

RESEARCH ARTICLE

Innovative Social Behavior in Chimpanzees (*Pan troglodytes*)

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We present evidence of agonistic buffering in captive chimpanzees, recorded from 1993 until 2005, mainly from ad libitum sampling in over 2000 hr of observation. A total of 33 agonistic buffering episodes were analyzed for context and effects of this complex social behavior. Agonistic buffering was directed at the whole chimpanzee colony as they supported an individual who initially received aggression from the alpha male, independently of the victim's age, sex or social rank. Chimpanzee agonistic buffering behavior is compared with that in other nonhuman primate species, and we describe some particularities of chimpanzee agonistic buffering: the status of the buffers used—socially important offspring such as those from the alpha female—and the social rank of the adult male responsible for the buffering episode—alpha male. Possible functions for this behavior in chimpanzees are suggested as appeasement of group members in a particularly crowded captive setting, and/or as a “forced reconciliation” mechanism. Chimpanzees exhibit behavioral flexibility by adapting themselves to new social and physical situations and use novel behavior to achieve social benefits. *Am. J. Primatol.* 70:54–61, 2008. © 2007 Wiley-Liss, Inc.

Key words: chimpanzees; agonistic buffering; captive setting; social rank; innovation; Machiavellian intelligence

INTRODUCTION

Deag & Crook [1971] described “agonistic buffering” in Barbary macaques (*Macaca sylvanus*) whenever a subordinate male approaching a higher-ranking male picked up an infant and presented her/him to the contender to inhibit a potential aggressive encounter. They concluded that the subordinate male exploited infantile features [see also Ransom & Rowell, 1972] to reduce the likelihood of being attacked; hence the name given to this behavior. According to Taub [1980], the males that displayed such behavior did so not because of potential agonism related to their rank differences, but because they both shared a special care-giving relationship with the infant used. To date, agonistic buffering has been observed in a variety of Old World monkey species [e.g. Barbary macaques: Deag & Crook, 1971; Deag, 1980; Smith & Peffer-Smith, 1982; Taub, 1980; gelada baboons: Dunbar, 1984; yellow baboons: Collins, 1984; olive baboons: Strum, 1987], but not reported from Neotropical primates or apes [but see Warren & Williamson, 2001]. Given the tactical importance of this behavior, its absence in such a political species as the chimpanzee is surprising. Complex social behavior, ranging from

reconciliation to deception, has been repeatedly described for both captive and wild chimpanzees [Arcadi et al., 1998; Boesch, 1991, 1992, 2003; Byrne & Whiten, 1989; de Waal, 1982, 1989, 1996, 2000; de Waal & Pokorny, 2005; de Waal & van Roosmalen, 1979; Goodall, 1986; Matsuzawa, 1996; Newton-Fisher, 1997; Nishida & Hiraiwa-Hasegawa, 1987; Whiten & Byrne, 1997]. Agonistic buffering might have passed unnoticed in chimpanzees because while reconciliation among macaques and baboons is typically directed from lower to the high-ranking individuals independent of the rank of the initiator of conflicts, the opposite is seen in chimpanzees [de Waal & Aureli, 1996]. Thus alpha male contacts to infants during aggression might have been considered

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as reconciliation rather than buffering. However, it is improbable that intense male–infant interactions following male aggression toward others would have been overlooked, given the thousands of hours of observations on chimpanzees. It seems unlikely, therefore, that agonistic buffering is a typical behavior among chimpanzees. We argue here that the development of agonistic behavior is a context-specific innovative tactical behavior [Reader & Laland, 2004], initiated by alpha males constrained in space, lacking social distance, and exposed to external stimuli that evoked potentially dangerous displays.

