Integration of New Males into Four Social Groups of Tufted Capuchins (*Cebus apella*)

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*We examined how aggressive, affiliative, and sexual behavior function to integrate male capuchins (*Cebus apella*) into a new social group. Nine males were exchanged among four social groups. We performed instantaneous scans and all-occurrence sampling during baseline, introduction, and follow-up periods. The study included three different introduction situations: 1) males familiar to one another were introduced to a group with no other adult male, 2) males unfamiliar to one another were introduced to a group with no other adult male, and 3) males familiar to one another were introduced to a group with an existing elderly, resident male. Severe aggression occurred in situations 2 and 3, but the introductions were peaceful in situation 1. In all cases proceptive females were among the first individuals to affiliate with the males, and males did not appear to compete for access to proceptive females. Following their period of proceptivity, the females that had cycled remained preferred social partners for the males. Immature animals also quickly affiliated with the new males, and the males tolerated the attention from immatures. Affiliative relationships between the males and nonproceptive females developed slowly, and while male-female aggression was mild, aggression among adult males (familiar and unfamiliar) had the potential to be severe.*

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INTRODUCTION

The potential for severe aggression makes the introduction of strangers into captive primate social groups problematic. In rhesus macaques (*Macaca mulatta*), new group members become integrated through aggression and the swift establishment of dominance relationships. For example, Bernstein (1964) found that rates of aggression peaked ≤20 min of introduction and then declined rapidly. Grooming, proximity, and individual activities, however, took over a week to stabilize. In pig tailed macaques (*M. nemestrina*) agonistic and affiliative response rates remained unstable for weeks after group formation, resulting in a longer period of social disruption than in rhesus macaques (Bernstein, 1969). Moreover, the successive introduction of individuals resulted in a higher rate of aggression and a longer period of social disruption than the simultaneous introduction of many individuals. In contrast, Westergaard *et al*. (1999) reported that for rhesus macaques a staged-group-formation method led to lower rates of severe injury than did a rapid-group-formation method. Among macaques, aggression is the initial, and probably most important, mechanism for integrating new members.

In other primate species, other responses to newcomers dominate. For example, male gibbons exhibit little aggression upon the introduction of adult males, but aggression builds up slowly over several days (Bernstein and Schusterman, 1964). In gelada baboons (*Theropithecus gelada*) pair-bonding proceeds through four stages: fighting, presenting, mounting, and then grooming (Kummer, 1974). Male-female dyads, however, typically skip the fighting stage.

Capuchins also do not conform to the macaque model of immediate aggression upon introduction, followed by rapid decline. *Cebus albifrons* had a lower overall rate of agonistic behavior during group formation than that of rhesus macaques, and aggression declined more gradually (Bernstein, 1965). Becker and Berkson (1979) suggested that, in capuchins, aggression toward strangers is mild and mainly limited to threats directed to new males. In tufted capuchins (*C. apella*), the introduction of strangers does not necessarily result in immediate aggression (Fragaszy *et al.*, 1994). In the absence of resident adult males, females and juveniles initiated affiliative social interactions with the introduced male, whereas the new male remained uninterested (Fragaszy *et al.*, 1994). Although infrequent, aggression in capuchins can be persistent and occasionally intense. The implication for captive management is that aggression does not always occur immediately following the release of monkeys, and may occur later.

To understand and to predict the consequences of an introduction, one must know the social organizations of the species. Capuchin females are philopatric, and males transfer among groups. Dominance relationships

are not as pervasive among capuchins as among macaques or baboons (Robinson and Janson, 1986). Some capuchins groom predominately down the dominance hierarchy (*Cebus olivaceus*: O'Brien, 1993; *C. apella*: Parr *et al.*, 1997), while other capuchins sometimes groom predominately up the dominance hierarchy (*C. capucinus*: Manson *et al.*, 1997; Perry, 1996). Female capuchins establish strong affiliative relationships with the alpha male (*Cebus apella*: Welker *et al.*, 1990; *C. olivaceus*: O'Brien, 1991; *C. capucinus*: Fedigan, 1993; Perry, 1997). Juveniles and infants also prefer to affiliate with the alpha male rather than other males (*Cebus olivaceus*: Robinson, 1981; *C. apella*: Welker *et al.*, 1990). The average male tenure length is 3.3 years in white-faced capuchins (*Cebus capucinus*) (Fedigan *et al.*, 1996), and ranges from 3 years in nonbreeding males to 9 years in breeding males in wedge-capped capuchins (*C. olivaceus*) (Robinson, 1988). Male turnover can result in severe aggression, occasionally culminating in the death of males, as well as females and infants (*Cebus capucinus*: Rose, 1994; Rose and Fedigan, 1995).

In *Cebus apella*, females initiate sexual interactions (Phillips *et al.*, 1994; Linn *et al.*, 1995), and they prefer dominant males, especially during periods of peak proceptivity (Janson, 1984; O'Brien, 1991). Female courtship behavior is related to ovulation, and appears to be the only cue available to males for determining female receptivity (Carosi and Visalberghi, in press). Conversely, in *Cebus capucinus*, males initiate courtship when females are in estrous (Manson *et al.*, 1997). In *Cebus apella*, Fragaszy *et al.* (1994) found that following the introduction of new males, some adult females exhibited species-typical proceptive behavior outside of possible ovulation. Female solicitations outside the typical estrous period are consistent with reports of postconception proceptivity (Phillips *et al.*, 1994; Carosi and Visalberghi, in press).

