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## Coppery titi monkey (*Plecturocebus cupreus*) pairs display coordinated behaviors in response to a simulated intruder

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### Abstract

Mate guarding and coordinated behaviors between partners are important for the maintenance of monogamous pair bonds. To study the effects of a perceived unfamiliar social intruder on females' behavior, we used coppery titi monkeys (*Plecturocebus cupreus*). We examined the effects of male aggressive temperament on females' behavior and the effects of each behavior performed by the male on the same female behavior. Using a mirror, we simulated a social intruder in the home territory and scored behaviors using an established ethogram. Based on our analysis of self-directed behaviors, females do not recognize themselves in the mirror. We then used general linear mixed models to predict percent change in females' behaviors as a function of 1) males' temperament, 2) males' behavior, and 3) an interaction between males' temperament and behavior. Male temperament did not significantly predict female behavior for any of our best fitting models. For percent change in female lip-smacking, male lip-smacking significantly predicted female lip-smacking ( $\beta = 0.74$ , SE = 0.22,  $t = 3.39$ ,  $P = 0.004$ ). There was a positive correlation between male and female agonistic behaviors such as back-arching/tail-lashing ( $\beta = 0.51$ , SE = 0.23,  $t = 2.22$ ,  $P = 0.04$ ) and for anxiety-related behaviors such as leaving the partner ( $\beta = 0.50$ , SE = 0.19,  $t = 2.68$ ,  $P = 0.015$ ), locomotion duration ( $\beta = 0.19$ , SE = 0.06,  $t = 2.98$ ,  $P = 0.02$ ), and locomotion frequency ( $\beta = 0.71$ , SE = 0.14,  $t = 5.17$ ,  $P < .001$ ). These findings on coordination of pair-mate behaviors may explain how titi monkeys display pair bond strength and ensure their reproductive success.

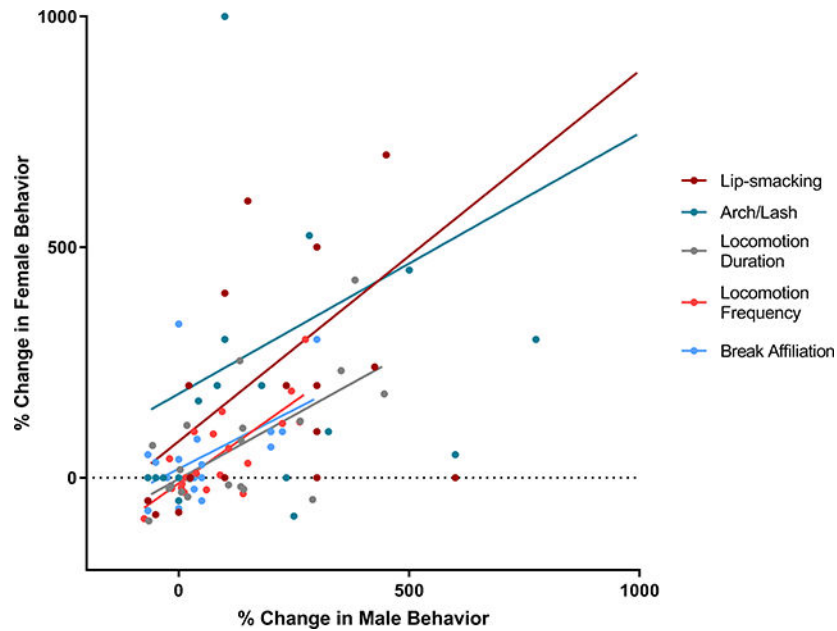
### Graphical Abstract

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Disclosure

The authors report no conflict of interests in this work.