The first episode of agonistic buffering was observed in 1995 by CC and occurred as a result of visitor disturbance to the chimpanzees. The alpha male responded to high visitor density and noise by performing a charging display, during which he hit a young female who screamed. All other colony members approached and supported the screaming female by hugging, embracing or standing nearby. The alpha male continued his display and again passed near the young female. The alpha male was then chased by all the other chimpanzees; he grabbed and carried ventrally an infant female who had been adopted by the alpha female. The rest of the colony ceased to chase the male while he carried

the infant ventrally and he then released the infant. No individual groomed, embraced or sat nearby the alpha male. At the time of first observation, the similarities were obvious between these behaviors and those described for agonistic buffering in other species. This behavior was then the focus of particular attention during subsequent observations. This paper thus provides a descriptive study of agonistic buffering in chimpanzees instead of attempting to test a specific hypothesis.

METHODS

Subjects

The study colony was housed in the Lisbon Zoo (Lisbon city, Portugal). Table I presents the details of the individuals in the group throughout the study. The enclosure measured 20.8 (width) × 4 (deep) × 5 (height) m, with a total area of 83.2 m². The enclosure was formed of 11 small-walled pens, which communicate by means of small doors (≈ 1 × 1 m). In addition, the number of pens occupied by the colony throughout the study (1993–2005) varied from four to seven due to the Zoo's policy management, and other primate species successively occupied several of these pens.

TABLE I. Chimpanzees' Ids (≈), Sex, Age and Further Information

Chimpanzee	Sex	Year of birth	Observations
Faustina	Female	1979	Alpha female since 1993 until the present ^{a,e}
Kali	Female	1981	Omega female in 1996 ^{c,e}
Cuca	Female	1985	Beta female that died in October 2001 ^{c,e}
Maria Pia	Female	1985	Temporary separately from the colony with offspring (Pascoal and Pipa) ^{b,e}
Joca	Female	1989	^e
Rita	Female	1991	Faustina's adoptive daughter ^{a,e}
Gugu	Female	1995	Maria Pia's first daughter ^f
Buba	Male	1979	Alpha male from 1993 until 1996 ^c , when he died ^{b,e}
Chico	Male	1977	Alpha male from 1996 ^d until 2000 when he became beta male ^{b,e}
Dári	Male	1986	Beta male from 1996 ^d and alpha male since 2000 ^{b,d}
Charlie	Male	1990	Transferred to Brazil in 1999 ^{b,e}
Tata	Female	1997	Joca's first daughter ^f
Andreia	Female	1997	Kali's first daughter ^f
Tina	Female	1997	Faustina's daughter ^f
Pipa	Female	2001	Maria Pia's second daughter ^f
Tuxa	Female	2001	Joca's second daughter ^f
Pascoal	Male	1999	Maria Pia's first son ^f
Kuca	Female	2002	Kali's second daughter ^f
Gabry	Female	2005	Gugu's daughter and Maria Pia's granddaughter ^f
Pepe	Male	2005	Maria Pia's second son ^f

^aSee Casanova [1996, 2002].

^bUnpublished data.

^cSee Casanova [1996].

^dSee Casanova [2002].

^eWild born. Initially hand raised by private owners and latter given to the Zoo.

^fCaptive born and raised by biological mothers.

The chimpanzees' diet consisted of fresh fruit and vegetables, several species of living insects (≈ 0.25 L for all individuals once per week), seeds, milk and eventually commercial dog food pellets. Animals were fed four times per day (08:00, 12:00, 14:30 and 17:30 during winter or 19:00 during the summer schedule). Until 1996, keepers provided water with a hose, without any rigid timetable. After 1996, clean water dispensers were installed in all pens.

