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Coping with Acute Crowding by *Cebus apella*

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Traditionally, scientists believed that crowded housing conditions increased aggression in animals. Recent research on captive primates fails to support a linear relationship between population density and aggressive behavior. Our study is the first to investigate the effects of acute crowding on a New World primate. We observed brown capuchins (Cebus apella) *under 2 different spatial conditions: a control that offered the full indoor space in the enclosure and a short-term experimental condition that restricted the capuchins to approximately half the amount of space of the control condition. We compared rates of self-grooming, aggression, contact sitting, social grooming, and play between both conditions. We conducted a mixed factorial ANOVA at the individual level while taking subject sex and age class into account. Intense aggression, play, and social grooming decreased significantly in crowded conditions, suggesting that capuchins avoid social encounters if spatially confined. Their strategy for coping with acute crowding via a decrease in all forms of social behavior is intermediate between chimpanzee and macaque strategies in similar experiments. The only behavior to increase under crowding was a nonsocial, self-directed behavior with the potential of reducing arousal: self-grooming.*

KEY WORDS: aggression; *Cebus apella*; coping model; crowding; husbandry.

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INTRODUCTION

Calhoun (1962) reported a connection between high population density and increased aggression in rodents. Initially, nonhuman primate studies supported the connection (Alexander and Roth, 1971; Elton and Anderson, 1977), but over the past few decades, contradictory findings have emerged (Bercovitch and Lebron, 1991; Eaton *et al.*, 1981). In primate literature, the coping model has now replaced the density/aggression model. According to the model, animals respond to crowded conditions by modifying their behavior to reduce the number and severity of aggressive encounters (Aureli and de Waal, 1997; de Waal, 1989a; de Waal *et al.*, 2000; Judge, 2000; Judge and de Waal, 1997).

Though advantageous for predator detection and territorial defense (van Schaik, 1983), group living increases competition within groups for access to food, mates (Lancaster, 1986), and space (Hall and Fedigan, 1997). To be beneficial, group living requires minimizing the costs, which primates achieve via carefully maintained social relationships. The density/aggression model proposes that normal social interactions break down during overpopulation (Calhoun, 1962). The coping model argues that the same social mechanisms that limit aggression in low population densities are activated more often in crowded conditions (de Waal, 1989a). As originally proposed, the coping model suggests that nonhuman primates modify their behavior to include more friendly and submissive interactions under conditions of unusual density to reduce the likelihood or severity of aggression (de Waal, 1989a).

Submissive signals by a subordinate individual to a more dominant one appease potential aggressors. Researchers have variously interpreted the signals to indicate fear (Maxim, 1982), showing friendly intentions in response to a threat (Andrew, 1965), an appeasement signal in place of withdrawal (de Waal and Luttrel, 1985), and a sign that the subordinate accepts the dominance relationship and thus eliminates the dominant's need to assert itself aggressively (de Waal, 1986; Judge, 2000), all of which help maintain social stability. Subordinates yield to dominants via submissive signals, thereby greatly reducing the potential of violence (Preuschoft and van Schaik, 2000).

Like submissive signals, grooming reinforces social relationships and reduces the likelihood of aggression. Terry (1970) argues that both being groomed and grooming reduce tension in situations in which group cohesion and solidarity are threatened. Grooming may also act as an appeasing mechanism to avoid aggression. A low-ranking female's chance of harassment is lower while grooming a high-ranking female than when a high-ranking female is simply in close proximity (Silk, 1982). O'Brien

(1993b) suggested that low-ranking females exploit the situation by soliciting grooming from approaching dominants in an attempt to redirect possible aggression. Monkeys are more likely to attend to the distress calls of a conspecific if the conspecific had groomed them earlier (Seyfarth and Cheney, 1988). Grooming also occurs in everyday contexts without any eminent threat of aggression. Juveniles use grooming to integrate themselves into the adult social system and to form lasting bonds (O'Brien, 1993a). Equal reciprocation of grooming time between partners characterizes affiliative grooming relationships in which the primary function seems to strengthen social bonds (O'Brien, 1993b). Grooming then becomes a central mechanism in both formation and maintenance of group cohesion.

