RESEARCH ARTICLE

Scream–Embrace Displays in Wild Black-Horned Capuchin Monkeys

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Reintroduction of capuchin monkeys (*Cebus apella*) into their social group in captivity can elicit sirena screams and embraces. Captive scream–embrace displays are male biased, and females never perform sirena screams. One hypothesis is that scream–embrace displays serve a tension-reduction or reconciliatory function between males with conflicting interests. Alternatively, these displays may function to maintain strong affiliative bonds between friendly male dyads. Scream and/or embrace displays in wild Brazilian black-horned capuchins were analyzed for social and ecological contexts, behavioral components, and individuals involved. Seventy-two displays were observed during the 199-day study period. Among the 66 displays for which both members could be identified by sex, there were 42 occurrences of male–male dyads, 17 of male–female dyads, and seven of female–female dyads. Scream–embrace dyads were male–male pairs significantly more often than expected from group membership, and the α male was the only male to engage in scream–embrace displays with females. Female–female pairs did embrace, but never emitted sirena screams. Displays most commonly occurred in ''reunion'' contexts, primarily the reuniting of subgroups after hours or days out of contact, but also after intergroup encounters, and across groups in ''intergroup'' displays. Displays were rare, but socially contagious, and subgroup reunions could elicit multiple displays in rapid succession. Although the occurrence of screams and embraces was positively correlated, both behaviors also occurred independently, and their functions may be different. Male sirena screams may be honest advertisements of united alliances, directed toward a third party, whereas the embrace may be a risky affiliative signal, directed primarily within the dyad. Am. J. Primatol. 70:551–559, 2008.
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INTRODUCTION

Embracing behavior in primates has generally been categorized as occurring within three social contexts: as a greeting during reunions, as an appeasement during group tension or excitement, or as a reconciliation after agonistic interactions [Kyes, 1989]. Embracing behavior in the genus *Cebus* has never been assessed quantitatively in the wild [Di Bitetti, 2001]. However, in captive experiments with *Cebus apella*, the reintroduction of a male into his social group frequently led to ''reunion displays,'' in which a reuniting dyad ran together emitting high-pitched loud vocalizations to join in a reciprocal frontal embrace [Matheson et al., 1996; Phillips & Shauver Goodchild, 2005]. For this study, I use the term ''scream–embrace'' displays instead of ''reunion'' displays to describe the two principal behaviors observed in this display without assuming the primary function of these behaviors in the wild.

The captive data suggest that scream–embrace displays are primarily a male–male activity [Matheson

et al., 1996; Phillips & Shauver Goodchild, 2005]. Perhaps, male–male relationships are more ''tense,'' because male capuchins disperse as juveniles and attain rank based on physical prowess, unlike females, who tend to stay in their natal group and inherit rank through the matriline. In fact, in captivity, females do occasionally participate in embraces; however, they do not emit the accompanying ''sirena'' scream [Matheson

et al., 1996; Phillips & Shauver Goodchild, 2005]. The sirena scream is the loudest vocalization in the capuchin monkey repertoire in *C. nigritus* [Di Bitetti, 2001], and it may be that the conspicuousness of this call benefits males, but not females, when broadcast to third parties.

During his study of vocalizations of wild *C. nigritus* in Argentina, Di Bitetti [2001] found that scream–embrace displays seemed to occur most commonly when individuals met again after having lost contact for several hours, either because the group had divided or one individual was lost. Thus, in wild observations, as in captivity, reunion after separation appears to be a social stimulus that elicits scream–embrace displays. However, in contrast to captive reports, Di Bitetti [2001] found that wild scream–embrace displays occurred not only between the α male and other high-ranking males, but also frequently between the α male and α female, although it was not clear whether the female herself vocalized during these displays. In this study, I examine a group from a different population of wild *C. nigritus* to quantitatively assess the relationship between age–sex class and participation in scream–embrace displays.

Phillips and Shauver Goodchild [2005] argue that male scream–embrace displays operate to reaffirm social relationships, particularly in the context of social tension. In their view, the tension-reducing function of the display is similar to olive baboon "diddling" [Smuts & Watanabe, 1990], stump-tailed macaque "hold-bottom rituals" [de Waal & Ren, 1988], bonobo "G-G rubbing" [de Waal, 1987], and the wheeze dances in white-faced capuchins [Perry, 1995]. If scream–embrace displays function to reduce tension between males, they might be expected to occur most frequently after fights, as seen in macaques [de Waal & Ren, 1988] and white-faced capuchins [Perry, 1995]. They might also be more frequent in the presence of a contestable resource, such as a high-quality fruit patch or a female displaying behavioral estrus.

