

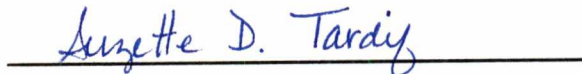
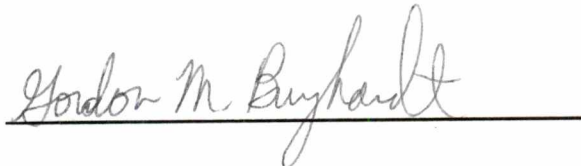
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FOOD COMPETITION IN PAIRS OF COMMON MARMOSETS (CALLITHRIX
JACCHUS)

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Anne Michels

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ABSTRACT

This study examined the effects of dispersal of food and amount of difficulty involved in obtaining food on food competition in common marmosets (Callithrix jacchus). Mated pairs of C. jacchus were presented with food in four different configurations, each of which involved food that was either dispersed or concentrated, and either difficult or easy to obtain. Analysis of each animal's food consumption, as well as searching and aggressive behaviors, showed that both dispersal and amount of difficulty in obtaining food had little effect on food competition. There were significant effects of both aggression and amount of time spent searching on amount of food consumed. Females obtained more food than males in all situations, apparently because they were more aggressive and more motivated to search for food than were males.

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CHAPTER 1

INTRODUCTION

Intraspecific competition for food is a topic of great interest to both ethologists and ecologists. Intraspecific, and especially intra-group, food competition are of particular interest in primates for several reasons. Intra-group food competition has long been postulated as an important determinant of primate social organization (e.g. Denham 1971; Eisenberg et al. 1972; Clutton-Brock and Harvey 1976; Janson 1988; Janson and van Schaik 1988). Furthermore, intra-group food competition has proven to be much more intense than inter-group competition in species such as brown capuchins (Cebus apella) and long-tailed macaques (Macaca fascicularis) (Janson 1985; van Schaik and van Noordwijk 1988).

Common marmosets (Callithrix jacchus), members of the family Callitrichidae, are native to edge and savannah-forests in eastern Brazil (Hershkovitz 1977; Wolfheim 1983; Goldizen 1986). Their adult body size ranges from approximately 270 to 390g, and they are not sexually dimorphic in this respect (Epplé 1970;

Hershkovitz 1977; Cicmanec 1978). The common marmoset is a convenient animal in which to study intra-group food competition because they are relatively easily housed and bred, and have been shown to have an unequal distribution of food within the social group (Tardif and Richter 1981).

Tardif and Richter (1981) found that when groups of common marmosets are offered a preferred food item, there are differences in the amount consumed in relation to sex and age class. Adult females usually consume the greatest portion of the food, followed by juveniles, and then by adult males (Tardif and Richter 1981). Furthermore, adult females frequently defend food, particularly against the adult male (Tardif and Richter 1981). In the wild, however, it is unlikely that such a concentrated food source as was presented in Tardif and Richter's study would ever be encountered.

Natural populations of C. jacchus experience a variety of feeding situations. Some foods, such as insects, other small animals, and, to a lesser degree, fruit, are usually dispersed, and individuals apparently split up to forage for them (Maier et al. 1982; Terborgh 1983). There is probably little direct competition among individuals for these foods (Maier et al. 1982). However, plant exudates such as gum and sap are also a large part

of the common marmoset's diet, and exudate trees are a more concentrated, renewable food source (Fonseca and Lacher 1984; Lacher et al. 1980, 1984; Maier et al. 1982). Since a group of C. jacchus usually concentrates on just a few exudate trees within its home range, and it usually visits them as a group, the opportunity for some individuals to aggressively defend food resources may exist in this case (Lacher et al. 1980, 1984; Maier et al. 1982). Whether this actually occurs in nature is unclear. Lacher et al. (1980) observed that only one C. jacchus fed from an exudate tree at a time, and that the most dominant animals apparently fed first, but others have observed members of small groups feeding on a tree simultaneously, although they did appear to space themselves out along the tree (Coimbra-Filho and Mittermeier 1978; Maier et al. 1982).

This diversity in the dispersion of foods in the diet of C. jacchus may lead to variation in the intensity of competition within a group. In order to investigate whether this flexibility exists, this study experimentally examined the behavior of C. jacchus in a variety of feeding situations.

Predictions

Feeding situations can be classified according to the spatial concentration of food and the amount of difficulty (i.e. searching) involved in obtaining it. In this study, pairs of C. jacchus were presented with food in four different configurations: food which is concentrated and easy to obtain, concentrated and difficult to obtain, dispersed and easy to obtain, and dispersed and difficult to obtain (for description of these treatments, see Chapter 2).

1. When food is concentrated and easy to obtain, a high amount of aggression and a large discrepancy in the amount consumed by each animal is expected, as was found by Tardif and Richter (1981). Increased intragroup aggression while feeding on concentrated food sources has been observed in other primates, such as indris, Indri indri (Pollock 1977), rhesus macaques, Macaca mulatta (Southwick 1967; Southwick et al. 1976), japanese macaques, Macaca fuscata (Mori 1977), mangabeys, Cercocebus albigena (Chalmers 1968), chimpanzees, Pan troglodytes (Wrangham 1974), and gorillas, Gorilla gorilla (Fossey and Harcourt 1977), and has been suggested as a rule for primates in general (Oates 1986). Such behavior has also been observed in birds (Zahavi

1978) and fish (Magnuson 1962; Rubenstein 1981).

2. When food is concentrated and difficult to obtain, a large discrepancy in the amount of food obtained by each individual is expected. This is consistent with the findings of Bloomstrand et al. (1986) with captive chimpanzees, and Markowitz (1982) with captive polar bears. A fairly high level of aggression is expected, as was found by Markowitz (1982). Although Bloomstrand et al. (1986) found no significant change in group levels of aggression upon introduction of a complex feeding mechanism, some individuals displayed increased levels of aggression.

3. When food is dispersed and easy to obtain, a decreased amount of aggression and a nearly equal distribution of the food is predicted. This is consistent with Tardif and Richter's (1981) findings for the cotton-top tamarin, Saguinus oedipus, as well as studies by Magnuson (1962), Southwick (1967), Chalmers (1968), Wrangham (1974), Southwick et al. (1976), Fossey and Harcourt (1977), Mori (1977), Pollock (1977), Zahavi (1978), Rubenstein (1981), and Oates (1986). In addition, this agrees with the predictions of game theory (Maynard Smith 1982) and Davies and Houston (1978).

