

*California Regional Primate Research Center, University of California, Davis*

## **Effects of Pair-Bond and Social Context on Male–Female Interactions in Captive Titi Monkeys (*Callicebus moloch*, Primates: Cebidae)**

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### **Abstract**

In monogamous species, an abiding relationship between a specific adult male and a specific adult female is a defining feature of the social system. The interactions between these individuals are influenced by many factors, including not only the history of their relationship (for example, development of a mutual bond), but also the immediate effects of the prevailing social context (for example, presence and sex of extra-pair conspecifics). In this study we examined the effects of an existing bond and of social context on interactions between adult heterosexual pairs of the monogamous titi monkeys (*Callicebus moloch*). Twelve adult males and 12 adult females were tested with their cagemates and with an unfamiliar partner of the opposite sex in five social contexts: (1) mated male–female pair; (2) unfamiliar pair; (3) single female; (4) single male; and (5) empty stimulus cage. Results show that mated pairs were more affiliative than unfamiliar pairs and differentiated social contexts more sharply. Males were more responsive to context than females. Distance between mates was less and physical contact was more frequent in the presence of male–female pairs or a single male, than in the presence of a single female or an empty cage. These findings suggest that the presence and sex of strangers have a stronger influence on male–female interactions when the pair has an existing relationship.

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## Introduction

Interspecific variation in social organization among related species reflects differences in social dispositions, social interactions, and patterns of social relationships. In socially monogamous species, the relationship between an adult male and adult female is the defining feature of the social system. The salient attributes of this relationship in the monogamous titi monkey (*Callicebus* spp.) in its natural habitat include frequent grooming, tail twining, small inter-animal distance, following, spatial exclusivity, and close coordination of the behavior of male and female during feeding, locomotion, resting, and the complex species-typical displays during territorial confrontations between neighboring groups (Mason 1966, 1968; Robinson 1979, 1981; Wright 1985; Kinzey 1997 for a review).

Monogamy is not a unitary trait, of course, and as with any abiding social relationship, the development and expression of the relationship between male and female in a monogamous social system will be influenced by many variables (Anzenberger 1992). We have examined some of these variables in research with captive titi monkeys (*Callicebus moloch*). An adult male and adult female that live together will form an emotional attachment or pair-bond that is evident in many aspects of their relationship. In addition to confirming behaviors that can be observed in free-ranging animals, experimental findings demonstrate that: both sexes strongly prefer each other over strangers in choice tests; they distinguish unequivocally between cagemate and stranger, even after mates have been alone for several days and a stranger is the only available partner; and when separated from each other they show increases in cortisol, heart rate, vocalizations, and locomotion (Cubicciotti & Mason 1975; Mason 1974, 1975; Mendoza & Mason 1986a, b; Anzenberger 1988; Fernandez-Duque et al. 1997).

The data also indicate that interactions between a specific male and female titi monkey are influenced by the presence of other animals and that the sexes differ sharply in their responsiveness to the social environment. Males are more highly aroused behaviorally than females by the presence of other animals and show stronger tendencies to approach members of the opposite sex and to give agonistic displays to members of the same sex (Cubicciotti & Mason 1978; Anzenberger et al. 1986; Mendoza & Mason 1986a; Anzenberger 1988; Fernandez-Duque et al. 1997).

These asymmetries in the social responsiveness of male and female titi monkeys have important implications for understanding the factors governing the formation and maintenance of pair-bonds. Interactions between animals that are in the process of forming a pair bond are expected to be influenced not only by the lack of familiarity between them, but also by the social context in which their interactions occur. Interactions between mated pairs, however, are expected to reflect primarily differences between males and females in their reactions to features of the social context.

A primary purpose of this study was to examine the influence of different aspects of the social context on mated and unfamiliar heterosexual pairs of adult titi monkeys. This was accomplished by observing animals with their mates and

with an unfamiliar partner in five different contexts, created by presenting strangers in a nearby cage: (1) a mated pair; (2) an unfamiliar pair; (3) a single female; (4) a single male; and (5) an empty stimulus cage.

## Methods

### Subjects

Subjects were 12 male and 12 female adult titi monkeys, *Callicebus moloch*, who had been living as heterosexual pairs in stable family units for at least 2 years at the start of the study. All adult pairs had produced offspring. Five males and four females were wild-born and imported as adults. The remaining subjects were captive-born and had been raised in stable family units. They ranged in age from 5 to 17 years. All animals were housed indoors in stainless-steel cages (1.2 × 1.2 × 2.1 m high) equipped with four parallel perches extending the width of the cage, and maintained according to established laboratory protocols. Temperature in the colony room ranged between approximately 22–33°C. Cleaning occurred in the morning and the animals were fed twice daily, morning and afternoon. Water was available ad libitum.

