MONKEY SEE AFFECTS MONKEY DO: DOES VISUAL PERSPECTIVE INFLUENCE PARTNER PREFERENCE IN A CALLITRICHID MONKEY?

A Thesis in Psychology
by
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Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science

May 2012
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ABSTRACT

Past research demonstrates that social context modulates nonhuman primate social behavior. In partner preference tests with cotton-top tamarin monkeys (*Saguinus oedipus*), focal animals spent more time investigating opposite sex strangers when their mate could not see them compared to when they could. It is unclear what aspect of social context drives this change in behavior. Changes in the focal monkey's social preferences may be due to the obstruction of the mate's view, suggesting the focal is sensitive to the knowledge state of others, or the obstruction of its own view, in which case the sensitivity to the knowledge state of others is undetermined. In this study, cotton-top tamarins explored a Y-maze in which their mate and an opposite sex unfamiliar monkey were placed at opposing ends of the maze. Visual access among the animals was manipulated across experiments such that all animals had full visual access to each other, visual access for all monkeys was occluded, or the focal monkey and its mate’s visual access was differentially occluded. Monkeys spent more time with the mate when the mate’s visual access was unoccluded and when visual access was differentially occluded among members of the triad. This suggests that cotton-top tamarins modulate their social behavior based on visual state of others.
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ACKNOWLEDGEMENTS

I would like to offer my gratitude to the following people (and tamarins) for their help and support in the completion of this thesis:

- Dr. Daniel Weiss, my advisor, without whose knowledge and guidance this work would not have been possible.
- Dr. Richard Carlson and Dr. Reginald Adams, for their service on my committee and for their support throughout the thesis writing process.
- Rebecca Roberts, Stephanie Bay, Shannon Jones, Angela Hill, Callie Serbonich, Lili Hadsell, Krista Liguori and all of the other Comparative Communication Laboratory research assistants who volunteered their time and energy to the completion of this project.
- Dr. Rena Kass and Dr. Leah Cream, without whose medical skill I would have been unable to complete this, or any, work.
- Don Madden, for his infinite patience, unending support, and extensive proofreading.
- The Comparative Communication Laboratory tamarins.
Chapter 1

Introduction

Among mammals, humans are unusually flexible with regard to their mating systems, engaging in polyandry, polygyny, and multi-male or multi-female breeding structures. Despite this flexibility, in much of the developed world, the prevailing mating strategy among humans is monogamy (Haviland, 1983; Obi, 1970; Schuiling, 2003). Even within societies that accept polygyny, the majority of marriages involve one man and one woman (Becker, 1981; Murdock, 1967).

Adherence to sexual monogamy confers reproductive benefits. At the least, monogamous individuals gain exclusive mating access to a single individual. In cooperative breeders, like humans, monogamy bestows additional benefits. Infant survival, and therefore genetic fitness, is facilitated by biparental care (Gubernick & Teferi, 2000), and a faithful partner reduces the chance of squandering resources on genetically unrelated offspring (Trivers, 1972). From an evolutionary fitness standpoint, entering into a monogamous relationship, however, is akin to taking a double-or-nothing bet. By sexually restricting oneself to a single mate, the reproductive success of the individual becomes entirely dependent on the reproductive fitness of one’s monogamous partner. Thus, the ideal strategy is to engage in non-monogamous copulations without risking the benefits gained from a monogamous relationship.

In societies that conform to monogamy, the potential repercussions of non-monogamous copulations are high. Marital infidelity (real or imagined) is the most common reason for divorce (Betzig, 1989) and the most common cause of spousal violence (Daly & Wilson, 1988). Despite the risks, infidelity in monogamous relationships is quite common. Nearly 1 in 4 married men and 11.6% of married women admit to extra-marital intercourse (Wiederman, 1997). Since the
potential costs of infidelity are high, the costs of non-monogamous copulations increase as the risk of detection increases. Thus, the most beneficial illicit copulations are those that go undetected.

Given the risks involved with extra-monogamous copulations, surreptitious cheating minimizes the chances of incurring costs. In humans, successful cheating often relies on skillful deception. Humans are not the only monogamous primates, however. Fourteen percent of primate species engage in monogamy (Rutberg, 1983), and extra pair copulations among monogamous primates are widespread (Baker, Bales & Dietz, 1993; Price & McGrew, 1991; Rothe & Koenig, 1991; Teborgh & Goldizen, 1985). Social intelligence theories suggest that the sophisticated cognitive functioning involved in concealing non-monogamous copulations may have evolved in response to living in complex social groups (Byrne & Whiten, 1998). The evolutionary basis for departures from monogamy and the evolutionary basis for deception may have risen from similar social pressures. If this is the case, then at least a subset of cognitive mechanisms used to successfully depart from monogamy may be shared by other monogamous primates, particularly those that live in social structures similar to those observed in humans. Investigations into departures from monogamy in nonhuman primates may allow us to ascertain the evolutionary roots of these behaviors.

Besides humans, exclusive mating relationships between a single pair of socially bonded individuals are not found in any species of Great Ape. Further, Old World monkeys, the non-ape primates most closely related to humans, rarely engage in monogamy. Monogamous relationships are, however, widespread among Callitrichidae, a more distantly related family of New World monkeys (Dixson, 1998). Cotton-top tamarins (Saguinus oedipus), a member of the Callitrichidae family of monkeys, represent a particularly interesting model for investigating the shared cognitive capabilities required for successful departures from monogamy. Like humans, the majority of cotton-top tamarins form long-term bonded mating relationships with a single
individual. Until the 1980s, this species was thought to live exclusively in monogamous breeding groups, comprised of a single dominant breeding pair and their offspring (Sussman & Garber, 1987). However, more recent evidence suggests that, like humans, their mating strategies are much more flexible. Both wild and captive cotton-top tamarins engage in a variety of mating strategies besides monogamy, including polygyny, polyandry, and multi-male/multi-female groups (Price & McGrew, 1991). Also like humans, even when part of an established, seemingly monogamous, pair, tamarins engage in copulations with individuals other than their bonded pair mate (Price & McGrew, 1991). While many tamarins appear to mate with exclusively with one partner, as in the nuclear family groups described above, the circumstances that give rise to departures from a monogamous mating structure and the cognitive skills that facilitate these departures from monogamy remain unclear.

In addition to their flexible mating structures, humans and cotton-top tamarins share another characteristic unusual among primates, namely cooperative breeding. Biparental care of offspring is thought to be a significant factor in the development of monogamous mating structures (Brotherton & Komers, 2003). Cotton-top tamarins give birth to infants that are heavy resource consumers, and both parents are heavily invested in infant care. Mothers typically produce twin offspring, each of which can weigh up to 10% of her body weight (Leutenegger 1973; 1979). Breeding females are generally unable to meet the metabolic demands of nursing and carrying the infant (Epple, 1978; Tardiff, 1994), and, in most groups, the father and subadult group members bear much of the burden of infant care (Cleveland & Snowdon, 1984). Infants are carried full-time by an adult, usually the father, for the first few weeks of life and sporadically for several months thereafter. In addition to carrying infants, fathers participate in a number of prosocial infant-directed behaviors, such as food provisioning and responding to infant distress calls (Kostan & Snowdon, 2002; Tardif, 1994).
Models of optimized breeding suggest that male and female tamarins may gain different benefits from adherence to monogamy (Dunbar, 1995). Males benefit most from a roving-polygyny strategy, in which they mate with multiple females. This mating strategy can double the number of offspring a male can potentially father, contributing to improved reproductive success (Dunbar, 2010). Females, on the other hand, gain reproductive benefits from monogamy. Females can successfully raise a greater number of offspring with parental involvement from the male, and males are more likely to coparent when paternal probability is high (Trivers, 1972). By mating with one male, she increases the likelihood of cooperative parenting and reduces the personal resource cost of each infant (Dunbar, 2010). Thus, males and females may express differences in the degree to which they conform to monogamy. To evaluate these differences, we examined the degree to which cotton-top tamarins expressed a preference for a monogamous pair mate or a novel individual.

While, to our knowledge, no studies have investigated this explicitly, data from a phonotaxis experiment suggests that male and female cotton-top tamarins may express differential patterns of partner preference. Miller and colleagues (2001) placed cotton-top tamarins in a maze with two arms extending from a central chamber. A loudspeaker was placed at the end of each arm. At the start of the experiment, one of the speakers played back a recorded call produced by an individual of the opposite sex (either the tamarin’s bonded pair mate, a familiar conspecific, or a novel tamarin) and the other speaker played an opposite-sex call produced by a different individual (from one of the aforementioned categories). Subsequent to these playbacks, the tamarin was allowed to roam freely in the maze and could approach either speaker. Preference for calls was determined by the speaker that was first approached by the focal tamarin. Miller and colleagues (2001) reported a sex difference in call type preference. Specifically, females preferentially approached speakers playing the vocalizations of familiar tamarins, with their mate being preferred over all other callers. In contrast, males preferred to
approach speakers playing calls produced by novel females rather than those produced by their mate. In sum, male cotton-top tamarins appeared to exhibit a novelty preference that was not shared by their female counterparts in the context of hearing recorded vocalizations.

