stable male dominance hierarchies and preferential male association by the female was evident (Baker *et al.*, 1993). They argued that this manifestation of polyandry stemmed from limited resources, including few available females and a saturated habitat. Accordingly, non-breeding males remain in the group and ultimately replace the breeding male because their lifetime reproductive success would be higher by staying in the group than if they dispersed (Baker *et al.*, 1993; Dunbar, 1995). However, it is likely that both reproductive and habitat constraints operate jointly to shape the character of polyandrous groups in the wild.

Studies on captive marmosets and tamarins have focused on the long-term social stability of polyandrous groups. Surveys of captive breeding colonies show that multimale-single female groups tend to be stable in captivity (Price and McGrew, 1991; Rothe and Koenig, 1991). In a study of golden lion tamarins 8 polyandrous groups remained stable over many months (Kleiman, 1978). However, in 3 of them the male was related to the female. Several other studies have demonstrated medium- to long-term stability in a small number of groups of saddle-back tamarins (Epple, 1975) and common marmosets (Siess, 1988 as cited by Rothe and Darms, 1993).

There was no report in which polyandrous groups of marmosets or tamarins had been studied in conjunction with hormonal measures in the males. Recent research suggests that both testosterone (T) and cortisol (CORT) vary across social contexts in male marmosets (Nunes *et al.*, 2001) and tamarins (Ginther *et al.*, 2001). Furthermore, our own research suggests that in captive marmosets adult sons in the natal group have lower T than their fathers (French and Schaffner, 1995), and in peer groups of marmosets composed of multiple adult males, subordinates have lower T

than the dominant male (Abbott, 1993). Such sensitivity in the interplay between social context, mating system and hormones, particularly T, has been thoroughly explored in avian taxa via the challenge hypothesis (Wingfield *et al.*, 1990). The hypothesis indicates that for monogamous and polygynous species in which males provision offspring, T should be elevated only during times of heightened competition among males because high T is incompatible with paternal care (Saino and Møller, 1995). Under stable conditions, once territories are established, relationships among males should be maintained by social inertia with males having relatively low T levels. For males that provision offspring, T spikes at the start of the breeding season and then progressively declines across phases of nesting, brooding and rearing young.

We examined whether evidence for a monopolizing or a non-monopolizing facultative strategy was present in polyandrous groups of Wied's marmosets (*Callithrix kuhlii*), consisting of 2 related males and 1 unrelated female across the first 80 days of group formation. We compared the behavioral and endocrine measures during the establishment of polyandrous groups and contrasted the behavioral and endocrine responses to group formation with analogous data collected on males housed in monogamous pairs. In addition, we compared the endocrine and behavioral profiles of the high- and low-mating polyandrous males across the female ovulatory cycles. We predicted that if males exhibited a non-monopolizing strategy, there would be little evidence for a preferential relationship with the female, either socially or sexually, by one of the males. Conversely, if the marmosets engaged in a monopolizing polyandry strategy, we expected to see considerable evidence of aggressive and agonistic competition between males and differential access to the female socially and sexually, particularly during the periovulatory period. Increased competition between males should also lead to elevated levels of T and CORT during the establishment of the polyandrous groups and during the female periovulatory periods, particularly if the represent instability in the relationships between the males (cf., Wingfield *et al.*, 1990). Thus, we predicted that one male in each polyandrous group would have higher T and CORT, particularly during periods when the female was most likely to conceive and that polyandrous males would have higher T and CORT than monogamous males throughout the observation period.

METHODS

Subjects

A total of 20 adult Wied's marmoset males (*Callithrix kuhlii*) contributed data to the study: 10 males from 5 newly-formed polyandrous groups (2 related males and 1 unrelated female Table I). We contrasted behavior and

Table I. Characteristics of male marmosets in polyandrous groups

Males in the same dyed	Type of relation	Ages when group formed (in years)	Experience parent (p) or helper (h)
Hum/Igg[a]	Father/son	8.0/1.6	p/no
Cal/Giz	Brothers	2.0/1.5	h/h
Moz/Ell	Brothers	2.2/2.8	h/h
Ken/Lea	Brothers	1.8/1.8	h/h
Ren/Xe	Brothers	2.4/1.5	h/h

[a] Abbreviated names of the males that served in the study. The ordering of the names corresponds to characteristics presented in the next 3 columns.

hormone profiles of polyandrous males with similar measures from males in newly-formed monogamous groups. Five of the monogamous males contributed behavioral data and 5 different monogamous males contributed hormonal data. Monogamous males were evenly matched for age. The males contributing behavioral data were on average 38 mo old and males contributing hormonal data were on average 34 mo old when placed into monogamous groups. None of the monogamous males had previous experience as a parent, and all but 3 males had experience as helpers in their natal family groups.

Housing and Husbandry

The subjects were at the Callitrichid Research Facility at the University of Nebraska at Omaha. All of them were socially housed within enclosures ranging from $0.9 \times 0.9 \times 1.2$ m. to $1.6 \times 1.2 \times 2.4$ m. There was olfactory, auditory and limited visual contact with neighboring groups, which was achieved with opaque screens. They ate a balanced and varied diet 2 times per day and had access to water at all times. Lighting was controlled on a 12:12 on/off cycle starting between 06:00 and 08:00 h, depending on colony room (Schaffner *et al.*, 1995). We treated the subjects in accordance with all local, state and federal laws pertaining to the care and use of animals in research. The Callitrichid Research Facility is a U.S.D.A. licensed and AAALAC accredited facility. The research was reviewed and approved by the UNO/UNMC IACUC (#91-110-03, #95-103-07).