Sampling Methods

The data presented in this paper come from three different observation periods. The first period (February 1993 to June 1995) [Casanova, 1996] comprises a series of ad libitum observations made during 1,037 observation hours (habituation period included). Only data collected during ad libitum samples are presented here, because this sampling technique was the only one that allowed for reliable characterization of agonistic buffering events. During scan and focal samples (627 hr) focused on particular individuals and/or behavior [Altmann, 1974] the primary observer (CC) was unable to identify the cause or onset of agonistic buffering events involving males while collecting detailed data on females. In the second period (July 1998 to September 1999) ad libitum, scan and focal sampling were done for 750 hr on all individuals. Agonistic buffering cases were then recorded during focal samples on males and infants because the observer was aware of the existence of these episodes and she used behavior-dependent focal sampling on males to capture these events. The criterion followed to switch the focal from a female to a male was the presence of large groups of visitors, because these potentially could disturb the colony and in previous observations, the charging displays of the male immediately followed this visitor context. Every time the observer switched the focal target to a male, agonistic buffering occurred ($N = 6$). Males were followed during these episodes until 10 min after the end of the episode. The episode terminated when infants were recovered by their mothers or after the infants were released by the males. Using behavior-dependent focal samples could potentially increase the possibility of the observer being biased toward focusing only on an alpha male. There is, however, a low probability for such a bias because both alpha and subordinate males were equally likely to be involved in any non-buffering agonistic interaction and females were never observed in an agonistic interaction with other females [see Casanova, 2002]. The third period (January 2004 to July 2005) also consists of ad libitum sampling (123 hr) combined with focal and scan samples (402 hr). There was thus a total of 2,312 observation hours with the group during which agonistic buffering was sampled.

RESULTS

Identity of the Participants

Thirty-three episodes of agonistic buffering were observed during observation hours (0.014 bouts/hr). Of these, 27 (81.8%) were recorded during ad libitum samples and six (18.1%) were observed during focal samples. In all instances the current alpha male was the perpetrator of agonistic buffering (Buba: 8/33; Chico: 19/33; Dári: 6/33; see Table II). Buba and Chico always used the alpha female's infant daughter (Table II), whereas Dári was more likely to use the daughter of a subordinate female (Kuca: 4/6).

During buffering events, the alpha male carried infants ventrally (17/33), dorsally (7/33), embraced (3/33), carried dorsal and embraced simultaneously (1/33) or embraced and simultaneously groomed the infant (1/33). In three cases it was not possible to determine how the infant was picked up and carried. Duration of infant carrying differed significantly among males (Kruskal Wallis $W = 9.4$, $df = 2$, $P < 0.01$; Fig. 1). Chico and Buba carried the infant for significantly longer periods than did Dári (post hoc tests, $P < 0.05$). The identity of the individual originally harassed by the alpha male was unrelated to the victim's age, sex or social rank, and the colony supported the harassed individual in all observed episodes. The identity of the infant buffer was in most of the episodes (87.9%) connected to the social rank of its mother, the alpha female. In 12 (36.3%) episodes the alpha female recovered her infant from the alpha male (Buba: 1/8; Chico: 10/19; Dári: 1/6) before the group calmed down. In 13 (39.3%) cases the infant remained sequestered by the male (Buba: 7/8; Chico: 6/19; Dári: 1/6). Whether the infant was recovered by the mother or simply released by the male was uncertain in the seven remaining episodes. The alpha female allowed Buba to retain her infant significantly more often than Chico (Fisher's exact probability test: $P < 0.0001$).

Agonistic Buffering Context

Before agonistic buffering episodes, individuals were engaged in normal foraging, resting or social activities. All agonistic buffering episodes occurred when visitor density was very high (visitor groups ranged from 50 to 160 individuals). Parties were composed of children and adults (pupils and teachers, families or large groups). These groups of visitors started making noise (screaming, shouting, throwing objects, running and stomping in front of the enclosure) increasing the animals' nervousness. The chimpanzees ceased their usual activities, turned their backs toward the visitors or looked for places to hide: individuals were agitated and infants immediately sought proximity with their mothers in what appear to be a highly stressful situation for the chimpanzees. The visitors' harassing activities

TABLE II. Summary of the Agonistic Buffering Episodes in Captive Chimpanzees at the Lisbon Zoo