## Keywords

pair bonding; temperament; coordination; anxiety; affiliation; aggression

## Introduction

In the wild, titi monkey (*Plecturocebus* spp.) families consist of a pair of two adults and two to four offspring living in a small territory (Fernandez-Duque, Di Fiore, & de Luna, 2013; Fuentes, 1998; Mason, 1966). Approximately 15% of primates are monogamous, including titi monkeys, which is one of the highest rates among mammals (usually estimated at 3–5%; Kleiman, 1977; Munshi-South, 2007). A monogamous social bond is characterized by distress upon separation, the partner's ability to buffer stress, and preference for maintaining close proximity to the partner (Anzenberger, 1988; Bales et al., 2017; Fernandez-Duque, Mason, & Mendoza, 1997; Mendoza & Mason, 1986a). Socially monogamous species are characterized by their preference for one partner. In titi monkeys, this preference is associated with affiliative behaviors (e.g., joint territorial defense, coordinated behaviors between the members of the pair, paternal care; Anzenberger, Mendoza, & Mason, 1986; Fuentes, 1998; Kinzey, Rosenberger, Heisler, Prowse, & Trilling, 1977; Mason, 1966; Mendoza & Mason, 1986b; Robinson, Wright, & Kinzey, 1987), and agonistic behaviors such as mate-guarding and restraining the mate when a same-sex stranger is in the vicinity (Mason, 1966; Spence-Aizenberg, Di Fiore, & Fernandez-Duque, 2016; Van Belle, Fernandez-Duque, & Di Fiore, 2016). These affiliative and agonistic behaviors play an important role in the maintenance of pair bonds (Fernandez-Duque, Vaggia & Mason, 2000; Mason, 1966; Fisher-Phelps et al., 2016).

Measuring responses to intruders can be useful in determining the level of agonistic behaviors that members of a pair bond engage in as part of pair bond maintenance. However,

live intruders come with the risk of injury to the subjects and the intruder. Using a mirror to mimic the presence of a territorial intruder has the advantage of being able to test in the home cage while using fewer animals and avoiding any risks of injuries (Fisher-Phelps et al., 2016). If a subject is tested with their partner and the entire home cage is reflected in the mirror, the subject's reflection in the mirror may be perceived as a same-sex stranger, an opposite-sex stranger, and/or a pair or unfamiliar titi monkeys, all of which may pose a threat to the pair bond (Anderson & Gallup, 2011; Fisher-Phelps et al., 2016). Two previous mirror studies using coppery titi monkeys (*Plecturocebus cupreus*; Fisher-Phelps et al., 2016; Witczak, Ferrer, & Bales, 2018), a socially monogamous New World monkey, found that subjects' responses to the mirror were comparable to those of previous studies using a live intruder (Cubicciotti & Mason, 1978; Fernandez-Duque et al., 1997; Fernandez-Duque et al., 2000; Mendoza & Mason, 1986a; Menzel, 1986; Menzel, 1993).

A previous study of male titi monkeys used the mirror as a tool to simulate the presence of an intruder in order to study males' behavioral and physiological responses to a stranger (Fisher-Phelps et al., 2016). Because the original goal of the study was not to test self-recognition, this study only scored the mirror-guided and self-directed behaviors, and determined that male titi monkeys did not recognize themselves in the mirror. Male titi monkeys responded robustly to a perceived male intruder, showing an increase in both affiliative and agonistic behaviors (Fisher-Phelps et al., 2016).

A second study compared the difference in coppery titi monkey males' responses to a mirror based on male temperament (Witczak et al., 2018). The aim of this study was to understand the relationship between aggressive temperament and the endogenous oxytocin (OT) system in a monogamous primate. Two different groups were determined based on previously observed behaviors: pairs with High-aggressive males and pairs with Low-aggressive males. High-aggressive males show persistent food-related and social aggression that sometimes results in injury. Low-aggressive males have never shown any aggression towards their partner or show low-levels of food-related aggression early in their pairing. For more details regarding how males were categorized, see Witczak et al., 2018. The same stimuli (a mirror) elicits opposite physiological responses in the two groups. Low-aggressive males showed a rise in their plasma OT level, whereas the High-aggressive males exhibited a drop in OT in response to a social threat (Witczak et al., 2018). In this study, the researchers also found that High-aggressive males spent less time in contact with their mates and lip-smacked less when confronted with a simulated intruder. Additionally, they found that High-aggressive males who exhibited a drop in OT displayed a smaller increase in time spent in proximity to their partners (Witczak et al., 2018).

The previous two mirror studies conducted using coppery titi monkeys only measured males' physiological and behavioral responses to a simulated intruder (Fisher-Phelps et al., 2016; Witczak et al., 2018). Given that titi monkeys are a pair-bonding species (Bales et al., 2017), it is important to understand how both members of the dyad react when facing a social stressor together. Partners play an important role in regulating each other's emotional and physiological responses (Cacioppo, 1994; Hofer, 1984; Diamond, Hicks, & Otter-Henderson, 2008; Mikulincer & Shaver, 2019; Shaver, Mikulincer & Cassidy, 2018). While supportive relationships can act as buffers from social stressors (Cohen & Wills, 1985;

Heinrichs et al., 2003), individuals with distressed or absent social relationship are at a higher risk for affective disorders (Coyne, Thompson, & Palmer, 2002; Davila, Karney, Hall, & Bradbury, 2003; Maselko, Kubzansky, Lipsit & Buka, 2011; Russek & Schwartz, 1997) and morbidity/mortality (Helgeson, 1991; Hibbard & Pope, 1993; Holt-Lunstad et al., 2015; Uchino, 2006).