An alternate hypothesis proposed by Matheson et al. [1996] is that the male–male scream–embrace displays are indicators of strong affiliative relationships between individuals, and not of tension between dyads. In this case, embraces in tufted capuchins may be more similar to the non-tense affiliative hugging that occurs for extended periods in male muriquis [Strier et al., 2002]. If scream–embrace displays function to maintain affiliative bonds, I expect that dyads with high rates of affiliation, not agonism, will engage in scream–embrace displays, and that these displays will co-occur with affiliative behaviors, such as grooming, playing, or lying in contact. In fact, in Matheson et al.'s [1996] study of captive capuchins, male–male scream–embrace displays never occurred in the context of within-group agonism.

This paper provides the first detailed analysis of scream–embrace displays in wild capuchins. Scream–embrace display data were analyzed for one group of black-horned capuchin monkeys over a 1-year period from Caratinga Biological Station, Minas Gerais, Brazil. This field site was ideal for testing the primacy of the "reunion" function hypothesis, because the capuchin study group here had a fission–fusion social organization, with the study group subdivided into smaller groups out of visual and vocal contact from one another on about half of the days of study [Lynch Alfaro, 2007]. In fact, evidence is accumulating that subgrouping or fission–fusion behavior may be relatively common in *C. nigritus* populations compared with other *Cebus* species [Izar, 2004]. Here, ecological and social contexts of scream–embrace displays, components of display behavior, and sex and age class of participants are considered.

First, I test whether participation in displays is biased by sex or status, with the following predictions based on previous studies: (1) Scream–embrace displays are exclusively male–male behaviors. (2) The α male participates in all scream–embrace displays. (3) Females may participate in embraces, but never emit sirena screams during embraces.

Second, I test for evidence that scream–embrace displays function primarily as greetings between individuals, with the following prediction: (4) Scream–embrace displays most frequently occur when individuals re-establish contact after being separated from vocal and visual contact with one another.

Third, I test for support of the tension-reduction hypothesis for the function of displays, with the following predictions: (5) Scream–embrace displays occur most frequently in tense social contexts, such as after agonism or in the presence of a contestable resource, and male–male scream–embrace displays commonly include "tense" behavioral elements, such as threats to others, fear grimaces, mounts with thrusting, or overlords. (6) Male–male dyads with a higher overall frequency of dyadic aggressive interactions are more likely to engage in scream–embrace displays together.

Finally, I test for evidence to support the hypothesis that displays reflect strong affiliative male–male bonds: (7) Frequency of affiliative interactions between dyads are positively correlated with frequency of scream–embrace displays between dyads; and scream–embrace displays most commonly co-occur with affiliative behaviors.

METHODS

Study Site and Study Group

Data were collected from September 1996 through August 1997 at Estação Biológica de Caratinga, a ~1000-ha fragment of Atlantic forest in Minas Gerais, Brazil. Observations were made on

one wild group of habituated capuchins [Rímoli & Ferrari, 1997], with 199 observation days during the study period. At the beginning of the study, there were 25 individuals in the group, including four adult males, six adult females, five juvenile (including subadult) males, eight juvenile (including subadult) females, and infants. The current α male had risen to his position by means of a within-group take-over and expulsion of the previous α male in May 1996 [Lynch & Rímoli, 2000]. Adult membership remained the same throughout the study period [Lynch & Rímoli, 2000]. Individuals were recognizable owing to pelage patterns, facial characteristics, size, and behavior [Di Bitetti & Janson, 2001; Izawa, 1980], and age classes followed Izawa [1980], with subadults and juveniles combined for the analyses in this paper.

Observation and Data Collection Methods

To determine rank of individuals within the group, data on both approach–retreat interactions and dyadic aggressive interactions were recorded, noting the individuals involved and the direction of signals [Lynch Alfaro, 2007; Lynch, 2001]. A dominance hierarchy was constructed using methods modified from Perry [1995] and Di Bitetti [1997]. Although the data did not define a unique linear hierarchy, the α male was clearly defined and always dominant to all other individuals in the group.

During a pilot study of the same group of capuchins, I made a qualitative observation that lost calls (or long distance whistle series), as described by Di Bitetti [2001] for *C. nigritus* and Digweed et al. [2007] for *C. capucinus*, sometimes preceded scream–embrace displays. Lost calls are easily recognizable, loud and harsh calls given by individuals when they become separated from the group [Digweed et al., 2007]. During this study, *all occurrence* sampling was employed for both sirena scream vocalizations and for lost call vocalizations (Table I).