Alpha male	Date	Harassed chimpanzee	Infant	Context that elicited agonistic buffering	Support given to the harassed chimpanzee	Displayed behaviors (duration) during buffering	Infant recovered by alpha female
Buba	17/05/95	Maria Pia	Rita	Charging display/public	Yes	Ventral carrying (53 ^a) ? ^b	No
Buba	23/06/95	Joca	Rita	Charging display/public	Yes		No
Buba	04/07/95	Charlie	Rita	Charging display/public	Yes	Dorsal carrying (83)	No
Buba	19/07/95	Dári	Rita	Charging display/public	Yes	Dorsal carrying (?)	No
Buba	29/07/95	Joca	Rita	Charging display/public	Yes	Ventral carrying (?)	No
Buba	03/09/95	Charlie	Rita	Charging display/public	Yes	Ventral carrying (93)	No
Buba	18/09/95	Faustina	Rita	Charging display/public	Yes	?	Yes
Buba	26/09/95	Chico	Rita	Charging display/public	Yes	Dorsal carrying (?)	No (?)
Chico	17/01/99	Maria Pia	Tina	Charging display/public	Yes	Dorsal carrying (?)	No
Chico	06/02/99	Dári	Tina	Charging display/public	Yes	Ventral carrying (?)	No
Chico	20/02/99	Cuca	Tina	Charging display/public	Yes	Ventral carrying (?)	No
Chico	03/03/99	Rita	Tina	Charging display/public	?	Embrace (?)	No
Chico	17/04/99	Dári	Tina	Charging display/public	Yes	Ventral carrying (?)	Yes
Chico	20/05/99	Cuca	Tina	Charging display/public	Yes	Ventral carrying (?)	Yes
Chico	03/06/99	Maria Pia	Tina	Charging display/public	Yes	Embrace (143)	No
Chico	12/06/99	Gugu	Tina	Charging display/public	Yes	Ventral carrying (31)	Yes
Chico	19/06/99	Dári	Tina	Charging display/public	Yes	?	Yes
Chico	24/06/99	Faustina	Tina	Charging display/public	Yes	Ventral carrying (?)	Yes
Chico	28/07/99	Cuca	Tina	Charging display/public	?	Ventral carrying (?)	?
Chico	05/08/99	Kali + Joca	Tina	Charging display/public	?	Ventral carrying (70)	?
Chico	10/08/99	Gugu	Tina	Charging display/public	?	Embrace + grooming (37)	?
Chico	27/04/99	Gugu	Tina	Charging display/public	Yes	Ventral carrying (59)	No
Chico	06/05/99	Tata	Tina	Charging display/public	Yes	Ventral carrying (19)	Yes
Chico	27/05/99	Rita	Tina	Charging display/public	Yes	Ventral carrying (44)	Yes
Chico	10/06/99	Kali + Tuxa	Tina	Charging display/public	Yes	Ventral carrying (13)	Yes
Chico	15/06/99	Faustina	Tina	Charging display/public	Yes	Ventral carrying (23)	Yes
Chico	13/07/99	Rita	Tina	Charging display/public	Yes	Ventral carrying (32)	Yes
Dári	1/01/04	Kali	Tina	Charging display/public	Yes	Embrace (5)	Yes
Dári	20/04/04	Kali	Kuca	Charging display/public	Yes	Dorsal carrying (?)	No
Dári	25/11/04	Joca	Kuca	Charging display/public	Yes	Dorsal carrying (11)	?
Dári	04/02/05	Kali	Kuca	Charging display/public	Yes	Dorsal carrying (27)	?
Dári	17/03/05	Rita	Kuca	Charging display/public	Yes	Embrace + dorsal carrying (?)	?
Dári	16/05/05	Chico	Tina	Charging display/public	Yes	Embrace (?)	?

^aTime in seconds.

^bQuestion marks stand for uncertain observations.