In humans, partner's temperament and attachment styles have been found to affect how they respond to acute stressors (Laurent & Powers, 2007). Animal studies have also demonstrated that the temperament of another individual can affect behavioral responses to stressors. For example, female rats paired with aggressive males exhibited greater depressive-like behavior (e.g., behavioral despair, anhedonia, depression-related anxiety; Belovicova, Bogi, Csatlosova, & Dubovicky, 2017; Pollak, Rey, & Monje; Walker, Wing, Banks, & Dantzer, 2018), particularly for females with an anxious temperament prior to exposure to the male (Cordero et al., 2012; Poirier, Cordero, & Sandi, 2013). Women are more likely to be diagnosed with affective disorders such as major depressive disorder than men (Weissman & Olfson, 1995). It is possible that social risk factors may contribute to women's increased likelihood of developing affective disorders (Kuehner, 2017). It is therefore important to study how differences in relationship quality may affect female behavioral outcomes. The present study is the first to examine how socially monogamous female non-human primates differentially react to an acute social stressor based on their partner's temperament and behavior.

To determine whether we could use the mirror as a model of an unfamiliar social intruder for females, we first measured females' self-directed and mirror-guided behaviors. We hypothesized that, when confronted with the mirror, females would not recognize themselves (Anderson & Gallup, 2015; Gallup, 1970; Fisher-Phelps et al., 2016). We then measured social behaviors, and compared the behavior of females paired with High-aggressive males to the behaviors of females paired with Low-aggressive males. We hypothesized that all females would show an increase in affiliative, agonistic, and anxiety-like behaviors in response to the mirror (Fisher-Phelps et al., 2016); however, the degree to which they exhibited behavioral changes would be influenced by the temperament of their mate (Witczak et al., 2018). In particular, we predicted that a High-aggressive male would inhibit the behaviors of his partner (Cloven & Roloff, 1993; Cordero et al., 2012; Kiewitz, Restubog, Shoss, Garcia, & Tang, 2016). We also compared the behavior of the two members of the pair to see if their responses to the mirror were similar. Because this species is known to exhibit coordination of territorial displays (Anzenberger et al., 1986; Fuentes, 1998; Robinson et al., 1987), we hypothesized that, for females paired with Low-Aggressive males, the way the male reacts to the presence of a social stressor would influence the behavior of the female. Given that Low-aggressive males in the previous mirror study exhibited a greater increase in time in contact with their mates and a greater increase in lip-smacking frequency (Witczak et al., 2018), we predicted that females paired with Low-aggressive males would also exhibit a greater increase in these affiliative behaviors. We also predicted that female's agonistic (e.g. back-arching/tail-lashing; Cubicciotti & Mason, 1978; Fernandez-Duque et al., 2000; Mendoza & Mason, 1986a) and anxiety-like (e.g. locomotion; Capitanio, Mason, Mendoza, Del Rosso, & Roberts, 2006; Ragen, Freeman,

Laredo, Mendoza, & Bales, 2015) behaviors would be correlated with those of their partner if they were paired with Low-aggressive males.