Early evidence that primates do not act according to the density aggression model emerged from a study of long-term crowding in chimpanzees. Nieuwenhuijsen and de Waal (1982) compared the behavior of a captive chimpanzee (*Pan troglodytes*) colony during the summer, while the chimpanzees lived in a large outdoor enclosure, and during the winter, while they lived in an indoor enclosure 20 times smaller than the outdoor area. Though aggression increased, it did so only slightly. More importantly, friendly and appeasing interactions, i.e., submissive greetings and grooming, increased significantly during the crowded months. Individuals did not simply intensify their typical behavioral patterns in response to greater density (*cf.* Freedman *et al.*, 1972); instead, they changed the frequency of certain behaviors in ways that were likely to reduce aggression.

A study comparing the behavior of groups of rhesus macaques (*Macaca mulatta*) living under varying density conditions also supported the coping model (Judge and de Waal, 1997). All groups were well established and had lived together for more than 8 years. Adult males uniformly increased grooming while aggression remained constant across densities. Female behavior was more variable than that of males depending on whether they were interacting with kin or nonkin. Judge and de Waal (1997) showed that primates modify their behavior based on spatial and social conditions, but did not necessarily become more aggressive as a result of crowding.

Short-term crowding studies suggesting some coping mechanisms require extended time to develop complement long-term studies supporting the coping model (Judge, 2000). Short-term crowding of rhesus monkeys resulted in increases of mild, but not severe, aggression and increases in submissive signals but a decrease in grooming (Judge and de Waal, 1993). The authors interpret the findings as not fully supporting either the density/aggression model or the coping model and instead propose a conflict avoidance strategy whereby crowded individuals respond by reducing most social behavior. The increase in mild aggression caused individuals to keep their distance; the increase in submissive signals attempted to appease dominants, and the decrease of grooming and other forms proximity reduced the likelihood of individuals entering into agonistic encounters. Another macaque study supported the use of a conflict avoidance strategy. Long-tailed macaques (*Macaca fascicularis*) decreased grooming, exploration, play, and counteraggression whereas mild aggressiveness increased under acute crowding (Aureli *et al.*, 1995).

The first study of short-term crowding of chimpanzees again upheld the conflict avoidance strategy as a way to limit aggression. The authors refer to the chimpanzees' behavior as an inhibition strategy (Aureli and de Waal, 1997). As in previous short-term crowding studies, adult chimpanzees decreased all forms of social behavior. In contrast to the macaques Judge and de Waal (1993) and Aureli *et al.* (1995) studied, chimpanzees decreased the frequency of both intense and mild aggression. The study also measured certain behaviors that indicate anxiety (Maestripieri *et al.*, 1992) and found that they increase in crowded conditions, which suggests that conflict avoidance may be the fastest way to limit aggression but that the resulting increase in stress drives development of more active tension reduction mechanisms that emerge in studies of long-term crowding (Aureli and de Waal, 1997).

To evaluate specific characteristics, we assessed the effects of short-term crowding on the behavior of 2 groups of brown capuchins (*Cebus apella*). This is the first study to investigate the effects of crowding on a New World primate. In the wild, brown capuchins have an average group size of 12–27 individuals (Fragaszy *et al.*, 2004). Adult males make up one third of the group, adult females another third, and immature individuals are the remainder (Fragaszy *et al.*, 2004). Capuchins share many characteristics with chimpanzees. Both *Cebus* and *Pan* are highly intelligent and manipulative in tool use and foraging (Ottoni and Mannu, 2001; Westergaard and Suomi, 1994; Westergaard *et al.*, 1997), form distinct cultures in the wild (Boesch and Boesch-Achermann, 2000; Goodall, 1986; Perry *et al.*, 2003; Whiten *et al.*, 1999), hunt and obtain other foods cooperatively (Fedigan, 1990; Boesch, 1994, 2002; Mendres and de Waal, 2000), share food (de Waal, 1997, 1989b; Perry and Rose, 1994; Rose, 1997; Westergaard and Suomi, 1997), and males of both genera cooperate in group defense (Goodall, 1986; Perry, 1996; Watts and Mitani, 2001). Because of the similarities, Rose (1997) speculated that convergent evolution between *Pan* and *Cebus* occurred. We hypothesized that, because capuchins and chimpanzees share many behavioral characteristics related to social tolerance, capuchins would respond to short-term crowding in the same way as chimpanzees. Macaques decreased only some social behaviors, viz., grooming, play, and intense aggression, while other behaviors, viz., mild aggression and submissive signals, increased (Aureli *et al.*, 1995; Judge and de Waal, 1993). However, chimpanzees, decreased all forms of social behavior including both mild and intense aggression (Aureli and de Waal, 1997). We hypothesized that the capuchins would decrease the amount of both mild and intense aggression along with all other social behaviors, using the inhibition strategy to avoid conflict.