### Design

Subjects were tested once in each of 10 unique conditions. This included two familiarity conditions (paired with mate, ‘mated pair’, and with opposite-sex stranger, ‘unfamiliar pair’, and five context conditions, mated pair, unfamiliar pair, single male, single female, empty stimulus cage). In other words, each of the 24 subjects underwent 10 tests. On five of those tests, while paired with its mate, the subject was tested in the presence of another mated pair, an unfamiliar pair, a single male, a single female, or an empty cage.

Except for familiarity with the mate, the subjects were unfamiliar with the other animals at the start of testing. A subject was considered ‘unfamiliar’ if it had never been housed with the other animals. Subjects could not see other ‘unfamiliar’ subjects while housed, but could hear and smell them. The sequence and order of conditions were approximately balanced across cohorts. Cohorts were tested on the same day in complementary conditions. Subjects were also used as stimulus animals (single male or single female).

The duration of the test period was 15 min. Only one condition was presented in a daily session and at least 24 h intervened between successive tests, during which subjects were housed in their home cages with mates and offspring.

### Apparatus

The test cage (2.5 × 4.0 × 2.3 m, Fig. 1) was located in an indoor room with controlled lighting and temperature (20°C). The cage was divided into two equal sections by a double partition made of 2.5 cm-poultry-wire panels, 15 cm apart. A remotely operated opaque curtain ran in the opening between the panels. A 2.5-cm diameter PVC runway traversed the length of each section, at a distance of 1 m

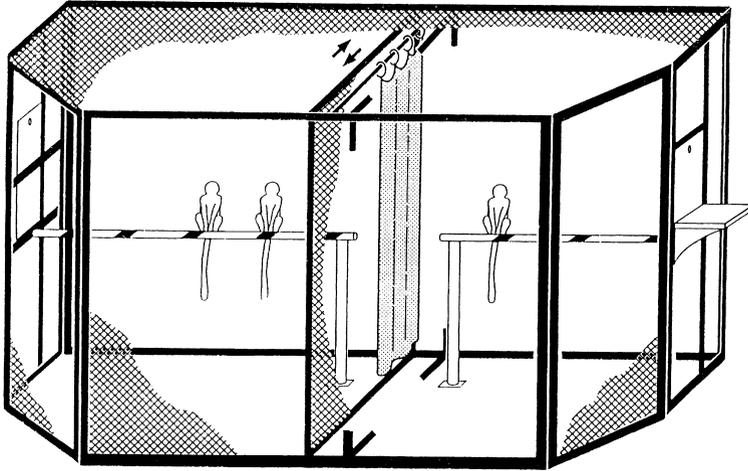


Fig. 1: Schematic view of apparatus

from the floor. Each end of the runway terminated at two adjacent entryways covered by remotely operated opaque and transparent doors. The runway, floor, ceiling, and walls of the cage were marked into sections 32.5 cm wide. Outside the cage, an enclosed booth with a screened observation window curtailed visual contact with observers. The subjects had been previously habituated individually to the test cage during ten 30-min sessions (Fernandez-Duque 1996).

#### Test Procedures

Each subject was transported individually from the home cage to the testing room in a small cage that was placed on one of the four release platforms mounted outside the testing cage. Animals on adjacent release platforms were unable to see or touch each other. To begin a social test, the opaque curtain running between the two sections was drawn and subjects were released simultaneously into the apparatus by raising the opaque and transparent entry way doors in quick succession. For scoring purposes, the 15-min test was divided into 60 15-s intervals, signaled by audible clicks of a timer.

Data were collected from all subjects present in the apparatus. For example, testing a mated pair confronting an unfamiliar pair provided data on the behavior of mated pairs in the presence of unfamiliar pairs and conversely, the behavior of unfamiliar pairs in the presence of mated pairs. Data on single stimulus animals (single male and single female) were collected following the same procedures as with paired subjects.

Data on behavior and spatial location were collected throughout the session. Spatial data provided information on the section of the runway, floor, ceiling, or wall in which the subject was located. These data were used to calculate inter-ani-

mal distance (for pairs) and use-of-runway (being on the runway with a companion was an indication of social tolerance, since titi monkeys strongly preferred to stay on perches when tested individually, Fernandez-Duque 1996) Spatial location and physical contact between pairs of subjects were scored using instantaneous sampling ('on the signal'). Other behaviors were recorded once for each interval in which they occurred (one-zero). For categories that involved two subjects (e.g. distance, contact), data were collected only on animals in the same section of the cage. Two observers participated in the study. Each observer collected data from only one section of the test cage.