The exchange of male tufted capuchins (*Cebus apella*) among four captive groups gave us the opportunity to investigate the mechanisms of social integration. We had three different introduction situations: 1) males familiar to one another were introduced to a group with no other adult male (groups B and C), 2) males unfamiliar to one another were introduced to a group with no other adult male (group D), and 3) males familiar to one another were introduced to a group with an existing elderly, resident male (group A). In situations 2 and 3 we were particularly concerned with the possibility of aggression among unfamiliar males. In situation 3 we expected females to support the elderly resident male and to buffer him from attack. We expected that females might immediately solicit the new males outside of their estrous periods and continue to associate with the new males after their period of proceptivity. In situation 3 we expected females initially to prefer the elderly resident male but to gradually shift their preference to the new prime-aged

males. We believed that juveniles might actively approach the new males but were unsure as to how the youngest animals would respond.

METHODS

Subjects and Study Sites

We moved two social groups of tufted capuchins (*Cebus apella*) (groups A and B) from the University of Georgia (UGA) to new enclosures at Laboratory Animal Breeders and Services of Virginia (LABS) in Yemassee, SC. They are the same social groups described in Fragaszy *et al.* (1994). In association with the move, we exchanged 3 males from these 2 groups with 5 males from 2 social groups at the Yerkes Regional Primate Research Center of Emory University (YRPRC): groups C and D. One male was exchanged between social groups at YRPRC, and one elderly male from UGA remained in his resident group. The exchange of males was intended to maintain genetic diversity in all 4 social groups. In Table I we list the males in the 4 study groups and describe their associations pre- and post-transfer. We transferred the 2 males that had previously lived together in group C to group A. Likewise, we transferred the 3 males from group D to group B, and the 2 males from group B to group C. Of the 2 males from group A, we transferred one to group D and did not transfer the other. We placed the male transferred to group D together with an additional male from group C.

Table I. The male capuchins and their associations before and after transfer

Male subject	Age (years)	Old group	Years in old group	New group
SH[a]	>36	A	6	A
UY	12	C	5	A
AD	11	C	5	A
PB	12	D	5	B
VN	10	D	5	B
MO[b]	4	D	4	B
IK	21	B	6	C
OZ[b]	8	B	6	C
YV	10	A	6	D
DR[b]	6	C	6	D

[a]This male was wild-caught and referred to as a young adult in 1963. We collected these data in 1995–96, 33 years later. Assuming characterization as a young adult meant that permanent canines had erupted, this male would have been ≥36 years old during this study. He was not transferred from group A.

[b]While the other males were adult, OZ and DR were subadult and MO was an older juvenile.

Before the move the UGA, social groups lived in two-room indoor enclosures (each room: $4.8 \times 2.3 \times 2.3$ m), divided by a walled partition with a 0.5×0.5-m opening. The rooms contained perches, bedding material, and plastic chains and toys. After their move to LABS, the groups lived in a larger indoor-outdoor enclosure. The indoor area ($5 \times 20 \times 3$ m) had a gravel floor and chain link fencing and contained plastic perches, climbing structures, and a feeder. The outdoor area (30×30 m) had natural grass fenced by corrugated aluminum and two multilevel platforms, two feeders, and climbing structures. The two enclosures at YRPRC contained an indoor ($5 \times 10 \times 2.3$ m) and outdoor area ($5 \times 4 \times 2.3$ m). The indoor area was divided into two sections by chain link fencing, and each section had perches, bedding material, and plastic climbing structures. The monkeys did not use the outdoor area during the introduction or follow-up periods.

Procedure

In Table II we report the number of males, females, and immatures in each study group. One observer collected baseline data for 10 weeks while groups A and B were housed at UGA. Baseline data collection consisted of scan samples at 10-min intervals on adult and subadult males and females. Behavior recorded during the scan samples included: proximity (≤ 0.5 m), affiliative contact, allogrooming, sexual behavior, agonistic behavior, and alone, i.e. engaged in none of these behaviors. We divided data collection into

Table II. Period of observation, number of subjects, hours of observation, and the number of scan samples

Group	Study period	# of males (>4 years)	# of females (>3 years)	# of Immatures (<3 years)[b]	Hours of observation	# of scans per male
A	Baseline	2	12	10–11	21.5	150
A	Introduction	3	12	11	24.3	291
A	Follow-ups 1–4	1–3[a]	12	11	12.0	48–144
A	Reintroduction	2	12	11	12.5	150
B	Baseline	2	11	6–11	19.5	140
B	Introduction	3	11	11	24.3	291
B	Follow-ups 1–4	3	11	11	16.0	192
B	Follow-up 5	3	11	11	8.3	100
C	Introduction	2	8	6	10.5	112
C	Follow-ups 1–4	2	8	6	8.7	104

[a] In group A some of the males were removed during the follow-up periods to receive medical care for their wounds. Systematic data collection was not possible on group D (not shown).
[b] On average immatures were 13 mo old. Five immatures were >6 mo old. In group A, one immature was 5 mo old, in group B two immatures were 5 mo old and one immature was 4 mo old, and in group C one immature was only 3 wk old.

a 5-day period immediately following the introduction, and 4 2-day follow-up periods occurring at one-week intervals. We conducted scan samples on the introduced males (and the resident male of group A) at 5 min intervals during the introduction and follow-up periods. We supplemented scan samples with all occurrence data collection on the directionality of grooming, agonistic behavior, and sexual behavior. Agonistic interactions used to indicate dominance relationships included clear submissive signals such as grimace, flee, and avoid. Before data collection, we obtained 85% agreement among 3 observers on focal samples using a pre-established ethogram that included the scan sample and all occurrence behavioral categories.