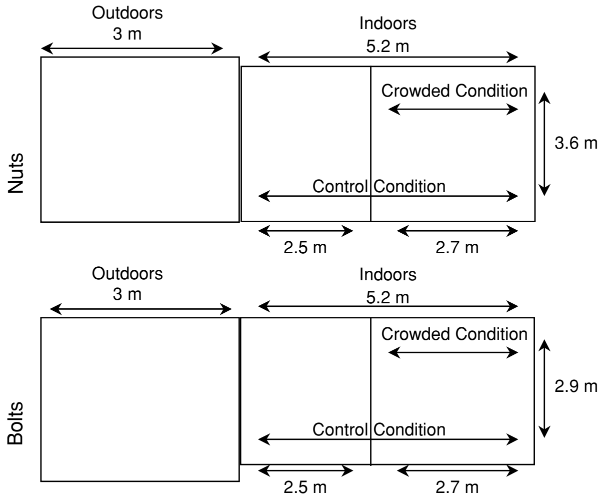
METHODS

Subjects and Housing

The 38 brown capuchins lived at the Yerkes National Primate Research Center in 2 separate, well established groups. Changes in the group composition since their establishment in October 1991 resulted from births, deaths, and removals or additions of adult males. The 2 groups had similar demographic composition. The Bolts, consisted of 3 adult males, 6 adult females, 8 immature males, and 2 immature females. The Nuts, had 3 adult males, 5 adult females, 6 immature males, and 5 immature females. No rank reversal occurred during the study. During testing, we removed some individuals temporarily for veterinary care.

We housed both groups in indoor/outdoor enclosures, with the Nuts having 31 m^2 total of floor space and the Bolts having 25 m^2 (Fig. 1). Both enclosures had swings and perches, with mesh ceilings and walls so the subjects could use most of the 3-dimensional space. Each enclosure consisted of 1 outdoor section separated from the indoor sections by an opaque wall. A chain-link fence partitioned each group's indoor section into 2 parts. There were interconnecting doorways between adjacent sections, and a tunnel between the 2 distant sections. The 2 social groups were visually separated by an opaque screen, but had auditory contact. The capuchins were restricted from indoor or outdoor access during daily cleaning, testing, or cold weather. Monkey chow and water were available *ad libitum* and the subjects had access to a tray of fresh produce, bread, and protein fluid daily after *ca.* 1600 h.

In the experimental condition—crowded—we restricted subjects to 1/2 of the indoor area totaling only 9.7 m^2 and 7.8 m^2 of the indoor floor space for the Nuts and the Bolts, respectively. During the control condition—control—we allowed subjects access to both indoor areas, but not the outdoor enclosure. Thus, both conditions were more crowded than when the capuchins have access to the entire enclosure. The setup allowed the capuchins about twice as much space as in the crowded condition as well as greater escape opportunity because of the mesh and open doors separating



Group One Animal Area		Group Two Animal Area	
Outdoors	12.3 m^2	Outdoors	10.2 m^2
Indoors (control)	18.6 m2	Indoors (control)	15.0 m^2
Indoors (crowded)	9.7 m2	Indoors (crowded)	7.8 m^2

Fig. 1. Subjects' indoor–outdoor enclosures. We collected control data when subjects had free range of entire indoor area. Floor area of the control test for the Nuts was 18.6 m^2 and 15.0 m^2 for the Bolts. In the crowded condition, subjects lived in the front section of the indoor run, 9.7 m^2 for Nuts and 7.8 m^2 for Bolts.

both areas. Restricting the capuchins to indoor access during the control condition allowed us to observe fully the whole colony at once. The combined indoor area measured 18.6 m^2 and 15 m^2 total floor space for the Nuts and the Bolts, respectively.