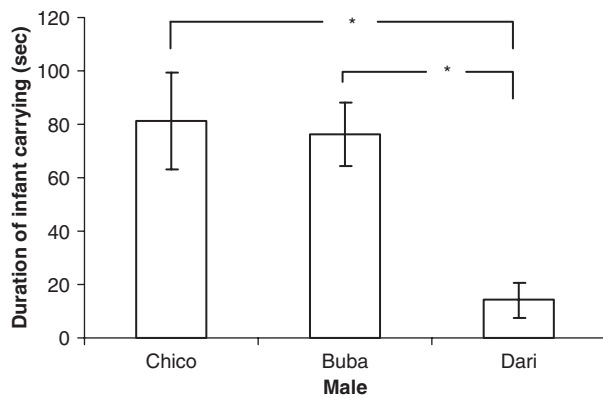


Fig. 1. Duration of infant carrying between males (post hoc contrasts). * $P < 0.05$.

provoked a charging display by the alpha male. During these charging displays, the alpha male might accidentally hit or push another group member in his way, and this individual might begin screaming and soliciting support. In all instances observed (Table II), while some colony members supported the harassed chimpanzee by embracing, hugging, grooming or maintaining close proximity with her/him, infants and juveniles near their mothers looked at the harassed chimpanzee or at the location of the alpha male. Most group members would then chase the alpha male, and he would display the behavior described here as agonistic buffering. As shown in Table II, chimpanzees supported any harassed animal, independently of their age, sex or social rank.

Effects of Agonistic Buffering

As soon as the alpha male ventrally or dorsally carried, embraced or groomed the alpha female's infant (or rarely, another available infant), chasing by other chimpanzees stopped immediately. The alpha male might continue displaying affiliative behavior toward the infant for some time. In 12 episodes (36.3%), when the group's arousal ended, the alpha male allowed the infant to return to its mother. In another 13 cases (39.3%) the alpha female actively recovered her infant, especially from Chico. The group would then resume typical activities (feeding, playing, grooming and resting). In the 10 min following an episode, the alpha male never received affiliative behavior from the rest of the colony once his buffering display was over.

Dári was the only alpha male who did not contact or carry the alpha female's daughter but rather, the daughter of a low-ranking female, Kali (Kuca: 4/33). At the time of Dári's tenure as the alpha male, the alpha female's daughter Tina was 8 years old (see Table I) and was large and heavy. Dári attempted to use her as a buffer twice, but Tina, with the help of her mother and other members of the

group, rejected Dári in only 5 sec (see Table II). Of the available infants, Kuca was very socially interactive within the group, in contrast to Tuxa or Pipa, who did not socialize frequently having histories of temporary separation from the rest of the colony along with their mother. Pepe and Gabry at the time were still suckling and hence clung to their mothers at all times. Despite the use of a subordinate infant, the group's agonistic behavior toward Dári ceased when he picked her up.

DISCUSSION

Our sample, although small, complies partially with Deag and Crook's [1971] definition of agonistic buffering, in that males performed this behavior to terminate an aggressive context rather than to avoid one. At the same time, we note some particularities of chimpanzee agonistic buffering in comparison to that of monkeys.

First, the context that elicited agonistic buffering was very artificial: zoo visitors harassed chimpanzees living in an enclosure that provided no means of escape from visitor attention. However, it was not the visitor harassment that elicited agonistic buffering, but the fact that alpha males while performing charging displays in response to visitors sometimes stepped on, hit or pushed another chimpanzee in their way. These "accidental" aggressive contacts elicited group agonistic support for the victim, as has been described for chimpanzees in other contexts [de Waal, 1982, 1989, 1996, 2000; Hemelrijk & Ek, 1991]. We suggest that Lisbon Zoo chimpanzees devised this form of agonistic buffering to quickly and efficiently appease group companions during a whole-group aggressive encounter. In this way the chimpanzees adjusted to the socio-spatial limitations imposed by their particular captive environment (little interindividual space, no escape from visitors, interlinked enclosures with low ceilings, which limit display and locomotion). The low number of episodes recorded here and specific to high visitor densities suggests that in the wild or in undisturbed, larger enclosures, agonistic buffering would seldom occur. Agonistic buffering was never observed following aggressive interactions that did not involve visitors. This is clearly an uncommon, subtle but complex behavior which makes its observation difficult [Casanova, 2002].