4. When food is dispersed and difficult to obtain, the distribution of the food is expected to be the

closest to equal. The amount of aggression should be at its lowest, since the animals are expected to concentrate on obtaining the food. This is in agreement with Novak's findings for captive Rhesus macaques (pers. comm.).

The chapters that follow explain the experimental procedures and statistical analyses used, detail the results, and discuss the findings in relation to other studies as well as future research in this area.

CHAPTER 2

METHODS

Subjects, Housing and Care

Research was conducted at the Oak Ridge Associated Universities Marmoset Research Center. The subjects were ten mated pairs of captive born Callithrix jacchus (Table 1). One animal died shortly after the beginning of the study, and all data for this pair were discarded. The main criterion used in selecting the subjects was length of pairing, and all pairs used in the study had been housed together for at least five months. This was to ensure that any relationship (e.g. pair bond) formed between the animals would be well established before the beginning of the study. Pairs which had previous offspring living with them were excluded, because provisioning of offspring by parents of both sexes would make it difficult to score which parent was obtaining a greater portion of the food. Females which were pregnant or lactating were also excluded, since it was expected that their hunger levels might differ from those of other females. Unfortunately, after the completion of the feeding tests, it was discovered that seven of the

Table 1: Summary of subject characteristics

Pair #	Sex	Animal number	Age	Weight	Length of pairing
1B*	F	5285	8.8yr.	340g	5.5 months
	M	5252	8.3	330	
4A*	F	5281	8.5	310	42.0
	M	5280	8.0	340	
10A*	F	5291	?	280	4.5
	M	5258	7.5	360	
13B*	F	5249	2.5	340	13.0
	M	5248	2.5	330	
15A	F	5397	3.3	330	21.0
	M	5398	6.1	340	
15B*	F	5401	4.4	340	40.0
	M	5402	5.2	360	
24A*	F	5403	3.0	360	20.0
	M	5404	2.8	370	
30A	F	5389	3.6	310	26.0
	M	5390	3.5	320	
34B*	F	5213	4.5	340	20.4
	M	5212	4.5	310	

* pairs in which female was pregnant during study

nine females had been in early stages of pregnancy during the study. Thus, reproductive state was controlled for during statistical analyses.

The subject pairs were housed in the marmoset breeding facility in 0.9 x 0.9 x 1.5m wire mesh cages suspended 0.6m from the floor (Clapp and Tardif 1985). Each cage contains an 18 x 20 x 41cm metal nest box. The temperature in the breeding facility was maintained at approximately 24-27°C during the study (Tardif pers. comm.).

The regular feeding schedule of the animals at the Marmoset Research Center includes an ad libitum feeding of a mixture of high protein monkey chow, bananas, applesauce, and supplemental vitamins and minerals at approximately 0730hr (Clapp and Tardif 1985). A second feeding, at 1400hr, consists of canned marmoset diet plus one or more of the following: grapes, peanuts, marshmallows, sweet potatoes, lettuce, and mealworms. This schedule was maintained for the study animals.

Experimental Design and Procedures

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 representing the hypotheses previously

posed:

1. **Concentrated and Easy to Obtain.** Eight raisin pieces in a 12.5cm diameter semicircular metal food cup were placed inside the animals' cage. This is similar to the manner in which the animals' food is normally presented.

2. **Concentrated and Difficult to Obtain.** A single food cup containing eight raisin pieces buried under 100cc of a sawdust-like chopped cornhusk material was placed inside the animals' cage.

3. **Dispersed and Easy to Obtain.** Four food cups, each containing two raisin pieces, were hung inside the animals' cage. The cups were arranged in a square configuration on the front wall of the cage with a distance of 40-44cm between each cup.

4. **Dispersed and Difficult to Obtain.** Four food cups, each containing two raisin pieces buried under 50cc of a sawdust-like chopped cornhusk material, were hung in the same configuration as described above.

Preliminary tests showed that the average amount of time spent searching during "difficult" tests was approximately nineteen times the average amount of time spent searching during tests which were categorized as "easy".

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. The experimental tests were conducted between 0930 and 1400hr, the period during which maximum response was observed during preliminary tests. The tests began on November 4, 1989, and ended on December 6, 1989. The total length of the testing period was kept as short as possible in order to minimize the chances of animals becoming pregnant during the testing period. Each pair of animals experienced only one test per day. Each pair received three replications of each of the four different feeding configurations, and these replicates were scheduled such that one occurred in the morning (0930-1100hr), one around noon (1100-1230), and one in the afternoon (1230-1400). The order of presentation in which each pair received the tests was randomized. The tests lasted until one minute after the last raisin was obtained, or for a maximum of twenty minutes for each trial.

Data were recorded using a hand-held Hewlett Packard 71B microcomputer programmed to function as an event recorder. For each trial, the number of raisin pieces consumed, the number and rate of aggressive displays, the

number and rate of acts of physical aggression, and the amount of time spent searching for food were recorded for each animal. The number of times and rate at which each animal displaced another from a food cup was also recorded (see Table 2 for definitions of behaviors). After completion of the study, all animals were weighed.

Statistical Analyses

Wilcoxon Rank Sum tests (Bhattacharyya and Johnson 1977) were used to determine whether pregnant and nonpregnant females differed in a) the amount of food consumed, b) the magnitude by which they differed from their mates in amount of food consumed, c) the number of times they displaced their mates, d) the magnitude with which they differed from their mates in number of displacements performed, e) the number of aggressive displays and acts of physical aggression performed, f) the magnitude by which they differed from their mates in number of aggressive displays and acts of physical aggression performed, g) the amount of time spent searching, and h) the magnitude by which they differed from their mates in the amount of time spent searching. Since no significant differences were found, pairs with pregnant and nonpregnant females were pooled for the

Table 2: Definitions of recorded behaviors

Behavior	Definition
aggressive display	ear tuft flicking, presenting, staring, piloerection, arch-walking, or frowning. Aggressive vocalizations such as the "erh-erh" vocalization (Stevenson and Poole 1976) were also recorded in this category, since displays were frequently accompanied by vocalizations, and vocalizations were almost always accompanied by displays.
physical aggression	any attempt to attack, chase, cuff, bite, or scratch another individual.
displacement	any occasion in which an animal leaves a food cup at the approach of another and is replaced at the food cup by the second individual was scored as a displacement for the second animal.
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 Harrison and Tardif 1988)

remainder of the analyses.

A repeated measures ANOVA was used to determine whether the four different testing conditions had a significant effect on the total (female plus male) number of displacements which occurred, the total rate of displacement, the total number of aggressive displays performed, the total rate of aggressive display, the total number of acts of physical aggression, and the total rate at which physical aggression occurred.