Behavioral Procedures

Formation of Groups

Before establishing polyandrous groups, we ensured that all males had stable social relationships with each other. Thus, we had them cohabit for

a period of ≥6 weeks and not >6 mo. From January 1993 until November 1995 5 dyads were formed. We conducted 2 series of observations to ascertain whether a dominance relationship was present in each dyad. We observed behavior during undisturbed conditions and during presentations of highly-prized food items. No aggressive interactions occurred during either condition. A clear winner emerged during the presentation of highly-prized foods in 2 dyads. All 5 dyads showed very stable social relationships as evidenced by allogrooming, a complete lack of aggressive interactions, and mutual maintenance of proximity.

At the end of the dyad cohabitation phase males were introduced to an unrelated, unfamiliar female in an enclosure that was novel for all 3 individuals. We monitored newly-formed groups very closely. An observer was either stationed in the room (first several hours of group formation) or made frequent checks of the social interactions among individuals ≥1 time/h for the first 3 days of group formation. Monogamous groups were formed in a similar fashion, with the exception that we paired a single male with an unfamiliar, unrelated female.

Behavioral Data Collection

We conducted observations across the first 80 days of group formation because our previous research indicated that changes in social and sexual relationships reach an asymptote between days 60 and 80 from pair formation (Schaffner *et al.*, 1995; Schaffner, unpublished data). We used instantaneous sampling every 30 s to indicate the female's proximity to the male as within one arm's reach or closer. Behaviors scored on an all occurrences basis included behaviors related to sexual activity, such as open-mouth-display (a rhythmic opening and closing of the mouth emitted by males and females that signals a readiness to mate), attempted mount, mount, copulation, and genital sniffing; agonistic behaviors (anogenital and suprapubic scentmarks, archwalking, and genital displays), aggressive behavior (strike, attack, tuft-flicks and erh-erh vocalization), follow, approaches (to within arm's reach or closer), and leaves (subject moves away more than arm's reach). We scored allogrooming via 1-0 sampling every 30 s (Schaffner *et al.*, 1995; Schaffner and French, 1997).

Thirty-min observations occurred 3–5 days per week. We observed polyandrous groups an average of 50 days (46–61) distributed evenly across the 80-day period. We observed monogamous pairs an average of 39 days (34–44) distributed evenly across the 80-day period. Three observers collected the data and interobserver reliability ranged between $r = .85$ and $r = .89$.

Urine Collection

Hormones were monitored via urine samples that were collected from each individual 4–7 days per week. We collected the first void of the day in aluminum pans or metal trays that temporarily lined the cage floor. Following collection, we centrifuged samples at 700 rpm and transferred the supernatant to a clean tube and froze it at $-20°$C until assay.

Assay Procedures

Testosterone EIA

We used a testosterone (T) enzyme immunoassay (EIA) that has been described and validated for marmosets (Nunes *et al.*, 2000). We hydrolyzed urine samples (10 μl) with 25 μl of β-glucurondase (Sigma Chemical Co., St. Louis MO, USA) and extracted T with 5.0 ml of diethyl ether. We evaporated the ether under nitrogen and the samples reconstituted with 4 ml EIA phosphate buffered saline (PBS).

Microtitre plates (Nunc-Immuno Plate MaxiSorp F56) were coated with T antibody (R156/7, Dr. Bill Lasley and Dr. Coralie J. Munro, University of California, Davis, CA). We added duplicate aliquots of T standard, (Sigma Chemical Corporation, St. Louis, MO) ranging from 1000 to 1.95 pg/well in halving dilutions and 50 μl of diluted urine extracts to the plates. We added T HRP conjugate (batch # 3/95) to all wells. After incubation and separation of unbound steroid, we added 100 μl of EIA substrate solution (ABTS and H_2O_2 in citrate buffer) to all wells. We read plates in a Dynatech MR5000 plate reader after color formation was complete.

Recovery for T following extraction phase was 78%. The assay sensitivity at 90% binding was 1.95pg. Displacement curves of halving dilutions of male urine pool and T standards were parallel in the 10–90% binding range. We determined the precision of the assay for the current study by assaying pooled urine samples that contained high and low concentration in each assay. Interassay variability for high pools (n = 25) was 4.1% and for low pools (n = 25) was 5.0%. Intraassay coefficients were 4.4% and 4.8% for high and low concentration pools, respectively.

Cortisol EIA

We assayed samples for urinary cortisol (CORT) with an EIA previously described and validated for the species by Smith and French (1997).

Standards ranged from 1000 to 1.95 pg/well in halving dilutions. The procedural details are identical to those for T EIAs, with the exception that no hydrolysis or extraction was required before assay. We determined the precision for the assay by assaying high and low concentration pooled urine samples. Interassay variability for high concentration pools (n = 24) was 3.7% and for low concentration pools (n = 24) was 5.0%. The intraassay coefficients of variability were 3.9% and 4.8% for high and low concentration pools, respectively.