In most episodes (87.9%) the infant used was the offspring (biological or social) of the alpha female. Male chimpanzees not only recognized the status of the alpha female's infant, but also knew how to profit from her/his importance. In baboons and macaques the infant participant is not necessarily the offspring of an alpha female. We also observed four cases (12.1%) where the infant used was the daughter of a subordinate female. We suggest that while a key element is the use of an infant as a buffer, whenever

possible males attempt to use socially important infants.

Although infant carrying by male chimpanzees has been reported [Nishida, 1983; Notmann & Munn, 2003], none of these descriptions fit with the contexts or behavior observed at the Lisbon Zoo. Alternative explanations for infant-carrying behavior such as paternal care [e.g. Warren & Williamson, 2001] are unlikely to be the case for these agonistic buffering episodes. First, paternity could only be identified for two offspring: Gugu (Buba's daughter) and Tina (Dári's daughter) [Knapp, 2001, personal communication; see also Paul et al., 1992]. Gugu was never carried by her father Buba, who instead carried the social daughter of the alpha female (see Table II). In the second case, Dári did briefly transport his biological daughter (see Table II) and this offspring was also the biological offspring of the alpha female. Because in the majority of the episodes Dári carried the daughter of a low-ranking female because no other independent infant was present.

In Nishida's [1983] study, adult males in Mahale, Tanzania, carried infants in non-agonistic contexts, but more briefly than did females and irrespective of the mother's reproductive stage. Nishida [1983] suggests that because all mothers mated exclusively with their own group males, these adult male alloparents could have been fathers of the infants. Males were developing genetically advantageous interactions with infants on a "collective basis" (p 28). The costs of caretaking to adult males were small (short bout lengths) while males might benefit by courting mothers through affiliation with their infants, the physical development and socialization of infants is stimulated by male contacts, infants may establish intimate relationships with the males who may protect them in the future, and finally the mothers may gain extra time for feeding or resting [Nishida, 1983]. Thus male parental care as an alternative explanation to the behavior reported here seems unlikely because an alpha male was risking injury to his offspring while being aggressively pursued by most group members. It would also be advantageous for the alpha male to flee the group without the extra weight of the infant. Nor did agonistic buffering episodes improve the male's opportunity to court the mothers of infants or contribute to the establishment of an intimate relationship between the infant and the alpha male. Mothers did not take advantage of the extra time to feed or rest; on the contrary, they pursued the alpha male and sometimes recovered their infants. Furthermore, within 10 min after the episode finished, in no case did the mother (or any other group member) groom or interact in an affiliative way with the alpha male.

Notmann & Munn [2003] described infant carrying by males in Budongo Forest, Uganda,

reporting one episode of a newborn male infant being cared for by a high-ranking adult male for 2 days until the death of the infant. Notmann & Munn [2003] discussed this case in the context of kidnapping and infanticide and argue that current proximate explanations for kidnapping should include the possibility that males are motivated by interest in infants as "possessions" and not solely as sources of meat or as ways to create reproductive opportunities (p 2). However, the context in which this infant "care" occurred was not overtly aggressive, whereas at Lisbon Zoo buffering episodes always occurred in aggressive contexts.

