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Cooper, M.A.; Bernstein, I.S.; Hemelrijk, C.K.

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RESEARCH ARTICLE

Reconciliation and Relationship Quality in Assamese Macaques (*Macaca assamensis*)

MATTHEW A. COOPER[1]*, IRWIN S. BERNSTEIN[2], AND CHARLOTTE K. HEMELRIJK[3]
[1]*Department of Psychology, Georgia State University, Atlanta, Georgia*
[2]*Department of Psychology, University of Georgia, Athens, Georgia*
[3]*Department of Theoretical Biology, University of Groningen, Groningen, The Netherlands*

A consistent conclusion in reconciliation research is that animals that reconcile are likely to have strong social bonds. This has led to the hypothesis that reconciliation occurs most often between valuable social partners. We tested this hypothesis in a group of Assamese macaques (*Macaca assamensis*) living near a temple in Assam, India. Using focal sample and ad libitum data collection, we recorded the occurrence of reconciliation, grooming, and agonistic aiding, and the outcomes of approach. We used matrix association methods (Tau_{Kr} correlation) to correlate reconciliation with grooming, aiding, and approach outcome. Females reconciled more often with females with which they had stronger grooming and aiding relationships. The correlation between reconciliation and aiding was significant for support to the aggressor and the victim. In contrast, no such correlations with reconciliation were found for males. This study provides evidence that females reconcile most often with valuable and compatible social partners. The results do not support the relationship-quality hypothesis for males, and we suggest that future studies give more consideration to the possibility that males reconcile for reasons other than to repair relationships with valuable partners. Am. J. Primatol. 65:269–282, 2005.

Key words: aiding; grooming; approach; relationship value; sex differences

INTRODUCTION

Social conflict is inevitable in gregarious species, and thus conflict management is a necessary part of life. When social conflict escalates to aggression, it may become necessary to resolve the dispute and restore the relationship. One such behavioral mechanism for conflict resolution is reconciliation.

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*Correspondence to: Matthew Cooper, Department of Psychology, P.O. Box 3966, Georgia State University, Atlanta, GA 30302-3966. E-mail: biomcc@langate.gsu.edu

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de Waal and van Roosmalen [1979] first used the term ''reconciliation'' to imply that friendly contact between former opponents shortly after a fight helps repair a relationship damaged by aggression. Several lines of evidence suggest that reconciliation does in fact function to repair relationships. Reconciliation reduces the probability of renewed aggression, which is typically increased after a fight [e.g., Aureli van Schaik, 1991; Castles & Whiten, 1998b; Cords, 1992; Kutsukake & Castles, 2001; Watts, 1995]. Reconciliation also reduces postconflict (PC) stress, as indicated by a rapid reduction in heart rate [Aureli & Smucny, 2000; Smucny et al., 1997], and reduced self-directed behavior compared to PC periods without reconciliation [Aureli & van Schaik, 1991; Castles & Whiten, 1998b; Kutsukake & Castles, 2001]. Reconciliation has also been shown to restore tolerance around a desirable resource [Cords, 1992].

There is considerable evidence suggesting that the occurrence of reconciliation varies with factors related to the quality of the social relationship between opponents (the relationship-quality hypothesis [Aureli et al., 1989; de Waal & Yoshihara, 1983; Kappeler & van Schaik, 1992]). According to Kummer [1978], social relationships can be viewed as investments, and, by extension, social partners have a certain value to those with which they interact. Cords and Aureli [2000] proposed that relationship quality is composed of relationship *value*, *compatibility*, and *security*. They suggested that relationship value should be restricted to those interactions with clear fitness consequences. ''Aiding'' is expected to be a good indicator of partner value because it can provide tangible benefits to the participants. In macaques, females often support their matrilineal kin, which promotes the inheritance of dominance rank [Bernstein & Ehardt, 1985; Chapais, 1988]. In some primate species, coalitions among males are common, and have been shown to influence the outcome of fights and increase access to receptive females [Bercovitch, 1988; Silk, 1993]. In nonhuman primates, rates of friendly behavior reflect social bonds. In macaques, social grooming is the most common type of friendly behavior, and in this study we use grooming as a measure of partner compatibility [Cords & Aureli, 2000]. The outcome of an approach reflects the degree of predictability and security in a relationship. Approaches that often result in negative outcomes, such as avoidance, silent bared-teeth displays, and other signs of tension, indicate less secure social relationships [Castles et al., 1996; Cords & Aureli, 2000].

If reconciliation repairs relationships damaged by aggression, then reconciliation should occur most often between partners with high-quality relationships because they risk losing, at least temporarily, the benefits associated with that relationship. Several studies have reported that animals reconcile more often with individuals with which they regularly exchange friendly behavior than with others [Arnold & Whiten, 2001; Aureli et al., 1989; Castles et al., 1996; de Waal & Ren, 1988; de Waal & Yoshihara, 1983; Preuschoft et al., 2002]. In macaque species that have strong matrilineal kinship networks, kin reconcile at higher rates than nonkin, whereas in species with less pronounced kinship networks no effect of kinship on reconciliation has been found [Aureli et al., 1997; Demaria & Thierry, 2001; de Waal & Ren, 1988]. Likewise, sex differences in the occurrence of reconciliation suggest that valuable relationships are characterized by high rates of reconciliation [Arnold & Whiten, 2001; Watts, 1995]. Experimental evidence also supports the relationship-quality hypothesis. Cords and Thurnheer [1993] found that reconciliation rates increased in pairs of long-tailed macaques (*M. fascicularis*) after they were trained to cooperate to obtain food.