It is unclear how well the phonotactic data approximate tamarin behavior when conspecifics are physically present. In the Miller et al. (2001) experiment, the tamarins approached a source emitting a single social cue, a contact vocalization. Social interactions with conspecifics, on the other hand, involve a variety of social cues. Tamarins must interpret and react to visual and olfactory information in addition to a diverse set of auditory signals. Thus, while the phonotactic data may provide some insight regarding the presumed partner preference of this species, the extent to which the reported behaviors will generalize is unclear.

We are unaware of any experimental investigations involving cotton-top tamarin partner preferences in the presence of conspecifics. However, some insights into the likely behavioral patterns are available from studies of other tamarin species (Buchanan-Smith & Jordan, 1992; Epple, 1990; Inglett, French & Dethleffs, 1990). These investigations indicate that partner preference is situational and changes according to social context. Specifically, visual access between animals appears to modulate partner preference, as the line of sight between individuals influences the allocation of time spent with others.

Several studies have demonstrated that other tamarin species prefer spending time with their bonded pair mate rather than an unfamiliar conspecific when all members of the triad share visual access to one another. In a study of partner preference in saddle-backed tamarins (Sanguinis fuscicollis), Epple (1990) placed three mesh cages, each housing a single saddle-backed tamarin, into a testing room. The central cage housed the focal animal and was connected via mesh tunnels to each of the other cages. The focal monkey’s bonded mate and an unfamiliar member of the opposite sex were each held in one of the attached cages. During testing, the focal monkey could travel through the tunnels to investigate either of the other individuals. All three
animals had continuous, unobstructed visual access to each other through the caging and tunnels during testing. Data was collected in 30 minute sessions that were divided into ten second increments. The author reported that male and female saddle-back tamarins spent more time in close proximity to their mate’s cage than the unfamiliar tamarin’s cage. Although Epple (1990) does not report first approach data, the dependent measure of partner preference used by Miller et al. (2001), she found a sex difference in the number of overall approaches the focal tamarin made towards other members of the triad. Males made a significantly higher number of approaches towards their mate’s cage than the unfamiliar tamarin’s cage. In contrast, there was no statistically significant difference in the number of approaches made by females towards the mate versus the unfamiliar tamarin. Contrary to Miller et al.’s study with cotton-top tamarins, these data suggest that male tamarins, rather than females, may show a familiarity bias, but that both males and females prefer close contact with a mate relative to an unfamiliar tamarin.

A related species, red-bellied tamarins (*Saguinus labiatus*), also display similar patterns of behavior. Buchanan-Smith and Jordan (1992) placed three cages adjacent to one another. A focal red-bellied tamarin was housed in the center cage, with its mate and an opposite-sex unfamiliar tamarin located in the adjacent cages. The central cage was fitted with two nest boxes, one on each side of the cage, and the authors measured time spent in each nest box as an indicator of the focal tamarin’s preference for the individual in the adjacent cage. The cages were designed such that wooden screens could be inserted into the central cage that prevented visual access between the two end cages and from one side of the central cage to the other. Animals were housed in the apparatus for two days before data collection began, and data was recorded over sessions lasting two hours in duration. Time spent in each half of the central cage and the frequency of affiliative and agonistic behaviors were analyzed. Consistent with the data from saddle-back tamarins, when the red-bellied tamarins had unobstructed visual access, both males and females spent more time in proximity to their mate than to unfamiliar tamarins. However,
when visual access was occluded, the focal tamarin showed no preference for its mate relative to the unfamiliar tamarin. This suggests that the familiarity bias observed in saddle-back tamarins may depend on the social context.

Partner preference data from golden lion tamarins (Leontopithecus rosalia) indicates modifications to the social context can result in changes in the expression of partner preference. Inglett, French and Dethlefs (1990) allowed focal tamarins to explore a T-shaped maze with a mate and an unfamiliar tamarin located on opposite arms of the maze. During some trials, an opaque partition was inserted into the center of the T-maze, such that visual access between the arms of the maze was disrupted (though access to both sides of the maze remained unrestricted for the focal monkey). Thus, the individuals at the ends of the maze could not observe the focal monkey interacting with the individual on the opposite end of the maze. Likewise, with the partition in place, the focal monkey could not see from one side of the maze to the other. Its visual access was restricted to the arm of the maze, and subsequently only the monkey at the end of that arm, closest to the focal monkey’s position at any given time. To observe the other animal, the focal monkey would have to travel around the barrier to the other arm of the maze, at which point no longer it no longer had visual access to the arm from which it came. When the partition was not in place, all three animals had unobstructed visual access to each other. Consistent with the aforementioned findings from saddle-back and red-bellied tamarins, both male and female golden lion tamarins spent significantly more time in proximity to their mates when the visual access between the three animals was unoccluded. Once the partition was in place, however, the amount of time spent in proximity to the unfamiliar tamarin increased significantly for both males and females.

Taken together, these studies present a clear pattern of behavior in several tamarin species, yet several open questions regarding partner preference in cotton-top tamarins remain. First, do cotton-top tamarins to behave differently than other species of tamarins, as the
phonotactic data would suggest (Miller et al., 2001)? The phonotactic data did not assess tamarin preferences in the presence of conspecifics. It is possible, that when cotton-top tamarins interact with physically present conspecifics, their behaviors may resemble those reported for other tamarin species. Differences in the social behavior between species may also result in differential expression of partner preference. Studies of social behavior in golden lion tamarins (Inglett, French, Simmons & Vires, 1989) and cotton-top tamarins (Snowdon & Pickhard, 1999) have indicated differential rates of male and female aggression between the species. If these species differ in the expression of aggression, they may also differ in their expression of partner preference. A final explanation may lie in the methodological differences between the cotton-top tamarin study and aforementioned studies with other tamarin species. Miller et al. (2001) used first approach as an indicator of tamarin preference whereas Epple (1990), Buchanan-Smith and Jordan (1992), and Inglett et al. (1990) used time spent in proximity to the other individual as a preference measure. While Epple (1990) reports sex based differences in the number of overall approaches, it is unclear whether an analysis of first approach data in other species would correspond to that observed by Miller et al. (2001).

A second unanswered question pertains to the changing partner preference observed in red-bellied and golden lion tamarins. In the aforementioned studies, both males and females were less likely to spend time in proximity to opposite sex strangers when in full visual access of their mate relative to when visual access was occluded. The cause of this phenomenon is unclear. Are changes to social preference modulated by the focal monkey’s visual access or do they change as a function of the mate’s visual access? In both the Buchanan-Smith & Jordan (1992) and the Inglett et al. (1990) study, the visual barrier(s) occluded one side of the apparatus from the other for all animals. Thus, while the bonded pair mate and unfamiliar conspecific could not see the focal animal interacting with the individual on the opposite side of the apparatus, the focal monkey also only had visual access to the monkey on one side of the cage at a time. Thus, it is
unclear whether the observed change in partner preference arises due to obstruction of the mate’s vision or obstruction of the focal tamarin’s vision.

Determining whose visual access causes the changes in the focal tamarin’s behavior may have implications for understanding tamarin cognition. In the simplest case, the tamarins may spend more time with the unfamiliar conspecific when visual access is disrupted because that is the only way it can observe the unfamiliar tamarin. When visual access is unoccluded, the focal tamarin can watch the unfamiliar tamarin while in proximity to its mate. However, with the occluder in place, the focal tamarin can only observe the unfamiliar tamarin by going around the visual barrier in the center of the apparatus, at which point it is in close proximity to the unfamiliar tamarin. Thus, in order to observe the unfamiliar tamarin, the focal tamarin must only spend time in proximity to it in the visually occluded condition. This account assumes that are few costs to investigating the unfamiliar conspecific.

