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SHORT COMMUNICATION

Sex Differences in Food Acquisition and Aggression in Captive Common Marmosets (*Callithrix jacchus*)

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ABSTRACT. Competition for food within the social group has been postulated as an important factor affecting primate social organization. This study examined how factors such as sex, aggression, dispersion of food, and amount of difficulty involved in obtaining food affect the distribution of food in common marmoset (*Callithrix jacchus*) social groups. Mated pairs of adult *C. jacchus* were presented with food that was either dispersed or concentrated, and either difficult or easy to obtain. The number of food pieces obtained, aggressive displays, incidents of physical aggression, and amount of time spent searching for food were recorded for each animal. Neither dispersion nor difficulty in obtaining food had significant effects on the distribution of food or any of the other behaviors examined. The primary factors affecting food distribution were aggression and amount of time spent searching. Females obtained more food than males in all situations because they were more aggressive and apparently more motivated to search for food than were males.

Key Words: Aggression; Sex; Food; Foraging; *Callithrix jacchus*.

INTRODUCTION

Intraspecific competition for food is a topic of great interest to both ethologists and ecologists. Intraspecific, especially intra-group, food competition is of particular interest in primates because it has long been postulated as an important determinant of primate social organization (e.g. EISENBERG et al., 1972; CLUTTON-BROCK & HARVEY, 1976; JANSON, 1988). Furthermore, intra-group food competition has proven to be much more intense than inter-group competition in some species (JANSON, 1985; VAN SCHAIK & VAN NOORDWIJK, 1988).

For species in which group members compete for food, the degree of dispersion of food sources and the amount of difficulty (i.e. searching, manipulation) involved in obtaining the food are likely to have significant effects on the amount of food obtained by each group member and the amount of food-related aggression. Groups feeding on a dispersed food source are expected to show less aggression and a more equitable distribution of food amongst group members than groups feeding on a concentrated food source (DAVIES & HOUSTON, 1978; MAYNARD SMITH, 1982). Such behavior has been found in a number of primate species (e.g. WRANGHAM, 1974; SOUTHWICK et al., 1976), and has been suggested as a rule for primates in general (OATES, 1986). Increasing the amount of difficulty involved in obtaining food has also been found to decrease aggression and equalize the amount of food obtained by each group member (CLUTTON-BROCK & HARVEY, 1976; MARKOWITZ, 1982; BLOOMSTRAND et al., 1986).

Common marmosets (*Callithrix jacchus*, Family Callitrichidae) live in groups of 3–13 animals and are native to edge and savanna-forests in eastern Brazil (HERSHKOVITZ, 1977; MAIER et al., 1982; STEVENSON & RYLANDS, 1988). Adult body size is not sexually dimorphic, and ranges from approximately 270 to 390g (EPPLE, 1970; HERSHKOVITZ, 1977). *C. jacchus* is ideal for the study of intra-group food competition, because wild *C. jacchus* encounter a variety of feeding conditions, and because captive *C. jacchus* have an unequal distribution of food within the social group (TARDIF & RICHTER, 1981).

Natural populations of *C. jacchus* experience a variety of feeding situations. Some foods (e.g. insects, fruit) are relatively dispersed, and groups apparently split up to forage for them (MAIER et al., 1982). There is probably little direct competition between individuals for these foods. However, plant exudates such as gum and sap are a major component of the diet, and exudate trees are a more concentrated, renewable food source (FONSECA & LACHER, 1984; SCANLON et al., 1989; RYLANDS & DE FARIA, 1993). Since a group of *C. jacchus* focuses on just a few exudate trees within its home range, and usually visits them as a group, the opportunity for some individuals to aggressively defend food may exist in this case (LACHER et al., 1980; MAIER et al., 1982; SCANLON et al., 1989).

When captive groups of *C. jacchus* are offered limited amounts of a preferred food item, there are differences in the amount consumed in relation to sex and age class (TARDIF & RICHTER, 1981). Adult females usually consume the greatest portion of the food, followed by juveniles, and then adult males. Furthermore, adult females frequently defend food, particularly against the adult male (TARDIF & RICHTER, 1981). However, TARDIF and RICHTER's (1981) study used food which was concentrated and easily obtained. Increasing the dispersion or the amount of difficulty involved in obtaining food could equalize the sex differences in aggression and food consumption seen in TARDIF and RICHTER's study. The present study examined the patterns of aggression and food consumption in mated pairs of *C. jacchus* presented with a variety of feeding situations.