Observational data on scream–embrace behaviors were recorded through *all occurrence* sampling (Table I), with an attempt to reduce bias and record all individuals engaging in displays by moving through the group to locate non-visible animals [Di Bitetti, 2001]. Scream–embrace displays were both rare and clumped in time. When they did occur, there were often many individuals screaming, embracing, or both in rapid succession. However, as the sirena screams are unlike any other vocalization and were such an obvious cue to scream–embrace displays, there was some observer bias toward collecting data on loud scream–embrace displays compared with embrace-only displays. As described in Di Bitetti [2001], it sometimes can be difficult to distinguish which individuals give the sirena vocalization

TABLE I. Behavioral Observation Methods for Scream and/or Embrace Displays and Their Social and Ecological Contexts

Target information	Sampling method	Protocol
Lost calls, screams, embraces	All occurrences	Note all auditory observations of scream or lost call series; if scream heard or running to embrace seen, identify individuals and record subsequent social interactions in the dyad; then move through group to assess for presence of further displays by other dyads
Affiliative behaviors after displays	All occurrences	Note presence of grooming, play, and/or lying in contact for the displaying dyad directly after scream and/or embrace behavior until dyad breaks contact
Tense behaviors associated with displays	All occurrences	Note presence in displaying dyad of threats toward others, fear grimaces, penile erections, mounting with thrusts, or overlords [Oppenheimer, 1973] during or directly after display until dyad breaks contact
Social and ecological contexts of displays	Post hoc analyses of scan, focal animal follow, *all occurrences* and ad libitum data	Data collection in a larger, related study during the same time period included *all occurrence* sampling of behavioral estrus in females [Lynch Alfaro, 2005; Lynch et al., 2002], intergroup encounters [Lynch, 2001; Lynch et al., 2002], subgroup composition and change [Lynch Alfaro, 2007], focal animal follow and ad libitum data on within-group aggression [Lynch, 2001; Lynch et al., 2002], and scan and focal animal sampling on food choice [Lynch Alfaro, 2007]. These data were analyzed post hoc for the presence of estrous females on the day of a display; the utilization of high-quality resources in the hour before a display; and within 15 min before a display, the presence of within-group aggression, a loud external event, an intergroup encounter, and/or the reunion of subgroups or individuals

during the scream–embrace displays, because often two or more individuals vocalize at the same time. In addition, when one individual gives the sirena scream, other individuals may simultaneously give other vocalizations [Di Bitetti, 2001]. For this reason, each display was categorized as with or without sirena scream, but vocalizations were not assigned to particular individuals within the display. Dyads were also observed running toward one another and screaming the sirena, without a final embrace, and so each display was categorized as including scream–embrace, scream-only, or embrace-only. Each dyad for a display was categorized as "male–male," "male–female," or "female–female." For each display, I recorded *all occurrence* data on affiliative and tense behavioral interactions that occurred during and immediately after the display (Table I). A display could be categorized as both "tense" and "affiliative." When possible, data were collected on dyadic interactions after displays until the individuals became separated by 1 m from one another.

To determine the contexts in which scream–embrace displays occurred, I quantified social and ecological contexts into the following categories (Table I): presence of female in behavioral estrus; foraging on high-quality, clumped resources; within-group aggression; intergroup encounter; reunion of individuals or subgroups; and loud external event (i.e. car backfire, gunfire, thunder, a tree falling to the ground). These categories were not mutually exclusive so one display could be coded as occurring within more than one context.

Displays occurring in the following contexts were considered "reunions": an intergroup encounter occurred immediately before the display, and members of both groups were overlapping in spatial use before the display; independently traveling subgroups reunited immediately before the display; one of the individuals in the display had been separated from group, i.e. this was the first sighting of that individual that day; lost calls occurred directly before the display; the display occurred in a dyad composed of individuals from two different groups (an intergroup display).

I considered a display to have occurred in a "reunion between subgroups" context when one established subgroup encountered other individuals from the main group. Stringent guidelines were used to distinguish "true" subgroups from a widely dispersed group that was traveling as a single unit, as described in detail in Lynch Alfaro [2007]. Observed individuals were considered to be a distinct subgroup only when the observer had (1) censused all individuals present, (2) recounted all these individuals at least twice, and (3) traveled with this group of individuals for at least 1 hr with no change in group membership.

Research complied with protocols approved by the University of Wisconsin-Madison Animal Use and Care Committee and adhered to the legal requirements of Brazil. The study was non-invasive and no animals were captured or harmed.

Statistical Analyses

Standard non-parametric tests for correlations, comparisons of means and of absolute frequencies were used as the data did not conform to a normal distribution.

RESULTS

Displays by Type

Seventy-two displays that included either a sirena scream, a running to embrace, or both were visually observed during the study period. This included 19 scream–embrace displays (26.4%), 20 scream-only displays (27.7%), and 33 embrace-only displays (45.8%). In other words, in only about one-fourth of cases did the sirena scream vocalization and the embrace behavior occur together in the same display, and the most common display type was the embrace-only display.