Creatinine Assay

We corrected the hormonal concentration for each sample for creatinine concentration via a modified Jaffe end-point assay (Burtis and Ashwood, 2001). The protocols have been validated and described by French *et al.* (1996). Coefficients of variations were 13% for interassay variation and 2.5% for intraassay variation.

Data Analysis

We determined for each polyandrous group which male had the greater number of mating events—mounts, attempted mounts and copulations—across the course of the study. We used this criterion to test for differences in frequencies of behaviors related to sexual activity by comparing the high-mating polyandrous males, the low-mating polyandrous males and the monogamous control males. We also examined only copulations in which ejaculation occurred, as attempted mounts and mounts represent unsuccessful mating attempts and could be higher in subordinate males. Finally, we contrasted the levels of T and CORT across the 3 different types of males, as levels of T are thought to be elevated in periods of group instability, such as the formation of a new group (Wingfield *et al.*, 1990). To test whether polyandrous males were overtly competitive with each other, we tested for differences in agonistic displays among the 3 types of males. Finally, to test whether males in polyandrous groups were aggressive toward each other, we compared the mean frequency of aggressive behavior, which included a composite measure of erh-erh vocalization, tuft-flicks, attacks and strike, between the high-mating polyandrous males and their partner males. We tested comparisons involving the 3 different males using a one-way between subjects analysis of variance (ANOVA), with type of male—high-mating polyandrous, low-mating polyandrous and monogamous control—as the factor. We performed statistical comparisons involving only high- and low-mating polyandrous males using paired *t*-tests.

We also tested for monopolization by one of the polyandrous males by comparing the effect of female ovulatory status on social, competitive and sex-related behaviors as well as hormone titres between high-and low-mating polyandrous males. This was accomplished by contrasting mean rates of behavior and urinary T and CORT levels during different phases of the female ovulatory cycles. We determined the day of ovulation by pregnandiol glucuronide profiles, a conjugate of progesterone, and signaled by a peak in luteinizing hormone. We then divided the cycle into 3 phases: periovulatory that occurred from −2 to +2 days around ovulation; follicular (−6 through −3 days before ovulation) and luteal (+3 through +8 days following ovulation). Two researchers not involved in the study independently pinpointed ovulation events for each female. The comparisons were made with a series of 2-factor mixed ANOVAs with the between-subjects factor being type of male (high-mating vs. low mating) and the within-subjects factor being phase of cycle (periovulatory vs. follicular vs. luteal).

Our previous data suggest that males and females change their behavior toward each during the early phases of pair formation (Schaffner *et al.*, 1995). Therefore we assessed the effect of the duration male-female relationships on the behavior and hormone profiles in the males at four 20-day intervals across the 80-day observation period. We contrasted mean frequencies of affiliative behavior per 30 min for males from monogamous and polyandrous groups. We used the Hinde Index (Hinde and Atkinson, 1970) to ascertain whether the males or the females assumed a greater role in maintaining contact. We derived the index by subtracting the proportion of bouts of social proximity in which the female left the male from the proportion of bouts in which the female approached the male, for each observation session. In addition, we compared mean levels of urinary CORT and T between the 2 types of males. We performed comparisons via a series of 2-factor mixed ANOVAs with the between-subjects factor being type of male (polyandrous vs monogamous) and the within-subjects factor being time (4 20-day blocks) following group formation. We further analyzed significant main effects for time via Tukey's honestly significant difference (HSD) post hoc comparison. We used the Huynh-Feldt correction for sphericity for any within-subjects components of all the analyses to reduce the risk of Type I error (Keppel, 1993). We adopted an alpha level of $P < 0.05$ for all tests.

RESULTS

Testing for monopolization

Before presenting statistics we must note the lack of success in forming 3 polyandrous groups of marmosets composed of unrelated males. Although

they cohabited successfully, aggression erupted between the 2 males immediately upon polyandrous group formation. In each instance, one of them systematically emitted erh-erh vocalizations toward the other male and followed him throughout the enclosure. The recipient responded to the aggression by emitting infant-like raspy vocalizations and retreated to the bottom of the enclosure. In our experience such behavioral exchanges signals the imminent expulsion of a group member; therefore, we disbanded these group. Accordingly, the analyses pertain only to polyandrous groups composed of related/familiar males.

High-mating males engaged in attempted mounts, mounts, and copulations much more frequently ($M = 59.8 \pm 28.85$ SE) than the low-mating males (13.2 ± 5.39) did. However, the difference is attributable to the difference in unsuccessful mating attempts, which was an average of 56.00 ± 29.61 for high-mating males and average of 11.00 ± 5.37 for low-mating males. Neither comparison is significantly different (Ps $\geq$ .13). We then tested to see whether high-mating polyandrous, low-mating polyandrous and monogamous control males differed in their interest in mating with females by comparing the frequencies of open-mouth displays and genital sniffing. There was a tendency for high- and low-mating males to emit open mouth displays more than monogamous males did, but there is no significant difference in the frequency of genital sniffing by the 3 types of males toward the female (Table II). All of the polyandrous males copulated—mating including actual ejaculation—with the female in full view of the other male. We did not observe males interfering in the mating activities of the other male and aggression did not occur in the context of mating. Only 2 of the 5 monogamous males copulated with their females. When we examined copulations across the 80-day observation period there was a nearly significant difference between the 3 types of males (Table II), with the monogamous males being the least active. When we collapsed the data for polyandrous males ($M = .05 \pm .01$) and contrasted it to monogamous males the difference was significant ($t_{13} = -2.13$, $P = .05$). However, there is no difference in the urinary T or CORT levels among the 3 different types of males (Table II).