Before the introductions to groups A and B, we locked the group members into the outdoor portion of their enclosure. The new males were taken into the outdoor area in transport boxes and released. We staggered the introductions in groups A and B in time to allow for observations immediately following each introduction. When weather permitted, we collected data from an observation tower and locked the groups outside. We otherwise restricted data collection to the indoor portion of the enclosure. The introductions for groups C and D were more gradual than for groups A and B. For 6 wk before introduction, the males were housed individually and in sight of one another. On the first day we released the males in groups C and D into the outer portion of the enclosure and exposed them to the resident group members through chain-link fencing. We removed the males in group C from the outer portion of the enclosure and separated them from each other on the first night, and put them back with the entire social group on the second day. On the second and third nights we removed the males from the social group, and they spent the night together. From the fourth day onward the males remained in the social group. In group D, the introduction procedure and data collection protocols could not be followed because of fighting between the males immediately upon being placed together but before they were introduced to the social group. We removed the victim of the fight (YV) for treatment and introduced him 2 wk later. YV pulled out his stitches in 3 days and was removed again. Four weeks later he was reintroduced.

Eighteen days after the introduction, fighting occurred in group A. We removed all 3 males and canceled data collection for follow-up period 2. Only one male (AD) was present during the third and fourth follow-ups, and we reintroduced the injured male (UY) 34 days after the fourth follow-up. Due to renewed fighting between AD and UY, we removed and reintroduced UY a total of 3 times. During the first reintroduction, we resumed regular data collection for 3 days, and the reintroduction provided the opportunity for an unplanned fifth follow-up period on group B, which we lumped with the other follow-up periods, except where

indicated. During the second and third reintroductions of UY we recorded observations *ad libitum*.

Analysis

We obtained rates of aggression during the introduction from the all-occurrence data set. All-occurrence sampling may have underestimated total agonistic behavior, especially threats and grimaces, but was likely accurate for more severe or noisy forms of aggression. We obtained baseline rates of aggression from focal samples conducted on males for a separate study. We excluded avoidance from the analysis of agonistic behavior.

We combined proximity and affiliative contact into a single measure of affiliation because they independently indicated similar trends but occurred rarely. We measured affiliation as a proportion of the number of partners in proximity or affiliative contact over the product of the total number of scans and the number of available partners. Proximity and affiliative contact among the new males themselves often inflated the amount of affiliation. Excluding familiar males from the number of partners with which the new males affiliated gave a more accurate measure of integration into the group. We divided affiliative partners into: 1) proceptive females: ones currently exhibiting species-typical proceptive behavior; 2) formerly proceptive females: ones having previously directed species-typical proceptive behavior toward the new males, but were not doing so currently; 3) nonproceptive females: ones having not exhibited species-typical proceptive behavior since the introduction; 4) immatures: under 3 yr.

When possible, we performed analyses using nonparametric tests that account for individual variation, such as Kruskal-Wallis tests or Wilcoxon signed ranks tests. We used intersubject, rather than intrasubject, tests when the number of males sampled at each time period differed. Sample sizes were often small. Accordingly, we used Chi-square tests. We set the significance level at $p < .05$ for tests that account for individual variation, and reduced it to $p < .01$ for Chi-square tests. Chi-square tests ignore individual variation by pooling subjects and should be interpreted cautiously. When possible, we presented individual variability in the tables and figures.

We performed individual comparisons to give an estimate of individual variability for Chi-square tests. We have presented the number of individuals whose data are in the same direction as a significant Chi-square after the p-value, e.g. 5 of 7 males. We compared individuals to themselves for comparisons between the introduction, follow-up periods, and reintroduction. We only collected baseline data on groups A and B, so we compared each new male to the most appropriate resident male for comparisons

involving baseline. We compared the new males in groups A and B to their counterparts before the introduction. For example, we compared the new alpha male to the former alpha male, and likewise for the subordinate(s). The new males in group C were the former males in group B; we compared them to themselves.

RESULTS

Introduction

Aggression. Serious fighting among the new males and the resident females did not occur immediately after introduction. Severe aggression among the new males in group A and the resident male occurred only during follow-up periods. The most severe aggression on the first day of the introduction occurred when two unfamiliar males were placed together before entering group D. DR attacked YV in the first minute after their release. YV was removed for treatment and returned two weeks later without aggression and was subordinate to DR.