For 30 of the 72 observed cases of displays, the observed display occurred immediately after a scream–embrace display by another dyad, an embrace-only display by another dyad, or a sirena scream vocalization recorded from elsewhere in the group. In 26 of these 30 cases, these sequential displays were observed in "reunion" contexts (20 when subgroups reunited, four during intergroup encounters, one when a lost individual returned to the group, and one in an intergroup display). For the other four cases of sequential displays, two occurred when the group was stable and in the presence of a female displaying behavioral estrus, and two had undetermined precipitating circumstances.

To test whether the first display in a series of displays was the most likely to include both a scream and an embrace, I used a χ^2 test to compare the frequency distribution of display types (scream–embrace, scream-only, and embrace-only) for "first" displays and "subsequent" displays occurring quickly after sirena screams performed by other individuals. There was no difference in frequency of display type for male–male displays, or for all displays, based on being a first or a subsequent display in a series.

Comparing days when the group traveled as a whole with days when the group was divided into independent subgroups for at least part of the time [Lynch Alfaro, 2007], the number of sirena screams per day (Mann–Whitney U test: $U = 3{,}917$, $N_1 = 92$, $N_2 = 100$, $P = 0.022$), the proportion of days with sirena screams (Pearson's χ^2: $\chi^2 = 4.434$, $N_1 = 92$, $N_2 = 100$, $P = 0.035$), the number of embraces per day (Mann–Whitney U test: $U = 3{,}955$, $N_1 = 92$, $N_2 = 100$, $P = 0.005$), and the proportion of days with

embraces (Pearson's χ^2: $\chi^2 = 7.435$, $N_1 = 92$, $N_2 = 100$, $P = 0.006$) were all significantly higher when the group divided into discrete subgroups. Across all observation days, frequency of sirena screams (Spearman rank correlation: $r_S = 0.387$, $N = 192$, $P < 0.001$) and frequency of embraces (Spearman rank correlation: $r_S = 0.461$, $N = 192$, $P < 0.001$) showed a significant positive correlation with the frequency of lost calls. When restricting the analysis to days with subgrouping only, the frequency of lost calls was still a strong positive predictor of the frequency of sirena screams (Spearman rank correlation: $r_S = 0.423$, $N = 100$, $P < 0.001$) and embraces (Spearman rank correlation: $r_S = 0.451$, $N = 100$, $P < 0.001$). Similarly, when restricting analyses to only those days when the group traveled as a cohesive unit, the frequency of lost calls was positively correlated with the frequency of both sirenas (Spearman rank correlation: $r_S = 0.343$, $N = 92$, $P = 0.001$) and embraces (Spearman rank correlation: $r_S = 0.271$, $N = 92$, $P = 0.009$).

Displays by Sex, Age, and Social Status

Both age and sex affected the frequency of displays and the type of displays in which individuals participated (Fig. 1). Among the 66 displays for which both members of the dyad could be identified by sex, there were 42 occurrences of male–male dyads (63.6%), 17 of male–female dyads (25.7%), and seven of female–female dyads (10.6%). In four of the six displays in which sex of both individuals could not be determined, the dyad was a male and an infant of unknown sex. Significantly more male–male dyads compared with male–female and female–female dyads were observed in displays than expected based on the total number of possible dyads of each type from group membership ($\chi^2 = 59.56$, $P < 0.001$). Nine out of nine males in the group participated in displays, and nine out of 14 females also participated in displays—this sex difference does not reach significance using a two-tailed Fisher's exact test ($P = 0.116$). When limiting the analysis to scream–embrace displays only, the sex difference is significant ($P = 0.013$), with seven out of nine males and only three of 14 females participating in this type of display through the course of the study. The sex difference is also significant when comparing scream-only displays ($P = 0.036$), but there is no significant sex difference in likelihood of individuals participating in at least one embrace-only ($P = 0.176$) display over the course of the study. When considering both age and sex class, adult males participated in scream–embrace displays at a significantly higher mean frequency than either adult or juvenile females (Fig. 1A), and adult males also performed scream-only displays at a significantly higher mean frequency than juvenile males or adult or juvenile females (Fig. 1B). In contrast, juvenile males
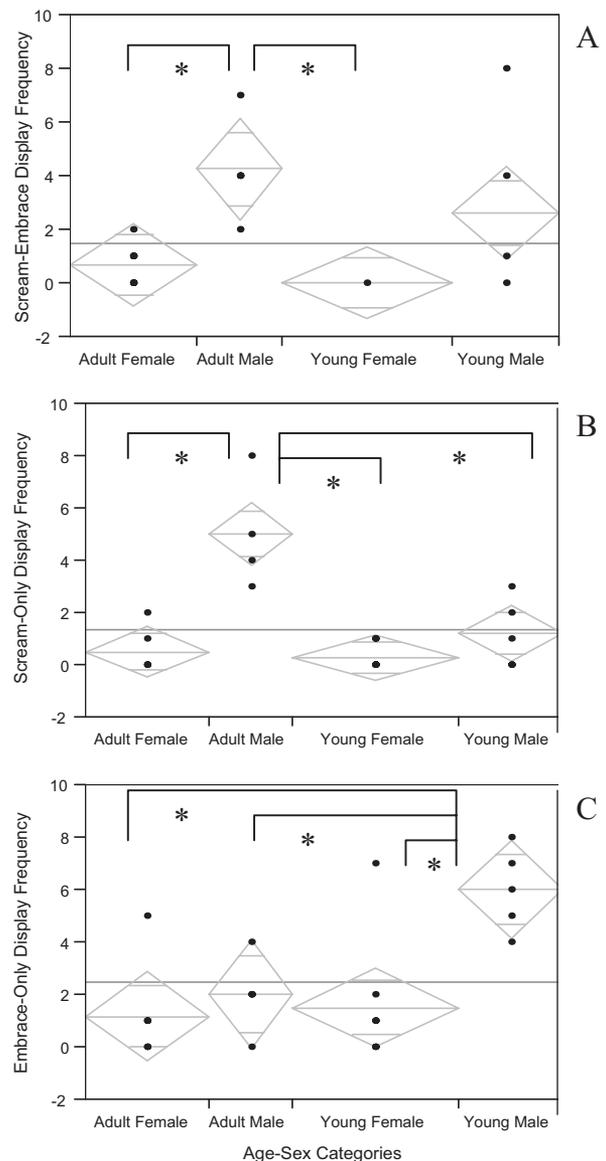