There was no evidence that high- and low- mating polyandrous males displayed more agonistic behavior than monogamous controls. Although high- and low-mating males circumgenital scentmarked more frequently than the monogamous controls did, there was a great deal of individual variability in the rate at which the behavior was displayed by different males within each classification and there is no significant difference (Table II). Similarly, there was no difference in the rate in which the different types of males suprapubic scentmarked. Archwalking was displayed at higher rates by the high- and low- mating polyandrous males than by the monogamous

Table II. Mean (SE) behaviors directed toward females by the different types of males[a] and their steroid hormone levels with relevant ANOVA results

Measure	High-mating	Low-mating	Monogamous	F (2,12)	P
Sex-related					
Open-mouth displays	0.39 (0.09)	0.90 (0.68)	0.24 (0.15)	2.94	0.09
Genital-sniffing	0.30 (0.15)	0.27 (0.14)	0.24 (0.06)	0.05	0.95
Copulations	0.07 (0.02)	0.04 (0.01)	0.01 (0.01)	3.30	0.08
Agonistic					
Circumgential scentmark	5.14 (1.46)	6.81 (2.94)	2.09 (1.19)	1.41	0.28
Suprapubic scentmark	0.30 (0.17)	0.15 (0.05)	0.13 (0.11)	0.64	0.55
Archwalking	0.50 (0.24)	0.44 (0.31)	0.02 (0.02)	1.36	0.29
Genital display	0.09 (0.05)	0.67 (0.28)	2.19 (1.66)	1.22	0.33
Hormone					
T (ng/mg creat)	3152 (566)	2543 (567)	2793 (432)	0.34	0.72
CORT (μg/mg creat)	19.74 (3.62)	20.62 (1.69)	24.16 (2.07)	0.81	0.47

Note. Rates of behavior are expressed as acts/30 min observation.
[a] High-mating polyandrous, low-mating polyandrous and monogamous males.

control males, but the difference is not significant and there is no significant difference in the rate of genital displays by the 3 types of males (Table II).

A composite measure of aggressive behavior did not indicate that males were aggressive toward each other. Aggression by the high- mating males toward the low- mating males occurred 3 times across the 5 groups and the 80-day observation period ($M = .01 \pm .006$ per 30 min), whereas low-mating males directed aggression toward the high-mating males only once ($M = .004 \pm .004$ per 30 min). The difference is not significant ($t_4 = .69$, $P = .53$).

Next, we examined behavior and hormone levels in only high- and low-mating polyandrous males across the reproductive cycle of the females. There is little evidence to suggest that one polyandrous male within each group monopolized mating or social access to the females during the different phases of their cycles. There is no significant main effect for type of male or phase of cycle for any of the behavioral measures (Table III). In addition, there is no significant interaction between the 2 factors for any of the behaviors (all Ps $\geq .19$). Two of the analyses approached significance. For copulation, type of male was nearly significant with high-mating males copulating with the female more than low-mating males did; however, in the periovulatory phase 3 of the 5 male dyads were tied in their frequency of copulating with the female. For male allogroom female there was a trend for both males not to allogroom females during the follicular phase. However, most of the data points for follicular phase occur during the initial 2 weeks of group formation when allogrooming between marmosets is very low. We were not able to statistically analyze T and CORT levels because not all males provided samples for all phases of the reproductive cycle, resulting in

Table III. The mean (SE) behaviors directed toward females by high- and low-mating males are presented across the reproductive cycle with the corresponding between and within subject components of the ANOVAs

Measure	Type of male	Periovulatory	Follicular	Luteal	Between F (1,8)	Within F (2,16)	P
Sex-related							
Open mouth displays	High	1.02 (0.55)	4.19 (2.23)	0.38 (0.22)	1.00		0.35
	Low	0.75 (0.31)	1.71 (1.51)	0.55 (0.24)		2.55	0.14
Genital-sniffing	High	0.40 (0.13)	1.00 (0.17)	0.35 (0.35)	0.10		0.76
	Low	0.89 (0.41)	0.63 (0.77)	0.23 (0.29)		1.7	0.22
Copulation	High	0.25 (0.14)	0.33 (0.21)	0.05 (0.05)	4.13		0.07
	Low	0.06 (0.05)	0 (0.00)	0.02 (0.02)		0.96	0.40
Affiliative							
Male groom female	High	0.41 (0.06)	0.0 (0.00)	0.13 (0.10)	0.99		0.35
	Low	0.44 (0.25)	0.15 (0.15)	0.75 (0.46)		3.50	0.07
Male follow female	High	3.26 (2.45)	6.54 (6.20)	0.82 (0.68)	1.10		0.33
	Low	0.45 (0.23)	0.27 (0.11)	00 (0.00)		1.14	0.32
Sit in contact	High	5.18 (2.54)	5.61 (3.63)	4.27 (2.22)	0.33		0.58
	Low	3.86 (0.78)	2.42 (0.73)	3.95 (0.97)		0.18	0.84
Agonistic							
Anogenital scentmarks	High	3.12 (1.19)	3.99 (1.76)	3.26 (1.32)	0.77		0.41
	Low	7.61 (3.21)	4.97 (2.35)	4.98 (1.85)		0.82	0.46
Suprapubic scentmarks	High	0.44 (0.30)	0.13 (0.10)	0.33 (0.07)	1.62		0.24
	Low	0.17 (0.12)	0.03 (0.03)	0.17 (0.07)		1.30	0.30
Genital displays	High	0.01 (0.01)	0.09 (0.06)	0.03 (0.03)	2.69		0.14
	Low	0.55 (0.34)	0.70 (0.37)	0.25 (0.19)		1.91	0.19
Archwalks	High	0.66 (0.38)	0.49 (0.38)	0.65 (0.41)	0.001		0.97
	Low	0.77 (0.62)	0.05 (0.05)	0.92 (0.84)		1.80	0.21
Hormone							
T (ng/mg creat)	High	2540 (802)	2858 (756)	2899 (565)			
	Low	3159 (667)	3053 (747)	2884 (751)			
CORT (μg/mg creat)	High	14.99 (3.7)	13.59 (1.6)	23.13 (8.5)			
	Low	29.89 (9.7)	19.38 (1.3)	28.20 (7.2)			