The rate of aggression received and initiated per male did not increase on the first day of the introduction ($M = 3.64$, $SE = 0.84$) compared to baseline ($M = 3.05$, $SE = 0.90$; Table III). The rate of aggression per group,

Table III. Rates of aggressive episodes per hour

Study period	[a]Mean rate of aggression per group (M ± SE)	[b]Mean rate of aggression per male (M ± SE)
Baseline	—	3.05 ± 0.90
Introduction		
Day 1	3.97 ± 1.04	3.64 ± 0.84[c]
Day 2–5	4.26 ± 1.64	2.14 ± 0.58
Follow-ups		
Follow-up 1	2.87 ± 0.23	1.11 ± 0.38
Follow-up 2	3.42 ± 1.54	1.00 ± 0.60
Follow-up 3	2.17 ± 1.58	1.54 ± 0.60
Follow-up 4	2.83 ± 1.46	1.20 ± 0.61
Follow-up 5 (group B)	7.76	1.92 ± 0.48
Reintroduction (group A)	2.15	0.60 ± 0.04

[a,b]No difference in the rate of aggression per group (Friedman $X^2 = 7.19$, df = 8, n = 3, p > .05) or per male (Kruskal Wallis $X^2 = 19.02$, df = 11, p = .061).
[b]Sample sizes for aggression per male were as follows: baseline $N = 4$; introduction $N = 7$; follow-up 1 $N = 7$; follow-up 2 $N = 5$; follow-up 3 $N = 6$; follow-up 4 $N = 6$; follow-up 5 $N = 3$; reintroduction $N = 2$.
[c]A Chi-square test failed to show a difference in the rate of aggression per male between baseline and the first day of the introduction.

and per male, also did not increase during the 5-day introduction period (Table III). We performed additional comparisons to examine a possible bias in the direction of aggression. Males and females initiated aggression in proportion to their numbers in the group (326 episodes initiated by 31 females, 88 episodes initiated by 7 males).

Males received far more aggression than expected based on the sex ratio [315 episodes received by 7 males, 99 episodes received by 31 females; $\chi^2(1) = 56.49$, $P < .01$]. The majority of aggression between males and females occurred when females initiated aggression against males. When males directed aggression against females it typically occurred in a sexual context (73.9% of 69 episodes). (For a description of species-typical sexual behavior, see Carosi and Visalberghi, in press). Although heterosexual fights were common, they never resulted in serious injury.

We observed a total of 130 coalitions involving new males, females, and immatures. The 98 female-female coalitions were more common than all other types combined [$\chi^2(1) = 67.02$, $P < .01$], and the 109 coalitions targeted at new males were more than any other age-sex class [$\chi^2(1) = 119.14$, $P < .01$]. The new males also formed more coalitions with resident females than with their male peers [22 coalitions with females vs. 5 coalitions with male peers; $\chi^2(1) = 11.94$, $P < .01$, 5 of 7 males], and they usually targeted other males (86.4% of 22). The elderly resident male directed the majority of his aggression against the new males (85.4% of 48 episodes). He formed coalitions with females more than any other age-sex class (97.6% of 41) directed them against the new males more than any other target (90.2% of 41). He received support from many females, but high-ranking females tended to give him more support.

Affiliation

In group A the elderly resident male (SH) and one of the introduced males (UY) engaged in an ambiguous affiliative display, consisting of mutual loud roaring/squealing vocalizations while oriented towards one an other, often while rearing back, raising eyebrows, chest-rubbing, and grimacing. They approached one another at the start of the display, occasionally making contact and even embracing. The first display occurred <30 min of introduction, and displays continued at a steady rate of 2.3 per hour over the next 5 days. Displays were typically 1–3 min in duration. The display appeared predominantly affiliative, and included a mixture of elements of courtship behavior (Phillips *et al.*, 1994; Carosi *et al.*, in press), and male greeting behavior (Matheson *et al.*, 1996). Even when not giving facial and postural signals, the males generally watched one another and coordinated their movements

to remain within a few meters of one another. The display is similar but not equivalent to wheeze dancing (Perry, 1998; Manson *et al.*, 1997). Both the display and wheeze dance involve back- and-forth movement, but the former includes rearing back and raised eyebrows and culminates in an embrace, while the latter includes protruded lips characteristic of courtship and culminates in mounting.

The males initially affiliated with fellow newcomers, rather than resident group members. Males were in proximity or affiliative contact or both with fewer group members during the introduction than resident males were during baseline [$\chi^2(1, N = 7, 4) = 45.26$, $P < .01$, 5 of 7 males] (Figure 1). The new males also had a lower rate of grooming during the introduction ($M = 4.61$, $SE = 2.34$) than the resident males did during baseline ($M = 6.93$, $SE = 2.41$) [$\chi^2(1, N = 7, 4) = 12.86$, $P < .01$, 6 of 7 males]. The reason for the decreased rate of grooming was that the new males initiated less grooming during the introduction than the resident males did during baseline [$\chi^2(1, N = 7, 4) = 16.88$, $P < .01$, 6 of 7 males] (Figure 2). New males also received more grooming than they initiated during the introduction [$\chi^2(1, N = 7) = 11.86$, $P < .01$, 4 of 7 males]. The new males typically received grooming from proceptive females. In fact, during the introduction period the new males groomed or received grooming only from proceptive females and familiar male peers.

The amount of time the elderly resident male spent in affiliation with others increased during the introduction (75% of 291 scans) compared to baseline (45% of 150 scans) [$\chi^2(1) = 39.61$, $P < .01$]. Although the male's affiliation during the introduction was greater than female-female affiliation during baseline (53% of 936 scans) [$\chi^2(1) = 43.85$, $P < .01$], it was no different than the rate for the alpha female (74% of 78 scans).