Data Collection

We collected data between 1000 and 1600 h from August 1998 through April 1999. May Lee Gong collected observational data once per group per day. We similarly distributed observations of both the crowded and control conditions over the times of day. Before data collection, we allowed subjects 30 minutes to adjust to the crowded situation, which they normally never encountered. Capuchins in the control condition did not need such adjustment, as they were merely locked indoors, which they were accustomed to during routine observations and daily cleanings. Under both conditions, each observation session lasted 30 minutes. The total number of sessions was 21 and 15 on the Nuts and Bolts, respectively, under the crowded condition, and 8 and 9 sessions under the control condition, respectively.

Behavioral sampling followed the methods of Altmann (1974). We collected agonistic encounters, play, and self-grooming with all-occurrence sampling. We collected instantaneous scans every 5 minutes, starting at the beginning of the observation period and ending at 30 minutes, i.e., 7 scans/observation session. We collected contact sitting and allogrooming behaviors during scans.

Operational Definitions

Affiliative behaviors included allogrooming (intently picking through the hair of another individual), contact sitting (≥ 2 individuals sitting in contact without grooming), and play. Play consisted of wrestling, chasing, and gnawing unaccompanied by any threat displays or vocalizations. Self-grooming included the same behaviors described for allogrooming but directed at the individual performing the grooming rather than at a conspecific.

We considered behaviors agonistic on the basis of specific facial threats, agonistic vocal displays, or biting. We also considered interactions agonistic if 1 individual responded to the other with counteraggression or vocal submissive displays (Verbeek and de Waal, 1997). We characterized agonistic encounters by the level of aggression, either intensely or mildly aggressive. We recorded only the highest level of aggression per episode per subject; in other words, if 1 individual began an agonistic encounter by threatening another and then proceeded to bite its opponent, the incident would count as 1 instance of intense aggression for only the instigator and not the recipient of the aggression. Mild aggression consisted of negative or intimidating behaviors such as pushing or mock biting as well as threats and lunges that evoked responses, such as flight or screaming. Threat displays consisted of open mouth stares (raised eyebrows, open mouth stares, and flattened ears), stares, swaying, head bobbing, forward thrust, and piloerection (Fragaszy *et al.*, 2004; Freese and Oppenheimer, 1981). Intense aggression included biting, hair pulling, and any other behavior that could cause physical damage. We considered aggressive encounters interrupted for pauses of ≥ 30 seconds or longer as 2 separate aggressive incidents.

Data Analysis

We expressed social grooming and contact sitting data as a percentage of samples taken. We calculated play bouts, mild aggression, intense aggression, and self-grooming data as hourly rates of behavior, separated for crowded and control conditions. After determining that the behavioral trends did not significantly differ between the groups, we combined the data to create a larger sample size of 38 individuals. We then subjected the individual data points to a mixed factorial analysis of variance (ANOVA) with age (adult vs. immature) and sex (male vs. female) as between-subject factors and condition (crowded vs. control) as a within-subject factor. We followed up significant interactions via Marascuilo and Serlin's (1988) procedure for interaction contrasts.

RESULTS

Agonistic Behavior

Figure 2 contains the hourly rate of mild aggression, which crowding did not significantly affect compared with the control condition ($F_{1,34} = 2.40$, NS). Adults tended to initiate more mildly aggressive encounters than immature capuchins did under both conditions (age: $F_{1,34} = 8.50$, $p = 0.006$). The sexes showed no significant difference in mild aggression (sex: $F_{1,34} = 0.02$, NS), nor was there a significant interaction between condition and age or sex.