Fig. 1. Mean individual frequency of displays by display type and age–sex class. For each age–sex class (adult female, $n = 6$; adult male, $n = 4$; juvenile female, $n = 8$; juvenile male, $n = 5$), the frequency of observations that each individual was involved in a display is represented by a square. Diamonds indicate means and confidence intervals. Asterisks indicate that the mean frequency is significantly different at the $P < 0.05$ level between the two groups indicated, using a Tukey–Kramer HSD. (**A**) Mean frequency of scream–embrace displays ($\chi^2 = 12.76$, df = 3, $P = 0.005$) was significantly higher for adult males than for juvenile females or adult females. (**B**) Mean frequency of scream-only displays ($\chi^2 = 12.38$, $P = 0.006$) was significantly higher for adult males compared with all other age–sex classes. (**C**) Mean frequency of embrace-only displays ($\chi^2 = 13.36$, df = 3, $P = 0.004$) was significantly higher for juvenile males than for all other age–sex classes. The term "Young" denotes the juvenile class, which includes subadults, as described in the Methods. HSD, honestly significant difference.

participated in embrace-only displays at a significantly higher mean frequency than the other three age–sex classes (Fig. 1C).

Seven of the eight adult–adult dyads always included a scream component to their displays, and the other adult–adult dyad (AC-TE) did include a scream in one of their two displays. In contrast, only two of 16 juvenile–juvenile dyads ever included a scream in their displays. Adult–juvenile dyads were intermediate, with 12 of 17 adult–juvenile dyads performing screams in all ($n = 11$ dyads) or some ($n = 1$ dyad) of their displays.

At least one male participated in every scream–embrace display dyad and every scream-only display dyad; the only kind of display seen for female–female pairs was the embrace-only display ($n = 7$ displays). All cases of male–female scream–embrace displays included the group's α male (AC, $n = 3$ female partners). The α male was disproportionately represented in displays compared with all other individuals in the group (see Fig. 2). However, he was a participant of only about one-third of all displays (23 of 72), and fewer than half of all scream–embrace displays (7 of 19). In fact, all age–sex classes performed displays without the α male (see Fig. 2). The previous α male (LU), ousted from the study group and now a member of a neighboring group, was also involved in one scream–embrace and one scream-only display with non-α males from the study group, and another α male (GO) from a neighboring group participated in a scream–embrace display with a non-α male from the study group.
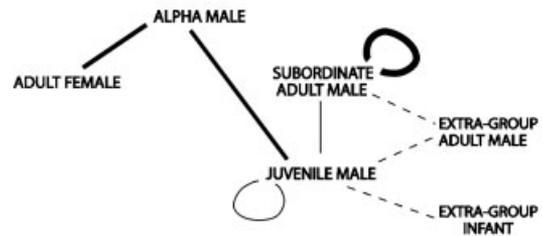
In regression analyses of the frequency per individual of participation in each type of display, there was a strong positive correlation between frequency of scream–embrace displays and frequency of scream-only displays (Spearman $\rho = 0.789$, $P < 0.001$), but there was no correlation between the frequency of embrace-only displays and either scream–embrace displays (Spearman $\rho = 0.298$, $P = 0.168$) or scream-only displays (Spearman $\rho = 0.325$, $P = 0.130$).