## Methods

### Selection of Subjects and Housing

For this study, we used video recordings from a previous study that analyzed the differences in male titi monkey behavioral and physiological responses to the presence of a mirror, using male temperament as a predictor (Witczak et al., 2018). We used 20 pairs ( $N = 20$  adult females in 20 separate pairs) of adult coppery titi monkeys (*Plecturocebus cupreus*) for the present study. Ten of the females were paired with High-aggressive males, ten were paired with Low-aggressive males, with a mean of  $9.80 \pm SE 0.74$  years of age at the beginning of the study. Female age did not significantly differ between females paired with High-aggressive males ( $10.74 \pm SE 1.01$  years) and Low-aggressive males ( $8.65 \pm SE 1.01$  years;  $t = -1.45$ ,  $df = 38$ ,  $P = 0.15$ ). Females also did not significantly differ in age from their male partners ( $t = -0.17$ ,  $df = 78$ ,  $P = 0.87$ ). High-aggressive and Low-aggressive males also did not differ significantly in age ( $t = .58$ ,  $df = 36.49$ ,  $p = 0.56$ ; see Witczak et al., 2018 for more details). The subjects were housed in the California National Primate Research Center (CNPRC) with their pair-mates and their offspring. Families were housed in a  $1.2 \text{ m} \times 1.2 \text{ m} \times 2.1 \text{ m}$  stainless steel cage or a  $1.2 \text{ m} \times 1.2 \text{ m} \times 1.8 \text{ m}$  with four horizontal perches, a food bowl, and two water dispensers. They were fed twice daily with New World monkey chow, rice cereal, carrots, apples, raisins, and bananas. They were kept on a 12 hours light, 12 hours dark cycle, in a room where the temperature is maintained at approximately  $21^\circ\text{C}$ . For additional information regarding animal husbandry, please see Tardif et al. (2006) and Mendoza and Mason (1986a). This study was approved by the IACUC of the University of California, Davis; and complied with legal requirements of the United States and the policies of the American Society of Primatologists on Ethical Treatment of Non-Human Primates.

While titi monkeys are quite affiliative with their partners, some males display aggression toward their pair-mates. In a previous study (Witczak et al., 2018), a scale was developed to sort males into two categories: High-aggressive and Low-aggressive. A score of 0 corresponds with a male who has never shown any sign of aggression, and a score of 1 with a male usually non-aggressive, displaying some food aggression at the beginning of the pairing but no more. A score of 2 represents a subject who has shown occasional bouts of non-food-related aggression. Males with a score of 0, 1, or 2 were classified as Low-aggressive ( $N = 10$ ). A score of 3 matches with a male who displays persistent food-aggression which sometimes results in injuries, and a male scored as a 4 corresponds with a subject who shows persistent non-food-related aggression that can lead to chasing and sometimes injuries. Males who scored a 3 or 4 on this scale were categorized as High-aggressive ( $N = 10$ ). For more details regarding temperament categorization, please see Witczak et al. (2018). All females in the present study were the partners of the males in Witczak et al., 2018. No females were considered to be High-aggressive.

## Mirror Exposure and Behavioral Assessment

We used a mirror as a stimulus for the female, predicting that she would be responding to 1) a same-sex stranger if viewing herself in the mirror, 2) an opposite-sex stranger if viewing her partner in the mirror, 3) an unfamiliar pair of titi monkeys if viewing herself and her partner in the mirror, and/or 4) her partner in her home cage. A previous mirror validation study revealed that titi monkeys do not show any signs of habituation to the mirror after having been tested twice per week for five weeks (Fisher-Phelps et al., 2016). Additionally, in this previous study, males did not recognize themselves in the mirror.

In the current study, we used a 33 cm × 22 cm mirror placed on a movable cart (81.6 cm in height). During the experiment, the mirror was moved in front of the cage for five minutes. Previous research has shown that titi monkey parents do not show any behavioral or physiological changes when separated from their offspring (Mendoza, 2017; Mendoza, Capitanio, & Mason, 2000; Mendoza & Mason, 1986b). Therefore, to keep testing conditions similar for pairs with and without offspring, any offspring over 6 months of age were removed from their parents during the test. Four High-aggressive pairs and seven Low-aggressive pairs had offspring over 6 months of age. Presence of offspring did not significantly predict any of our outcome variables and therefore was not included as a covariate in our analyses. No pair had infants under 6 months of age during this study.

From 4/29/2016 to 3/10/2017, every pair was tested once in a control condition (showing the back of the mirror to the subjects) and once in a mirror condition (showing the front of the mirror), with a break of two weeks between the two conditions. The order in which the front and back of the mirror was presented was counter-balanced and we randomized whether subject experienced the control or experimental condition first. During the test, subjects were filmed and behaviors were later scored using Behavior Tracker 1.5 ([www.behaviortracker.com](http://www.behaviortracker.com)). Two ethograms were used: one targeting self-directed and mirror-guided behaviors (Table 1; Fisher-Phelps et al., 2016), and another focusing on social behaviors (Table 2; Fisher-Phelps et al., 2016; Witczak et al., 2018). One person scored all of the female behaviors from the previously recorded videos using these established ethograms. Male behaviors had all been previously scored for the Witczak et al., 2018 study. We used the same two-step validation process as the one used by Witczak et al. (2018) to validate behavioral scoring for female behaviors. First, to achieve >95% inter-rater reliability, two observers scored behaviors for three separate mirror test sessions. The second observer was an experienced graduate student who was already validated on scoring behaviors for the mirror study. The two observers first scored the male behaviors that had previously been scored for the Witczak et al. (2018) study. After the observers achieved >95% agreement on all three sessions, the first observer then scored three new sessions for female behaviors three times each. The observer was considered validated when they achieved >95% agreement three times in a row for all three mirror test sessions.