Note. Rates of behavior are expressed as acts/30 min observation.

some cells in the analyses having only 3 data points. The descriptive statistics indicate that the distributions for hormone levels are largely overlapping between the 2 types of males. We performed no analysis for aggressive behavior between the males because only one aggressive behavior occurred across the 3 phases of the female cycles. The overwhelming indication from the analyses is that males in polyandrous groups do not monopolize social or sexual access to females. Therefore, in subsequent analyses we do not distinguished polyandrous males from each other, but contrast them together versus monogamous males.

Behavioral Contrasts Over Time

Monogamous males were in proximity with females in nearly half of the instantaneous samples, significantly more often than polyandrous males ($F_{1,13} = 27.35$, $P < .001$, Fig. 1a), and the levels did not change across the 80 days of group formation ($F_{3,39} = .85$). Unlike proximity, rates of allogrooming the female did not vary systematically, either as a function of type of male ($F_{1,13} = .73$) or across group formation ($F_{3,39} = .86$), and there was no significant interaction ($F_{6,39} = 1.49$, Fig. 1b). Similarly, there was no difference in the frequency that females allogroomed males in monogamous versus polyandrous groups ($F_{1,13} = .53$, $P = .48$), though there was a tendency for females to allogroom males more frequently the longer the group was together ($F_{3,39} = 2.23$, $P = .10$, Fig. 1c).

When we examined whether polyandrous males differed in their role in proximity maintenance with females, we found no difference in their patterns of proximity maintenance versus monogamous males ($F_{1,13} = .09$). However, the male role in regulating proximity changed over time ($F_{3,39} = 2.88$, $P < .05$), with both monogamous and polyandrous males assuming more responsibility for maintaining contact with females early during group formation, while later during group formation maintaining contact was less skewed. Comparisons post hoc revealed significant differences among the first 2 time blocks versus the latter 2 time blocks ($P < .01$, Fig. 2). There is no significant interaction effect ($F_{3,39} = .78$).

Hormonal Contrasts Over Time

Endocrine function in males was not affected by the demography of the social group (Fig. 3). For urinary T there is no significant difference in levels between monogamous and polyandrous males ($F_{1,13} = .09$), nor is there a significant change over time ($F_{3,39} = .25$), and there is no significant interaction between the factors ($F_{3,39} = 1.99$). Urinary CORT tended to decrease for both types of males across the 3 time blocks following group formation ($F_{3,39} = 2.56$, $P < .11$, but there is no effect of type of male ($F_{1,13} = 1.78$), and no significant interaction ($F_{3,33} = 1.78$).