Due to the nature of social monogamy, however, the focal tamarin may incur costs by investigating an unfamiliar member of the opposite sex. In this case, if the focal tamarin understands that the presence of an occluder prevents its mate from observing its behavior, then the focal tamarin may be more willing to investigate the unfamiliar tamarin when the occluder is in place. This supposes that the focal tamarin is capable of assessing the visual state of another individual and realizing that it is obstructed by the presence of the opaque barrier. The ability to recognize that another individual’s viewpoint is different than one’s own is referred to as level-1 perspective taking (Flavell, Everett, Croft, & Flavell, 1981). Individuals capable of level-1 perspective taking recognize what another individual can and cannot see based on features such as visual attention, line of sight, visual obstruction, and whether the individual has its eyes open. Successful performance in hiding or occlusion tasks is generally considered as evidence for an understanding of level-1 perspective, and humans demonstrate full mastery of this skill by age 3 (Flavell et al., 1981).
To the best of our knowledge, no one has yet investigated the role of perspective taking in the context of partner preference tasks. However, perspective taking abilities in other nonhuman primates has been the subject of much recent attention. All species of Great Apes, our closest nonhuman relatives, and some Old World monkey species appear capable of utilizing the perspective of others to optimize decision-making (Flombaum & Santos, 2005; Hare, Call, & Tomasello, 2001; Shillito et al., 2005; Tanner & Byrne, 1993). It is unclear however, if any species of New World monkey, which are more distantly related to humans, understands level-1 perspective taking. Monogamous breeding structures are more common in New World monkeys than Old World monkeys or apes, and perspective taking abilities could facilitate successful departures from monogamy in these species.

Experimental investigations of level-1 perspective taking in New World primates have been met with mixed results. Capuchin monkeys (*Cebus apella*, a non-monogamous New World species) fail to consider the visual perspective of others in a food competition task (Hare et al., 2003), although both capuchin and spider monkeys (*Ateles geoffroyi*) appear to account for the presence of a visual barrier when using conspecific’s gaze to locate a food reward (Amici et al., 2009). Data from common marmosets (*Callithrix jacchu*), a monogamous Callitrichid species closely related to tamarins, is particularly interesting. Burkhart & Heschl (2007) placed a focal marmoset in an apparatus with a more dominant conspecific. The focal animal was then given a choice between a food reward visible to the dominant conspecific and a food reward that was hidden from the dominant animal. Consistent with level-1 perspective taking, the marmosets consistently chose the food that was not visible to the dominant animal. A further analysis of the data, however, found that the marmosets may have been choosing on the basis of the dominant’s gaze not the dominant’s visual perspective. Thus, it is unclear whether marmosets are utilizing perspective taking abilities or associative learning when making their choice.
A more basic form of joint attention, gaze following, is thought to be a subcomponent of level-1 perspective taking (Emery, 2000). Unlike level-1 perspective taking, which presumes an understanding that knowledge states differ between individuals, gaze following can be explained by associative learning. No species of New World monkey has exhibited convincing evidence of level-1 perspective taking, but many New World primates, including cotton-top tamarins, show evidence of gaze following (Burkhart & Heschl, 2006; Itakura, 1996; Rosati & Hare, 2009; Vick & Anderson, 2000). Cotton-top tamarins co-orient their gaze with conspecifics (Neiworth, Burman, Basile, & Lickteig, 2001) and utilize gaze to predict future actions in others (Santos & Hauser, 1990). Thus, while tamarins may not exhibit evidence of level-1 perspective taking, they appear to glean information from the gaze of others.

The four experiments discussed in this thesis have been designed to explore two main questions. First, we explored the discrepancy between the phonotaxis data from cotton-top tamarins and the partner preference data produced by closely related species. Experiment 1 was designed to examine whether a familiarity bias exists for cotton-top tamarins in the presence of conspecifics. In this experiment, the focal tamarin explored a Y-shaped maze (See Figure 2-1) housing a bonded pair mate on one end and an unfamiliar conspecific on the other. The focal tamarin was allowed to roam the maze for 120 seconds, and the time spent in each arm was measured as an indicator of preference. If a familiarity bias exists, then we predicted that the focal tamarins would exhibit sex differences in their willingness to approach and spend time with the unfamiliar tamarins.

In Experiment 2, we manipulated the social context by disrupting visual access between the focal monkey, the mate, and the unfamiliar monkey. In this manner, we investigated whether cotton-top tamarins exhibit context dependent partner preference akin to that observed in other species. This also allowed us to determine if the familiarity bias found by Miller et al. (2001) would manifest when the tamarins no longer had visual access to each other. An opaque barrier
was placed between the arms of the maze to preclude the focal monkey from seeing from one side of the maze to the other. Likewise, the mate was unable to view the focal tamarin’s interactions with the unfamiliar conspecific and vice versa. As in previous experiments with other species (see above), the data from this experiment was compared with that from Experiment 1 to assess changes in partner preference. Deviations from the patterns of partner preference observed in Experiment 1 would suggest that social context plays a role in the expression of partner preference.

Having established that tamarin partner preference depends, at least in part, on the visual access among conspecifics, Experiment 3 was designed to explore whether that effect was due to a disruption in the focal monkey’s visual access or the mate’s visual access. In Experiment 3, we differentially manipulated the mate and the focal monkey’s visual access. In this experiment, the mate retained full visual access to both the focal and the unfamiliar monkey during the course of each trial. Except upon entry of the maze, the focal monkey no longer had full visual access to both arms of the maze at any given time. By erecting an opaque occluder along the arm of the Y-maze that housed the mate, the focal monkey could no longer see the unfamiliar monkey from the arm of the maze that housed the mate. Thus, as in Experiment 2, in order to observe the unfamiliar monkey, the focal monkey was forced to leave the arm of the maze in which it could see the mate and enter the opposite arm of the maze. This experiment was designed to replicate the experience of Experiment 1 (full visual access) for the mate and the experience of Experiment 2 (occluded visual access) for the focal monkey (when on the mate’s side of the maze). If the data from Experiment 3 resemble that of Experiment 2, it would suggest that the focal monkey’s visual access to its mate modulates the focal monkey’s behavior in this social preference task. However, if the mate’s visual access modulates changes in the focal monkey’s social preference, then we should expect the focal monkey’s behavior to resemble that observed in Experiment 1 in which there was no occluder present.
If the focal monkey modulates its partner preference on the basis of the mate’s visual access, we can make two predictions. The first is that the focal monkey will prefer the mate relative the unfamiliar monkey in situations in which the mate has unrestricted visual access to the focal monkey’s behavior. Experiment 3 was designed to test this hypothesis. The second prediction is that the focal monkey will exhibit an increased preference for unfamiliar monkey in conditions in which the mate’s visual access is obstructed. The fourth experiment was designed to test this hypothesis. In Experiment 4, as in Experiment 3, the focal monkey’s visual access and the mate’s visual access were manipulated differentially. However, contrary to Experiment 3, in Experiment 4 the focal monkey retained full visual access while the mate’s visual access was occluded. If the focal monkey’s partner preference is influenced by disruptions to its mate’s visual access, the focal monkey should behave as it did in Experiment 2 (full visual occlusion). If the changes in the focal monkey’s partner preference stem from disruptions to its own visual access, however, the data should resemble that seen in Experiment 1 (full visual access). In this regard, the data from Experiment 4 should contrast with that seen in Experiment 3.
Chapter 2

Experiment 1

Methods

Subjects

Ten cotton-top tamarins (five males and five females) participated in the experiment. All monkeys were born at the New England Regional Primate Research Center in Southborough, Massachusetts and were brought to The Pennsylvania State University in June 2005. The tamarins are housed in mated, opposite sex pairs in a single colony room. The monkeys have been paired with the same cagemate since their arrival. During the course of data collection, physical injuries required two bonded pairs of subjects to be separated for extended periods of time by a clear, Plexiglas barrier. These pairs maintained full visual access to each other at all times and were granted physical access to each other for limited periods of time. All subjects had previous experience with a Y-maze apparatus but no previous experience with the current experimental paradigm. Use and care of the tamarins conformed to the rules and regulations of the Institutional Animal Care and Use Committee at the Pennsylvania State University.

Apparatus

Subjects were tested in a Y-maze constructed from a wood frame with transparent Plexiglas panels on the top and bottom of the maze. White foam board panels were placed beneath the Plexiglas on the bottom of the maze to provide an opaque floor. The sides of the
maze were constructed of wire mesh (see Figure 2-1). Visual access was unobstructed through the mesh sides, ensuring that the focal animal had visual access to all parts of the maze from any position within the apparatus.

The maze was elevated three feet above the ground and consisted of three compartments: a holding area and two approach arms. The holding area (30cm x 30cm x 30cm) was located at the base of the approach arms (91cm x 30cm x 30cm), which extended at 45° angles from the holding area. A removable transparent Plexiglas barrier prevented the focal animal from entering the maze until the experiment began. The terminal ends of the arms of the maze were covered
with a thin wire mesh that allowed for visual, auditory, and olfactory communication between individuals on either side while limiting physical contact.