The relationship-quality hypothesis has been evaluated mainly with data from captive primate groups. We tested this hypothesis in a free-living, provisioned group of Assamese macaques (*M. assamensis*). These animals live in a relatively natural environment, in which dispersal is a potential response to aggression. In a previous study we demonstrated reconciliation in this group [Cooper & Bernstein, 2002]. In this study, we measured the correlations between the proportion of reconciliation and the proportions of agonistic aiding, frequency of grooming, and outcomes of approach.

MATERIALS AND METHODS

Study Site and Subjects

This study was conducted on a group of Assamese macaques living near the Tukeswari temple near Goalpara, Assam, India. The group lived on the temple grounds and on the steep, rocky hill behind the temple. The hill was sparsely forested and surrounded by farmland. One other group of Assamese macaques lived in the vicinity, and animals have been known to immigrate between groups. The main temple was at the base of the hill and a second, smaller temple was at the top of the hill, 110 m above the temple grounds. The monkeys raided nearby rice fields, and stole food from shops and houses. Local priests fed the monkeys daily at each temple site, and the monkeys received food from tourists as well. The sporadic, clumped offerings produced a competitive feeding environment.

The group consisted of 64 animals, all of which were well habituated and individually recognizable. Twelve females and 11 males were classified as adults, 10 females and eight males were classified as subadults, and the remaining 23 animals were classified as juveniles or infants. Age estimates were based on body size and the eruption and size of canines in males. Kinships were unknown.

Data Collection

The study was conducted from October 1997 to February 1998, which overlapped with the end of the mating season. We performed focal observations on all 23 adult animals, and observed each subject for 4 hr (approximately 24 samples, 10 min each). During focal samples we recorded the identity of the initiator and recipient, the type of behavior, and the time when the behavior occurred. We recorded affiliative behavior, agonistic behavior, and approaches. Our ethogram was modeled after the behavior of stumptail macaques (*M. arctoides*) [Bertrand, 1969]. We also included the lip-grin, as described for Assamese macaques [Hill & Bernstein, 1969]. Other behavioral definitions match those used by de Waal and Luttrell [1989] and Castles et al. [1996]. Affiliative contact included grooming, passive contact, embracing, playing, muzzle contact, and sexual and nonsexual mounting. Aggressive behaviors included (in order of increasing intensity) open-mouth threats, lungeing, charging, chasing, manual contact aggression, biting, and severe biting. Submissive behaviors included avoiding, fleeing, and silent bared-teeth display. We summarized approaches (within 1 m) according to outcome. We defined positive approach outcomes as either participant initiating affiliative contact within 10 sec of approach, as long as it was not followed by agonistic behavior. We defined negative approach outcomes as either participant showing a silent bared-teeth display, or rough pushing and pulling, or aggression by the approachee, or approachee withdrawal

within 10 sec of approach. So that focal samples could be matched with PC samples, we recorded the identity of every animal in view and its distance from the focal subject prior to the start of each focal sample. Distances from the focal subject were divided into three categories: within 5 m, between 5 and 25 m, and over 25 m.

We also recorded data on grooming and aggression ad libitum during 1,008 hr of observation. For bouts of grooming, we recorded the identity of the initiator and recipient. We defined ''aid'' as any third-party involvement initiated during the course of an ongoing agonistic interaction. We recorded agonistic responses for each individual in triadic interactions, indicating the direction of support. When three or more animals directed aggression toward others, we recorded ''aid'' for each dyad. To be sure we accurately identified the initiator and recipient of aggression, we analyzed only those episodes in which we were confident we had observed the beginning of the encounter. Occasionally, two or more animals jointly initiated aggression, and we considered the animal that attacked the longest to be the initiator.

We performed a 10-min PC sample after all observed agonistic episodes between adult animals that involved a charge or more intense aggression. The PC sample began immediately following the last agonistic response in the conflict. If fighting started again within 2 min, it was considered part of the same episode, and the PC sample was started anew. We used the same data collection protocol for the PC samples as for the focal samples. We selected the initiator or the recipient of aggression as the focal subject, and in polyadic fights we selected one of the two main opponents. The main victim was the animal that was initially attacked, and the main aggressor was the animal that attacked for the longest duration. In polyadic fights we collected multiple PC samples by recording interactions between the focal subject and each opponent. Priority as a focal subject was given to the animal for which we had the least amount of data. We attempted to sample each subject an equal number of times as an initiator and recipient of aggression. Complete counterbalancing could not be achieved because some animals were rarely the recipients of aggression.