The remaining analyses focus on the differences between the male and female of a pair, rather than on the behavior of individual animals, because of the competitive nature of the testing situation. For example, if we hypothesize that the amount of aggression an animal performs 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 still more aggressive.

Repeated measures ANOVA was used to determine whether the magnitude of the difference between females and males differed across the four feeding configurations for the following behaviors: amount of food consumed,

number and rate of displacements performed, 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. Paired t-tests were performed 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 displacements performed, 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.

In order to determine whether other factors, such as weight or length of pairing, affected the distribution of food within pairs, the data were examined for correlation between the following pairs of variables: a) difference in the weight of animals in a pair (female's weight minus male's weight) and difference in the amount of food consumed (female's average food intake minus male's average), b) difference in number of aggressive acts (female's number of aggressive displays and acts of physical aggression minus male's) and difference in amount of food consumed, c) difference in number of aggressive acts and difference in amount of time spent searching, d) difference in number of aggressive acts and difference in percent of time spent searching, e)

difference in the amount of time spent searching and
difference in amount of food, f) difference in percent of
time spent searching and difference in amount of food, g)
length of pairing and difference in amount of food, h)
length of pairing and difference in number of aggressive
acts, and i) length of pairing and total number of
aggressive acts.

CHAPTER 3

RESULTS

A summary of the data can be found in Tables 3 and 4. For detailed lists of data for each behavior, see Tables A-1 through A-9, Appendix.

Data for pregnant and nonpregnant females did not differ significantly for any of the following behaviors: a) amount of food consumed ($Z=.7350$, $p=.4623$), b) magnitude by which they differed from their mates in amount of food consumed ($Z=.7319$, $p=.4642$), c) number of times they displaced their mates ($Z=-.2965$, $p=.7668$), d) magnitude by which they differed from their mates in number of displacements performed ($Z=1.025$, $p=.3055$), e) number of aggressive displays ($Z=1.181$, $p=.2376$) and acts of physical aggression ($Z=-.4608$, $p=.6450$), f) magnitude by which they differed from their mates in number of aggressive displays ($Z=1.667$, $p=.0956$) and acts of physical aggression ($Z=-.1495$, $p=.8811$), g) amount of time spent searching ($Z=1.318$, $p=.1887$), and h) magnitude by which they differed from their mates in amount of time spent searching ($Z=1.318$, $p=.1877$). Thus, data for pairs with pregnant and nonpregnant females were pooled for the remainder of the analyses.

Table 3: Average number of occurrences and average duration of various behaviors for females and males.

	Female	Male
<u>Amount of Food</u>		
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
<u>Displacement</u>		
Overall	.57	.67
Concentrated and Easy	.21	.07
Concentrated and Difficult	.69	.84
Dispersed and Easy	.19	.33
Dispersed and Difficult	1.11	1.40
<u>Aggressive Display</u>		
Overall	.37	.06
Concentrated and Easy	.48	.11
Concentrated and Difficult	.48	.11
Dispersed and Easy	.15	0
Dispersed and Difficult	.37	0
<u>Physical Aggression</u>		
Overall	.20	.05
Concentrated and Easy	.11	.04
Concentrated and Difficult	.26	.07
Dispersed and Easy	.07	0
Dispersed and Difficult	.37	.07
<u>Amount of Searching (seconds)</u>		
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

Table 4: Average rate of performance of various behaviors by females and males.

	Female	Male
<u>Rate of Displacement</u>		
Overall	.08	.08
Concentrated and Easy	.10	.02
Concentrated and Difficult	.05	.05
Dispersed and Easy	.06	.11
Dispersed and Difficult	.10	.14
<u>Rate of Aggressive Display</u>		
Overall	.08	.01
Concentrated and Easy	.16	.03
Concentrated and Difficult	.06	.01
Dispersed and Easy	.07	0
Dispersed and Difficult	.05	0
<u>Rate of Physical Aggression</u>		
Overall	.03	.01
Concentrated and Easy	.05	.01
Concentrated and Difficult	.02	.01
Dispersed and Easy	.03	0
Dispersed and Difficult	.03	.003
<u>Percent of Time Searching</u>		
Overall	18.4	12.1
Concentrated and Easy	.7	1.3
Concentrated and Difficult	29.9	19.2
Dispersed and Easy	3.0	3.3
Dispersed and Difficult	40.1	24.5

Neither dispersal of the food nor the amount of difficulty involved in obtaining food had a significant effect on the total (female plus male) number of aggressive displays performed, the total rate of aggressive display, the total number of acts of physical aggression, or the total rate of physical aggression (Table 5). The total number of displacements performed was significantly affected by both dispersal of the food and difficulty in obtaining food. Paired t-tests showed that although there was no significant difference in the number of displacements which occurred during concentrated and easy and dispersed and easy tests ($t=-1.515$, $p=.1682$), animals displaced each other significantly more times during dispersed and difficult than concentrated and difficult tests ($t=-2.311$, $p=.0496$), during concentrated and difficult than concentrated and easy tests ($t=-2.986$, $p=.0174$), and during dispersed and difficult than dispersed and easy tests ($t=-3.375$, $p=.0097$). However, these differences in the total number of displacements performed were apparently due to differences in the length of tests for the four treatments, since the total rate of displacement was not significantly affected by either dispersal or difficulty in obtaining food.

Table 5: Repeated measures ANOVA statistics for effects of dispersal of food and difficulty in obtaining food on total (female plus male) number of occurrences and total rate of various behaviors.

	F	p
<u>Displacement</u>		
Dispersal	6.60	.0332*
Difficulty	12.06	.0084**
Interaction	3.09	.1169
<u>Rate of Displacement</u>		
Dispersal	4.62	.0638
Difficulty	.87	.3792
Interaction	2.34	.1646
<u>Aggressive Display</u>		
Dispersal	3.20	.1115
Difficulty	.63	.4492
Interaction	1.06	.3330
<u>Rate of Aggressive Display</u>		
Dispersal	1.58	.2442
Difficulty	4.08	.0781
Interaction	1.40	.2705
<u>Physical Aggression</u>		
Dispersal	.01	.9180
Difficulty	1.92	.2035
Interaction	.23	.6463
<u>Rate of Physical Aggression</u>		
Dispersal	.17	.6914
Difficulty	.04	.5506
Interaction	.33	.5819

*significant at .05 level

**significant at .01 level

The magnitude of the difference between males and females in amount of food obtained was not significantly affected by dispersion of the food or the amount of difficulty involved in obtaining food (Table 6). Neither dispersal nor difficulty in obtaining food significantly affected the amount of difference between males and females in any of the following behaviors: number of displacements, rate of displacement, number of acts of physical aggression, and rate of physical aggression (Tables 6 and 7). Neither dispersion nor difficulty in obtaining food had a significant effect on the magnitude of the difference between males and females in the number of aggressive displays performed, but there was a significant interaction effect of these two factors. However, there were no significant effects of dispersion, difficulty in obtaining food, or an interaction between them on the difference between males and females in the rate at which aggressive displays were performed. The difference between males and females in amount of time spent searching was not significantly affected by dispersion, but 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

Table 6: Repeated measures ANOVA statistics for effects of dispersal of food and difficulty in obtaining food on the difference between females and males in average number of occurrences and average duration of various behaviors.