Sexual Behavior

Two females exhibited proceptive behavior on the first day of introduction, and they began soliciting the new males ≤20 min of their release. In group C, wherein the males were released into the outer portion of the enclosure on the first day of introduction, one female mated with a new male through the chain link fencing. The only proceptive female in group A during the introduction period directed her solicitations toward one of the new males (UY). They mated in full view of the resident male without receiving aggression. While the 8 females showing proceptive behavior during the 5-day introduction period was not greater than expected, 3 females showed behavioral signs of estrus when they were not fertile; two females mated with males while they were pregnant, and one female mated while caring for her 3-week old infant.

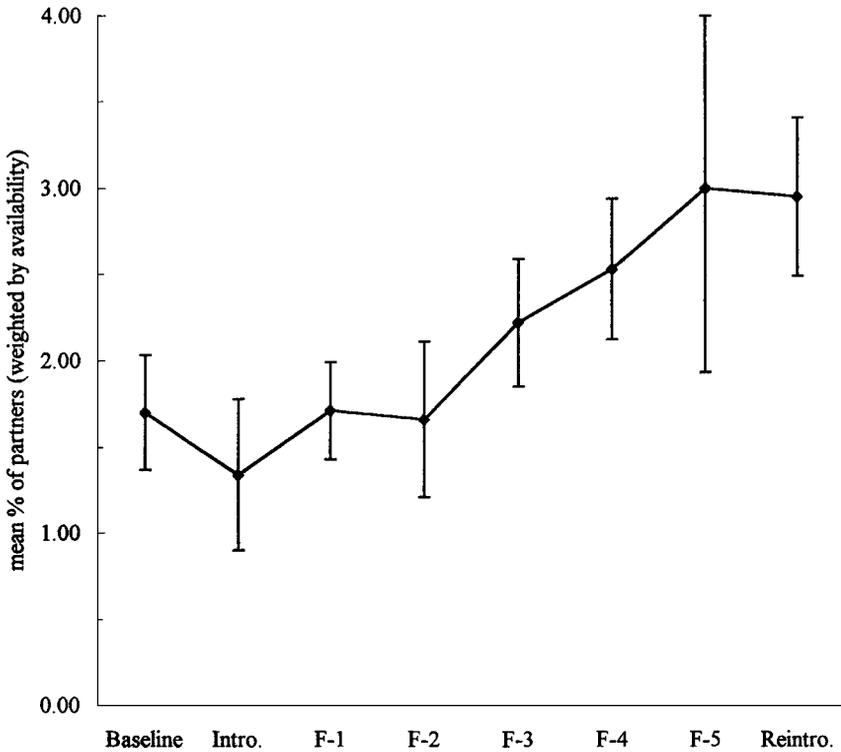## Mean Proportion of Partners
that Affiliated with Males

Fig. 1. Proportions were calculated per male as the number of partners with which the male was in proximity or affiliative contact, divided by the product of the number of scans and the number of available partners. A Kruskal Wallis test indicated no significant difference in the mean proportion of affiliation at different time periods [Kruskal Wallis $\chi^2(5) = 6.26$, $P = .28$]. Significant Chi-square tests are presented in the text. Sample sizes are as follows: baseline $N = 4$; introduction $N = 7$; follow-up 1 $N = 7$; follow-up 2 $N = 5$; follow-up 3 $N = 6$; follow-up 4 $N = 6$; follow-up 5 $N = 3$; reintroduction $N = 2$.

Affiliation among new males and resident group members decreased from baseline to introduction, and we divided the resident group members into 4 categories to see where the difference was coming from. While all types of partners tended to affiliate with the new males less during the introduction than with the resident males during baseline, only nonproceptive females affiliated with the new males significantly less often [Mann-Whitney $U(7, 4) = 0.0$, $P = .007$]. During the introduction, proceptive females
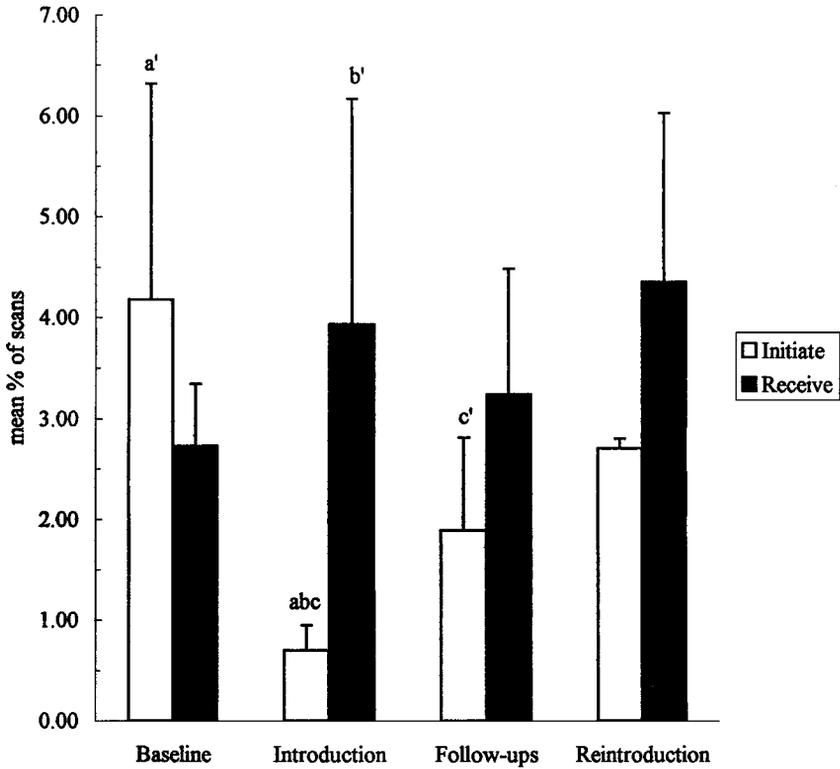
Time Males Spent Grooming