Considering all adult and juvenile males in the study group, a comparison of display frequency and frequency of agonism for each dyad across the study period revealed no significant relationship between agonistic interactions and the frequency of scream and/or embrace displays (Spearman rank correlation: $r_S = -0.365$, $N = 21$ dyads, $P = 0.105$). In contrast, a comparison of frequency of grooming bouts and frequency of scream and/or embrace displays across the same male dyads revealed a positive relationship between grooming bouts and display frequency (Spearman rank correlation: $r_S = 0.442$, $N = 21$ dyads, $P = 0.045$).
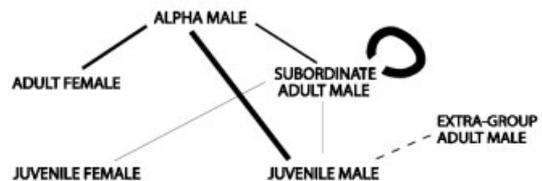
Social and Ecological Contexts of Displays

The most common context in which displays occurred was when two or more individuals were reunited after loss of visual and vocal contact ($n = 54$ cases; Fig. 3). The most common type of reunion was
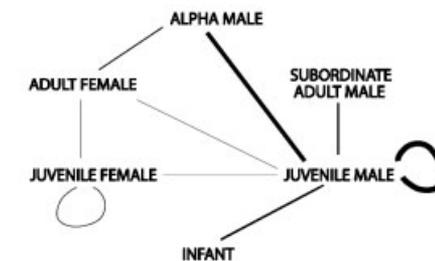

Fig. 2. Relative average frequency of displays per dyad by sex–age class and type. Solid lines indicate within-group displays. Relative average frequency was calculated across and within sex–age classes by taking the total number of displays observed within or across a class, and dividing this by the total number of possible dyads within or across this class. The thickness of lines indicates the relative frequency of the displays compared within and across age classes, and is directly comparable across the three display types. Dashed lines indicate intergroup displays (an individual in the focal group performing a display with a non-group member) and here thickness does not indicate relative average frequency. (**A**) Relative average frequency of scream–embrace displays per dyad by sex–age class. (**B**) Relative average frequency of scream-only displays per dyad by sex–age class. (**C**) Relative average frequency of embrace-only displays per dyad by sex–age class.

when two subgroups reunited ($n = 32$ cases; Fig. 3). Individuals returning to their own group after participating in an intergroup encounter ($n = 9$ cases) or after having been isolated from the group ($n = 5$) also performed displays. Another reunion context for displays was across groups ("intergroup display," $n = 5$); in these cases, one of the study group members performed a display together with an individual from a different group.

Displays also occurred at a low frequency when the study group was traveling as a stable unit. No single ecological or social circumstance seemed to
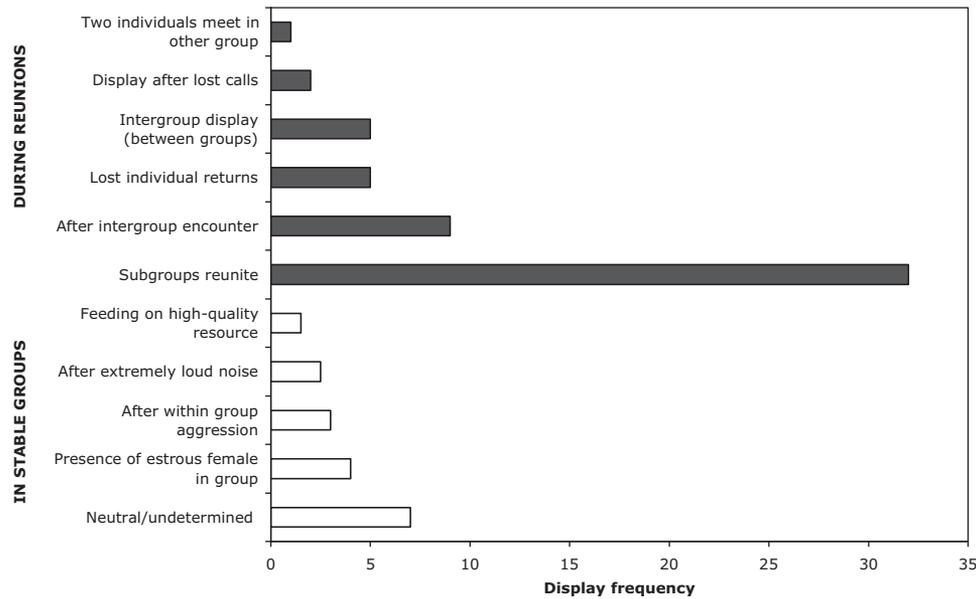
Fig. 3. Frequency of displays when group membership was unchanging and when individuals were reuniting after separation. Categories are explained in more detail in the Methods section of the text and Table I. In one case, a display occurred after the group had fed on a high-quality resource and there was a loud noise, so this case was counted as 0.5 for each of the two categories.