During each trial, the focal subject’s mate and the unfamiliar tamarin were placed at the opposite terminal ends of the Y-maze. The mate and the unfamiliar tamarin remained in their transport boxes (30cm × 23cm × 30cm), which were covered by wire caging on the front and top, transparent Plexiglas on the sides and a metal door in the rear. The transport boxes were aligned with the terminal ends of the Y-maze such that the wire-mesh front was adjacent to the wire-mesh terminal end of the Y-maze arms, thereby allowing visual access to the focal tamarin inside the maze.

**Procedure**

Experimental trials were conducted with triads consisting of a focal tamarin, its mate, and an unfamiliar tamarin of the opposite sex. Each triad was assessed for kin relationships so that no genetically related individuals belonged to the same triad. In order to limit the extent of previous contact between (non-mated) members of the triad, animals housed in adjacent cages in the colony room were never in the same triad. Each member of the ten bonded pairs appeared with two different unfamiliar individuals (on the opposite arm of the mate), resulting in a total of 20 unique triads. Every triad was tested twice, counterbalancing the side of the mate and unfamiliar tamarins.

Prior to the start of a trial, transport boxes holding the mate and unfamiliar monkey were placed at the terminal ends of the Y-maze arms. Once the non-focal animals were in place, an experimenter covered the terminal end of each arm of the maze with opaque foam board (31.5cm x 51.5cm). This prevented the focal animal from having visual access to the other individuals until the start of the experiment. The focal animal was then brought into the experiment room
and given access to the holding area of the maze. Once the focal animal entered the holding area, the foam board occluders at the end of each approach arm were removed. Subsequently, an experimenter removed the transparent barrier from the holding area, and the focal animal was allowed to enter and explore the maze. Once the focal animal left the holding area, the transparent barrier was replaced, ensuring that the focal animal did not leave the arms of the maze until the end of the trial.

Focal animals were allowed to freely explore the Y-maze for 120 seconds upon entry into the maze. During this time, the focal animal’s movements were recorded via a digital video camera suspended above the maze. After 120 seconds had elapsed, the barrier to the holding area was removed, allowing the focal animal to return to its transport box, and the mate and unfamiliar tamarin were removed from the room.

Data analysis

Video data from the experiment were analyzed using proprietary software developed for this project. Data analysis began at the point that the focal tamarin left the holding area and continued for 120 seconds. We recorded the first arm of the maze the focal monkey entered, total time spent on each side of the maze, time spent within one body length of the end of each arm (i.e., close proximity), and the number of times the focal monkey crossed from one arm to the other.

Results

When full visual access was available, focal tamarins preferred spending time with their mate relative to the unfamiliar tamarin. Results from a paired samples t-test indicated that over
In the course of the two minute trial, focal tamarins spent significantly more time in the arm housing the mate ($M = 69.4s$, $SD = 20.60$) relative to the arm housing the unfamiliar tamarin ($M = 50.6s$, $SD = 20.60$; $t(39) = 2.88$, $p = .006$; See Figure 2-2). Of the ten monkeys tested, seven spent more time with their mate than the unfamiliar monkey (See Figure 2-3). The time spent within close proximity of the mate and unfamiliar monkey was calculated by dividing the time the focal monkey spent within one body length of the end of the arm by the total time spent in that arm. Tamarins exhibited a significant preference for being within close proximity to their mate ($M = .53$, $SD = .28$) and the unfamiliar tamarin ($M = .38$, $SD = .28$; paired samples t-test; $t(39) = 2.99$, $p = .005$; See Figure 2-4).

Figure 2-2: Time spent with the mate versus the unfamiliar monkey overall and by sex in Experiment 1.
An analysis of sex differences was conducted to determine whether individuals of either gender were more likely to spend time with their mate or the less familiar individual. A repeated
measures ANOVA revealed no significant difference in the proportion of time males ($M = 66.7s$, $SD = 23.02$) and females ($M = 72.1s$, $SD = 18.05$) spent in the arm proximal to the mate, $F(1,8) = .572, p = .471$. Males ($M = .53, SD = .29$) and females ($M = .53, SD = .28$) also did not differ significantly in the proportion of time they spent in close proximity to their mate ($F(1,8) = .001, p=.97$) or the unfamiliar monkey; ($M_{Males} = .37, SD_{Males} = .28; M_{Females} = .40, SD_{Females} = .30; F(1,8) = .04, p = .844$).

In Experiment 1 (and subsequent experiments) the side of the maze on which the mate and unfamiliar monkeys were placed was counterbalanced between trials. Therefore, if the tamarins exhibited a systematic preference for one individual relative to another, we would expect focal monkeys to first approach both the left and right sides of the maze 50% of the time. Of the ten monkeys tested, however, nine demonstrated a preferred side of first approach (i.e., a side bias; See Figure 2-5). A one-sample binomial analysis of first approach data across all trials in all experimental conditions found a significant side bias, $p = .021$. Differences in the overall time spent on each side, however, were not significant, (paired samples t-test, $M_{Left} = 56.3s$, $SD_{Left} = 22.38; M_{Right} = 63.7s$, $SD_{Right} = 22.38; t(39) = -1.05, p=.302$). Thus, when comparing the overall time spent on each side, the monkeys did not appear to exhibit a side bias.
Experiment 1 was designed to assess the presence of a familiarity bias in cotton-top tamarin partner preference. In Miller et al.’s (2001) phonotactic experiment, an analysis first approach data indicated that males preferred the vocalizations of novel conspecifics while females preferred the vocalizations of their mates. However, the first approach data from Experiment 1 found no systematic preference for the mate or the unfamiliar monkey. Rather, the overall amount of time spent with each individual appeared to be more informative and in line with similar studies conducted with related species (e.g., Epple, 1990; Buchanan-Smith & Jordan, 1992; Inglett et al., 1990). When visual access among animals was unrestricted, both males and females preferred spending time in the arm of the maze proximal to their mate. Both sexes also

**Discussion**

Figure 2-5: Percentage of first approaches towards the preferred side for each individual across all trials in Experiments 1, 2, 3, and 4.
spent a significantly greater proportion of their time in close proximity to the mate compared to the unfamiliar monkey. These data are not consistent with the findings reported in previous phonotaxis work (Miller et al., 2001) in that both males and females exhibited a preference for their mate over an unfamiliar tamarin. Thus, the novelty bias displayed by the males in the phonotaxis experiment did not extend to situations in which both conspecifics were physically present.

Data from other tamarin species has found that obstructions to visual access can result in the elimination of a previously observed partner preference (Buchanan-Smith & Jordan, 1992; Inglett et al., 1990). Having found in Experiment 1 that cotton-top tamarins, like other species of tamarin, display a significant preference for the mate when visual access is unoccluded, we investigated whether manipulations to the visual access between individuals would influence cotton-top tamarins’ displayed pattern of partner preference. To this end, we occluded visual access between the sides of the maze in Experiment 2.
Chapter 3

Experiment 2

Methods

Subjects

The subjects were the same ten cotton-top tamarins as in Experiment 1 and same triads were used as in Experiment 1.

Apparatus

A white Tyvek occluder (105 cm x 101 cm) was placed between the arms of the maze (See Figure 3-1). The occluder was attached to the crook of the maze and extended to the wall behind the maze. With the occluder in place, visual access between both sides of the maze was unavailable. The mate was only able to see the focal monkey when the focal monkey was in the same arm, and likewise for the unfamiliar individual on the opposite side. As a result, the mate did not have visual access to the unfamiliar monkey, nor could it see the focal monkey when it was located in the distal arm of the maze. Similarly, the focal monkey did not have visual access to the opposite arms of the maze. The focal monkey could gain visual access to both arms of the maze only at the point of entry from the holding area.
Procedure

The procedure was identical to that in Experiment 1. As in Experiment 1, each triad was tested twice, counterbalancing the side of the mate and the unfamiliar triad and a total of 40 trials were conducted.