	F	p
<u>Amount of Food</u>		
Dispersal	1.61	.2406
Difficulty	.95	.3587
Interaction	.07	.7997
<u>Displacement</u>		
Dispersal	.59	.4661
Difficulty	1.67	.2320
Interaction	.18	.6803
<u>Aggressive Display</u>		
Dispersal	.55	.4799
Difficulty	1.21	.3026
Interaction	5.37	.0491*
<u>Physical Aggression</u>		
Dispersal	.28	.6121
Difficulty	1.49	.2570
Interaction	.16	.7020
<u>Amount of Searching</u>		
Dispersal	.80	.3978
Difficulty	5.41	.0485*
Interaction	.88	.3756

*significant at .05 level

**significant at .01 level

Table 7: Repeated measures ANOVA statistics for effects of dispersal of food and difficulty in obtaining food on the difference between females and males in average rate of various behaviors.

	F	p
<u>Rate of Displacement</u>		
Dispersal	2.08	.1877
Difficulty	1.87	.2089
Interaction	4.15	.0760
<u>Rate of Aggressive Display</u>		
Dispersal	.44	.5267
Difficulty	2.19	.1775
Interaction	.66	.4414
<u>Rate of Physical Aggression</u>		
Dispersal	.09	.7704
Difficulty	.34	.5780
Interaction	.08	.7886
<u>Percent of Time Searching</u>		
Dispersal	1.74	.2235
Difficulty	5.74	.0434*
Interaction	1.29	.2887

*significant at .05 level

**significant at .01 level

difficult feedings ($t=-2.956$, $p=.0182$); there was no significant difference in the amount by which males and females differed in this behavior between the concentrated and easy and concentrated and difficult configurations ($t=-1.681$, $p=.1312$). Similarly, the difference in the percent of time males and females spent searching was not affected by dispersion, but was significantly affected by difficulty in obtaining food. Again, this was due to a significantly larger difference between females and males during dispersed and difficult tests than dispersed and easy tests ($t=-3.184$, $p=.0129$). There was no significant difference between the concentrated and easy and concentrated and difficult tests in the difference in percent of time males and females spent searching ($t=-1.632$, $p=.1414$).

Females obtained significantly more food than males overall, as well as within each of the four feeding configurations (Table 8). Males and females did not differ significantly in the number of times they displaced each other, except during the concentrated and easy configuration, in which females displaced their mates more often than males. Results for the rate at which males and females displaced their mates showed the same pattern (Table 9). Females performed significantly more aggressive displays overall, as well as during all

Table 8: Paired t-test statistics for differences between females and males in average number of occurrences and average duration of various behaviors. (Degrees of freedom=8 for all tests).

	Mean	Std. Error	t	p
<u>Amount of Food</u>				
Overall	2.32	.493	4.683	.0008**
Concentrated & Easy	2.26	.894	2.529	.0177*
Concentrated & Difficult	3.26	1.169	2.788	.0118*
Dispersed & Easy	1.30	.454	2.859	.0106*
Dispersed & Difficult	2.48	.685	3.622	.0034**
<u>Displacement</u>				
Overall	-.11	.133	-.834	.4284
Concentrated & Easy	.15	.058	2.530	.0353*
Concentrated & Difficult	-.15	.158	-.928	.3807
Dispersed & Easy	-.15	.168	-.872	.4087
Dispersed & Difficult	-.30	.395	-.749	.4752
<u>Aggressive Display</u>				
Overall	.31	.093	3.384	.0048**
Concentrated & Easy	.37	.151	2.442	.0202*
Concentrated & Difficult	.37	.171	2.169	.0309*
Dispersed & Easy	.15	.098	1.512	.0845
Dispersed & Difficult	.37	.087	4.233	.0014**
<u>Physical Aggression</u>				
Overall	.16	.079	1.990	.0409*
Concentrated & Easy	.07	.121	.614	.2782
Concentrated & Difficult	.18	.158	1.170	.1378
Dispersed & Easy	.07	.049	1.512	.0845
Dispersed & Difficult	.30	.180	1.643	.0695
<u>Amount of Searching</u>				
Overall	43.32	7.777	2.162	.0626
Concentrated & Easy	-1.09	.601	-1.821	.1061
Concentrated & Difficult	76.71	46.020	1.667	.1341
Dispersed & Easy	-2.31	2.444	-.947	.3714
Dispersed & Difficult	99.93	36.091	2.769	.0243*

*significant at .05 level

**significant at .01 level

Table 9: Paired t-test statistics for differences between females and males in rates of behavior. (Degrees of freedom=8 for all tests).

	Mean	Std. Error	t	p
<u>Rate of Displacement</u>				
Overall	-.006	.032	-.177	.8637
Concentrated & Easy	.079	.026	3.093	.0148*
Concentrated & Difficult	-.007	.012	-.607	.5609
Dispersed & Easy	-.050	.070	-.712	.4969
Dispersed & Difficult	-.045	.058	-.782	.4565
<u>Rate of Aggressive Display</u>				
Overall	.074	.027	2.734	.0129*
Concentrated & Easy	.130	.066	1.967	.0424*
Concentrated & Difficult	.054	.035	1.560	.0787
Dispersed & Easy	.067	.050	1.341	.1083
Dispersed & Difficult	.043	.011	3.848	.0024**
<u>Rate of Physical Aggression</u>				
Overall	.023	.015	1.542	.0808
Concentrated & Easy	.031	.049	.622	.2757
Concentrated & Difficult	.007	.013	.552	.2980
Dispersed & Easy	.030	.024	1.251	.1231
Dispersed & Difficult	.024	.011	2.124	.0332*
<u>Percent of Time Searching</u>				
Overall	6.359	3.245	1.959	.0857
Concentrated & Easy	-.573	.386	-1.484	.1761
Concentrated & Difficult	10.711	6.830	1.568	.1555
Dispersed & Easy	-.314	1.602	-.196	.8493
Dispersed & Difficult	15.622	5.748	2.718	.0263*

*significant at .05 level

**significant at .01 level

of the feeding configurations except dispersed and easy. The rate of aggressive display was higher for females in all cases except the concentrated and difficult and dispersed and easy configurations. 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. There were no sex differences in the rate of physical aggression, except that females were more physically aggressive than males during the dispersed and difficult configuration. Males and females did not differ in the amount of time they spent searching, except during dispersed and difficult feedings, in which females searched significantly more than males. The sex differences in the percent of test time that animals spent searching showed the same pattern.