Table 1 describes the behavior categories used in this study. In the presentation of results, we consider these categories within two major groups: attraction/affiliation and behavioral arousal. The first group includes measures of social distance, approach, contact, use-of-runway, mounting/thrusting and grooming; the second includes species-characteristic behaviors (Mason 1966; Moynihan 1966). Anogenital inspection, arching, chest-rubbing, gnashing, holding, locomotion, piloerection, tail-lashing, and vocalization were used to assess excitement or arousal.

### Data Analysis

Data for social distance (calculated from spatial location data) and physical contact were analyzed using the pair as the unit of analysis ( $n = 12$ ). For the remaining behavioral categories, data were analyzed by subject using the total number of intervals in which each animal performed the behavior under each of the 10 testing conditions (maximum possible = 60/condition/subject,  $n = 24$ ).

Unless otherwise indicated, statistical outcomes are based on the non-parametric Friedman two-way analysis of variance, Wilcoxon matched-pairs or Mann-Whitney tests (Siegel 1956). The Sequential Bonferroni correction was used whenever multiple tests were made (Rice 1989) and only corrected p-values are reported. Figures and tables present data as mean percentage of the maximum possible score, based on the number of 15-s intervals during which the behavior was observed at least once. Whenever used, 'frequency' or 'time' refer to number of intervals, not actual frequencies or durations of the behavior.

## Results

### Effects of Familiarity

An existing relationship between male and female had major effects on their behavior in the test situation, particularly on measures of affiliation and attraction. This can be seen in Table 2, which summarizes results and statistical outcomes by familiarity for the combined social context conditions. As compared to unfamiliar pairs, members of mated pairs were closer to each other, were more often on the runway, and approached and contacted each other more frequently. Grooming, although relatively infrequent, followed the same trend as other affiliative behaviors, occurring a total of 19 times in six mated pairs and once in one unfamiliar

Table 1: Behavior categories

Behavior Categories	Description
Attraction/Affiliation Approach	One subject moves within arm's reach of a stationary subject and they remain in proximity for at least 3 s. If both subjects move into proximity simultaneously and remain in proximity for at least 3 s, 'approach' is scored for both.
Contact	Common usage.
Grooming	Combing through cagemate's fur with the hands.
Mounting and/or thrusting	Common usage. Only recorded for males. Not observed in females.
Tail-twining	Sitting quietly side by side with tails intertwined (i.e. wrapped around each other for at least one turn).
Behavioral Arousal	
Anogenital inspection	Sniffing, licking, or otherwise exploring partner's anogenital area.
Anogenital-rubbing	The anogenital region, which probably includes circumanal glands, is in contact with the perch and the rear part of the body is slid forward or moves laterally.
Arching	Back arched sharply (as in frightened cat), subject may raise trunk until arms leave perch or arms may be bowed.
Chest-rubbing	The chest region, where a visible sternal gland is located, is moved with pressure and friction against the perch or other surface by sliding the body forward. It may also be pressed in a downward motion with hands and/or arms.
Gnashing	Repeated and rapid opening and closing of mouth, accompanied by sounds of lips and/or teeth.
Holding	Grasping and seemingly restraining the partner.
Locomotion	Movement of at least one body length.
Piloerection	Hair erect, most noticeably in the tail.
Tail-lashing	Repetitive swinging of the whole tail from side to side (arcs greater than 45°).
Vocalizations	Includes squeaks, whistles, moans (low-pitched vocalizations), and loud, sustained calling (full calls and duetting).

Table 2: Effects of familiarity and social context on measures of affiliation/attraction and behavioral arousal