DISCUSSION

We predicted that if groups exhibited a non-monopolizing polyandry strategy there would be little evidence for a monopoly of social or sexual behavior with the female by one of the males. Conversely, if the marmosets engaged in a monopolizing polyandry strategy there would be evidence of competition in the form of aggression, heightened agonistic displays,
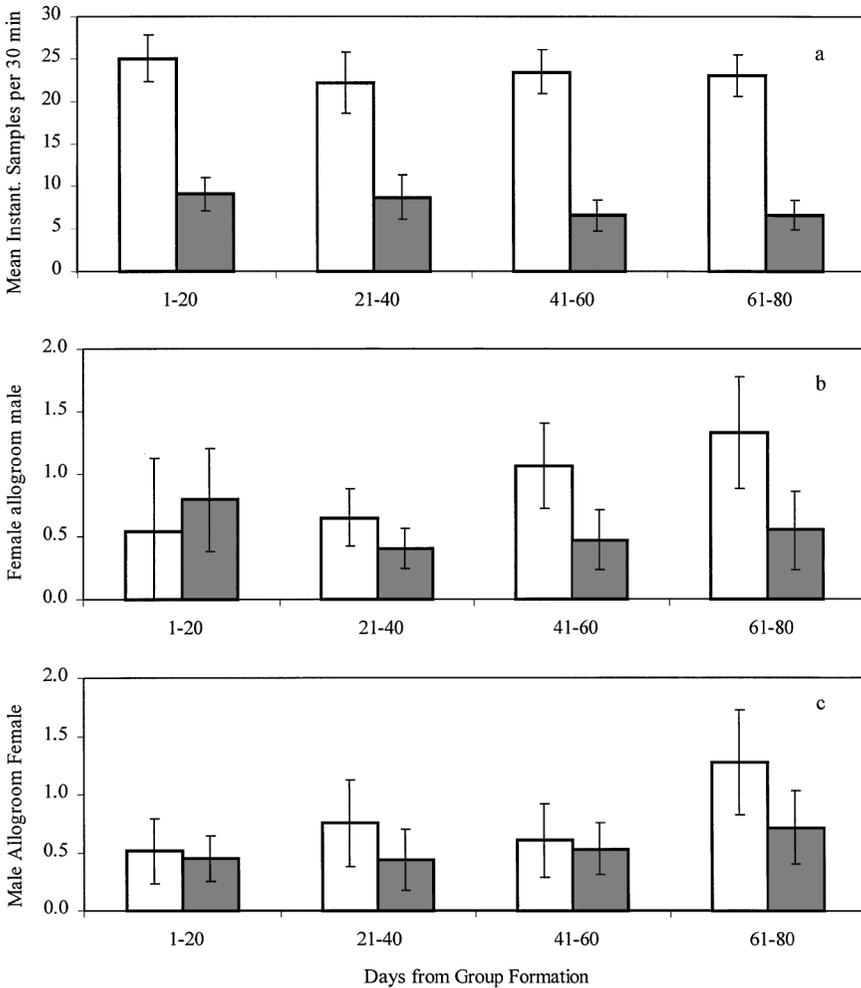
Fig. 1. Mean (±SE) instantaneous samples in contact per 30 min (a), mean (± SE) one-zero frequencies of male allogrooming female per 30 min (b), and mean (± SE) one-zero frequencies of female allogrooming male (c) across the 4 time blocks. Monogamous males are represented by open bars and polyandrous males are represented by filled bars. For (a) there is a significant main effect for type of male.

increased urinary T levels and differential access to the female both socially and sexually. Our findings point to a non-monopolizing facultative strategy, as there was little overt competition and little difference in the frequency in the behavior of polyandrous males with the females and no difference in urinary T and CORT levels compared to those of monogamous males.
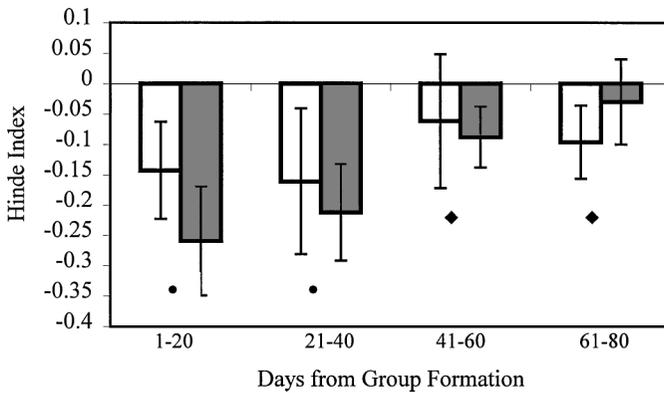
Fig. 2. Mean (±SE) Hinde index across the 4 time blocks (derivation in text). Monogamous males are represented by open bars and polyandrous males are represented by filled bars. There was no difference between the type of male at any of the 4 time blocks. Pairs of bars with different symbols represent statistically different comparisons post hoc ($P < .01$) for both comparisons.

Although polyandrous males did not differ from monogamous males in the majority of behaviors, there are 2 key differences. Polyandrous males were less frequently in proximity with the females and they copulated more frequently with the female than monogamous males did.