Data analysis

Data analysis procedures were identical to those in Experiment 1.
Results

With the visual occluder in place, the focal monkey no longer exhibited a preference for its mate. Results from a paired samples t-test indicated no significant difference in the amount of time the focal monkey spent with its mate ($M = 58.35s, SD = 28.48$) and the unfamiliar monkey ($M = 61.09s, SD = 28.46$, $t(39) = -.251, p = .80$; See Figure 3-2). Of the ten monkeys that participated in Experiments 1 and 2, seven spent less time with their mate when visual access was occluded (Experiment 2) relative to when visual access was unoccluded (Experiment 1; See Figure 3-3). The same seven individuals spent more time with the mate than the unfamiliar individual in Experiment 1. A repeated measures ANOVA indicated a marginally significant effect of occluder on the time spent with the mate in the full visual access condition (Experiment 1) compared to time spent with the mate in the occluded condition (Experiment 2); $F(1,9) = 4.37, p = .07$. If we restrict our analysis to the seven monkeys that demonstrated a preference for the mate in Experiment 1, this difference reaches statistical significance (repeated measures ANOVA, Greenhouse-Geisser corrected, $F(1,6) = 55.92, p < .001$). As in Experiment 1, focal monkeys in Experiment 2 preferred to spend time in close proximity (within one body length) to their mate ($M = .54, SD = .25$) relative to the unfamiliar monkey ($M = .44, SD = .27$). This difference was marginally statistically significant, $t(39) = 1.87, p = .07$ (See Figure 3-4). A repeated measures ANOVA found no significant main effect of the occluder on the proportion of time spent in close proximity to the mate ($F(1,9) = .01, p = .93$) or the unfamiliar tamarin ($F(1,9) = 1.46, p = .26$) between Experiment 1 and Experiment 2.
Figure 3-2: Time spent with the mate versus the unfamiliar monkey overall and by sex in Experiment 2.

Figure 3-3: Time spent with the mate by individual in Experiment 1 (No occluder) compared to Experiment 2.
The change in partner preference observed between Experiment 1 and Experiment 2 does not appear to be sex dependent. Males \((M = 64.65 \text{ s}, SD = 22.832)\) and females \((M = 59.7 \text{ s}, SD = 33.41)\) did not differ significantly in the amount of time spent with their mate, \(F(1,8) = .289, p = .61\) (See Figure 3-2). A mixed model ANOVA also found no significant differences in the proportion of time males \((M = .56, SD = .23)\) and females \((M = .51, SD = .27)\) spent in close proximity to the mate \((F(1, 8) = .17, p = .67)\) or in close proximity to the unfamiliar monkey \((M_{Males} = .46, SD_{Males} = .25; M_{Females} = .42, SD_{Female} = .29; F(1,8) = .18, p = .69)\).

**Discussion**

When all individuals had full visual access to each other in Experiment 1, the focal monkey demonstrated a significant preference for its mate over the unfamiliar monkey. This partner preference disappeared and the focal monkey spent nearly equal time with the mate and the unfamiliar monkey when visual access between the sides of the maze was occluded. This
suggests that partner preference in cotton-top tamarins, like golden lion and red-bellied tamarins, is not static (Inglett et al. 1990; Buchanan-Smith & Jordan, 1992). Rather, manipulations to the visual access between conspecifics result in a change in partner preference.

In Experiment 2, focal monkeys spent a smaller proportion of time in close contact with their mate and a greater proportion of time in close contact with the unfamiliar than in Experiment 1. However, they still preferred close contact with their mate over the unfamiliar tamarin, and this difference trended towards significance. This suggests that while the focal monkeys may be more willing to spend time on the unfamiliar animal’s side of the maze, this does not extend to close investigation of the unfamiliar tamarin. One potential explanation for this pattern of behavior involves mechanisms of communicating reproductive status in cotton-top tamarins. Cotton-top tamarins communicate a variety of sexual information via olfactory cues (Washbaugh & Snowdon, 1999). It is possible focal tamarins refrained from close investigation of the unfamiliar tamarin in order to avoid scent cues that could later be detected by the mate.

On the basis of Miller et al.’s (2001) phonotaxis data, we predicted female cotton-top tamarins might exhibit a familiarity bias while males would exhibit a novelty bias. We did not find this to be the case. No significant sex differences in partner preference were found in Experiments 1 or 2. These data indicate that the results reported in the phonotaxis experiment (Miller et al, 2001) did not generalize to situations in which other monkeys were physically present.

In comparing the partner preference in Experiment 1 to Experiment 2, we found that when the visual access between individuals was restricted in Experiment 2, the bias for the mate displayed in Experiment 1 was eliminated. In Experiment 2, the barrier erected between the arms of the maze disrupted visual access between all three monkeys. Thus, we are unable to conclude if the focal monkey’s partner preference changed because its own visual access was disrupted or if its partner preference changed because its mate’s visual access was disrupted. If the focal
monkey is accounting for its mate’s visual access when it makes social decisions, it may be utilizing a rudimentary form of perspective taking. To investigate this possibility, in Experiment 3, we disrupted the focal monkey’s visual access (somewhat similar to the experience in Experiment 2), while leaving the mate’s visual access intact (as in Experiment 1).
Chapter 4

Experiment 3

Methods

Subjects

Five of the ten monkeys, three males and two females, which participated in Experiments 1 and 2 participated as focal monkeys in Experiment 3. As a practical consideration, we restricted our sample to monkeys that reliably entered the transport box from their home cage. This was done to reduce the time required for data collection and to decrease the burden on the colony. Due to the reduction in sample size, monkeys were exposed to different triads than used in Experiments 1 and 2. As in previous experiments, no monkeys in any triad shared kin relationships, although monkeys housed in adjacent cages were run as part of the same triad. Subsequent to the completion of Experiment 2 and prior the beginning of Experiment 3, the two mated pairs that had been separated were reunited. As in Experiments 1 and 2, each member of the five bonded pairs appeared with two different unfamiliar individuals (on the opposite arm of the mate), resulting in a total of ten unique triads. Every triad was tested twice, counterbalancing the side of the mate and unfamiliar tamarin, for a total of 20 trials.

Apparatus

A white Tyvek occluder was attached to the arm of the maze in which the mate was placed (See Figure 4-1). The occluder extended from the crook of the maze to the terminal end of
the arm housing the mate. The occluder blocked the visual access of the focal monkey to the opposite arm and the unfamiliar individual while it was on the side of the mate, though the mate’s visual access to the opposite side (and the unfamiliar individual) was undisturbed. Thus, the mate’s visual access was the same as that in Experiment 1 (full visual access).

![Y-maze apparatus in Experiment 3. The red bar represents the visual occluder, which was flush against the side of the maze on which the mate had been placed. In this example, the unfamiliar monkey is on the left side of the maze while the mate is on the right. From the focal monkey’s position in the maze, it could see the mate, but not the unfamiliar tamarin. The mate, on the other hand, had visual access to both members of the triad.]

**Figure 4-1:**

**Procedure**

In all other respects, the procedure was identical to Experiment 1 and Experiment 2.

**Data analysis**

Data analysis procedures were identical to those in Experiments 1 and 2.
Results

As in Experiment 1 (full visual access), a paired samples t-test indicated that focal tamarins preferred their mate ($M = 74.72, SD = 35.91$) relative to the unfamiliar tamarin ($M = 45.26s, SD = 35.92$), and this difference approached significance; $t(19) = 1.83, p = .08$ (See Figure 4-2). Four of the five tamarins tested in Experiment 3 spent more time with their mate than the unfamiliar tamarin, indicating the effect was widespread across our sample (See Figure 4-2). Unlike in Experiment 1 (full visual access) and Experiment 2 (full occluder), in Experiment 3, focal tamarins also demonstrated a significant preference for being in close contact to the cagemate ($M = .70, SD = .30$) over the unfamiliar tamarin ($M = .38, SD = .28; t(19) = 3.25, p = .004$; See Figure 4-3). Due to the smaller sample size and the lack of sex differences found in the previous experiments, sex differences were not analyzed in this condition.

Figure 4-2: Time spent with the mate versus the unfamiliar monkey by focal monkey in Experiment 3.
In order to assess the strength of the similarities of the partner preference across the first three experiments, a repeated measures ANOVA analyzed the effect of type of occlusion between Experiments 1, 2, and 3. In both Experiment 1 and Experiment 3, the focal monkey spent more time with the mate than the unfamiliar monkey, and there was no significance difference between the time spent with the mate in Experiment 1 (full visual access) and the time spent with the mate in Experiment 3 (focal occluded), $F(1, 4) = .41, p = .56$. The difference in time spent with the mate in Experiment 2 (full occluder) compared to Experiment 3 (focal occluded) approached significance ($F(1, 4) = 5.21, p = .085$; See Figure 4-4). This indicates that the partner preference exhibited in Experiment 3 is not significantly different than the partner preference exhibited in Experiment 1. As was the case with Experiment 1, however, Experiment 3 is compared to Experiment 2, in which the tamarins displayed no preference for the mate, the difference approaches significance.
Discussion

In situations in which focal monkeys are visible to their mate, the focal monkeys should spend less time with the unfamiliar tamarin compared to time spent with the mate. The pattern of data observed in Experiment 3 (focal occluded) conforms to this prediction. In both Experiment 1 (full visual access) and Experiment 3 (focal occluded), the mate had unobstructed visual access to the focal tamarin’s behavior. Accordingly, in both of these experiments, focal tamarins spent more time with their mate than the unfamiliar tamarin. This contrasts with patterns of behavior observed in Experiment 2 (full occluder), in which focal tamarins spent nearly equal time with their mate and the unfamiliar tamarin. Although visually, Experiment 3 most resembled Experiment 2 from the focal tamarin’s perspective, the focal tamarin’s behavior was most similar to its behavior in Experiment 1. Focal tamarins spent more time with its mate in Experiment 3 relative to Experiment 2.