Since ANOVA results indicated that there were no significant differences between treatments for most of the behaviors, overall differences between the male and female of each pair were used for correlation analyses. No significant correlation was found between the difference in the weight of animals in a pair and difference in amount of food consumed ($r = -.1974$, $p = .6107$), the length of pairing and difference in amount

of food ($r=.5771$, $p=.1038$), length of pairing and difference in number of aggressive acts ($r=.2548$, $p=.5082$), and length of pairing and total number of aggressive acts ($r=-.2298$, $p=.5520$). The correlation between difference in the percent of time spent searching and difference in amount of food consumed was very close to significance ($r=.6543$, $p=.0559$). There were significant correlations between a) the difference in the number of aggressive acts and the difference in amount of food consumed ($r=.8123$, $p=.0078$) (Figure 1), b) the difference in the number of aggressive acts and difference in amount of time spent searching ($r=.7876$, $p=.0017$) (Figure 2), and c) the difference in amount of time spent searching and difference in amount of food consumed ($r=.7260$, $p=.0268$) (Figure 3). 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 a) difference in number of aggressive acts and difference in amount of food consumed ($r=.5676$), b) difference in the number of aggressive acts and difference in amount of time spent searching

($r=.4933$), and c) difference in amount of time spent searching and difference in amount of food consumed 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.

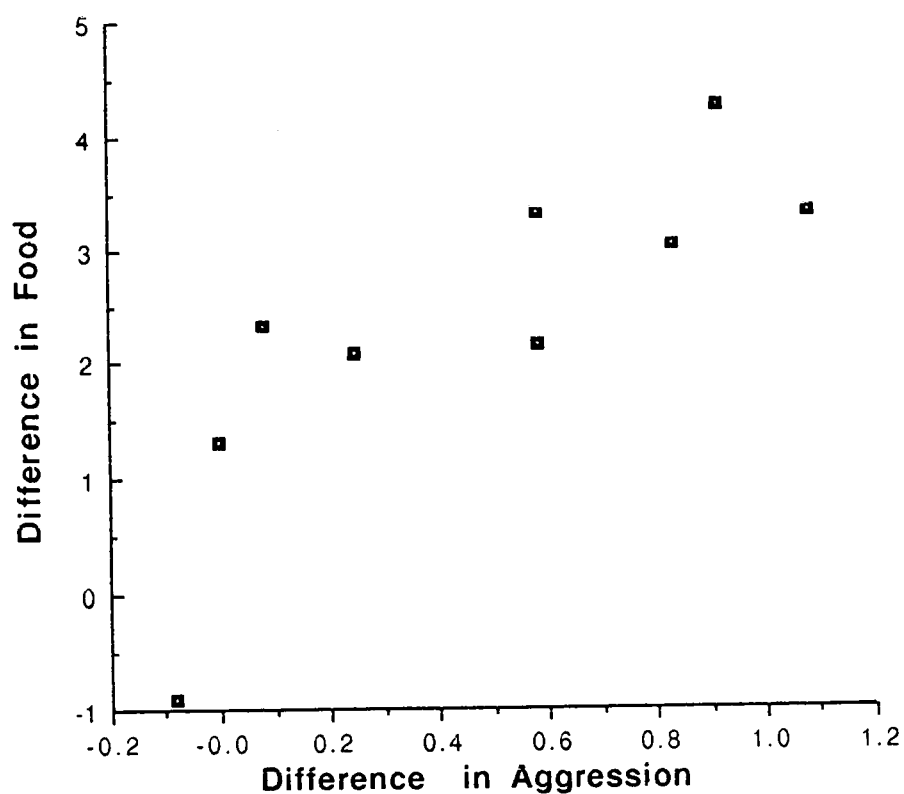


Figure 1: The relationship between amount of aggression and amount of food obtained. Each point represents the difference in average number of aggressive acts (female minus male), plotted against the difference in average amount of food consumed for each pair.

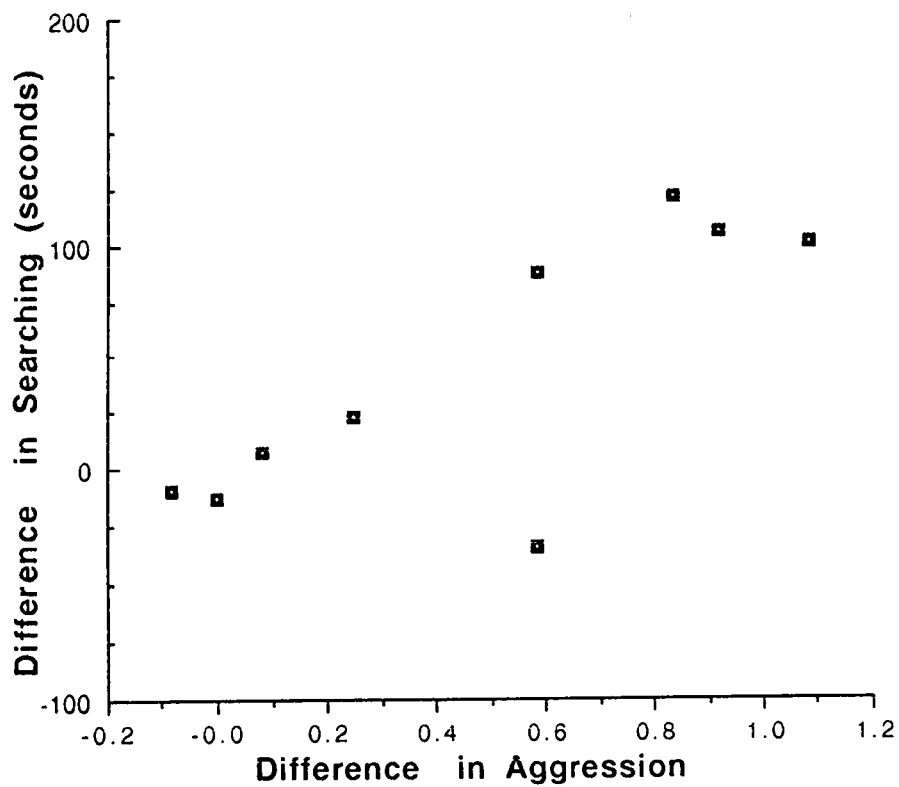


Figure 2: The relationship between amount of aggression and amount of time spent searching. Each point represents the difference in average number of aggressive acts (female minus male), plotted against the difference in average amount of time spent searching for each pair.