	Context condition	Mated Pair	Unfamiliar Pair	p-value
<b>Affiliation and attraction</b>				
Approach	Social	6.8 ± 7.2	3.9 ± 6.2	<b>0.02</b>
	Empty	5.7 ± 4.8	4.4 ± 5.7	0.66
Contact	Social	48.8 ± 20.6	10.5 ± 12.2	<b>0.00</b>
	Empty	21.6 ± 16.6	8.8 ± 12.4	<b>0.03</b>
Social distance	Social	28.8 ± 31.9*	95.3 ± 28.1*	<b>0.00</b>
	Empty	58.5 ± 33.1*	94.9 ± 30.9*	<b>0.02</b>
Use-of-runway	Social	82.8 ± 20.3	61.6 ± 27.1	<b>0.00</b>
	Empty	74.9 ± 23.3	64.2 ± 27.8	<b>0.02</b>
<b>Behavioral arousal</b>				
Anogenital inspection	Social	0.8 ± 1.5	0.6 ± 2.0	0.11
	Empty	1.7 ± 3.7	0.3 ± 1.8	<b>0.02</b>
Arching	Social	14.8 ± 16.9	13.8 ± 16.6	0.86
	Empty	1.2 ± 2.1	3.9 ± 6.3	0.07
Chest-rubbing	Social	6.8 ± 7.9	6.2 ± 9.1	0.20
	Empty	7.5 ± 10.1	4.5 ± 8.3	0.21
Gnashing	Social	27.8 ± 25.2	16.0 ± 19.7	<b>0.00</b>
	Empty	12.9 ± 15.1	7.1 ± 12.6	<b>0.03</b>
Holding	Social	4.5 ± 8.4	1.7 ± 3.2	0.06
	Empty	0.7 ± 1.3	1.0 ± 1.8	0.42
Locomotion	Social	28.2 ± 17.6	43.4 ± 18.0	<b>0.00</b>
	Empty	31.3 ± 16.0	47.9 ± 23.7	<b>0.00</b>
Piloerection	Social	13.3 ± 18.6	11.8 ± 16.9	0.48
	Empty	0.8 ± 1.6	1.6 ± 2.7	0.09
Tail-lashing	Social	4.1 ± 6.9	1.5 ± 4.4	<b>0.00</b>
	Empty	0.1 ± 0.5	0.2 ± 0.7	0.56
Vocalizing	Social	4.1 ± 9.6	3.8 ± 9.0	0.59
	Empty	1.6 ± 6.1	6.7 ± 12.8	<b>0.03</b>

Numbers indicate mean percentage (± SD) of 15-s intervals in which the behavior was observed.

\* Data for social distance are presented in centimeters.

Bold numbers, p-value smaller than significance level after sequential Bonferroni correction for k = 4-tests (affiliation/attraction) or k = 9-tests (behavioral arousal).

Table 3: Effects of familiarity on the response to different social conditions

Behavior categories	Mated Pairs				Unfamiliar Pairs				$\chi^2$	p	
	Mated	Unfamiliar	Single female	Single male	Mated	Unfamiliar	Single female	Single male			
Affiliation and attraction											
Approach	9.5 ± 11.1	6.1 ± 5.9	6.2 ± 6.2	5.3 ± 5.6	6.4 ± 8.9	4.4 ± 6.7	2.3 ± 4.5	2.4 ± 4.8	9.0	<b>0.03</b>	
Contact	56.7 ± 22.3	49.5 ± 28.0	35.3 ± 25.3	53.4 ± 25.3	18.1 ± 26.6	6.5 ± 12.8	6.9 ± 14.3	10.5 ± 20.9	2.9	0.41	
Social Distance	21.4 ± 34.6	30.3 ± 32.5	37.2 ± 36.0	26.3 ± 2.7	84.0 ± 47.1	100.3 ± 61.8	104.2 ± 34.0	92.7 ± 41.6	5.7	0.13	
Use-of-runway	83.1 ± 22.8	80.4 ± 21.6	81.2 ± 23.6	85.0 ± 20.7	64.9 ± 32.7	61.8 ± 32.7	58.4 ± 33.6	60.1 ± 38.2	1.2	0.76	
Behavioral arousal											
Anogenital Inspection	0.8 ± 1.8	0.3 ± 0.8	1.6 ± 3.7	0.7 ± 2.1	0.5 ± 1.7	0.2 ± 0.6	0.7 ± 2.5	1.1 ± 3.5	2.2	0.53	
Arching	22.7 ± 22.2	13.0 ± 17.0	6.8 ± 8.9	16.9 ± 19.5	16.2 ± 16.1	19.2 ± 21.5	7.2 ± 9.5	12.7 ± 16.7	14.4	<b>0.00</b>	
Chest-rubbing	5.9 ± 10.2	6.3 ± 10.9	7.8 ± 9.4	7.3 ± 11.5	5.6 ± 9.7	5.5 ± 8.4	7.9 ± 13.2	6.0 ± 10.2	2.4	0.49	
Gnashing	35.1 ± 19.5	25.8 ± 25.6	20.3 ± 19.2	29.9 ± 26.4	19.0 ± 20.6	21.1 ± 24.4	10.2 ± 15.4	13.8 ± 18.4	8.7	<b>0.03</b>	
Holding	8.6 ± 19.2	4.8 ± 8.3	1.9 ± 2.7	2.3 ± 3.5	1.9 ± 3.5	2.1 ± 3.6	1.0 ± 2.1	1.9 ± 3.7	3.8	0.28	
Locomotion	31.3 ± 23.2	28.2 ± 15.0	30.9 ± 23.0	25.0 ± 18.1	40.4 ± 24.6	48.0 ± 26.5	45.8 ± 18.0	39.4 ± 20.9	4.3	0.23	
Piloerection	23.9 ± 30.4	15.5 ± 19.6	3.9 ± 7.6	9.6 ± 16.9	15.5 ± 21.0	18.6 ± 24.5	3.1 ± 5.7	10.2 ± 16.4	17.5	<b>0.00</b>	
Tail-lashing	10.2 ± 16.9	2.9 ± 5.1	0.6 ± 1.1	2.7 ± 4.7	2.5 ± 6.9	1.7 ± 4.6	0.1 ± 0.3	1.7 ± 5.7	7.5	0.06	
Vocalizations	8.8 ± 19.8	6.2 ± 12.9	0.0	1.4 ± 5.8	7.6 ± 15.8	3.8 ± 8.7	2.6 ± 7.8	1.3 ± 3.5	4.4	0.22	