Analysis

Using the PC matched-control (PC-MC) method, we previously showed that reconciliation occurs in this study group [Cooper & Bernstein, 2002] (see de Waal and Yoshihara [1983] for the PC-MC method). Also, using the time-rule method, we previously classified affiliative contact between former opponents occurring within 2 min following a fight as reconciliation [Cooper & Bernstein, 2002] (see Aureli et al. [1989] for the time-rule method). The present data set is limited to fights between 19 adults, and consists of 157 PC samples and 24 reconciliations based on the 2-min criterion. Four adults were excluded from analysis because they had less than four PC samples with other adults. The data set contained 33 PC samples from polyadic fights. These polyadic fights were included in the analysis because we previously found that including them with dyadic fights did not significantly alter the frequency of reconciliation [Cooper & Bernstein, 2002]. Moreover, we noted that polyadic fights were evenly distributed among different sex combinations of opponents.

We summarized data from nine adult males and 10 adult females into symmetrical matrices of reconciliation, grooming, aiding, aiding the aggressor, aiding the victim, and positive and negative outcomes of approach (Tables I–IV).

TABLE I. Reconciliation Matrix Symmetrical*

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	M1	M2	M3	M4	M5	M6	M7	M8	M9
F1	x	2(4)	1(3)	–	1(5)	1(3)	0(1)	–	0(1)	0(1)	0(4)	0(3)	0(1)	–	–	–	–	–	
F2	2(4)	x	–	0(2)	0(4)	1(2)	0(1)	–	–	0(3)	3(5)	1(3)	0(2)	0(1)	1(2)	0(1)	–	–	–
F3	1(3)	–	x	–	0(1)	1(1)	–	–	–	–	0(1)	0(1)	0(2)	–	0(1)	–	–	–	–
F4	–	0(2)	–	x	0(1)	–	–	–	–	–	1(2)	0(2)	0(2)	–	–	0(1)	–	–	–
F5	1(5)	0(4)	0(1)	0(1)	x	–	–	–	–	0(1)	0(3)	–	0(1)	–	–	–	–	–	–
F6	1(3)	1(2)	1(1)	–	–	x	–	–	–	–	0(1)	0(2)	0(1)	–	0(1)	–	–	–	–
F7	0(1)	0(1)	–	–	–	–	x	–	–	0(1)	0(1)	–	–	0(1)	0(1)	1(2)	–	0(1)	–
F8	–	–	–	–	–	–	–	x	0(2)	0(1)	–	–	–	–	0(2)	0(1)	–	–	–
F9	0(1)	–	–	–	–	–	–	0(2)	x	–	–	–	–	–	0(1)	0(2)	–0(1)	–	
F10	0(1)	0(3)	–	–	0(1)	–	0(1)	0(1)	–	x	–	–	–	–	0(1)	–	–	–	–
M1	0(4)	3(5)	0(1)	1(2)	0(3)	0(1)	0(1)	–	–	–	x	2(6)	1(8)	0(5)	0(2)	0(1)	–	–	0(1)
M2	0(3)	1(3)	0(1)	0(2)	–	0(2)	–	–	–	–	2(6)	x	1(3)	0(1)	0(3)	0(3)	0(1)	0(2)	–
M3	0(1)	0(2)	0(2)	0(2)	0(1)	0(1)	–	–	–	–	1(8)	1(3)	x	1(4)	2(2)	0(2)	0(1)	–	0(1)
M4	–	0(1)	–	–	–	–	0(1)	–	–	–	0(5)	0(1)	1(4)	x	1(1)	0(2)	–	0(1)	0(1)
M5	–	1(2)	0(1)	–	–	0(1)	0(1)	0(2)	0(1)	0(1)	0(2)	0(3)	2(2)	1(1)	x	1(1)	0(2)	–	–
M6	–	0(1)	–	0(1)	–	–	1(2)	0(1)	0(2)	–	0(1)	0(3)	0(2)	0(2)	1(1)	x	–	0(1)	0(1)
M7	–	–	–	–	–	–	–	–	–	–	–	0(1)	0(1)	–	0(2)	–	x	0(2)	1(4)
M8	–	–	–	–	–	–	0(1)	–	0(1)	–	–	0(2)	–	0(1)	–	0(1)	0(2)	x	–
M9	–	–	–	–	–	–	–	–	–	–	0(1)	–	0(1)	0(1)	–	0(1)	1(4)	–	–

*The number of fights reconciled is shown, and the number of opportunities to reconcile is shown in parentheses. Empty cells were partialled out of the analyses. Analyses were conducted on the proportions.
F, female; M, male.

TABLE II. Grooming Matrix Symmetrical (Top) and Aiding Matrix Symmetrical (Bottom)*