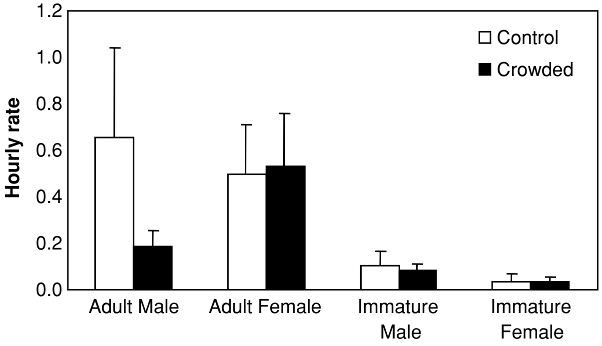


Fig. 2. Mean + SEM rate per hour of mild aggression—pushing, mock biting, or other negative or intimidating behaviors—during control and crowded conditions. Data are separated for each age and sex class. There is no significant difference between crowded and control conditions.

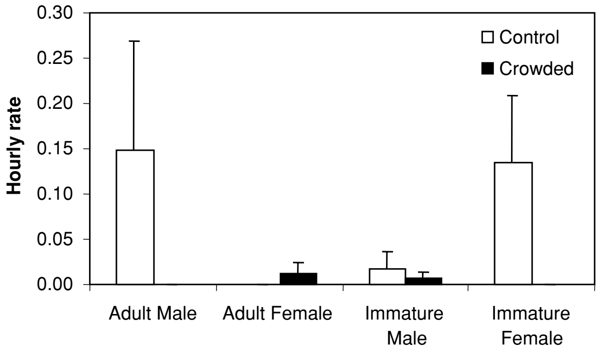


Fig. 3. Mean + SEM rate per hour of intense aggression, i.e., frequency of chasing, biting, hair pulling and any other potentially damaging behavior during control and crowded conditions. Data are separated for each age and sex class. There was significantly less intense aggression in the crowded than the control condition, but no significant effect of subject age or sex.

Intense aggression decreased significantly in the crowded condition ($F_{1,34} = 9.62$, $p = 0.004$; Fig. 3). Results indicate a significant interaction between age and sex ($F_{1,34} = 6.34$, $p = 0.016$). Following Marascuilo and Serlin (1988), we used visual inspection of the data to design a hypothesis for *post hoc* testing—in this case, that both adult males and juvenile females are more aggressive than adult females and juvenile males. As this hypothesis involves specific groups from each independent variable in the study, it is a single-interaction contrast. Results are significantly different, $t_{34} = 1.79$, $p < .05$. The interaction between age, sex, and condition is significant also ($F_{1,34} = 9.77$, $p = 0.004$). Adult males and immature females were the most aggressive in the control condition, while adult females and immature males were most aggressive during crowding ($t_{34} = 8.08$, $p < .005$). There is no significant interaction for condition and age or condition and sex.

Affiliative and Play Behavior

Play behavior (Fig. 4) decreased significantly under the crowded condition ($F_{1,34} = 13.62$, $p = 0.001$), and immature individuals played at a significantly higher rate than adults did ($F_{1,34} = 13.23$, $p = 0.001$). Immature capuchins decreased their rate of play significantly more than adults did under crowded conditions (age × condition: $F_{1,34} = 10.21$, $p = 0.03$; interaction contrast: $t_{34} = 3.37$, $p < 0.005$). There is no significant interaction for age, sex, and condition or for sex and condition.

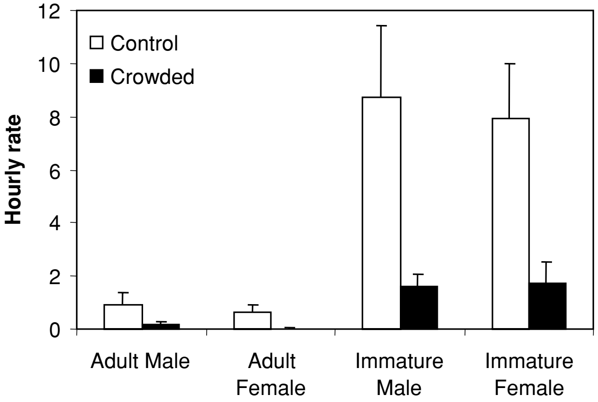


Fig. 4. Mean + SEM hourly rate of play bouts. Data are separated for each age and sex class per condition. There was significantly less play in the crowded condition than the control with the greatest drop in frequency in juvenile males.