These patterns of results suggest that the differences in partner preference seen between
Experiment 1 and Experiment 2 are unlikely to be caused by changes to the focal tamarin’s own visual perspective. Instead, changes in the mate’s visual perspective appear to motivate the observed change in partner preference. One potential explanation for these results is that focal tamarins are using level-1 perspective taking skills to evaluate the visual state of the mate and adjusting their partner preference accordingly. If cotton-top tamarins are capable of level-1 perspective taking, then we might expect them to spend more time investigating unfamiliar potential breeding partners in situations in which their mates cannot see them. While these data do not prove that tamarins are capable of level-1 perspective taking, they are consistent with this idea.

While the difference in time spent with the mate relative to the unfamiliar tamarin was more pronounced than that reported in Experiment 1 (full visual access), the difference only approached marginal significance. This is likely due to the reduced sample size used in Experiment 3. By increasing the sample, we hope to evaluate whether the failure to reach statistical significance is due to the size of the effect, which appears unlikely, or the low N.

All but one monkey preferred to spend time with the mate relative to the unfamiliar tamarin in Experiment 3. An analysis of the five individuals participating in the first three experiments found that two of the five monkeys spent more time with their mate in Experiments 1 and 3, in which their mate had full visual access to their behavior, compared to Experiment 2, in which the mate’s visual access was occluded (See Figure 4-5). If the monkeys are capable of level-1 perspective taking, we would expect this pattern to be more widespread throughout our sample. Before we dismiss the role of level-1 perspective taking, however, we should consider practical reasons that we may see this pattern of results as well. As noted above, our sample size in Experiment 3 was quite small. At this point, more data is needed to assess whether the discrepancy between data and theory is an artifact of our limited sample size. This will be the focus of future work.
Figure 4-5: Time spent with the mate in Experiment 1 (No occluder), Experiment 2 (Occluder) and Experiment 3 (Focal occluded) by individual. Total column reflects the overall mean time spent with the mate in each experiment.
Chapter 5

Experiment 4

Methods

Subjects

Five monkeys, 3 males and 2 females, were run as focal monkeys. Due to a death in our colony, a pair that participated in Experiments 1, 2 and 3 did not participate in Experiment 4. Three of the monkeys that participated in Experiments 1, 2, and 3 participated in Experiment 4. Two additional monkeys that participated in Experiments 1 and 2 were included in the sample (See Table 5-1). All other sampling procedures remained the same as those in Experiment 3.

Table 5-1: Monkeys participating in Experiment 1, 2, 3, and 4

<table>
<thead>
<tr>
<th>Focal monkey</th>
<th>Experiment 1 (no occlusion)</th>
<th>Experiment 2 (full occlusion)</th>
<th>Experiment 3 (focal occluded)</th>
<th>Experiment 4 (mate occluded)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bart</td>
<td>Yes</td>
<td>Yes</td>
<td>---</td>
<td>Yes</td>
</tr>
<tr>
<td>Elaine</td>
<td>Yes</td>
<td>Yes</td>
<td>---</td>
<td>Yes</td>
</tr>
<tr>
<td>George</td>
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<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Homer</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>---</td>
</tr>
<tr>
<td>Jerry</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Lisa</td>
<td>Yes</td>
<td>Yes</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Maggie</td>
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<td>Yes</td>
<td>---</td>
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</tr>
<tr>
<td>Marge</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>---</td>
</tr>
<tr>
<td>Milhouse</td>
<td>Yes</td>
<td>Yes</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Susan</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>
Apparatus

Occluders constructed of acoustic foam were placed on the pedestals housing the mate and unfamiliar monkey during previous experiments. The occluders consisted of two rectangles of acoustic foam (45 cm x 40 cm x 5 cm) attached in an L-shape (See Figure 5-1). To control for any confounding effect of the presence of the occluder, occluders were placed on both the mate’s side of the maze and the unfamiliar tamarin’s side of the maze. The occluder on the mate’s side of the maze was placed such that the visual access to the all but the closest arm of the maze was occluded. Therefore, the mate could only see the focal monkey when it was in the arm of the maze closest to the mate. The occluder placed on the unfamiliar tamarin’s arm of the maze was placed such that the unfamiliar tamarin had full visual access to the rest of the maze. The occluders abutted the terminal ends of the maze. To further ensure that the mate could not see the focal animal’s activity in the maze, opaque, white paper (22 cm x 28 cm) was attached to the side of the maze, such that, for functional purposes, the occluder extended 28 cm into the arm of each maze. This completely blocked visual access to the opposite arm of maze from all possible viewing angles available to the mate. With the occluders in place, the mate was unable to see any part of the maze except the arm on which it was housed. With the exception of the 28 cm at the end of the mate’s arm of the maze, the focal monkey’s visual access was unoccluded. This replicated Experiment 1 (full visual access) for the focal monkey while replicating Experiment 2 (occluded visual access) for the mate.
**Procedure**

In contrast to the previous experiments, in Experiment 4, the mate entered the room first and was positioned behind the occluder prior to any other members of the triad entering the room. This ensured that the mate did not have visual access to other members of the triad before the trial began. Once the mate was positioned and the occluder was in place, the unfamiliar tamarin and the focal tamarin were brought into the experiment room together and trials proceeded as in Experiment 1, 2, and 3.

In addition to the overhead camera, video cameras were positioned on the each side of the maze to record the behavior of the mate and unfamiliar monkey. Directional microphones were also positioned near the terminal ends of the maze to capture vocalizations produced by the mate and the unfamiliar monkey. Audio data was captured via a Marantz hard disk recorder.

*Figure 5-1:* Y-maze apparatus in Experiment 4. The red bars represents the extension of the visual occluder, which was flush against each the side of the maze. In this example, the mate is on the left side of the maze while the unfamiliar monkey is on the right.
Data analysis procedures were identical to those in Experiments 1, 2 and 3.

Results

After a preliminary analysis of the data was conducted, we terminated data collection before all planned trials had been completed. Of the five monkeys tested in Experiment 4, we collected complete data for four of them. For the remaining monkey, we collected data from two trials. As a result, we analyzed data from 18 trials rather than the expected 20 trials.

Focal animals spent significantly more time with the mate \( (M = 82.41, SD = 21.98) \) than the unfamiliar monkey \( (M = 37.58, SD = 21.98) \) in Experiment 4, \( t(17) = 4.33, p < .001 \) (See Figure 5-2). Four out of the five monkeys that participated in this experiment exhibited a preference for their mate relative to the unfamiliar monkey (See Figure 5-2). The difference between the time spent with the mate in Experiment 4 and Experiment 2 (full visual occlusion) was not significant (repeated measures ANOVA, \( F(3,9) = 2.02, p = .18 \); See Figure 5-3). Focal monkeys also spent a significant proportion of time in close proximity to the mate \( (M = .63, SD = .20) \) relative to the unfamiliar monkey \( (M = .45, SD = .27) \); \( t(17) = 2.22, p = .04 \); See Figure 5-4).
Figure 5-2: Time spent with the mate versus the unfamiliar monkey by focal monkey in Experiment 4.

Figure 5-3: Time spent with the mate versus the unfamiliar tamarin in Experiment 1, 2, 3 and 4.
We collected two measures as proxies for the monkeys’ arousal level across experiments. Vocalization rate was collected as an indicator of overall arousal level among the triad. The number of times the focal monkey crossed from one arm of the maze to the other served as an index of the focal monkey’s arousal. If arousal levels differed between experiments, we would expect to see significant differences reflected in these two measures. A repeated measures ANOVA, however, found no significant main effect of experimental condition on either the rate of vocalizations ($F(3,6) = 1.07, p = .43$) or rate focal monkeys crossed the maze (Greenhouse-Geisser corrected, $F(1,2) = 5.35, p = .14$).