Numbers indicate mean percentage ( $\pm$  SD) of 15-s intervals in which the behavior was observed.

\* Data for social distance are presented in centimeters.

$\chi^2$  based on Friedman test bold numbers, p-value smaller than significance level after sequential Bonferroni correction for  $k=4$ -tests (affiliation/attraction) or  $k=9$ -tests (behavioral arousal).

pair ( $p = 0.03$ ,  $U = 0$ ,  $n = 6$ ). The only measure of affiliation that occurred more frequently in unfamiliar pairs than in mated pairs was mounting/thrusting (61 times, four males vs. 18 times, two males), although the difference fell short of statistical significance ( $p = 0.07$ ,  $U = 0$ ,  $n = 4$ ).

Several measures of behavioral arousal also differed between mated and unfamiliar pairs (Table 2). For the combined context conditions, mates had significantly higher scores for gnashing and tail-lashing and significantly lower scores for locomotion. The frequencies of other behaviors indicative of arousal (anogenital inspection, arching, chest-rubbing, holding, piloerection, vocalization) were similar for mates and strangers and did not differ significantly.

To assess the effect of familiarity in the absence of intruders, we compared the behavior of mated and unfamiliar pairs in the empty condition (Table 2). Mated pairs were closer, spent more time on the runway, and made more frequent contacts than did unfamiliar pairs. They also showed higher levels of gnashing and anogenital inspection and lower levels of vocalization and locomotion.

### Effects of Social Context

Although social context influenced both mated and unfamiliar pairs, the effect of the presence of strangers was stronger and more extensive on mated pairs (Table 2). Compared to the empty condition, mated pairs in the presence of strangers (combined social conditions) were closer, spent more time on the runway, made more contacts, and showed a substantially higher level of behavioral arousal as measured by arching, gnashing, holding, piloerection, and tail-lashing. Mated pairs were closest and made most contacts in the presence of another male, whether the male was presented as a single stimulus or paired with an opposite-sex partner (Table 3).

Unfamiliar pairs were less affected by the presence of strangers. Measures of affiliation and attraction for the combined social conditions did not differ significantly from the empty condition for unfamiliar pairs and only three measures of behavioral arousal (arching, gnashing, piloerection) were reliably higher in the presence of strangers, compared to five measures for mated pairs (Table 2). Furthermore, Friedman tests indicated that mated pairs reliably differentiated among the four social conditions on six behavioral measures (contact, arching, gnashing, piloerection, tail-lashing and vocalization), whereas unfamiliar pairs did so on four measures (approach, arching, gnashing, piloerection, Table 3).

### Effects of Sex

An important factor in the results, regardless of the effects of familiarity with the partner or the presence of strangers, was the difference in responsiveness between the sexes (Table 4). Males showed substantially higher levels of behavioral arousal than females under all conditions. When paired with their mates in the empty condition, males had reliably higher scores for arching, chest-rubbing, gnashing, and holding. The same results were obtained in the empty condition for arching and gnashing when they were paired with unfamiliar females. The sexes

also differed in their willingness to interact socially with their partners, as indicated by their use of the runway (a measure of social tolerance). Females were off the runway significantly more often than males when tested with an unfamiliar male, whereas the difference fell short of statistical significance when tested with their mates.