Fig. 2. The amount of grooming initiated and received was calculated for each male as a proportion of the number of scans grooming or being groomed out of the total number of scans. The total amount of time spent grooming is equivalent to the sum of initiated and received grooming. Sample sizes are as follows: baseline $N = 4$, introduction and follow-ups $N = 7$, reintroduction $N = 2$.
[abc]a' is significantly greater than a, likewise for b and c (P < 0.5).

($M = 10.40$, $SE = 3.28$) affiliated with the new males at a higher rate than nonproceptive females ($M = 0.10$, $SE = 0.03$) and immatures ($M = 0.33$, $SE = 0.13$) did [Wilcoxon Signed Ranks $Z(7) = 2.37$, $P = .018$; $Z(7) = 2.37$, $P = .018$, respectively] (Table IV). Formerly proceptive females also affiliated with the new males at a higher rate than nonproceptive females and immatures did [Wilcoxon signed ranks $Z(7) = 1.86$, $P = .063$; $Z(7) = 1.99$, $P = .046$, respectively]. The same partner preferences occurred during baseline, but the differences are not statistically significant.

Table IV. The mean proportion of scan samples females and immatures were in affiliative contact or proximity with males

Study period	Proceptive females	Formerly proceptive females	Non-proceptive females	Immatures
Baseline				
mean (S.E.)	18.68 ± 9.96	—	$1.17 \pm 0.39^{b'}$	1.00 ± 0.32
Introduction				
mean (S.E.)	$10.40 \pm 3.28^{a'}$	$12.26 \pm 4.74^{a'}$	0.10 ± 0.03^{abc}	0.33 ± 0.13^{ae}
Follow-ups				
mean (S.E.)	$18.39 \pm 5.85^{d'}$	$10.29 \pm 4.12^{d'}$	$0.76 \pm 0.22^{c'd}$	$2.11 \pm 0.46^{e'}$
Reintroduction				
mean (S.E.)	—	1.30 ± 0.10	2.25 ± 0.05	5.25 ± 2.25

[abcde]a' is significantly greater than a, likewise for b, c, d, and e (P < .05).

Follow-up Periods

Aggression

During the follow-up periods, severe aggression occurred between the males in group A. Although AD (one of the new males) had remained apart from the group and avoided all others during the first 5 days following introduction, he apparently fought with and wounded the resident male (SH) and the other new male (UY). The fight occurred 2 days before the first follow-up period. We did not observe the fight, but wounding was evident. The aggression subsided quickly and SH and UY were not seriously injured, so the males remained in the group. Fighting occurred again the day before the second follow-up period. This time SH was killed and UY was severely injured and removed for medical treatment. The reintroduction of UY initially occurred without conflict, but 5 days later AD began relentlessly chasing UY and the males were separated. The reintroduction was tried a second time, and again the males initially ignored one another. Two days later, however, AD began relentlessly chasing UY and UY was removed. On the third reintroduction AD attacked UY <15 min and UY was permanently removed. Before the male transfer, AD and UY had lived together for 5 years, and UY used to dominate AD. Thus, the male transfer resulted in reversal of their previous dominance relationship.

Despite the severe aggression between the males in group A, the rate of aggression remained low during the follow-up periods (Table III). Males and females continued to initiate aggression in proportion to their numbers in the group, and males continued to receive more aggression than females. Whereas females occasionally used contact aggression in

heterosexual fights, males did not. Of the 249 aggressive episodes initiated by females, 222 were directed at the new males. None of the 27 fights among females occurred in a sexual context, indicating minimal female-female competition for males. Males threatened and/or lunged at infants 14 times. None of the episodes became more severe, and females never interfered.

Affiliation

The proportion of group members that affiliated with the new males gradually increased during the follow-up periods (Figure 1). We performed a few pairwise comparisons to document the change in affiliation. Group members affiliated with the new males more during follow-up period 4 ($M = 2.53$, $SE = 0.41$) than during the introduction ($M = 1.34$, $SE = 0.44$) [$\chi^2(1, N = 6, 7) = 112.72$, $P < .01$, 4 of 6 males]. Group members also affiliated with the new males more during follow-up 4, follow-up 5 ($M = 3.0$, $SE = 1.07$), and the reintroduction ($M = 2.95$, $SE = 0.46$) compared to baseline ($M = 1.70$, $SE = 0.33$) [$\chi^2(1, N = 6, 4) = 18.29$, $P < .01$, 4 of 6 males; $\chi^2(1, N = 3, 4) = 48.67$, $P < .01$, 2 of 3 males; $\chi^2(1, N = 2, 4) = 34.92$, $P < .01$, 2 of 2 males, respectively].