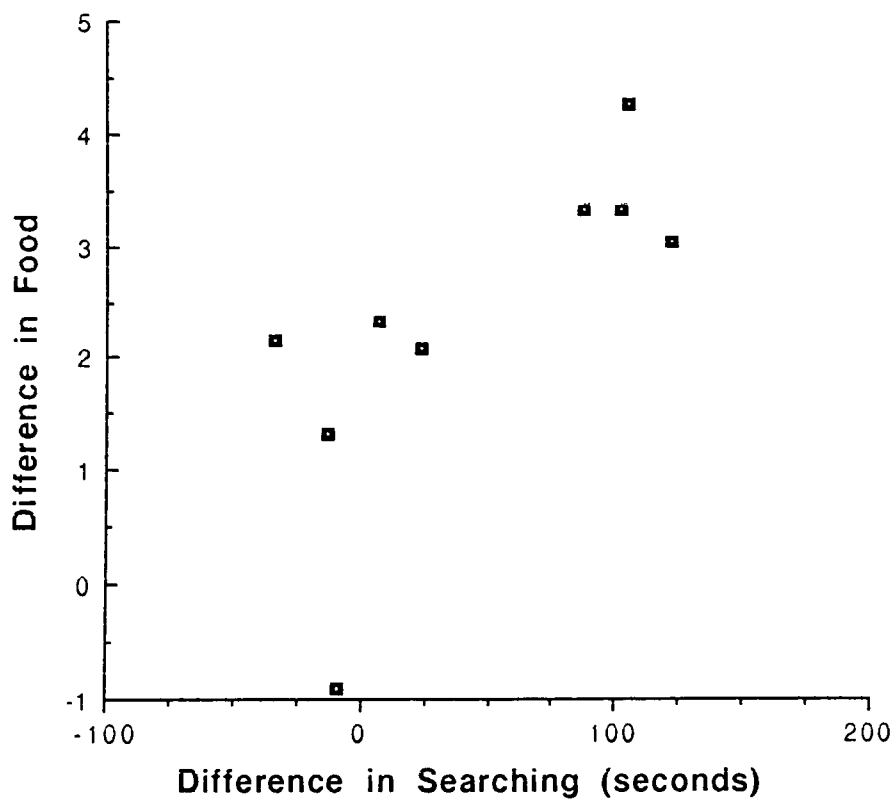


Figure 3: The relationship between amount of time spent searching and amount of food obtained. Each point represents the difference in average amount of time spent searching (female minus male), plotted against the difference in average amount of food consumed for each pair.

CHAPTER 4

DISCUSSION

The results of this study agree closely with those of Tardif and Richter (1981) with respect to distribution of food and levels of aggression. There was a marked sex difference in amount of food consumed, and females obtained more food than males in all feeding configurations. Females performed more aggressive displays than males in virtually all situations, and were also more physically aggressive overall.

There were virtually no sex differences in the number or rate at which animals displaced their mates. Furthermore, once test duration was taken into account, neither dispersal nor difficulty in obtaining food affected displacement behavior. Although displacement has previously been cited as an important behavior in primate food competition (Chalmers 1968; Watts 1985; Janson and van Schaik 1988), it is possible that in this species or in this type of captive, experimental situation, displacement simply was not an important or relevant behavior.

In this study, dispersal of food had no significant

effects on how the food was distributed between animals, searching behavior, or performance of aggressive behaviors. This is in disagreement with many other studies which have found dispersal to be quite an important factor in food competition (Magnuson 1962; Southwick 1967; Chalmers 1968; Wrangham 1974; Southwick et al. 1976; Fossey and Harcourt 1977; Mori 1977; Pollock 1977; Zahavi 1978; Rubenstein 1981; Oates 1986). However, most of the species in these previous studies have a very different social organization from C. jacchus. It is also possible that the food was not sufficiently dispersed in this study. It was observed that in some of the mated pairs, one animal simply prevented the other from gaining access to the front of the cage. Thus, the feedings which were classified as dispersed may not have differed functionally from those classified as concentrated. Unfortunately, preliminary trials in which food cups were positioned on the sides of the cage revealed that it was extremely difficult to observe animals obtaining food, and the back wall of the cage could not be reached from the door at the front. Tardif and Richter's (1981) study in this same colony, which found a significant effect of dispersion on food distribution and aggression in cotton-top tamarins, involved animals housed in cages consisting of two cage units connected by a small doorway. Since one

food cup was placed in each of these cage units, the food was more dispersed and probably more difficult to defend than in the present study.

Similarly, difficulty in obtaining food failed to have significant effects on aggression and how food was distributed between animals. This is in contrast to studies such as Novak's (pers. comm.), in which the use of foraging devices for presenting food to Rhesus macaques (Macaca mulatta) led to a decrease in aggression and a more equal distribution of the food than in less difficult feeding situations. The effect seen in Novak's study was mainly due to the fact that the foraging devices prevented the dominant animal from obtaining more than one piece of food at a time; therefore, he could not collect and hoard large amounts of food. However, such hoarding of food was not observed in Callithrix jacchus; only once was an animal observed to take more than one raisin piece at a time, even when the food was easy to obtain. This may be an indication of species differences in behavior patterns, or it may have been due to characteristics of the animals' cages. The solid floor of Novak's macaque cages permitted an animal to collect and guard a large pile of food. But the wire mesh floor of the cages in the present study made it impossible for an

animal to collect more food than it could hold.

The information on correlated variables probably provides the best clue as to what affects the distribution of food in pairs of C. jacchus. The correlation between difference in amount of aggression and difference in amount of food (Figure 1) 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. Similarly, animals which were much more aggressive than their mates searched much more than their mates (Figure 2), and animals which searched much more than their mates obtained much more food (Figure 3). Thus, there are two variables, aggression and searching, which are closely related to which animal of a pair obtains more food. One might be inclined to explain this situation as follows: animals which were more aggressive had greater access to the food cups, and thus were able to search more. Therefore, they obtained more food. However, partial correlation showed that the relationship between searching and amount of food obtained was not entirely due to aggression. Furthermore, 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 for any of the other configurations. Thus, females obtained more food than males not only because they were more aggressive, but because (in some situations) they apparently were willing to spend more time searching than males were.