The differences between the sexes increased in the presence of strangers in the opposing cage. Males had higher scores than females – particularly for measures of behavioral arousal – and they differentiated among social contexts more sharply. To convey these contrasts in arousal simply and economically, we constructed a composite behavioral arousal score by summing the principal species-characteristic measures of arousal (arching, chest-rubbing, gnashing, piloerection, holding, vocalizing, tail-lashing). Sex differences were statistically significant for all context conditions for both mated pairs and unfamiliar pairs (Mann–Whitney, Fig. 2). Males also differentiated context conditions reliably by the Friedman test, whether they were with their mates ( $\chi^2 = 34.26$ ,  $p < 0.001$ , Fig. 2) or with unfamiliar partners ( $\chi^2 = 33.4$ ,  $p < 0.001$ , Fig. 2). Females failed to differentiate context conditions reliably, regardless of familiarity of the partner (mate:  $\chi^2 = 4.24$ ,  $p = 0.38$ ; unfamiliar partner:  $\chi^2 = 2.01$ ,  $p = 0.73$ , Fig. 2). Analysis of differences among contexts indicated that males were least responsive to the empty conditions and, among social contexts, were most responsive to conditions that included another pair (mated pair, unfamiliar pair), followed by single males and single females. Pairwise comparisons among contexts indicated that differences in composite arousal between the empty and the three social conditions which included a male (mated pair, unfamiliar pair and single male) were statistically significant for males with their mates (all  $p$ -values  $< 0.033$ ). Differences between responses to the single female and each of the other social conditions were also statistically significant (all  $p$ -values  $< 0.005$ ). Male composite arousal scores were also higher in response to another mated pair, compared to an unfamiliar pair or a single male, but the differences fell short of statistical significance once the Bonferroni corrections were applied. Differences between responses to the unfamiliar pair and the single male were not statistically significant.

The same pattern of outcomes was obtained for males paired with unfamiliar females, as that obtained for males paired with their mates, except that the difference in behavioral arousal in response to mated and unfamiliar pairs was not significant. In spite of the similarities in the male reaction to context when paired with familiar or unfamiliar partners, the overall level of behavioral arousal was higher in the presence of intruders when paired with familiar partners (311.17 vs. 244.50,  $p = 0.031$ ,  $z = 2.2$ ,  $t = 11.5$ ).

Regardless of familiarity, it is possible that the presence of a partner may have increased responsiveness to the social context. To test this proposition, we compared the behavior of each animal when it was alone (single subject) with its behavior when it was with its mate or with an unfamiliar partner during confrontations with a single stimulus of the same sex. For example, the behavior of a male paired with its mate when confronting a single male was compared with the behavior of the same male as a single stimulus confronting a mated pair. We con-

Table 4: Sex differences on measures of affiliation/attraction and arousal in the absence of strangers (empty condition)

	Mated pairs			Unfamiliar pairs		
	Males	Females	p	Males	Females	p
Affiliation and attraction						
Approach	6.5 ± 4.7	5.0 ± 4.8	0.33	5.9 ± 6.9	2.8 ± 3.7	0.35
Use-of-runway	83.6 ± 14.2	66.3 ± 26.6	0.05	77.2 ± 15.7	39.7 ± 15.2	<b>0.01</b>
Behavioral arousal						
Anogenital-rubbing	1.8 ± 2.2	0.6 ± 1.0	0.09	2.1 ± 2.9	0.4 ± 1.0	0.04
Arching	2.4 ± 2.6	0.1 ± 0.5	<b>0.00</b>	7.6 ± 7.3	0.1 ± 0.5	<b>0.00</b>
Chest-rubbing	12.2 ± 10.0	2.9 ± 7.8	<b>0.00</b>	8.3 ± 10.4	0.7 ± 1.8	0.02
Gnashing	22.1 ± 15.5	3.6 ± 6.7	<b>0.00</b>	13.7 ± 15.3	0.4 ± 1.4	<b>0.00</b>
Holding	1.4 ± 1.6	0.0	<b>0.01</b>	1.1 ± 2.4	1.0 ± 1.1	0.49
Locomotion	32.6 ± 14.3	30.0 ± 17.3	0.64	45.4 ± 23.5	50.4 ± 23.6	0.45
Piloerection	1.4 ± 2.1	0.1 ± 0.5	0.05	2.5 ± 3.2	0.7 ± 1.6	0.12
Tail-lashing	0.3 ± 0.6	0.0	0.15	0.3 ± 1.0	0.1 ± 0.5	0.95
Vocalizations	3.2 ± 8.6	0.0	0.07	8.3 ± 13.8	5.1 ± 11.4	0.22

Numbers indicate mean percentage (± SD) of 15-s intervals in which the behavior was observed.

Bold numbers, p-value smaller than significance level after sequential Bonferroni correction for k = 2-tests (affiliation/attraction) or k = 9-tests (behavioral arousal).