METHODS

The experimental subjects were nine mated pairs of adult *C. jacchus* housed at the Oak Ridge Associated Universities Marmoset Research Center in Oak Ridge, Tennessee. To ensure that any relationship (e.g. pair bond) between the animals was well established, all pairs had been housed together for at least five months. None of the pairs had offspring living in the cage with them. I excluded females which were lactating or noticeably pregnant, since I expected that their hunger levels might differ from those of other females. However, after completion of the study, it was discovered that seven of the nine females had been in early stages of pregnancy during the study.

The subject pairs were housed in 0.9×0.9×1.5m wire mesh cages (CLAPP & TARDIF, 1985). Between their regularly scheduled feedings, half-pieces of raisins, which are a familiar and highly preferred food item (TARDIF, pers. comm.), were presented to the study animals in the following feeding configurations:

Concentrated and easy to obtain: A 12.5cm diameter semicircular metal food cup containing eight raisin pieces was hung in the animals' cage. This is similar to the manner in which food is normally presented.

Concentrated and difficult to obtain: A food cup containing eight raisin pieces buried under 100cc of cornhusks chopped to the consistency of sawdust was hung in the animals' cage.

Dispersed and easy to obtain: Four food cups, each containing two raisin pieces, were hung in the cage. The cups were arranged in a square pattern on the wall of the cage with a distance of 40–44cm between each cup.

Dispersed and difficult to obtain: Four food cups, each containing two raisin pieces buried under 50cc of chopped cornhusks, were hung in the same pattern as described above.

Prior to the beginning of testing, each pair of animals experienced two practice sessions with the dispersed and difficult configuration. Observations indicated that upon conclusion of these sessions, all animals were able to find the raisins buried in the chopped cornhusk.

Each pair of animals experienced only one test per day, and received three replications of each of the four feeding configurations. The order of the tests and the time at which each test was given were randomized. Each test lasted until 1 min after the eighth raisin was obtained, or for a maximum of 20 min.

All observations were made from a blind. For each test, the number of raisin pieces consumed, aggressive displays, and acts of physical aggression, as well as the amount of test time spent searching for food was recorded for each animal (Table 1). Since tests involving the "difficult" feeding configurations usually lasted longer than "easy" tests, I statistically examined both the number and rate of performance (per minute) of each behavior to correct for effects of test length.

Table 1. Definitions of recorded behaviors.*

Behavior	Definition
Aggressive display	Ear tuft flicking, presenting, staring, piloerection, arch-walking, frowning, or producing the erh-erh (cackle) vocalization
Physical aggression	Any attempt to attack, chase, cuff, bite, or scratch another individual
Searching	Scanning the inside of a food cup, or using the hands to search or dig through chopped cornhusk material

*Based on STEVENSON and POOLE (1976), LIPP (1978), and STEVENSON and RYLANDS (1988).

I used Wilcoxon Rank Sum tests to determine whether pregnant and nonpregnant females differed in any of the recorded behaviors. Since no significant ($p \leq .05$) differences were found, pairs with pregnant and nonpregnant females were pooled for the remainder of the analyses.

I used two-way repeated measures ANOVA to determine whether the four feeding configurations had a significant effect on the total number and rate of aggressive displays, and the total number and rate of acts of physical aggression.

The remaining analyses focused on the differences between the male and female of a pair because of the competitive nature of the testing situation. If we hypothesize that the amount of aggression an animal exhibits affects the amount of food it obtains, we must examine the relative amounts of aggression and food consumption within each pair, because a particular animal could be very aggressive, but not obtain a large proportion of the food if its mate is even more aggressive.

I performed paired *t*-tests to determine whether females differed from males overall, as well as within each of the four test types, for the following behaviors: number of raisin pieces consumed, number and rate of aggressive displays, number and rate of acts of physical aggression, amount of time spent searching, and percent of time spent searching. I used two-way

repeated measures ANOVA to determine whether the magnitude of the difference between females and males differed across the four feeding configurations for these same behaviors.