Males had a higher rate of grooming during the follow-up periods ($M = 5.13$, $SE = 1.36$) than during introduction ($M = 4.61$, $SE = 2.34$) [$\chi^2(1, N = 7) = 6.92$, $P < .01$, 6 of 7 males]. The reason for the increased rate of grooming is that males initiated more grooming during the follow-ups than during the introduction [$\chi^2(1, N = 7) = 13.11$, $P < .01$, 5 of 7 males] (Figure 2).

Sexual behavior. Nonproceptive females affiliated with the new males more during the follow-ups ($M = 0.76$, $SE = 0.22$) than during the introduction ($M = 0.10$, $SE = 0.03$) [Wilcoxon signed rank $Z(7) = 2.20$, $P = 0.28$], but proceptive and formerly proceptive females did not significantly increase their affiliation with the new males (Table IV). Most importantly, proceptive ($M = 18.39$, $SE = 5.85$) and formerly proceptive females ($M = 10.29$, $SE = 4.12$) continued to affiliate with the new males more than nonproceptive females did [Wilcoxon signed rank $Z(7) = 2.37$, $P = .018$; $Z(7) = 2.20$, $P = .028$, respectively] (Table IV). Immatures also affiliated with the new males more during the follow-ups ($M = 2.11$, $SE = 0.46$) than during the introduction ($M = 0.33$, $SE = 0.13$) [Wilcoxon signed rank $Z(7) = 2.37$, $P = .018$]. Although the data are not available from scan samples, notes *ad libitum* suggest that immatures initiated affiliative contact with males more than males initiated contact with them.

DISCUSSION

Aggression Against the Newcomers

The introductions were remarkably peaceful when males familiar to one another were introduced to a group with no other adult male (groups B and C). Severe aggression occurred when males unfamiliar to one another were introduced to a group without other males (group D), or when males familiar to one another were introduced to a group with an existing adult male (group A). Upon introduction, the resident male (SH) and one of the new males (UY) immediately began coordinating their movements and engaged in prolonged mutual displays. We did not observe them fighting. Eighteen days after the introduction, the third male (AD) apparently killed SH and severely injured UY. The strong support from females, which SH received, may have delayed the fight. We did not observe the fight, and cannot say if the fight resulted from a loss of female support. Also, UY had the support of the females in his old group, and the absence of this support could have contributed to his losing the fight with AD. Overall, aggression among the males appeared to build up slowly, and the potential for severe aggression increased with continued exposure. For example, aggression between UY and AD began more quickly during each reintroduction.

The resident male (SH) was the leader in most agonistic encounters with the intruders. Females, however, supported the resident male in these encounters, and occasionally initiated aggression themselves. Female involvement was different from wild *Cebus apella* in which only the alpha male defends the group (Defler, 1982), and from wild *C. capucinus*, in which females are rarely involved in intergroup encounters (Perry, 1996b; Rose, 1994). Furthermore, female aggression against the new males did not depend on the presence of a resident male. In groups without resident males (groups B and C), females initiated aggression and jointly formed coalitions against the intruders. Initially, coalitions against the new males included many females, if not most of the group. Regardless of the number of females involved, these fights rarely resulted in contact aggression.

The potential for severe aggression among males remained regardless of the release method used, but the cause of the aggression was unclear. In group A, the new males had lived together peacefully for 5 years. While their transfer to a new group resulted in a fight, they were not obviously fighting over females or dominance. First, the victim (UY) continued to mate successfully after the initial fight without receiving aggression from AD. Secondly, although the fight resulted in a reversal of their previous dominance relationship, the aggressor did not cease his attack following repeated submissive signals by the victim (Mason, 1993). In group D, the new males were

unfamiliar, and were given visual access to each other while singly housed before the introduction. Again, the males were not obviously fighting over females or dominance. First, the attack occurred before the pair was released into the social group and thus not in the presence of females. Secondly, while the dominance relationship was clearly defined upon reintroduction, there were no prior agonistic signals between the pair.

Three important points should be made for persons attempting ca-puchin introductions. First, introductions involving multiple males have the greatest potential for severe aggression. Secondly, male-male aggression may not occur immediately, but instead days later. Thirdly, familiarity between males may reduce the risk, but does not preclude severe aggression. The males transferred into groups B and C had lived together, and their intro-ductions proceeded without serious aggression. Severe aggression in group A occurred between SH and AD, which were unfamiliar, but also between UY and AD, which had lived in the same group for 5 years. Finally, visual access before introduction did not prevent serious aggression between the unfamiliar males in group D.

Sexual Behavior and Affiliative Bonds

The resident males had lived in their old groups for 4–6 yr before transfer and had developed strong social relationships with the resident females. Wild capuchins can form strong heterosexual relationships as well (Fedigan, 1993; Rose, 1994; Perry, 1997), but the degree of male-female bonding probably depends on male turnover. Males often emigrate singly, but occasionally multiple males may move between groups. When several males enter a group there is often severe aggression among the males and a period of social disruption as the females still prefer the old males (Rose, 1994; Rose and Fedigan, 1995).