The lack of robust evidence to support a monopolizing strategy stems from the results that male marmosets did not show competitive behavior or elevations in hormone levels. When examining studies on other groups of marmosets and tamarins, there is no definitive pattern of behavioral evidence for either a monopolizing or non-monopolizing strategy on the part of males in polyandrous groups. For wild populations aggression between males in polyandrous groups is remarkably low (Baker *et al.*, 1993; Garber *et al.*, 1993; Goldizen, 1987; Heyman, 1996; Soini, 1987). However, in cases where a clear dominant male has been identified, it is he that engages in more sexual behavior with the female during times when she is likely to conceive (*Cebuella pygmaea*: Soini, 1987; *Leontopithecus rosalia*: Baker *et al.*, 1993). Just as often, researchers are unable to identify dominance differences between polyandrous males and rates of sexual activity do not appear to differ between the males (*Saguinus fuscicollis*: Goldizen, 1987; *S. mystax*: Garber, *et al.*, 1993; *Callithrix jacchus*: Lazaro-Perea *et al.*, 1999). We found no evidence in our polyandrous groups that males were aggressive toward each other or that they monopolized mating. They were related ($r = .50$) and at least one of them had known the other male all of his life. Evidence from wild marmosets, in which newly-formed polyandrous groups likely consisted of
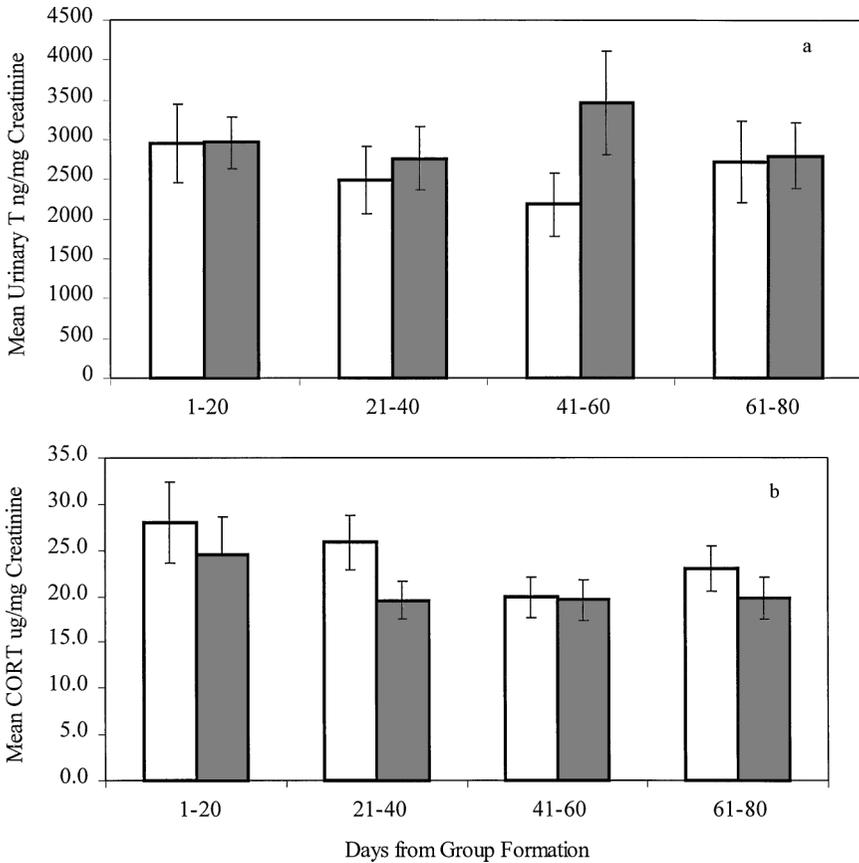
Fig. 3. The mean (±SE) concentrations for urinary T(a) and urinary CORT (b) are presented across the 4 time blocks. Monogamous males are represented by open bars and polyandrous males are represented by filled bars.

related males that were familiar, revealed a similar lack of competition and shared reproductive activity (Lazaro-Perea *et al.*, 1999). Thus, relatedness could be a critical factor in lowering overt competition between males. When we attempted to form polyandrous groups composed of unrelated males (n = 3), in which the males cohabitated together peacefully for ≥6 weeks before being introduced to a female, the groups were immediately unstable. Similarly, 2 of 3 polyandrous groups of captive cotton-top tamarins composed of unrelated males became unstable as evidenced by aggression toward one of the males shortly after the groups were established (Price and McGrew, 1991). It may be that long-term familiarity and relatedness (by growing up

in the presence of one another) is a prerequisite for facultative polyandry at least in some callitrichid species.

There are several possible explanations why it is difficult to ascertain dominance relationships between polyandrous males and why dominance, if established, does not parlay into different rates of successful reproductive activity in them. First, they may compete via sperm competition and not via overt aggression. Testes are larger in primates with a multimale mating system (Dixson, 1993; Harcourt *et al.*, 1981), and in a closely related species, the cotton-top tamarins (*Saguinus oedipus*), testicular weight is greater than expected for a monogamous species (Harcourt *et al.*, 1981). However, when Dixson (1993) compared testicular volume versus body mass in several species of callitrichids, he found little evidence for sexual selection due to sperm competition. Data on wild moustached tamarins (*Saguinus mystax*) reveal a systematic pattern of variability among functionally polyandrous males, in which one male in each group had significantly larger testes than those of other breeding males (Garber *et al.*, 1996). Garber and colleagues (1996) suggested that the mechanisms underlying the variation in testicular size may be due to different levels of T and luteinizing hormone in males. This makes sense as callitrichids experience dramatic changes in reproductive function under varying social environments (Abbott, 1993; French and Schaffner, 1999; Smith *et al.*, 1998). We found no evidence that T values are different between the polyandrous males or monogamous males, and T levels did not fluctuate meaningfully across the ovulatory cycle of the females or across the first 80 days of group formation. However, our polyandrous males copulated more than monogamous males did, which suggests that competition may occur at the gamete level.

A second possible reason why polyandrous males did not behave competitively in our study is the duration of the relationship between the males and the female. In an investigation of polyandry in captive saddleback tamarins, the male that engaged in more sexual interactions with the female had allogroomed the female more often (Epple, 1975). Heymann (1996) identified a similar pattern in allogrooming in 2 groups of wild moustached tamarins, but the observations of sexual behavior with the female did not reveal more mating with the female by one of the polyandrous males. In our polyandrous groups, the males did not differ from monogamous males in the frequency of allogrooming, whereas previous analysis of allogrooming by males toward females in newly-formed monogamous groups revealed a significant increase in the behavior over time (Schaffner *et al.*, 1995). In addition, our data revealed that polyandrous males were much less often in proximity with the female than the monogamous males were. The two behavioral differences between polyandrous and monogamous males suggest that the time it takes for social bonds to form between males and females

in polyandrous groups may be prolonged relative to the establishment of social bonds in monogamous groups. Consequently, males in newly-formed polyandrous groups may have essentially equal access to females simply because not enough time has elapsed for a strong social bond to develop.