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	M1	M2	M3	M4	M5	M6	M7	M8	M9
F1	x	120	106	28	116	67	3	1	2	4	42	3	0	36	4	0	0	0	0
F2	2(318)	x	29	24	24	83	1	0	1	14	105	3	0	21	2	0	0	0	0
F3	2(221)	1(249)	x	13	10	40	12	4	0	9	58	1	6	4	5	5	0	0	0
F4	0(249)	0(255)	0(156)	x	23	12	10	4	3	78	96	20	12	27	19	10	2	0	1
F5	0(225)	1(263)	0(166)	0(182)	x	34	42	7	10	16	146	9	0	25	30	0	0	0	0
F6	2(246)	9(250)	5(151)	0(173)	0(179)	x	9	10	3	33	51	0	16	27	42	1	1	0	0
F7	0(241)	0(247)	0(142)	0(166)	0(172)	0(161)	x	11	24	42	5	1	7	20	50	11	0	3	3
F8	0(247)	0(263)	0(146)	0(168)	0(178)	0(165)	0(146)	x	6	1	0	0	5	9	9	6	5	3	4
F9	0(217)	0(233)	0(114)	0(142)	0(152)	0(188)	0(126)	1(108)	x	8	2	0	3	4	31	5	8	8	0
F10	0(233)	0(243)	0(140)	0(162)	0(260)	0(155)	0(140)	0(144)	0(124)	x	16	3	1	9	53	6	1	0	0
M1	5(459)	14(485)	7(396)	2(410)	5(412)	1(413)	0(420)	0(428)	0(400)	0(416)	x	1	40	6	1	15	3	0	0
M2	4(336)	13(350)	5(247)	4(273)	2(283)	1(268)	1(275)	0(279)	0(251)	1(273)	55(519)	x	23	0	1	19	3	0	1
M3	0(427)	0(429)	0(334)	0(350)	0(378)	0(351)	0(348)	0(358)	0(326)	0(346)	14(522)	7(403)	x	6	0	31	2	0	3
M4	1(284)	2(302)	0(189)	0(213)	1(223)	3(204)	0(195)	0(201)	0(174)	0(197)	4(429)	3(316)	4(353)	x	2	3	0	0	0
M5	0(303)	0(305)	0(196)	2(218)	0(236)	0(213)	4(200)	0(208)	1(183)	0(204)	3(458)	2(327)	2(382)	1(249)	x	7	2	0	4
M6	0(355)	0(361)	0(246)	0(272)	0(284)	0(367)	0(254)	1(260)	1(228)	0(252)	0(514)	5(373)	9(448)	2(307)	0(308)	x	11	4	3
M7	0(259)	0(275)	0(158)	0(180)	0(190)	0(173)	0(164)	2(168)	0(141)	0(162)	1(430)	1(278)	2(366)	1(207)	4(218)	11(274)	x	8	14
M8	0(295)	0(309)	0(192)	0(214)	0(228)	0(211)	0(196)	0(204)	0(169)	0(188)	0(468)	0(309)	0(406)	0(241)	1(246)	1(284)	2(186)	x	0
M9	0(227)	0(243)	0(126)	0(150)	0(160)	0(145)	0(134)	0(136)	0(110)	0(132)	0(410)	0(259)	1(336)	0(181)	0(180)	1(232)	0(132)	0(170)	x

*The frequency of grooming (minus those instances that occurred during reconciliation) is shown in the top half of the matrix. The frequency of aiding is shown in the bottom half of the matrix, and the number of opportunities to aid is shown in parentheses. For aiding, analyses were conducted on the proportions.
F, female; M, male.

TABLE III. Aid Aggressor Matrix Symmetrical (Top) and Aid Victim Matrix Symmetrical (Bottom)*