We analyzed females' affiliative (lip-smacking, initiating contact with the partner, initiating proximity to the partner, and tail-twining), agonistic (arching/tail-lashing, restraining, and acts of aggression such as biting, hitting, or grabbing the partner), and anxiety-related (locomotion and breaking affiliation) behaviors (Table 2). Because we wanted to focus on analyzing possible links between female's behaviors and male's temperament and behaviors,

we did not analyze mirror-guided behaviors such as latency to approach the mirror and duration of time spent in proximity to the mirror.

## Data Analysis

**Self-directed and mirror-directed behaviors**—We first wanted to identify whether or not females recognized themselves in the mirror. We measured self-directed behaviors displayed when females saw the front of the mirror (experimental condition) and the back of the mirror (control condition). For all outcome measures, we performed a Shapiro Wilk test of normality and transformed non-normally distributed variables as necessary (Royston, 1983). Using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in R Statistical Software (version 3.6.1, R Core Development Team, 2019), we used a general linear mixed model (LMM) to determine whether mirror condition (fixed effect) predicted females' self-directed behaviors. We included females' ID as a random, repeated-measures effect. For all models, we performed a log likelihood ratio test to compare the fit of our model to that of a null model. Among the self-directed and mirror-directed behaviors scored during this study (Table 1), four of them did not occur and therefore were not analyzed (self-groom, adjust, tool, and examine). For the behavior “touches body”, we examined total body touching in addition to touching of individual body parts (hand, foot, chest, belly, back, arm, flank, head, neck, and other). Therefore, we used LMM to analyze the effects of mirror condition on a total of 14 female self-directed and mirror-directed behavioral outcomes. We had a strong *a priori* hypothesis that females would not recognize themselves in the mirror (Anderson & Gallup, 2015). All tests were two-tailed and the significance threshold was set at .05.

**Behavioral responses to mirror exposure**—We were also interested in understanding how male temperament (High-aggressive or Low-aggressive) and behavioral responses of males affected the females' behavioral responses to an acute social stressor. Because we were focusing on females' reactions to the presence of a perceived intruder, for social behaviors, we calculated percent change in behavior from the control to the experimental condition. Percent change scores have been used in other studies on changes in non-human primate behavior and physiology (Adams, Stanhope, Grant, Cummings, & Havel, 2008; Capitanio et al., 2011; Gust, Gordon, Brodie, & McClure, 1996; Kromrey, Czoty, Nader, Register, & Nader, 2016; Schwandt, Higley, Suomi, Heilig, & Barr, 2008). This was also the same method used for studying the effects of temperament on male titi monkeys' behavior (Witczak et al., 2018). Using a percent change score enables us to take into account the natural variation in behavioral responses between females. Additionally, the percent change score allows us to examine amount and directionality of change in behavior in response to an acute social stressor. For all outcome variables, we performed a Shapiro-Wilk test of normality and measured skewness and kurtosis. All non-normally distributed variables were transformed as necessary using a log or square root transformation (Royston, 1983). Male behaviors had been previously quantified and transformed. Transformation of male behavioral outcomes are described in Witczak et al., 2018.

We used LMM to model percent change in behavioral responses from the control to the mirror condition as a function of male temperament (fixed effect), percent change in male behavior (fixed effect), and an interaction effect between male temperament and male



behavior. For all models assessing females' responses to the mirror, we also included a random effect of whether or not females saw the front or the back of the mirror first (random, repeated-measures effect). We did not expect the order in which the mirror was presented to the subject to significantly predict behavior based on findings from a previous study that exposed titi monkey pairs to this same mirror testing paradigm 10 times over a 5-week period (Fisher-Phelps et al., 2016). Among the social behaviors scored during this study (Table 2), two of them occurred too infrequently to be analyzed (percent change in tail-twining and aggression). Therefore, we used LMM to analyze the effects of male temperament, male behavior, and their interaction on a total of 8 female social behavioral outcomes.