explain these displays (see Fig. 3). However, female–female displays were restricted to reunion contexts only, and male–female displays were the most common type of display observed when the group was traveling as a stable unit.

Scream–embrace, scream-only, and embrace-only displays were categorized as ''tense,'' ''affiliative,'' ''tense/affiliative,'' or ''neutral'' interactions, on the basis of behaviors observed during or directly after the display in the displaying dyad. The majority of displays occurred in otherwise ''neutral'' interactions; in other words, for most displays, the scream and/or embrace formed the only behavioral component of the interaction between the individuals in the dyad, and after the display, the two individuals separated without further affiliative or agonistic interaction. For ''tense/affiliative'' displays, all male–male cases involved either (1) the α male and another male within the study group, or (2) a subordinate male from the study group with a male from another group (an intergroup display). For male–male dyads, affiliative behavior occurred significantly more often during displays that included sirena screams compared with displays without sirenas (Fig. 4; Pearson's χ^2: $\chi^2 = 7.38$, $N_1 = 26$, $N_2 = 16$, $P = 0.007$). In contrast, neither the presence of sirena screams nor the presence of embraces in the display showed a significant impact on the likelihood of tense behavior during or immediately after the display.

Analyzing the proportion of displays involving ''tense'' interactions by age class of dyad, adult–uvenile dyads were significantly more likely to perform ''tense'' displays ($\chi^2 = 9.93$, $P = 0.020$) compared with the average

for all dyads. The proportion of displays involving affiliative interactions was not affected by age class of dyad. Sex class of dyads did not affect the likelihood of either tense or affiliative interactions associated with displays; however, this was a weak test as females participated in displays at such low rates overall.

DISCUSSION

The functional components of the scream–embrace display as described in captivity—running together, sirena scream, and embrace [Matheson et al., 1996; Phillips & Shauver Goodchild, 2005]—are not linked together inextricably as the vocal and physical components of one fixed action pattern in the wild. Although embraces and screams can co-occur, they may also be performed independently, and so I have categorized wild displays as scream–embrace, scream-only, and embrace-only.

Males were more likely than females to participate in scream–embrace and scream-only displays. The α male was the most frequent participant in displays overall, and the only male to give scream–embrace displays in dyads with adult females. Female–female displays were always embrace-only displays, although there is some evidence that females may give a sirena scream vocalization when displaying with the α male. Juvenile–juvenile displays were almost exclusively embrace-only displays, whereas adult–adult displays were most frequently scream–embrace.

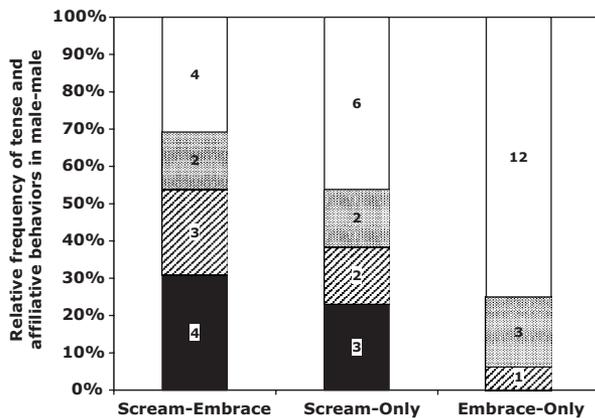When the group was traveling as a cohesive unit, no single ecological or social circumstance, such as an

Fig. 4. Relative frequency of affiliative and tense elements in male–male scream–embrace, scream-only, and embrace-only displays. Black bars indicate proportion of displays with both tense and affiliative components, light gray bars indicate proportion of displays with affiliative components only, dark gray bars indicate those with tense components only, and white bars indicate proportion of "neutral" displays (with no affiliative or tense components). The number inside each bar indicates the absolute frequency of observed displays of this type.

agonistic interaction, or the availability of high-quality food, seemed to be a strong predictor for the onset of displays. This argues against the hypothesis that displays are used for tension reduction or reconciliation [Phillips & Shauver Goodchild, 2005]. For male–male dyads, relatively high frequency of agonistic encounters between dyads did not predict an increase in displays for that dyad. This also seems to refute the hypothesis that displays were used for reconciliation or to decrease tension between adversaries, at least in this capuchin group. In contrast, male–male dyads with stronger affiliative bonds, as indexed by higher frequency of grooming bouts together, were significantly more likely to engage in displays with one another. This supports Matheson et al.'s [1996] hypothesis that displays act as a reinforcement of affiliative bonds for male dyads, and is similar to Whitham and Maestripieri's [2003] findings that high grooming frequency is associated with high diddling and embracing frequency in male guinea baboon dyads.