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	M1	M2	M3	M4	M5	M6	M7	M8	M9
F1	x	1(206)	1(140)	0(143)	0(120)	0(137)	0(130)	0(163)	0(121)	0(114)	3(428)	4(271)	0(260)	1(181)	0(205)	0(257)	0(178)	0(166)	0(135)
F2	1(112)	x	1(133)	0(124)	1(118)	7(118)	0(112)	0(150)	0(108)	0(98)	11(420)	8(257)	0(240)	2(169)	0(185)	0(239)	0(165)	0(152)	0(122)
F3	1(81)	0(116)	x	0(58)	0(52)	2(51)	0(42)	0(74)	0(31)	0(29)	6(358)	4(188)	0(175)	0(95)	0(113)	0(164)	0(89)	0(76)	0(46)
F4	0(106)	0(130)	0(98)	x	0(49)	0(51)	0(43)	0(74)	0(34)	0(29)	1(354)	3(190)	0(172)	0(96)	1(113)	0(166)	0(89)	0(76)	0(47)
F5	0(105)	0(145)	0(114)	0(133)	x	0(43)	0(45)	0(68)	0(28)	0(19)	4(344)	2(184)	0(175)	1(90)	0(111)	0(161)	0(83)	0(72)	0(41)
F6	2(109)	2(132)	3(100)	0(122)	0(136)	x	0(36)	0(68)	0(27)	0(21)	0(351)	0(183)	0(168)	1(87)	0(106)	0(159)	0(81)	0(70)	0(40)
F7	0(111)	0(135)	0(100)	0(123)	0(137)	0(125)	x	0(54)	0(17)	0(9)	0(350)	0(182)	0(162)	0(78)	3(95)	0(148)	0(72)	0(58)	0(30)
F8	0(84)	0(113)	0(72)	0(94)	0(110)	0(97)	0(92)	x	1(38)	0(41)	0(384)	0(214)	0(197)	0(111)	0(129)	1(181)	2(104)	0(102)	0(61)
F9	0(96)	0(125)	0(83)	0(108)	0(124)	0(110)	0(109)	0(70)	x	0(4)	0(343)	0(173)	0(155)	0(70)	1(90)	1(137)	0(64)	0(49)	0(21)
F10	0(119)	0(145)	0(111)	0(133)	0(145)	0(134)	0(131)	0(103)	0(120)	x	0(336)	0(169)	0(149)	0(67)	0(85)	0(135)	0(59)	0(42)	0(17)
M1	2(31)	3(65)	1(38)	1(56)	1(68)	1(62)	0(70)	0(44)	0(57)	0(80)	x	44(493)	12(438)	4(384)	3(413)	0(467)	0(394)	0(383)	0(357)
M2	0(65)	5(93)	1(59)	1(83)	0(99)	1(85)	1(93)	0(65)	0(78)	1(104)	11(26)	x	6(283)	2(232)	2(252)	4(301)	1(227)	0(208)	0(186)
M3	0(167)	0(189)	0(159)	0(178)	0(203)	0(183)	0(186)	0(161)	0(173)	0(197)	2(84)	1(120)	x	4(194)	2(223)	5(282)	2(210)	0(200)	0(168)
M4	0(103)	0(133)	0(94)	0(117)	0(133)	2(117)	0(117)	0(90)	0(103)	0(130)	0(45)	1(84)	0(159)	x	1(149)	1(204)	1(123)	0(110)	0(83)
M5	0(98)	0(120)	0(83)	1(105)	0(125)	0(107)	1(105)	0(79)	0(94)	0(119)	0(45)	0(75)	0(159)	0(100)	x	0(219)	4(143)	1(127)	0(97)
M6	0(98)	0(122)	0(82)	0(106)	0(123)	0(108)	0(106)	0(79)	0(89)	0(117)	0(47)	1(72)	4(166)	1(103)	0(89)	x	10(197)	1(172)	0(149)
M7	0(81)	0(110)	0(69)	0(91)	0(107)	0(92)	0(92)	0(64)	0(78)	0(103)	1(36)	0(60)	0(156)	0(84)	0(75)	1(77)	x	2(92)	0(68)
M8	0(129)	0(157)	0(116)	0(168)	0(156)	0(141)	0(138)	0(112)	0(123)	0(146)	0(85)	0(101)	0(206)	0(131)	0(119)	0(112)	0(94)	x	0(57)
M9	0(92)	0(121)	0(80)	0(103)	0(119)	0(105)	0(104)	0(75)	0(89)	0(115)	0(53)	0(73)	1(168)	0(98)	0(83)	1(83)	0(64)	0(113)	x

*The frequency of aid given to the aggressor is shown in the top half of the matrix, and the number of opportunities to aid is shown in parentheses. The frequency of aid given to the victim is shown in the bottom half of the matrix, and the number of opportunities to aid is shown in parentheses. Analyses were conducted on the proportions.
F, female; M, male.

TABLE IV. Positive Approach Matrix Symmetrical (Top) and Negative Approach Matrix Symmetrical (Bottom)*