**Discussion**

We predicted that, when the mate’s visual access was occluded, the focal monkey would show an increased preference for the unfamiliar monkey relative to when the mate’s visual access
was unoccluded. In Experiment 4, the focal monkeys’ behavior was inconsistent with these predictions. The focal monkeys exhibited a significant preference for the mate relative to the unfamiliar monkey despite the mate’s visual occlusion. This effect was robust across individuals.

It is unclear whether the monkeys’ behavior reflects a lack of perspective taking ability or methodological issues. Several methodological changes were made between Experiment 3 and Experiment 4. Rather than use a white Tyvek occluder, as we had in the other experiments, we used blue acoustic foam to occlude the mate’s vision. We made this choice in an effort to control for the effect of vocalizations between the animals. The acoustic foam, which was darker in color and surrounded the monkey on two sides, may have been more imposing than the Tyvek occluders. Cotton-top tamarins seek contact with known conspecifics when distressed (Kostan & Snowdon, 2002). If the animals found the foam occluder more distressing or threatening than the Tyvek occluders used in previous experience, they may display an increased preference for their partner in response. Additionally, unlike in the other experiments, in which the occluder was out of the reach of all members of the triads, the mate and unfamiliar monkey could reach the acoustic foam occluder and occasionally manipulated it during the course of the experiment.

During several trials, monkeys at the ends of the arms of the maze became interested in trying to detach the white paper from the side of the maze. If the monkeys are capable of level-1 perspective taking, manipulations to the visual occluder by the conspecifics may have made the occluder seem like an unreliable visual disruptor. If the focal monkey was not confident that the mate was unable to observe its behavior, it may behave as it did when the mate’s vision was unoccluded. Finally, these manipulations of the occluders were frequently noisy and occasionally appeared to startle the focal monkey. Thus, the increased preference for the partner may be a result of distress experienced by the focal monkey in response to these behaviors.

The addition of video and audio recording equipment may have also caused anomalous results in Experiment 4. In order to film the monkeys at the end of each arm, a camcorder on a
tripod and a microphone were placed in between the arms of the maze. While the equipment did not completely occlude the focal monkey’s visual access at any point in the maze, it did disrupt visual access between the arms of the maze. Turning on and synchronizing the additional recording equipment also resulted in longer total trial lengths, and triad members spent longer periods of time out of their home cages before the trials began. This additional stressor may have resulted in the focal monkey seeking the comfort of a familiar individual rather than investigating an unfamiliar conspecific.

Another possible explanation for the pattern of partner preference observed in Experiment 4 is that our monkeys may not have recognized the function of the visual occluder. As mentioned above, the occluder used in Experiment 4 was visually distinct from those used in previous experiments. While the data from Experiments 1, 2 and 3 suggest our monkeys recognized the effect of the Tyvek occluders on the mate’s visual access in those experiments, they may not have generalized this knowledge to the acoustic foam occluders used in Experiment 4.

Subsequent data collection in our lab may also explain the increased preference for the partner observed in Experiment 4. As part of an unrelated experiment, we have collected observational data on affiliative behaviors, such as grooming, play, and sexual contact, between pairs. Z-scores for the four individuals that exhibited a preference for the mate in Experiment 4 were above the colony mean (See Figure 5-5). This indicates that the monkeys chosen to participate in Experiment 4 may have shared particularly strong social bonds with their mate compared to other pairs in the colony. Interestingly, the one monkey who did not exhibit a mate preference in Experiment 4, Bart, scored below the mean on the measure of affiliative behavior.
Figure 5-5: Z-scores computed for the number of affiliative acts an individual displayed towards its partner.
Chapter 6

General Discussion

Summary of Findings

In Experiment 1, focal cotton-top tamarins were given 120 seconds to explore a Y-maze with the focal animal’s mate and an unfamiliar conspecific of the opposite sex housed next to each terminal end of the maze. In this experiment, all animals had unlimited visual access to each other. Based on time spent in each arm of the maze, both male and female focal animals showed a significant preference for their mate relative to the unfamiliar animal. In Experiment 2, a visual occluder was erected between the arms of the maze. The procedure was identical in all other regards. Once visual access between members of the triad was disrupted, the tamarins no longer displayed the partner preference observed in Experiment 1. Experiments 3 and 4 were designed to determine whether the visual access of the focal monkey or its mate influenced the pattern of results observed in the first two experiments. In Experiment 3, an occluder attached to one arm of the maze disrupted the focal monkey’s visual access (when on the side of the mate) while the mate retained full visual access throughout the experiment. As in Experiment 1 (with full visual access), focal monkeys exhibited a strong preference for the mate in Experiment 3. In Experiment 4, the mate’s visual access was occluded while the focal monkey’s visual access was unrestricted. In this experiment, focal monkeys also exhibited a significant preference for the mate. From this pattern of results, we conclude that the expression of partner preference is dependent on the degree of visual access between individuals.

In Experiments 1 and 2, our findings were consistent with patterns of partner preference observed in experiments with other tamarin species. Saddle-back (Epple, 1990), red-bellied
(Buchanan-Smith & Jordan, 1992) and golden lion tamarins (Inglett et al., 1990) evinced a clear preference for the bonded pairmate relative to an unfamiliar conspecific when members of the triad had unrestricted visual access to each other. Consistent with our findings, the golden lion and red-bellied tamarins’ preference for the mate was eliminated when visual access between members of the triad was restricted. This lends further supporting evidence that cotton-top tamarins, like other tamarin species, alter their partner preference due to changes in visual access among conspecifics.

One notable difference between the experimental paradigms used in our experiments and those with red-bellied tamarins (Buchanan-Smith & Jordan, 1992) and golden lion tamarins (Inglett et al., 1990) was the length of time the animals were in the testing situation. Inglett et al. (1990) collected data in multiple trials spanning 30 minutes each. Buchanan-Smith and Jordan (1992) altered the monkeys’ housing, allowing them to stay in the experimental apparatus for multiple days and collecting data in sessions that spanned several hours. By contrast, our tamarins only explored the maze for two minutes, yet the pattern of behavior we observed mirrored that of the animals in longer recording sessions. Thus, our study indicates that tamarin partner preferences are evident in a shorter timespan than previously known. While longer periods of data collection may have allowed for the emergence of more robust effects, our findings confirm that enduring social choices in primates may be achieved over relatively short timescale, a phenomenon that is true for humans as well (e.g., Ambady & Rosenthal, 1992).

Theories of social intelligence, such as the Machiavellian intelligence hypothesis, posit that the sophisticated cognitive skills exhibited by humans may have developed in response to the selective pressures inherent in living in complex social groups (Byrne & Whiten, 1988). Consequently, the roots of these abilities may be evident in other group-living species that similarly contend with the intricacies of navigating multiple social relationships. The robust nature of the tamarins’ partner preference observed in our data, which is consistent with data from
multiple closely related species, suggests that these underlying patterns of partner preference are likely to be shared, i.e., homologous, across closely related species. That these behaviors are reflected in the deceptive mating behaviors seen in humans suggests that the human behaviors may have developed from a shared cognitive lineage.

The results of our study were inconsistent with the previous phonotaxis study conducted with the same species (Miller et al., 2001). In that study, males approached speakers playing calls produced by novel members of the opposite sex and females preferentially investigated speakers playing calls produced by their mate. Our data indicate that both males and females preferred the familiar conspecific (i.e., the mate) when all animals had full visual access to one another. Given that focal individuals had no visual access to conspecifics while in the phonotaxis apparatus, the closest approximation of this situation in our study is Experiment 2, in which visual access among triad members was occluded. Thus, while we might have expected the greatest degree of consistency between the Miller et al. (2001) results and ours to occur when visual access was most disrupted among individuals (i.e., in Experiment 2), tamarins of both sexes spent nearly equal time with the mate and the unfamiliar monkey in those circumstances.

Several methodological differences may explain the disparity between our data and the Miller et al. (2001) data. Perhaps the most obvious difference is that, in our experiments, focal tamarins investigated physically present conspecifics whereas in the Miller et al. (2001) work, the tamarins investigated speakers producing combination long call vocalizations. Physically present conspecifics are capable of producing communicative signals, such as body postures and olfactory cues, which playbacks do not capture. Furthermore, physically present individuals can create dynamic interactions. The monkeys at the ends of the maze can respond, via scent marking, affiliative gestures, agonistic behavior, or vocalizations, to the focal monkey’s approach or departure. The unfamiliar monkey could also interact visually and vocally with the mate in Experiments 1 and 3. In this sense, the presence of the triad members, created a social
environment that could vary both within trials and between trials. In contrast, in the phonotaxis study, the stimuli were played at the onset of the trial and ceased before the focal animal entered the experimental apparatus. In this sense, the social environment remained stable over the course of the trial.