It seems reasonable that females might have a higher motivation to search for food if it is true that amount of food obtained is more directly related to fitness in female primates than in males (Wrangham 1979; van Schaik and van Noordwijk 1988). It is certainly logical that pregnant or lactating females would have a higher motivation to search (Gittleman and Thompson 1988), and since C. jacchus reproduce aseasonally, it is likely that healthy, mated females are either pregnant or lactating much of the time (Eppler 1970; HersHKovitz 1977). Thus, C. jacchus females may have evolved a tendency to search for food more than males even when they are not pregnant or lactating. This may also explain why no behavioral differences were found between pregnant and nonpregnant females. Females have been found to spend more time than males in feeding and foraging behavior in many other species of primates, such as indris (Pollock 1977), mantled howler monkeys, Alouatta palliata (Smith 1977),

mangabeys (Waser 1977), geladas, Theropithecus gelada (Dunbar 1977), red colobus monkeys, Colobus badius (Clutton-Brock 1973), and siamangs Symphalangus dactylus (Chivers 1977). Female waterbuck (Kobus defassa) and warthog (Phacochoerus aethiopicus) also forage for larger amounts of time than males (Spinage 1968; Clough and Hassam 1970).

It is possible that the sex differences in searching behavior and food consumption found in this study were related to the use of differing search strategies. After an animal has found a food item, there are two main strategies which may determine where it will search for the next item (Olton et al. 1981). It may return to the location where it obtained the first item (a "win-stay" strategy), or it may leave and search elsewhere (a "win-shift" strategy) (Olton et al. 1981). In this study, an animal using a win-shift strategy would probably obtain more food than one which persisted with win-stay, since there were only two pieces of food in each cup during dispersed feedings. (During concentrated feedings, win-shift was not an option, since there was only one food cup at which to search.) Thus, if females were more likely to follow win-shift than were males, this could explain why they obtained more food. Sex differences in choice of foraging location have been observed in red

colobus monkeys (Clutton-Brock 1973), hamadryas baboons, Papio hamadryas (Kummer 1971), indris (Pollock 1977), and orang-utans Pongo pygmaeus (Rodman 1977), but these do not necessarily represent differences in searching strategy. It is not clear why C. jacchus males and females would adopt different searching strategies, unless this was related to different dietary needs in the wild. Sex differences in diet composition have been found in wild mangabeys (Waser 1977), red colobus monkeys (Clutton-Brock 1977) orang-utans (Rodman 1977) and gorillas (Fossey and Harcourt 1977), and Hladik (1977) has suggested that females may have higher protein requirements than males, and may therefore eat more insects and other animal prey. Since animal prey are probably the most dispersed food eaten by wild C. jacchus, while fruit, and especially plant exudates, are more clumped, this is the food which would favor a win-shift strategy most (Olton et al. 1981). Thus, if female C. jacchus require more protein than males, it is possible that they would spend more time foraging for insects and other animals, and would adopt a win-shift strategy more often than males. This possible sex difference in tendency to adopt particular strategies might then carry over to captive studies like the present

one. However, this still does not explain why females searched more than males did. Furthermore, although this study was not designed to analyze the animals' searching strategies, it was the experimenter's impression that, in general, animals appeared to follow a win-stay pattern, with no obvious sex differences.

An alternative hypothesis to explain why females were more aggressive, obtained more food, and (in some cases) searched more than males 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.

Another reasonable hypothesis is that the heavier animal of a pair obtained more food, but analyses indicated no correlation between difference in weight and difference in amount of food consumed.

Since the relationship between mated C. jacchus has been shown to change over time (Woodcock 1982; Evans and Poole 1984), it seems likely that this would affect levels of aggression and distribution of food. However, no relation was found between either of these variables

and length of pairing.

Future studies of this type could be improved by increasing the sample size, particularly the number of pairs with nonpregnant females. This would allow for a more thorough examination of any differences that may exist between pregnant and nonpregnant females. It might also be interesting to examine the behavior of animals in various stages of pregnancy and lactation. A similar experiment could be performed using different foods, particularly foods that are encountered by wild C. jacchus. It would also be important to determine whether the behavior of the animals differs during other times of the year. More replications of each feeding configuration for each pair could also be useful. It would be particularly interesting to examine food competition during feedings in which the food was much more dispersed than in this study. As discussed previously, however, this may prove difficult unless the animals are housed differently. To determine whether females have a higher motivation to search, animals could be presented with a difficult feeding configuration in the absence of their mates, and searching time compared between males and females. Future studies might also be able to determine whether males and females follow different searching

strategies. Similar studies on other monogamous species would be extremely interesting.

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

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APPENDIX

Table A-1: Average number of raisins consumed by each animal

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	2.7	4.3	2.7	5.7	4.0	3.0	3.3	3.3	3.2	4.1
4A	4.7	1.7	8.0	.3	3.3	3.3	7.0	.7	5.8	1.5
10A	3.0	3.7	7.0	1.3	2.7	3.3	6.0	2.0	4.7	2.6
13B	3.7	3.3	7.3	.3	5.0	3.0	5.0	1.0	5.3	1.9
15A	7.3	.7	6.0	1.7	4.7	3.0	4.3	3.7	5.6	2.3
15B	6.7	3.0	4.3	4.3	5.7	2.0	5.3	3.3	5.5	3.2
24A	4.0	3.0	4.0	2.3	4.0	3.7	5.3	3.0	4.3	3.0
30A	4.7	1.0	6.0	1.3	3.7	2.7	5.0	2.3	4.8	1.8
34B	5.3	1.0	3.3	2.0	4.7	2.0	4.0	3.7	4.3	2.2
Mean	4.7	2.4	5.4	2.1	4.2	2.9	5.0	2.6	4.8	2.5

Table A-2: Average number of displacements performed by each animal

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	.3	0	.3	.3	0	.7	1.0	3.3	.4	1.1
4A	0	0	.3	.3	0	0	0	0	.1	.1
10A	0	0	.7	1.0	0	.7	1.3	2.3	.5	1.0
13B	.3	.3	1.0	1.3	0	.3	1.3	1.7	.7	.9
15A	.3	0	0	.3	.7	0	1.0	.3	.5	.2
15B	0	0	.3	.7	0	.3	0	1.7	.1	.7
24A	0	0	1.3	.7	.3	.7	1.0	1.0	.7	.6
30A	.3	0	.3	0	0	.3	.7	0	.3	.1
34B	.7	.3	2.0	3.0	.7	0	3.7	2.3	1.8	1.4
Mean	.2	.07	.7	.8	.2	.3	1.1	1.4	.6	.7