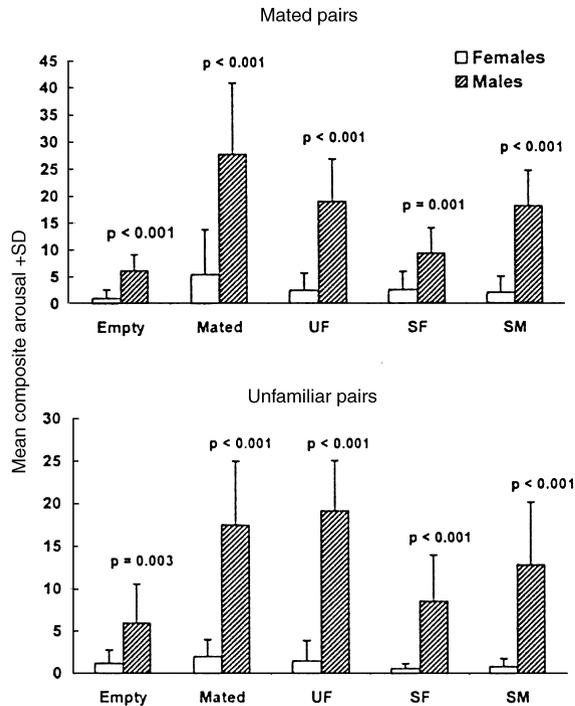


Fig. 2: Sex differences in behavioral arousal for mated and unfamiliar pairs in different context conditions. All Mann-Whitney tests were statistically significant after sequential Bonferroni correction for  $K = 10$  tests. UF, unfamiliar pair; SF, single female; SM, single male

structured a composite behavioral arousal score by summing the principal species-characteristic measures of arousal that were relevant to both the paired and single stimulus conditions (arching, chest-rubbing, gnashing, piloerection, holding, vocalizing, tail-lashing). The large sex differences between single males and females were consistent with findings for the paired conditions. As single subjects, males were more aroused than females, whether confronting a mated ( $U = 4$ ,  $n = 12$ ,  $p < 0.0001$ ) or an unfamiliar pair ( $U = 0$ ,  $n = 12$ ,  $p < 0.001$ , Fig. 3). The most surprising finding was that there were no reliable differences in arousal between the single stimulus and the paired conditions (Fig. 3).

### Discussion

This study shows, conclusively, that mated and unfamiliar pairs differed in the quality of their affiliative interactions, in good agreement with previous findings (Cubicciotti & Mason 1978; Anzenberger et al. 1986; Anzenberger 1988; Fernandez-Duque et al. 1997). Except for mounting/thrusting, all measures of attraction and affiliation indicated a higher degree of affiliation between mates

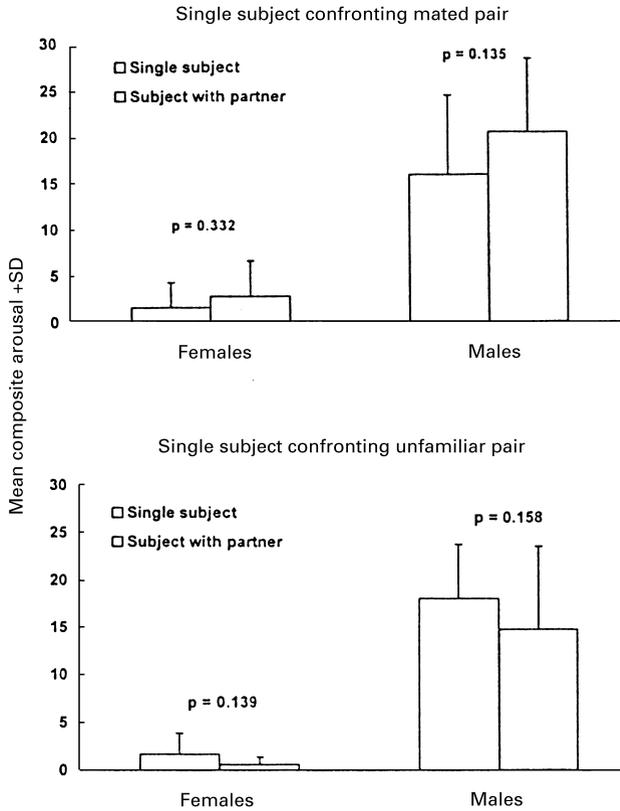


Fig. 3: Behavioral arousal of subjects as a single animal confronting a pair and as a member of a pair confronting a same-sex single stimulus

than between unfamiliar subjects. On the other hand, most measures of behavioral arousal did not differentiate between mated and unfamiliar pairs. This is in general agreement with data from a previous study: behavioral arousal during a test with an opposite-sex partner was primarily influenced by the time since separation from the mate, but not by familiarity with the testing partner (Fernandez-Duque et al. 1997).

Mated and unfamiliar pairs also differed in their responses to social context. The presence of strangers had profound effects on the affiliative interactions between mates, whereas it did not affect the affiliative interactions of unfamiliar pairs. Mates stayed, on average, within arm's reach, made more contacts, and spent more time on the runway in the presence of strangers than they did in the empty condition. These findings provide further evidence that the presence of strangers draws the mates closer to each other (Cubicciotti & Mason 1978). The data also suggest that the number and attributes of other individuals present differ-

entially affected the interactions between mates. The presence of another male, either as a single stimulus or while paired with an opposite-sex partner, drew mates closer than the presence of a single female. On the other hand, the spatial relationship between strangers remained unchanged regardless of the features of the social context. The effects of the social context on measures of behavioral arousal did not differ markedly in mated and unfamiliar pairs.