The characteristics of the vocalizations used by Miller et al. (2001) may also explain the differences observed between the two studies. They played a combination long call (CLC), which are known to be elicited in a variety of circumstances. They are typically produced when an individual is isolated from group members (Snowdon, Cleveland, & French, 1983). CLCs also appear to have a role in pair bonding and mating (Ghazanfar & Hauser, 2001) and sexual advertising (Cleveland & Snowdon, 1982). Additionally, CLCs have been found to elicit increased aggressive behavior when produced by an unfamiliar conspecific (Snowdon, Cleveland, & French, 1983). In the context of our experiments, CLCs were very rare, with only five being produced in 118 trials (across all four experiments). Thus, by playing the CLCs, Miller et al. (2001) may have created expectations regarding the social situation the focal monkeys were likely to encounter. Studies of cotton-top tamarins have found sex differences in vigilance behaviors, and it is possible that, given potentially aggressive context in which CLCs are produced, the sex differences that are reflected in Miller et al.’s (2001) first approach data may be related to the vigilance response (Savage, Snowdon, Giraldo, & Soto, 1996).

The differential results in the Miller et al. (2001) study and our own may also be due to different dependent measures. In this context of the Miller et al. (2001) paradigm, the direction of the monkey’s first approach was found to be the most informative measure of preference. Given that the stimuli ceased before the focal animal entered the maze, the monkeys were assumed to approach the speaker they deemed the most interesting first. In our paradigm, with physically present conspecifics, the time spent in each arm of the maze proved to be the most informative measure. Because our stimuli (i.e., the conspecifics), continued for the duration of the trial, time
spent in proximity to either animal was taken to indicate a preference for that animal in the moment.

Additionally, an analysis of the first approach data across all four of our experiments revealed a significant side bias. This may be a manifestation of the hysteresis effect, in which, in low risk environments, cotton-top tamarins (among other species) rely on previously used motor plans rather than generate new ones (Weiss & Wark, 2009). Evidence of side biasing was not reflected in the time focal animals spent in each arm of the maze, so we chose to use this, rather than first approach, as our dependent measure.

Having established that changes in visual access among conspecifics can result in changes to the expression of partner preference, we wanted to further investigate the factors underlying this change. To that end, we designed Experiments 3 and 4 to differentiate between the role of the focal monkey’s visual access and the role of the mate’s visual access in determining the focal monkey’s partner preference. In Experiment 3, we occluded the focal monkey’s visual access such that, while in the arm of the maze closest to the mate, it resembled the focal monkey’s visual access from Experiment 2. We did not occlude the mate’s visual access, thereby preserving the mate’s ability to observe the focal monkey’s behavior anywhere in the maze. We predicted that focal monkeys would be more likely to investigate the unfamiliar monkey in situations in which they could not be observed by the mate. Our monkeys’ behavior in Experiment 3 is consistent with this prediction. When their mate’s visual access was unoccluded, the focal monkeys spent more time with the mate compared to the unfamiliar monkey. They also spent less time with the unfamiliar monkey when the mate’s visual access was unoccluded than they did when the mate’s visual access was occluded in Experiment 2. From these data, we concluded that the focal monkeys exhibit a reliable partner preference in situations in which they are observed by their mate.

If we restrict our analysis to the data from Experiments 1, 2, and 3, the tamarins appear to
be behaving in a manner consistent with level-1 perspective taking. Level-1 perspective taking abilities would indicate that the monkeys are capable of understanding that their mate’s knowledge state is related to its visual perspective and that visual perspective, and therefore knowledge, can be disrupted by occlusion. If cotton-top tamarins are capable of level-1 perspective taking, then the focal monkey should spend more time with the mate in Experiments 1 and 3, in which the mate’s visual access is undisturbed, and more time with the unfamiliar monkey in Experiment 2, in which the mate’s visual access is occluded. Indeed, this interpretation is supported by the pattern of partner preference our tamarins exhibited in Experiments 1, 2, and 3. However, it should be noted that the data from Experiment 4 did not conform to the predictions suggested by an understanding of perspective taking. In Experiment 4, the mate’s visual access was occluded, such that it could not see the focal monkey interact with the unfamiliar tamarin. If tamarins understand perspective taking, we would expect an increase in the amount of time the focal monkey spends with the unfamiliar individual in this experiment. In contrast, our data reflect the opposite pattern of behavior. Focal monkeys spent significantly more time with the mate than the unfamiliar monkey in Experiment 4.

Given the data from Experiment 4, it is difficult to interpret the role of the mate’s visual access in the expression of tamarin partner preference. It is possible that, after multiple exposures to the unfamiliar individuals, focal animals became habituated to them. Thus, the partner preference observed in Experiment 4 may speak less to level-1 perspective taking and more to the rate at which cotton-top tamarins habituate to conspecifics.

Another explanation for the data observed in Experiment 4 may be that the strength of the affiliative relationship between pair mates may differ, and pairs that express higher rates of affiliative behavior may be less likely to investigate individual members of the opposite sex. As described above, due to a death in the colony, we included two individuals in Experiment 4 that had not participated in Experiment 3. Observational data regarding the frequency of affiliative
behaviors between mates collected after the completion of Experiment 4 indicated a particularly high rate of prosocial behaviors between these two individuals. The monkeys in Experiment 4 may not have increased the time spent with the unfamiliar monkey because they shared particularly strong bonds with their cagemate. Strongly bonded mates may be less motivated to explore extra monogamous mating opportunities. Alternately, they may be adverse to leaving their mate, regardless of the situation. If this is the case, pairs that display more normative rates of affiliative behaviors may display stronger evidence of level-1 perspective taking.

**Future Directions**

One subject that bears investigating is the role of the unfamiliar monkey’s visual access in the focal monkey’s partner preference. While it seems likely that the focal monkey’s behavior changes in response to alterations in its own visual access or in response to alteration in the mate’s visual access, the unfamiliar monkey’s visual access may also exert an effect on the focal monkey’s behavior. In Experiments 1, 3, and 4, the unfamiliar monkey’s visual access was unoccluded. In these experiments, the focal monkey spent more time with the mate than the unfamiliar monkey. Perhaps the occlusion of the unfamiliar monkey’s visual access in Experiment 2 is responsible for the decreased time the focal monkey spent with the mate in that experiment. If this is the case, the changes in partner preference exhibited in response to the visual environment may be related to intergroup dynamics rather than intrapair dynamics.

This work also raises questions about the costs of departures from monogamy in cotton-top tamarins. Our predictions regarding level-1 perspective taking stem from an assumption that non-monogamous behavior incurs costs if observed by the mate. These assumptions are supported by evidence that many monogamous animals actively enforce sexual monogamy in their bonded partners. These enforcement behaviors, known as mate guarding, are common
among socially monogamous species (see review in Brotheron & Komers, 2003), and have been observed in multiple Callitrichid species (De Vleeschouwer, Heistermann, Van Elsacker, & Verheyen, 2000; Golidzen, 1989; Huck, Lottker, & Heymann, 2004; Schaffner, 1996). Given the similarity with which cotton-top partner preference resembles partner preference exhibited by other tamarin species, it is likely that cotton-top tamarins would also engage in some form of mate guarding. The form that mate guarding behavior takes in cotton-top tamarins, however, is unclear. Understanding the mechanisms cotton-top tamarins use to prevent extra pair mating could additional provide insight into the factors that influence the expression of partner preference.

A more nuanced understanding of partner preference in cotton-top tamarins may facilitate our understanding of the inconsistent pattern of results observed in Experiments 3 and 4. Explicit investigations into perspective taking in cotton-top tamarins may also inform our interpretation of these results. While the results of Experiments 1, 2, and 3 are consistent with level-1 perspective taking, the current work does not directly investigate these abilities in tamarins. However, the data from Experiments 1, 2, and 3 and results from closely related species (Burkhart & Heschl, 2007) suggest that tamarins may be capable of level-1 perspective taking. Direct investigations of perspective taking abilities using a cooperative paradigm may lead to clearer evidence of the state of tamarin perspective taking abilities.

**Conclusions**

In summary, our results provide strong evidence that cotton-top tamarin partner preference changes in response to alterations in visual access among group members. These changes manifest quickly and do not appear to differ between the sexes. The pattern of behavior observed in our results is consistent with those seen in other tamarin species and may reflect the
roots of the homologous behaviors seen in other nonhuman primates. While it seems probable that cotton-top tamarins react to changes in their mate’s visual access, it is unclear to what extent they account for the mate’s visual access when making partner preference decisions.
References


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