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	M1	M2	M3	M4	M5	M6	M7	M8	M9
F1	x	4(15)	5(13)	4(6)	5(14)	5(6)	0(1)	0(0)	0(0)	0(3)	2(23)	2(18)	0(1)	4(10)	0(2)	0(0)	0(0)	0(1)	0(0)
F2	2(15)	x	0(2)	2(4)	2(9)	0(12)	0(2)	0(0)	0(0)	1(2)	1(17)	0(15)	0(2)	1(14)	0(4)	0(0)	0(0)	0(0)	0(0)
F3	0(13)	1(2)	x	1(8)	0(5)	1(7)	0(1)	0(0)	0(0)	0(4)	3(10)	1(8)	0(5)	3(4)	1(2)	0(5)	0(1)	0(1)	0(0)
F4	0(6)	1(4)	3(8)	x	2(5)	1(1)	1(5)	0(0)	0(1)	2(5)	9(15)	1(6)	0(8)	2(9)	1(5)	0(0)	0(2)	0(0)	0(0)
F5	2(14)	6(9)	1(5)	1(5)	x	2(5)	3(4)	1(2)	0(0)	0(1)	5(19)	0(2)	0(0)	0(8)	1(5)	0(0)	0(0)	0(0)	0(2)
F6	0(6)	3(12)	2(7)	0(1)	1(5)	x	0(1)	2(3)	0(1)	1(2)	3(4)	0(6)	3(7)	1(7)	2(6)	0(2)	1(1)	0(0)	0(0)
F7	0(1)	0(2)	1(1)	0(5)	0(4)	1(1)	x	0(3)	5(7)	2(7)	1(6)	4(7)	1(4)	1(7)	6(14)	0(4)	0(0)	0(0)	0(0)
F8	0(0)	0(0)	0(0)	0(0)	0(2)	0(3)	1(3)	x	0(4)	0(1)	0(0)	0(0)	1(1)	0(3)	2(2)	1(6)	4(9)	0(0)	0(4)
F9	0(0)	0(0)	0(0)	0(1)	0(0)	1(1)	0(7)	1(4)	x	0(0)	0(0)	1(2)	0(0)	0(3)	1(2)	1(6)	1(5)	0(1)	0(5)
F10	1(3)	1(2)	1(4)	1(5)	0(1)	0(2)	5(7)	1(1)	0(0)	x	0(2)	0(0)	1(1)	1(3)	0(1)	0(1)	0(0)	0(0)	0(1)
M1	0(23)	2(17)	3(10)	3(15)	5(19)	1(4)	4(6)	0(0)	0(0)	2(2)	x	0(8)	1(4)	1(15)	1(4)	0(3)	0(1)	0(0)	0(0)
M2	5(18)	3(15)	0(8)	2(6)	0(2)	2(6)	0(7)	0(0)	1(2)	0(0)	1(8)	x	0(3)	1(8)	1(4)	1(4)	0(1)	0(1)	0(0)
M3	0(1)	2(2)	2(5)	3(8)	0(0)	0(7)	1(4)	0(1)	0(0)	0(1)	1(4)	0(3)	x	1(5)	2(3)	1(11)	0(2)	1(3)	1(1)
M4	1(10)	2(14)	0(4)	1(9)	4(8)	1(7)	0(7)	2(3)	0(3)	0(3)	1(15)	0(8)	0(5)	x	0(4)	0(5)	0(0)	0(3)	0(0)
M5	0(2)	1(4)	0(2)	2(5)	1(5)	0(6)	2(14)	0(2)	0(2)	1(1)	1(4)	0(4)	0(3)	1(4)	x	0(5)	1(1)	0(5)	1(1)
M6	0(0)	0(0)	1(5)	0(0)	0(0)	0(2)	0(4)	5(6)	2(6)	0(1)	2(3)	1(4)	1(11)	0(5)	0(5)	x	0(6)	0(3)	0(0)
M7	0(0)	0(0)	0(1)	1(2)	0(0)	0(1)	0(0)	1(9)	2(5)	0(0)	1(1)	1(1)	1(2)	0(0)	0(1)	6(6)	x	0(3)	3(6)
M8	0(1)	0(0)	0(1)	0(0)	0(0)	0(0)	0(0)	0(0)	1(1)	0(0)	0(0)	1(1)	1(3)	1(3)	1(5)	1(3)	2(3)	x	0(1)
M9	0(0)	0(0)	0(0)	0(0)	1(2)	0(0)	0(0)	1(4)	0(5)	0(1)	0(0)	0(0)	0(1)	0(0)	0(1)	0(0)	0(6)	0(1)	x

*The frequency of approaches that resulted in positive outcomes is shown in the top half of the matrix, and the total number of approaches is shown in parentheses. The frequency of approaches that resulted in negative outcomes shown in the bottom half of the matrix, and the total number of approaches is shown in parentheses. Analyses were conducted on the proportions.
F, female; M, male.

We did not analyze the direction of reconciliation, because it was sometimes unclear which individual initiated reconciliation. Therefore, we made the reconciliation matrix symmetrical. Because the reconciliation matrix was symmetrical, we correlated it with symmetrical matrices of grooming, aiding, and approach outcomes.

Whenever possible, we corrected matrices for opportunity to interact by expressing cell values as proportions. We corrected the frequency of reconciliation for opportunity by expressing it as a proportion of the number of fights for each dyad (Table I). We studied 10 adult females (thus 45 female–female dyads). We recorded 38 fights in 19 of the 45 dyads, and seven fights were reconciled in six dyads. We recorded 62 fights in 27 of the 36 male–male dyads, and 10 fights were reconciled in eight dyads. We recorded 57 fights in 34 of the 90 male–female dyads, and seven fights were reconciled in five dyads. In the reconciliation matrix, zero values indicate the absence of reconciliation, and empty cells indicate that no reconciliation was possible due to a lack of conflict. We used a dummy matrix to partial out the empty cells from the reconciliation matrix [Hemelrijk, 1990b]. We corrected the frequency with which an individual aided another for opportunity by expressing it as a proportion of the number of fights in which the recipient of aid was involved, excluding fights between the recipient of aid and the potential aider (Tables II and III). We corrected positive and negative approach outcomes for opportunity by expressing the frequency as a proportion of the total number of approaches for that dyad (Table IV). Since the animals were not directly limited in their opportunity to groom, we did not correct the grooming matrix for opportunity to interact (Table II). However, the frequency of grooming observed may be affected by visibility, and thus correlations should be treated with caution. In addition, animals used grooming as a means of reconciling on six occasions, and these six bouts of grooming were removed from the grooming matrix.

Using the individual-based Tau_{Kr} test [Hemelrijk, 1990a], we performed analyses at the group level for females and males, and between the sexes. In the latter case, correlations can be performed with the females in the rows and the males in the columns, or vice versa. The outcomes differ slightly because of the difference between the numbers of males and females (nine males and 10 females). Since both correlations are equally important, we report the average of their Tau_{Kr} values.