Since weight and length of pairing are likely to affect the distribution of food and levels of aggression within pairs, I examined whether these factors were correlated. To examine whether aggression or searching behavior affected the amount of food obtained, I also examined the data for correlation between pairs of these variables. Since ANOVA results indicated that there were no significant differences between feeding configurations for most of the behaviors, overall differences between the male and female of each pair were used for the correlation analyses. The overall difference between the male and female of a pair was defined as the female's value for a variable (i.e. average number of times she performed a particular behavior) minus the male's value for that variable. The difference between male and female values was chosen for consistency, since the paired *t*-tests used to examine sex differences in behavior also focus on the difference between male and female values. Since aggressive displays and physical aggression did not occur frequently, they were pooled for each animal for these analyses and referred to as aggressive acts. I examined the data for correlation between the following pairs of variables: (1) difference in the weight of animals in a pair and difference in the amount of food consumed; (2) difference in number of aggressive acts and difference in amount of food consumed; (3) difference in number of aggressive acts and difference in amount of time spent searching; (4) difference in the amount of time spent searching and difference in amount of food; (5) length of pairing and difference in amount of food; (6) length of pairing and difference in number of aggressive acts; and (7) length of pairing and total number of aggressive acts.

RESULTS

Paired *t*-tests showed that females obtained significantly more food than males overall, as well as within each of the four feeding configurations (Table 2). Females performed significantly more aggressive displays overall, as well as during all of the feeding configurations except dispersed and easy. Females performed significantly more acts of physical aggression overall, but since this was a fairly rare behavior, there was insufficient evidence to make conclusions about sex differences within any of the individual treatments. Males and females did not differ in the amount of test time they spent searching, except during dispersed and difficult feedings, in which females searched significantly more than males. Since results for rates (per minute) of all behaviors showed patterns very similar to those for number of occurrences, results for rates of behaviors will not be discussed further. The detailed data and results of all statistical tests may be found in MICHELS (1990).

Two-way repeated measures ANOVA indicated that with few exceptions, neither dispersion of the food nor difficulty in obtaining food had a significant effect on the total number of occurrences of any recorded behaviors, the magnitude of difference between males and females in amount of food obtained, or the magnitude of difference between males and females in the number of occurrences of any recorded behaviors. However, the difference between males and females in amount of time spent searching was affected by the amount of difficulty involved in obtaining food. Paired *t*-tests showed that this was because females and males searched for similar amounts of time during dispersed and easy feedings, but females searched more than males during dispersed and difficult feedings ($p=.0182$). There was no significant difference between concentrated and easy and concentrated and difficult feedings in the amount by which males and females differed in amount of time spent searching.

Table 2. Average number of occurrences per test of various behaviors.

	Female	Male
Amount of food (No. of pieces)		
Overall	4.8	2.5*
Concentrated and easy	4.7	2.4*
Concentrated and difficult	5.4	2.1*
Dispersed and easy	4.2	2.9*
Dispersed and difficult	5.0	2.6*
Aggressive display (No. of occurrences)		
Overall	.37	.06*
Concentrated and easy	.48	.11*
Concentrated and difficult	.48	.11*
Dispersed and easy	.15	0
Dispersed and difficult	.37	0*
Physical aggression (No. of occurrences)		
Overall	.20	.05*
Concentrated and easy	.11	.04
Concentrated and difficult	.26	.07
Dispersed and easy	.07	0
Dispersed and difficult	.37	.07
Amount of searching (seconds)		
Overall	118.0	74.6
Concentrated and easy	1.3	2.4
Concentrated and difficult	228.1	151.4
Dispersed and easy	4.1	6.4
Dispersed and difficult	238.3	138.3*

*Significant differences between females and males ($p<.05$).