The carrying and manipulation of infants appeared to require an absence of action by the mother, who was almost always the alpha female. Sometimes the mother allowed the alpha male to finish his agonistic buffering display and release the infant, whereas on other occasions she actively sought to recover her offspring. We suggest that the absence of action by the mother was based on familiarity with the risks posed by the alpha male, producing intermale variance in rates and duration of infant use. The presence or absence of opponents during the alpha's tenure and his tenure duration might be plausible explanations for differences in female response. Buba was the alpha male for much longer than the other two, and thus was the best known and had the longest history of affiliative bonds within the group. Furthermore, Buba had no opponents while he was alpha male; Chico, the beta male, never initiated aggression, whereas Dári was still very young. Chico had only a relatively short tenure as alpha male and was constantly challenged by Dári [Casanova, 2002]; thus the group members may have had greater experience with the behavior of Dári and therefore more overt trust. Thus, Buba appeared to be the most trusted male, followed by Dári, whereas little confidence was placed in Chico. The nature of alpha male's relations with other group members and responses to challenges from other males suggest that assessment underlies variation in buffering and that the males are acting for political profit. Factors such as the personalities of the alpha males deserve further investigation.

The high capacity for behavioral innovation among chimpanzees is demonstrated by the "invention" of this novel form of interaction by the first alpha male. Chimpanzee agonistic buffering contains elements of both of the generation of novelty and the ability to apply such novelty to political ends. This study reiterates the political abilities of chimpanzees to manipulate social affairs. Unlike macaques [de Waal & Aureli, 1996], chimpanzees, and particularly dominant ones, tend to behave in a fair way akin to a sense of justice [de Waal, 1992, 1996; de Waal & Pokorny, 2005; Flack & de Waal, 2000]. For instance, the dominant initiates reconciliation among chimpanzees, whereas in macaques the initiator tends to

be a subordinate or defeated animal [de Waal & Aureli, 1996]. This dominant-to-subordinate directionality in interactions took the same course in the agonistic buffering cases described here.

Our data do not allow us to assume sympathetic feelings or ethical reasoning by the alpha males rather than a Machiavellian [Byrne & Whiten, 1989; Whiten & Byrne, 1997] use of behavior and infants. Nonetheless, the specificity of the context that elicited this behavior makes agonistic buffering appear as a post-aggressive interaction where infants are used as facilitators of colony social maintenance. At the same time, the alpha male might be demonstrating that he was acting on behalf of his group's well-being by displaying against visitor stress, because agonistic buffering only occurred when the alpha male aggressively contacted a group member during displays against humans. Such accidental contact with a group member outside a visitor context did not elicit agonistic buffering.

There were no other contexts in which group members acted aggressively in unison toward the alpha male in this colony and no other contexts where infants were used as buffers. Moreover, the preferential use of the alpha female's infant may also suggest that the male was using the alpha female's power as an intermediary in conflict resolution. During buffering and in other very specific agonistic contexts (e.g. a subordinate male copulating with a female), the alpha female was solicited by the alpha male to intervene, acting as a peacemaker (e.g. de Waal 1982, 1989, 1996).

CONCLUSIONS

1. Agonistic buffering was concluded to be part of the behavioral repertoire of one group of captive chimpanzees, innovated by the alpha male.
2. This form of agonistic buffering differs from that of monkeys because the infant used as a buffer was typically the offspring of the alpha female. In contrast to macaques, chimpanzees discriminate among infants on the basis of the mother's rank. In addition among chimpanzees, the behavior is performed by the alpha/dominant males, whereas in monkeys subordinate males use infants as buffers.
3. Agonistic buffering episodes in chimpanzees could act as a form of "apology" and thus function as a general form of reconciliation. Alpha males perceive the alpha female as an individual that can mediate post-conflict interactions.
4. Chimpanzees exhibit behavioral flexibility and innovation by adapting to new situations and using novel behavior to achieve social benefits. Behavioral plasticity allows chimpanzees to respond to challenges posed by a variety of captive enclosures and different social contexts through the use of innovative behavior patterns. Plasticity

is an advantage when individuals want to achieve political and social benefits.

5. The agonistic buffering episodes observed are complex polyadic interactions and further observations are needed to assess with more detail the significance of this behavioral mechanism.

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