We performed the Tau_{Kr} test with the computer software MATRIXTESTER (a sequel to MATSQUAR and MATRECT, developed by C.H.). The Tau_{Kr} method is an extended version of the Kr method in that it corrects for ties and the number of individuals. With this method, correlations are performed per individual and then summed over all individuals. For instance, we tested whether individuals were more often involved in reconciliation with partners with which they groomed more frequently. The significance of the Tau_{Kr} correlation is calculated by means of the ''quadratic-assignment'' method. This implies that complete rows and columns (instead of single cells) are permuted randomly. Thus interdependent cells (that belong to the same individual) are kept together. Note that in the matrices, zero values are real data points as long as the animals had the opportunity to interact. However, to be conservative, if an individual failed to interact with any partners (or received no interaction), we omitted them from the statistical analysis. Since correlations were performed for each individual on an ordinal scale, extreme data values will not bias the results. The significance level of the test is shown at $P < 0.05$ and $P < 0.01$, one-tailed. We used one-tailed tests because we investigated directional hypotheses.

RESULTS

Female–Female Interactions

Females reconciled more often with females with which they were often involved in grooming and aiding (Table V). The correlation between reconciliation and aiding was significant for support of the aggressor and the victim (Table V). Reconciliation did not significantly correlate with the outcomes of approach. The proportion of approaches that resulted in positive outcomes correlated with the proportion of approaches that resulted in negative outcomes (Table V).

Interactions Between the Sexes

Reconciliation between the sexes did not correlate with grooming, aiding, or outcomes of approach (Table V). Reconciliation between the sexes occurred in seven of 43 fights during the nonmating season, whereas it was not observed during the 14 fights in the mating season. This difference was not statistically significant (χ^2 (1, n = 19) = 2.60, P = 0.18).

Male–Male Interactions

Reconciliation among males did not correlate with grooming, aiding, or outcomes of approach (Table V).

DISCUSSION

Female Relationships

Agonistic aid is valuable in terms of gaining access to resources, and, at least in macaques, in promoting the inheritance and stability of female dominance relationships [Bernstein & Ehardt, 1985; Chapais, 1988; Chapais & St. Pierre, 1997]. While agonistic aid can be valuable, its effect on reconciliation has been difficult to demonstrate [Cords & Aureli, 1993; Kappeler & van Schaik, 1992; Preuschoft et al., 2002]. Even though our sample of fights was relatively small, and reconciliation was infrequent, we were able to document a correlation between reconciliation and agonistic aid among females. Correlations with

TABLE V. Tau_{Kr} Correlations Among Females, Males, and Between the Sexes

Correlations	Among females Tau_{Kr}	Among males Tau_{Kr}	Between the sexes Tau_{Kr}
1) Reconciliation with			
a) Grooming	0.226*	0.172	0.106
b) Aid	0.390**	–0.007	0.085
c) Aid aggressor	0.451**	0.152	0.117
d) Aid victim	0.601**	0.001	0.229
e) Positive approach	0.085	–0.142	–0.156
f) Negative approach	–0.050	–0.142	–0.082
2) Special			
a) Positive and negative approach	0.368**	–0.092	0.161

The Tau_{Kr} values are based on 2,000 matrix permutations. Empty cells in the matrices occurred when grooming was not observed or when animals had no opportunity for aid, positive approach, negative approach, or reconciliation. Empty cells in the reconciliation matrix were partialled out of the analysis using a dummy matrix. TauKr values for between the sexes were averaged between male to female and female to male values. Females, n=10; Males, n=9. *$P<0.05$; **$P<0.01$, one–tailed.

reconciliation were significant for support of the aggressor and the victim. Identifying support of the victim is important because these are situations in which we would expect aid to be most valuable. This study provides support for the relationship-quality hypothesis, and demonstrates that increased reconciliation with valuable partners is not an artifact of captivity.

We also found that females reconciled more often with other females with which they often groomed. It is possible that differential visibility biased the grooming data and thus the correlation with reconciliation. However, we think this possibility is unlikely, because in a separate analysis we found that reconciliation among females correlated significantly with grooming given but not grooming received (data not shown). A correlation specific to grooming given should not be contaminated by visibility issues, since for any grooming dyad each individual has an equal opportunity to be actor or recipient. Numerous studies have demonstrated that within groups, dyads with ''strong'' social bonds reconcile more than dyads with ''weak'' social bonds [Aureli et al., 1989; Call et al., 1999; Castles et al., 1996; Schino et al., 1998]. These studies often used a composite measure of high affiliation and low aggression to define ''strong'' social bonds. Cords and Aureli [2000] suggested that the frequency and duration of affiliative behavior reflect partner compatibility. The correlation between reconciliation and grooming in this study adds further support to the relationship-quality hypothesis, and suggests that the occurrence of reconciliation among females depends, at least in part, on partner compatibility.

Cords and Aureli [2000] suggested that approaches with negative outcomes were an indication of insecure relationships, and proposed that animals were motivated to reconcile with former opponents when relationship security was low. Their proposal was based in part on their finding that immature long-tailed macaques were more likely to reconcile with non-kin than with kin, and they suggested that non-kin relationships might be less secure [Cords, 1988; Cords & Aureli, 1993]. However, relationship security is expected to affect reconciliation only when relationships are valuable [Cords & Aureli, 2000]. We found no relationship between reconciliation and negative approach outcomes, but we did not have enough data to restrict the correlation to valuable partners only. Thus, our results may be due in part to our inclusion of valuable and non-valuable partners alike. Also, using the proportion of approaches with negative outcomes to indicate less secure relationships is problematic because the matrices of positive and negative outcomes of approach were correlated. This demonstrates that whether or not a female approaches another is a more important factor than the outcome.