Two other studies provide support for our findings. Lazaro-Perea *et al.* (1999) reported a lack of competition in 4 newly-formed groups of wild common marmosets that contained >1 breeding male, and in each case all males copulated with the new female(s) without conflict over mating opportunities.

In a laboratory investigation of common marmosets, in which father/son dyads were briefly introduced to unrelated females there was almost no aggressive behavior scored between the 2 males and the males did not differ in the rates at which they mated with the female (Baker *et al.*, 1999). In contrast, observations on wild common marmosets indicate that in well-established groups males monopolize mating with the breeding female via mate guarding (Lazaro-Perea *et al.,* 1999). Thus, a preferential relationship may develop between the female and one of the males over time, but it is unclear whether this would lead to increased overt competition between the males.

A third reason why polyandrous groups of marmosets are not overtly competitive may stem from the need for multiple group members to support infant care, which in turn is a consequence of the high reproductive output of callitrichid females (French, 1997). In fact, high costs have been implicated for males. Cotton-top tamarin males experience significant weight loss while carrying infants in the first 8 weeks following their birth (Achenbach and Snowdon, 2002; Sánchez *et al*., 1999). In addition, weight loss was most pronounced in males from small family groups (Achenbach and Snowdon, 2002), suggesting the reproductive cost is particularly high in newly-formed groups (contra Nievergelt and Martin, 1999). Thus, due to the high mother-to-infant birth weight ratio, the rate at which females can potentially reproduce, and the costs to fathers, additional adults (beyond that of a breeding pair) are believed to be essential to successfully rear offspring in the wild (Goldizen *et al.*, 1996). Once group size increases through birth, the level of tolerance between polyandrous males could theoretically decline. Schaffner and French (1997) found such a pattern of small group tolerance and large group intolerance in marmosets when breeding females were exposed to potential reproductive competitors. Therefore, the tolerance observed between the polyandrous males living in small groups in our study—low aggression and an absence of interfering in mating activities—agrees with previous studies that support a flexible mating strategy on the part of marmosets and tamarins (Savage and Baker, 1996).

If polyandry is a facultative strategy used by marmosets and tamarins, particularly when groups are small, how can we account for the differences in

reproductive access between males in polyandrous groups of lion tamarins, in which a monopoly on mating occurred between one of the polyandrous males and the female (Baker *et al.,* 1993) and saddle-back tamarins in which no monopoly was detected by Goldizen, (1987)? One explanation may lie in the extent to which factors that influence reproductive skew, such as relatedness of potential breeders and resource availability (Clutton-Brock, 1998), fluctuate between the 2 species. When groups are small, males that participate in a polyandrous system may gain more reproductive benefits than males that engage in a monogamous strategy do. That is to say a single male and female may have lower reproductive success than in cases where in 2 males join a female. Goldizen (1987) suggested that in saddle-back tamarins, polyandry may be a necessary strategy when groups are newly-formed. Small group size could represent a situation in which concessions are made by males, in the form of low aggression and breeding opportunities, which represent incentives for more than one breeding male to remain in the group (Keller and Reeve, 1994). When group size increases via recruitment in the form of maturing offspring, staying incentives could theoretically decline and males emigrate as observed by Goldizen.

Polyandry is also a strategy adopted by lion tamarins, particularly when groups are small (Baker, personal communication), though their groups differ from saddle-back tamarin groups in two ways. Polyandrous groups of lion tamarins are characterized by the presence of a distinguishable dominance hierarchy among males of breeding age (Baker *et al.*, 1993), whereas male saddle-back tamarins are not (Goldizen, 1987), and the lion tamarins live in more saturated habitats than the saddleback tamarins observed by Goldizen did. Therefore, the strategy of emigrating when group size increases is the least successful strategy for lion tamarin males (Baker and Dietz, 1996), and the transition from demographically polyandrous groups to groups with a single breeding male appears to arise from the death of one of the potential breeding males (Baker, personal communication). The pattern of polyandry in lion tamarins suggests that subordinate males require less staying incentives because the habitat is saturated (Clutton-Brock, 1998). Thus, for callitrichid males in saturated habitats, staying and cueing for breeding opportunities may be the best option.

Our data support the notion that cooperative polyandry is a non-monopolizing strategy adopted by closely related male marmosets and is highly stable when groups are small, but it remains to be thoroughly tested whether the strategy is successful when group size increases. Our colony records suggest that the relationships between polyandrous males becomes unstable under disturbed conditions, such as visual access to neighboring groups or the temporary removal of >1 resident breeding individual as a part of the protocol for other research projects.

In conclusion, we found no evidence of overt competition in polyandrous groups composed of related and highly familiar individuals. The formation of groups may represent a special situation in which the need for members to get along is paramount and overt competition too costly when males are related. Detailed observations on well-established polyandrous groups need to be gathered in order to know if preferential relationships or dominance hierarchies or both influence the pattern of social and sexual relationships between males and females. Whether males engage in facultative polyandry likely depends on a variety of factors including the degree of relatedness among breeding males, the number of adult helpers available, and the extent to which habitats are saturated.

ACKNOWLEDGMENTS

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