Table A-3: Average rate of displacement for each animal

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	.15	0	.03	.06	0	.30	.05	.48	.06	.21
4A	0	0	.03	.02	0	0	0	0	.01	.01
10A	0	0	.03	.09	0	.37	.13	.29	.04	.19
13B	.12	.02	.08	.07	0	.06	.13	.10	.09	.06
15A	.16	0	0	.02	.16	0	.13	.08	.11	.02
15B	0	0	.02	.03	0	.08	0	.13	.004	.06
24A	0	0	.07	.03	.10	.04	.07	.07	.06	.04
30A	.15	0	.05	0	0	.15	.06	0	.07	.04
34B	.33	.17	.10	.15	.29	0	.30	.13	.25	.11
Mean	.10	.02	.05	.05	.06	.11	.10	.14	.08	.08

Table A-4: Average number of aggressive displays performed by each animal

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	.67	.67	0	0	0	0	.33	0	.25	.17
4A	1.33	0	1.00	0	0	0	0	0	.58	0
10A	.33	0	.67	.67	0	0	.33	0	.33	.17
13B	.67	.33	1.67	.33	0	0	.67	0	.75	.17
15A	.67	0	.33	0	.67	0	.67	0	.58	0
15B	0	0	0	0	0	0	.33	0	.08	0
24A	0	0	0	0	0	0	0	0	0	0
30A	.67	0	.67	0	.67	0	.67	0	.67	0
34B	0	0	0	0	0	0	.33	0	.08	0
Mean	.48	.11	.48	.11	.15	0	.37	0	.37	.06

Table A-5: Average rate of aggressive display for each animal

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	.26	.26	0	0	0	0	.07	0	.08	.07
4A	.57	0	.32	0	0	0	0	0	.22	0
10A	.20	0	.03	.03	0	0	.08	0	.08	.01
13B	.03	.02	.12	.02	0	0	.07	0	.06	.01
15A	.31	0	.02	0	.16	0	.09	0	.14	0
15B	0	0	0	0	0	0	.02	0	.01	0
24A	0	0	0	0	0	0	0	0	0	0
30A	.07	0	.05	0	.44	0	.06	0	.15	0
34B	0	0	0	0	0	0	.02	0	.004	0
Mean	.16	.03	.06	.01	.07	0	.05	0	.08	.01

Table A-6: Average number of acts of physical aggression performed by each animal

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	0	.33	0	.33	0	0	0	0	0	.17
4A	1.00	0	0	0	0	0	.33	0	.33	0
10A	0	0	.33	.33	0	0	.33	0	.17	.08
13B	0	0	1.33	0	.33	0	.33	0	.50	0
15A	0	0	0	0	0	0	0	0	0	0
15B	0	0	0	0	0	0	0	0	0	0
24A	0	0	0	0	0	0	0	0	0	0
30A	0	0	.33	0	.33	0	0	0	.17	0
34B	0	0	.33	0	0	0	2.33	.67	.67	.17
Mean	.11	.04	.26	.07	.07	0	.37	.07	.20	.05

Table A-7: Average rate of physical aggression for each animal

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	0	.13	0	.06	0	0	0	0	0	.05
4A	.41	0	0	0	0	0	.04	0	.11	0
10A	0	0	.02	.02	0	0	.08	0	.02	.004
13B	0	0	.09	0	.06	0	.02	0	.04	0
15A	0	0	0	0	0	0	0	0	0	0
15B	0	0	0	0	0	0	0	0	0	0
24A	0	0	0	0	0	0	0	0	0	0
30A	0	0	.03	0	.22	0	0	0	.07	0
34B	0	0	.02	0	0	0	.12	.03	.03	.01
Mean	.05	.01	.02	.01	.03	0	.03	.003	.03	.01

Table A-8: Average amount of time spent searching by each animal (in seconds)

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	.5	.7	52.5	144.5	4.2	7.7	209.7	150.8	66.7	75.9
4A	.8	5.2	375.0	188.0	2.8	2.8	367.8	129.0	186.6	81.3
10A	.5	1.2	200.5	170.0	9.2	2.7	172.5	115.5	95.7	72.3
13B	1.3	.8	231.8	32.8	3.5	1.5	254.8	51.0	122.9	21.5
15A	.7	4.5	340.8	106.5	0	2.8	197.7	75.8	134.8	47.4
15B	2.3	1.8	215.3	229.8	2.7	17.0	241.5	184.7	115.5	108.3
24A	1.5	1.7	125.3	182.8	5.5	12.5	238.0	224.3	92.6	105.3
30A	4.0	4.2	257.2	9.8	9.2	1.2	267.0	36.0	134.3	12.8
34B	0	1.5	254.8	298.5	0	9.7	195.5	277.8	112.6	146.9
Mean	1.3	2.4	228.1	151.4	4.1	6.4	238.3	138.3	118.0	74.6

Table A-9: Average percent of time spent searching by each animal

Group #	Test									
	Conc. & Easy		Conc. & Diff.		Disp. & Easy		Disp. & Diff.		Overall	
	F	M	F	M	F	M	F	M	F	M
1B	.3	.8	15.5	34.3	4.2	5.8	36.2	23.7	14.0	16.2
4A	.7	3.8	55.2	30.0	2.7	2.2	51.8	22.7	27.6	14.7
10A	.5	1.2	33.2	28.2	9.2	2.2	39.5	31.2	20.6	15.7
13B	1.3	.8	25.3	3.5	1.8	.7	33.2	7.3	15.4	3.1
15A	.5	1.3	39.8	9.3	0	1.5	48.7	22.0	22.3	8.5
15B	1.5	.7	23.3	25.7	1.0	7.7	36.3	30.0	15.5	16.0
24A	1.0	1.0	10.5	15.5	1.2	1.5	35.2	37.0	12.0	13.8
30A	.7	.8	45.2	1.3	6.7	.8	52.5	8.2	26.3	2.8
34B	0	1.2	21.2	25.0	0	7.2	27.3	38.0	12.1	17.8
Mean	.7	1.3	29.9	19.2	3.0	3.3	40.1	24.5	18.4	12.1

VITA

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