Intersexual Relationships

We previously showed that males and females rarely reconcile in this group [Cooper & Bernstein, 2002]. Some studies in macaques and baboons have found that males and females reconcile less often with each other than with same-sex opponents [Schino et al., 1998], whereas others have found no effect [Castles & Whiten, 1998a; Demaria & Thierry, 2001]. Sex differences, when observed, may be partly due to an effect of reproductive season. In one study, reconciliation occurred less often during the mating season than in the non-mating season [Schino et al., 1998]; however, in another study no effect was found [Kutsukake & Castles, 2001]. In this study, we did not find an effect of reproductive season, but most of our data were collected during the non-mating season. Because of the low frequency of reconciliation between males and females, it was difficult to

investigate the effect of relationship quality. In gorillas, sex differences in relationship quality appear to correlate with reconciliation. Males and females reconcile more often than other sex combinations, and this may be due to the valuable relationships expected between male and female gorillas based on their social structure [Watts, 1995].

Male Relationships

We found that the occurrence of reconciliation among males was unrelated to grooming, aiding, or outcomes of approach. Consequently, our data do not support the relationship-quality hypothesis for males. There are several possible reasons for this. A larger sample might have revealed a correlation between relationship quality and reconciliation in males. However, the effect of relationship quality is at least weaker in males than in females, since we had more data on reconciliation for males than for females. Also, grooming, aiding, and approach outcomes may not indicate the quality of male social relationships. However, Assamese macaque males appear to be strongly bonded, as indicated by frequent aiding, grooming, and triadic male–infant interactions, and the occurrence of male–male mounting and genital touching [Bernstein & Cooper, 1998; Cooper & Bernstein, 2000]. Social bonds between Assamese macaque males appear similar to those reported for stumptail, bonnet, and Barbary (*M. sylvanus*) macaques [Estrada, 1984; Paul et al., 1996; Preuschoft et al., 1998; Silk, 1994].

It seems reasonable to assume that aggression damages social relationships among males. The few studies available found that males, like females, exhibit increased rates of self-directed behavior following aggression. These behaviors are reduced following friendly reunions between opponents, suggesting that males experience PC stress that is reduced by reconciliation [Castles & Whiten, 1998b; Kutsukake & Castles, 2001]. It has been proposed that high levels of PC stress mediate the increased rates of reconciliation that are often observed among valuable social partners [Aureli, 1997; Aureli et al., 2002]. It remains possible, however, that PC stress is not disproportionately elevated in males following aggression between valuable partners.

Finally, it is possible that males reconcile for reasons other than to repair relationships damaged by aggression. This is best described by the benign-intent hypothesis, which proposes that reconciliation signals the former opponent that the conflict is over and that it is safe to resume peaceful interactions [Silk, 1997, 2002]. The benign-intent hypothesis predicts that animals will reconcile to obtain short-term objectives, such as access to desirable resources or preferred partners. It is difficult to distinguish between the relationship-repair hypothesis and the benign-intent hypothesis because they make overlapping predictions. In fact, the benign-intent hypothesis can be viewed as a proximate mechanism by which reconciliation might ultimately function to repair relationships. One difference between the two hypotheses involves predictions about the initiation of reconciliation. The benign-intent hypothesis predicts that aggressors will initiate reconciliation more often than victims. The relationship-repair hypothesis refrains from making a prediction, given the difficulty of measuring initiative to reconcile, but suggests that ideally the victim should initiate contact more often after fights than during control conditions because the victim has a greater motivation to reduce hostility and uncertainty [Aureli et al., 2002]. While we acknowledge the limitations in measuring the initiation of reconciliation, in a previous study we found that aggressors in this study group initiated reconciliation in 75% of interactions [Cooper & Bernstein, 2002]. Furthermore, male

aggressors initiated reconciliation in 82% of interactions, which is consistent with the benign-intent hypothesis. We suggest that males may reconcile in a goal-oriented fashion, rather than as a means of repairing relationships with valuable and compatible partners. A similar sex difference has been reported for aiding in chimpanzees (i.e., females support those with which they have a social bond, whereas males support others more opportunistically) [Hemelrijk & Ek, 1991].

In this study, we did not consider how reconciliation might modify existing social relationships. Compared to female macaques, males have less stable dominance ranks and more-frequently contested agonistic encounters [Cooper & Bernstein, 2002; Whitten & Smith, 1984]. Given the dynamic nature of male dominance relationships, and the prevalence of male coalitions in this species, it seems reasonable to propose that males may use reconciliation as a tool to help build alliances.

In sum, females reconciled more often with females they groomed and aided. These results are consistent with the view that partner compatibility and value affect the occurrence of reconciliation, and supports the relationship-quality hypothesis for females. In contrast, the results do not support the relationship-quality hypothesis for males. We should at least consider the possibility that males use reconciliation opportunistically to gain access to specific individuals and build alliances, rather than to repair existing relationships with valuable partners.

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