The development of male-female relationships takes considerable time, and no doubt depends on recent history. We apparently did not witness the complete formation of male-female relationships during the course of this 10-wk study. Affiliation between males and females decreased after introduction, but gradually increased during the follow-up periods to levels greater than baseline. The initial lack of affiliative behavior between females and new males and subsequent increase is consistent with previous research (Fragaszy *et al.*, 1994), but we also found that a period of intense socialization occurs before levels of affiliation return to baseline. For example, 66 days after the male transfer, proximity and affiliative contact between males and females were still greater than baseline.

Nonconceptive sexual behavior among nonhuman primates occurs in a variety of situations. For example, in *Cebus capucinus*, males mounted females in coalitions and after fights (Manson *et al.*, 1997). In *Cebus apella*, some females showed a rapid onset of proceptive behavior following the introduction of a male (Fragaszy *et al.*, 1994). In stump tailed macaques (*Macaca arctoides*) males directed high rates of sexual behavior to females that had been briefly separated from the group (Bernstein *et al.*, 1992). In our study, 2 females solicited the new males <20 min of their release, and 3 other females mated when they were not able to conceive. Thus, female proceptive behavior has the potential to occur outside of ovulation, given the appropriate stimulation (Carosi and Visalberghi, in press). Male deprivation may have facilitated female proceptive behavior in group B. However, male deprivation does not appear to be the cause, because the females in groups A and C had the opportunity to mate before we exchanged the males.

We found very little evidence of male-male competition for females. For example, the resident male (SH) did not attempt to interfere in the courtship between the females and new males. Conversely, the dominant male in group C followed the subordinate male during female solicitations, which functioned to break-up the subordinate's courtship nonaggressively. In *Cebus apella*, females have a rich repertoire of proceptive behavior, which provide the primary, if not the only, cues males have of female receptivity (Carosi *et al.*, in press). Thus, we are unable to reject evidence that male capuchins only recognize estrous females by solicitations directed towards themselves (Phillips *et al.*, 1994).

In our study, the females that solicited the new males continued to approach and to contact them long after they were proceptive. For a female to be classified as formerly proceptive during the introduction period she would have had to solicit the males very recently. Conversely, females classified as formerly proceptive during the follow-up periods could have solicited the males weeks earlier. This decrease in the salience of formerly proceptive females probably accounts for the fact that males were more often in proximity and contact with them during the introduction than the follow-ups. Despite the changing characteristics of formerly proceptive females, they still affiliated with the new males more than with nonproceptive females. In addition, follow-ups occurred only 2 days per week and some females could have cycled in our absence. Thus, the nonproceptive female category may have included some formerly proceptive females during follow-ups, and this could explain the increased affiliation between males and non proceptive females. This crude categorization of females shows that sexual interactions helped to integrate the new males into the group, and females that were the last to cycle were the last to affiliate with the new males.

Sexual behavior serves to establish and to maintain bonds among chimpanzees, and particularly bonobos (Manson *et al.*, 1997; de Wall, 1989). Female langurs direct sexual behavior to the new adult male following the takeover of their social group (Hrdy, 1979). This atypical pattern of sexual behavior has been interpreted as a strategy by females to counter infanticide. In capuchins, infants have been killed during male takeovers (Rose and Fedigan, 1995), and males will directly attacking infants (*Cebus olivaceus*: Valderrma *et al.*, 1990; *C. capucinus*: Rose, 1994; *C. apella*: Darren Long, personal communication). In our study, however, the initiation of sexual behavior to counter infanticide seems unlikely. Immatures initiated contact and played with the new males more than they did with the old males. This is consistent with the understanding that immature capuchins are curious of newcomers and frequently initiate affiliative contact (Fragaszy *et al.*, 1994). The males' responses included gently reciprocating play, tolerating the immature's contact, completely ignoring the youngster, or moving away. Males were not aggressive towards immatures, and females did not prevent their offspring from approaching males. Female tolerance of male-infant interactions, and the interest of immatures in males, is inconsistent with the avoidance of attacks by males. If infanticide is a pattern in capuchins, then we may have found negative results for two reasons. First, attacks on infants may not occur within the first 10 weeks of a male take-over. Secondly and more likely, attacks may only occur on very young infants. The immatures subjects ranged 3 wks to 3 yr. The two- and three-year-olds were the most active with the males, but no attack occurred on the 5 infants <6 mo. For example, in group C, a new male mated with a female carrying a three-week-old infant, and did not attack it. Despite the risk of infanticide, immatures affiliated with the new males and, along with proceptive females, helped to facilitate the long process of male social integration.

Conclusions

Introductions involving unfamiliar males have the greatest potential for severe aggression. Severe aggression occurred when males unfamiliar to one another were placed together before introduction to the social group, and when males familiar to one another were introduced to a group with a resident male. When males familiar to one another were introduced to a group without a resident male, the introductions were peaceful. However, severe aggression can occur between males familiar to one another when they are introduced to a new group, such as the case with UY and AD. In all cases many weeks were required to establish affiliative relationships with the resident females. Proceptive females and immatures were the first group

members to approach and to contact the new males. Females continued to affiliate with the new males after their period of proceptivity, and the last females to cycle were the last to affiliate with the new males.

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