As found in captive studies, the most common display context was that of reunion of individuals or subgroups. Most displays observed in this study occurred when two subgroups reunited after having been out of visual and vocal contact. In these instances, multiple displays could occur in rapid succession as various individuals from one subgroup arrived and approached members from the other subgroup. Importantly, this was not a generalized increase in embracing behavior, but specifically dyads that had been out of contact from each other that either in tandem or taking turns embraced various individuals from the other subgroup. It is interesting that fission–fusion social organization has characterized groups into two populations of

C. nigritus in Southeastern Brazil, and displays are reported for this species, but not other species, in the wild. However, this may simply be an artifact of lack of information on displays from other wild *Cebus* populations; captive tufted capuchins are rarely identified to species or sub-species level, and may be kept in hybrid or mixed-species groups, and so data from captivity shed little light on the likely geographical distribution of displays in the wild.

Display frequency was positively correlated to the frequency of lost calls. In practice, lost calls often directly preceded screams and embraces. Individuals or subgroups would make vocal contact from a long distance, and lost calls by one or both parties would continue until visual contact was made, at which time the screams, running together, and/or embraces would occur. It appears, then, that a primary function of the display is as a greeting, and perhaps a sign of re-acceptance of individuals into the group.

It is well documented that wild tufted capuchin monkeys maintain individual relationships across groups after group division [Izar, 2004; Izawa, 1994; Lynch Alfaro, 2007]. Izawa [1994] hypothesized that capuchin monkey populations have a superstructure above the group level, which represents the history of splitting apart of matrilines through time, and that males preferentially transfer between a finite number of groups that have budded out of a single group. Izawa [1994] also found that intergroup encounters among these neighboring groups were affiliative and rarely agonistic, perhaps as a result of retained memories of past affiliative interactions with known individuals. In this study, capuchin males performed intergroup displays with males that had previously belonged to their group, as well as with males in groups they were "visiting," possibly in preparation for group transfer. It appears that for males, one function of displays may be to maintain old and form new social bonds across groups.

Future Directions

The results of this study generate several hypotheses concerning the function of sirena screams and embraces that can be tested through the use of acoustic analyses and playback experiments. Screams and embraces frequently occurred in the absence of each other and may serve distinct functions. Screams were performed predominantly by adult males and were the strongest predictor of affiliative interactions associated with displays. The sirena scream, the loudest vocalization in the diverse vocal repertoire of tufted capuchins [Di Bitetti, 2001], often occurs after the lost call, another extremely loud vocalization-type signaling separation from the group and, hence, vulnerability [Di Bitetti, 2001; Digweed et al., 2007]. Screams given after lost calls may function as honest advertisement of reunited alliances, directed at third

parties. In captivity, scream–embrace displays sometimes directly preceded coordinated intergroup threats by the same males toward the neighboring captive group [Matheson et al., 1996], suggesting that screams may serve to organize group males and reaffirm social bonds in preparation for coalitionary aggression toward other groups.

The absence of screams in female–female and juvenile–juvenile displays suggests that there may be no functional advantage to advertising alliances to third parties for these sex–age classes. This is not surprising, as females and juveniles rarely engage in intergroup encounters in this population [Lynch, 2001]. However, adult females emitted screams during scream–embrace displays with the α male within the stable group. All adult males were dominant to adult females in dyadic contests, but adult females' alliances with the α male changed the dominance ranking to the female's advantage in triadic interactions [Lynch, 1999, 2001], potentially increasing the incentive for females to broadcast information about alliances with the α male.

Embraces were used across diverse age–sex classes. Embraces may function as an honest indicator of affiliative relationships. Juvenile males were the most common participants in embrace-only displays, and had the most diverse sex–age classes for partners in embraces, suggesting the importance of a network of social bonds for young male capuchins. Embraces may be risky for adult males because of the vulnerability inherent in close physical contact, and for some male dyads this risk may serve as a test of the strength of their trust [Whitham & Maestripieri, 2003; Zahavi & Zahavi, 1997]. Other, less-bonded adult male dyads might be unwilling to risk close physical contact with one another, but still profit from advertising their alliance in scream-only displays.

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