The overall rate of grooming (Fig. 5) decreased significantly during crowding ($F_{1,34} = 20.75, p < 0.001$) and the grooming rate of adults dropped more dramatically than that of immature capuchins, as indicated by a significant interaction between age and condition ($F_{1,34} = 13.65, p = 0.001$). Also, there are significant results for sex, age, and the interaction of the two, such that the sex difference is not significant for immature monkeys but it is for

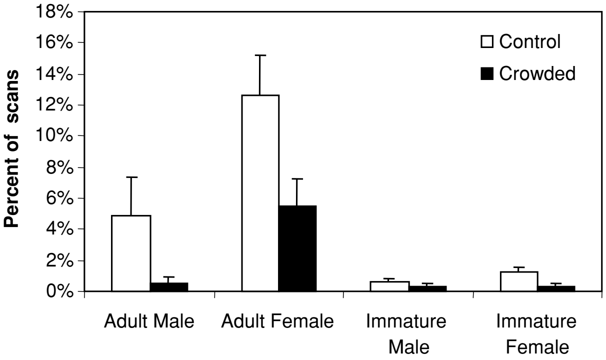


Fig. 5. Mean + SEM of social grooming rates in control and crowded conditions. Data are separated for each age and sex class per condition. The percentage of samples that involved social grooming significantly decreased in all age and sex categories under the crowded condition.

adults (age: $F_{1,34} = 18.83$, $p < 0.01$; sex: $F_{1,34} = 7.59$, $p = 0.009$; interaction between age and sex: $F_{1,34} = 6.10$; $p = 0.019$; interaction contrast: $t_{34} = 0.712$, NS). There is no significant interaction for age, sex, and condition or sex and condition.

Contact sitting showed a nonsignificant drop during crowded conditions ($F_{1,34} = 8.56$, $p = 0.072$), with no significant difference in age and sex categories, no significant interaction between age or sex and condition, and no significant 3-way interaction (age: $F_{1,34} = 0.54$, NS; sex: $F_{1,34} = 2.91$, NS).

Self-Grooming

The hourly rates of self-grooming for each age/sex class under both crowded and control conditions are in Fig. 6. Generally, adults groomed themselves more than immature individuals did and males did so more than females did (age: $F_{1,34} = 15.83$, $p < 0.001$; sex: $F_{1,34} = 4.83$, $p = 0.035$). Self-grooming was the one behavior to increase significantly under crowding ($F_{1,34} = 18.28$, $p < 0.001$). There is also a significant interaction between condition and age ($F_{1,34} = 4.52$, $p = 0.041$) such that adults increased their rate of self-grooming more than immatures ($t_{34} = 2.24$, $p = 0.025$). Condition and sex interacted significantly ($F_{1,34} = 13.47$, $p = 0.001$), showing that males were more affected by the crowded condition than females were ($t_{34} = 3.88$, $p < 0.005$). There is no significant 3-way interaction between age, sex, and condition.

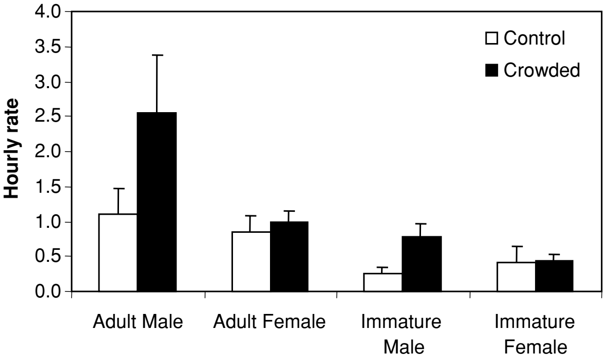


Fig. 6. Mean + SEM percentage of samples in which adult males, adult females, juvenile males, and juvenile females self-groomed during control and crowded conditions. Rates of self-grooming increased significantly during the crowded condition, with adult males showing the greatest increase.

DISCUSSION

The density aggression model clearly does not account for the observed response in capuchins because it would predict increased aggression under crowding. However, we found that there was no increase in any form of aggression under crowding. Moreover, intense aggression decreased under crowding, supporting the view that primates successfully cope with high-density situations.