A third important finding was the ubiquitous sex differences in responsiveness, regardless of the effects of familiarity with the partner or the presence of strangers. Sex differences in behavioral arousal were more pronounced in mated pairs than they were in unfamiliar pairs. Males scored higher than females on all measures of behavioral arousal in the absence of strangers (empty condition). Males interacted affiliatively with unfamiliar partners more than females, as indicated by the males' more frequent use of the runway (an indication of social tolerance, Menzel 1986), as well as a weak tendency to approach their partners more frequently. In contrast, females tended to run away from unfamiliar males.

Sex differences persisted in a social context. Regardless of the number, sex, and relationship between individuals comprising the social context, males were always more aroused and differentiated social conditions more than females did. Regardless of familiarity with the partner, the presence of a same-sex stranger (mated pair, unfamiliar pair or single male) elicited the highest response from males. Although we anticipated that males might perceive the presence of a single male as the most serious threat of cuckoldry, this did not occur. When paired with their mates, males responded the most to another mated pair. It is not clear what the qualities of a mated pair are that make it the strongest stimulus. Behavioral arousal does not seem to be a satisfactory explanation since males in mated pairs and unfamiliar pairs did not differ profoundly in their level of arousal. Our observations in the current and previous studies (Fernandez-Duque et al. 1997) lead us to suggest that the spatial relationship between individuals (e.g. distance between them, time spent in contact) may be more important in conveying information about the pair-bond than the display of species-specific behaviors.

Contrary to our expectations, the arousal of individuals when tested as single stimulus did not differ markedly from their arousal when tested with an opposite-sex partner. For example, the arousal of a male paired with his mate while confronting a potential competitor (another male) was not different from the arousal it showed when confronting, alone, a mated pair.

Our findings, as described in the previous paragraphs, convincingly show that male and female titi monkeys differ in their contributions to the maintenance of the pair-bond between them. In the following paragraphs, we discuss the possible implications of these findings for an understanding of the behavioral mechanisms underlying monogamous bonds.

The pronounced sex differences in the response to same-sex strangers found in this study indicate that males and females may be under different selective pressure. The males' main role in maintaining proximity with his mate could be taken as an indication that there is a risk of cuckoldry and therefore a need for mate guarding. Moreover, our observations that males were willing to interact with

other females is further evidence that mate guarding would be advantageous to males. Although accounts of extra-pair copulations in monogamous primates are not as abundant as in birds (for comprehensive reviews in birds: Birkhead & Moller 1992; Black 1996), extra-pair copulations have been reported in titi monkeys (Mason 1966), siamangs (*Hylobates syndactylus*, Palombit 1994), and white-handed gibbons (*Hylobates lar*, Reichard 1995).

It has also been suggested that the pair-bond in some monogamous primates may function as a defense mechanism against infanticidal males (Van Schaik & Dunbar 1990). In a recent comprehensive review of infanticide and pair-bonds in non-human primates, Palombit (1999) concluded that the absence of an important number of unmated 'floating' males may be one of the reasons that infanticide has not been observed among the monogamous hylobatids. Demographic data on titi monkeys and owl monkeys (*Aotus* spp.) also suggest the absence of a population of potentially infanticidal males. Bossuyt (pers. comm.) found that adult male offspring in titi monkey groups (n = 9) in Manú National Park, Perú may not leave their natal groups until they are four years old or even older, suggesting that they may delay dispersal until a reproductive opportunity is available. In one case, a dispersing male joined a widowed female and lived peacefully with an 8-month-old juvenile which most likely he had not sired. Demographic data from a population of the monogamous owl monkeys of Argentina (Fernandez-Duque, E., Rotundo, M. & Sloan, C., unpublished data) provides a remarkably similar picture. Extremely low infant mortality and stable groups of five or six individuals can be taken as an indication that the risk of infanticide through adult unmated males may be low. Based on these limited and indirect data, there would be no support for the hypothesis that titi monkey males are protecting infants from infanticidal males.

In conclusion, male-female interactions in titi monkeys are clearly affected by the degree of familiarity between members of the pair, as well as by the social context in which those interactions take place. Mated and unfamiliar pairs differed sharply in their affiliative interactions. The form and frequency of those interactions were affected by the presence of strangers when the pair had an existing relationship, but remained unchanged when the pair was unfamiliar. Males were reliably more responsive than females and differentiated among social conditions more than females did.

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