There were no significant effects of weight or length of pairing on any of the behaviors examined. Significant correlations were found between (1) the difference in the number of aggressive acts and the difference in amount of food consumed ($r=.8123$, $p=.0078$); (2) the difference in the number of aggressive acts and difference in amount of time spent searching ($r=.7876$, $p=.0017$); and (3) the difference in amount of time spent searching and difference in amount of food consumed ($r=.7260$, $p=.0268$). Since the difference in number of aggressive acts, difference in amount of time spent searching, and difference in amount of food consumed were all correlated, partial correlations were performed for each pair of these variables while holding the third constant. The partial correlations between (1) difference in number of aggressive acts and difference in amount of food consumed ($r=.5676$); (2) difference in the number of aggressive acts and difference in amount of time spent searching ($r=.4933$); and (3) difference in amount of time spent searching and difference in amount of food consumed ($r=.2399$) were all found to be nonsignificant ($p>.05$). Thus, the correlation between any two of these variables is partially (but not entirely) due to the third variable.

DISCUSSION

These results indicate marked differences between male and female *C. jacchus* in food acquisition and food-related aggression. Females obtained more food than males, and were more aggressive in defense of food than males, regardless of how the food was presented.

In *C. jacchus*, neither dispersion of food nor difficulty in obtaining food had significant effects on aggression or distribution of food between animals. This disagrees with studies that found these factors to be quite important to food competition in other primates (e.g. WRANGHAM, 1974; SOUTHWICK et al., 1976; BLOOMSTRAND et al., 1986). Why *C. jacchus* responded differently than other primates is unclear. However, it is important to note that the primates in these other studies are behaviorally different from *C. jacchus* in many ways (e.g. mating system, social organization, infant care), so it is not unexpected that they would differ in feeding behavior as well. It is possible that the marked sex differences in feeding behavior in *C. jacchus* simply override the effects that dispersion and difficulty produce in other species.

One hypothesis to explain the sex differences found in *C. jacchus* feeding behavior is that females had a stronger preference for raisins or were not satiated as quickly as males. However, the total amount of food presented (four raisins) was quite small, and it is unlikely that any of the animals became satiated. Furthermore, TARDIF and RICHTER (1981) found no evidence for sex differences in preference or amount of consumption during feedings of isolated *C. jacchus*. Relative weight of the animals and the length of time they had been paired could also affect feeding and aggressive behaviors. However, statistical analyses indicated no correlation between these factors and any of the behaviors measured.

Several correlated variables provide the best information as to what affects the distribution of food in mated pairs of *C. jacchus*. The correlation between difference in amount of aggression and difference in amount of food obtained indicates that animals which were much more aggressive than their mates obtained much more food than their mates, while those which were only slightly more aggressive obtained only slightly more food. This same relationship was found between aggression and searching, as well as between searching and obtaining food. Thus, both aggression and searching are closely related to which animal of a pair obtains more food. It is possible that the relationship between searching and obtaining food was simply a result of aggression. In other words, more aggressive animals may have had greater access to the food cups, and thus were able to search more and obtain more food. Partial correlation analyses indicated it was not clear whether searching had an effect on food consumption independent of aggression. However, females searched significantly more than males only during dispersed and difficult feedings, but the difference between females and males in amount of aggression was no higher during these feedings than any of the others. Thus, females obtained more food than males not only because they were more aggressive, but because (in some situations) they also searched more than males did.

Females might have a higher motivation to search for food if it is true that food intake is more directly related to fitness in female primates than in males (WRANGHAM, 1979; VAN SCHAIK & VAN NOORDWIJK, 1988). It is certainly logical that pregnant or lactating females would have a higher motivation to search, and since *C. jacchus* reproduce aseasonally, it is likely that healthy, mated females are either pregnant or lactating much of the time (EPPLE, 1970; HERSHKOVITZ, 1977). Thus, female *C. jacchus* may have evolved a stronger tendency to search for food than males even when not pregnant or lactating. This may explain why no behavioral differences were found between pregnant and nonpregnant females. Females spend more time on feeding and foraging behavior than males in many other species (e.g. CLUTTON-BROCK, 1973; CHIVERS, 1977; WASER, 1977).

These results are of importance to captive breeding of *C. jacchus*, since they indicate that diet composition should not be based on the assumption that group members consume equal amounts of each food type provided. In addition, the difficult feeding configuration in this study provides a simple and inexpensive foraging device which could be used for environmental enrichment.

In summary, dispersion of food and amount of difficulty involved in obtaining food had little effect on food distribution in *C. jacchus*. Females were able to obtain more food than males regardless of the manner in which the food was presented because they were more aggressive and more motivated to search for food than were males.

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