The results may seem counterintuitive because they show that capuchins crowded together temporarily in a small space actually spend less time in social interactions than when in larger enclosures. The spacing response to acute crowding, together with the reduction in intense aggression, appears to be an inhibition strategy similar to that in chimpanzees (Aureli and de Waal, 1997). Like chimpanzees, capuchins decreased affiliative as well as intensely aggressive behavior in crowded conditions. Though different from coping strategies as originally conceptualized (de Waal, 1989a), the inhibition strategy appears to limit aggression during short-term crowding. Chimpanzees and capuchins share many behavioral traits, including a high degree of social tolerance and cooperation (Boesch, 1994; Kauffman *et al*., 2004; Rose, 1997; Watts and Mitani, 2001). The high tolerance level may explain why neither species increases its rate of intense aggression in short-term crowding. The same social behaviors that allow capuchins and chimpanzees to cooperate in normal conditions allow them to reduce aggression successfully in crowded situations.

In terms of mild aggression, our capuchins fall somewhere in between the patterns seen in chimpanzee and macaque crowding studies. Unlike chimpanzees, capuchins did not decrease their rate of mildly aggressive encounters (Aureli and de Waal, 1997), nor did they increase their rates of mild aggression as is typical of macaques (Judge and de Waal, 1993); instead, they showed no significant change in rates of mild aggression. There are two possible explanations for the finding.

First, both the experimental and control conditions gave the capuchins less space than typically provided. Had we given the capuchins full access to the enclosure in the control condition, we may have seen a decrease in mild aggression. A second possibility for our results is that the period of crowding was too brief for the capuchins to adjust fully to the condition. Most short-term crowding studies allow subjects to habituate for at $\geq$1 h (Aureli and de Waal, 1997; Judge, 2000; Judge and de Waal, 1993), but we crowded them for only 30 minutes before data collection. A longer adjustment period might have resulted in a reduction of mild aggression as well as intense aggression. We consider the explanation that the capuchins may have responded to the novelty of the crowded condition rather than the reduction of space unlikely because we collected the crowding data over numerous occasions, thereby greatly reducing the novelty of the situation.

In addition to the significant results of our experimental manipulation, we also found significant differences between age and sex classes. Age and sex differences are selectively advantageous; male capuchins are considerably larger than females and equipped with large canine teeth (Freese and Oppenheimer, 1981), making for greater physical risk during aggressive encounters. Females and juveniles would not have the same associated cost as adult males. Risk evaluation may explain why adult females and juveniles engaged in intensely aggressive encounters in the crowded condition whereas adult males did not have a single intensely aggressive encounter under this condition. The explanation could also account for immature females having a high rate of intense aggression during the control condition. Young females are less likely to seriously injure each other because of their smaller canines and body size.

The potentially greater risk of aggression to males may also explain the sex difference in the rate of self-grooming. Males self-groom more than females in the same age class. Maestripieri *et al.* (1992) argue that self-grooming is one of many displacement behaviors that can be used to infer a state of anxiety, which relates to the causation of displacement behavior. Functionally, displacement behavior may have a self-calming effect. In the same way that grooming reduces stress and anxiety in the recipient (Aureli *et al.*, 1999; O'Brien, 1993b), self-grooming may reduce stress and anxiety in the self-groomer.

Allogrooming may be more effective in reducing tension. Taylor (2002) has argued for a sex difference in the tendency. Seeking social support in response to stress seems typical of female primates, including humans. Given the alternative stress-reducing behaviors, it is interesting that the female capuchins increased allogrooming under crowded conditions whereas the males increased auto grooming.

Though recent short-term crowding studies, including ours, have revealed specific differences in response to crowded conditions, a general pattern of social inhibition is evident (Aureli and de Waal, 1997; Aureli *et al.*, 1995; Judge and de Waal, 1993). The scientific literature no longer supports notions of a direct relationship between crowding and aggression, though they are still widely held. Now that we know increased spatial density does not necessarily correlate with increased aggression, we need more studies on a greater variety of genera to understand how specific characteristics mediate the crowding response. The success with which various primate species limit aggression under stressful conditions seems to vary with the degree of social tolerance, conciliatory tendency, and cognitive ability of the species, but to determine what role each of these factors plays, researchers need to employ a much broader cross-species perspective.

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