To determine the best-fitting model, we followed the same procedures described by Witczak et al. (2018). We used backwards selection to remove any non-significant fixed effects (Bentler & Mooijaart, 1989). We used a log likelihood ratio test to compare model fit to determine whether removing any non-significant fixed effects resulted in a better fitting model (Vuong, 1989). We then performed a log likelihood ratio test to compare the fit of our best model to that of the null model where we removed all main effects as a predictor of females' percent change in behavior (Vuong, 1989; West, Taylor, & Wu, 2012). The resulting final model, determined using a model comparison based on the likelihood of the model to the data, is the only one in which we evaluated the significance of the remaining parameters. For each of our 8 female social behaviors, we had one final model where we looked at significance level. The one final model represented the most likely hypothesized relationship between parameters given the data. Because we only evaluated parameter significance in one model per outcome, post hoc corrections were not necessary (Vuong, 1989; West, Taylor, & Wu, 2012). We had strong *a priori* hypotheses that females' behavioral responses would be inhibited if paired with a High-aggressive male (Clove & Roloff, 1993; Cordero et al., 2012; Kiewitz et al., 2016), and would be coordinated with those of their partner if paired with a Low-aggressive male (Anzenberger et al., 1986; Fuentes, 1998; Robinson et al., 1987; Witczak et al., 2018). All tests were two-tailed and the significance threshold was set at .05. The data that support the findings of this study are available on request from the corresponding author.

## Results

### Self-directed and mirror-guided behaviors

There was no significant effect of condition on self-directed behaviors (Table 3). Our model did not fit better than the null model, based on the results of our log likelihood ratio test, suggesting that there is no effect of the presence of the mirror on the self-directed and mirror-guided behaviors (Supplementary Table 1).

The second way we determined whether or not females recognized themselves in the mirror was by identifying whether we saw a decrease in social behaviors in response to the mirror (Gallup, 1970). We used percent change in mirror-directed, affiliative, agonistic, and anxiety-related behaviors to measure the response of the female facing a social stressor. As expected, we observed an increase in mirror-directed, affiliative, agonistic and anxiety-related behaviors in the presence of the mirror, suggesting females reacted to the front of the

mirror differently from the back of the mirror (Supplementary Table 2). Of the behaviors we scored, aggression and tail-twining occurred too infrequently to be analyzed. Because we did not find evidence that suggests females recognize themselves in the mirror, we were able to proceed with our analyses for females' behavioral responses to the mirror based on male temperament and behavior.

### Behavioral responses to mirror exposure

**Affiliative partner-directed responses to the mirror**—We used percent change in frequency of female lip-smacking, female initiation of social contact, female initiation of social proximity, and duration of time spent tail-twining to measure change in amount in time spent in affiliative contact with the male from the control to the mirror condition. When females were in the presence of a social stressor, their average percent change in lip-smacking increased by  $331.7 \pm \text{SE } 119.8\%$  relative to the control condition. Percent change in female lip-smacking was not normally distributed; therefore, we used a log transformation to normalize the data. Following a log transformation, the data were normally distributed ( $W = 0.97, P = 0.75$ ). Results from a log likelihood ratio test suggested that the best fitting model included both main effects of percent change in male lip-smacking and male aggression score but no interaction effect (Supplementary Table 3A). Moreover, when we take into account both percent change in male lip-smacking and male temperament, percent change in male lip-smacking significantly predicts percent change in female lip-smacking (Table 4A; LMM:  $\beta = 0.74, \text{SE} = 0.22, t = 3.39, P = 0.004$ ), while male temperament did not predict percent change in female lip-smacking (Table 4A; LMM:  $\beta = -0.80, \text{SE} = 0.41, t = -1.92, P = 0.07$ ). With regards to effect size, percent change in male lip-smacking had a medium positive effect on female percent change in lip-smacking (Table 4A;  $D = 0.76$ ; Cohen, 2013; Hedges, 1982) while male temperament had a small negative effect (Table 4A;  $D = -0.43$ ). These findings suggest that males' percent change in lip-smacking was positively correlated with females' percent change in lip-smacking (Figure 1). A log likelihood ratio test suggested this model fit better than the null model (Supplementary Table 3B:  $X^2 = 75.74, \text{df} = 1, P < .001$ ).

Average percent change in frequency of females initiating social contact increased  $61.3 \pm \text{SE } 39.0\%$  from the control to the mirror condition. Our data on percent change in female initiating social contact were not normally distributed; therefore, we used a log transformation. Following this transformation, percent change in frequency of females initiating social contact was normally distributed ( $W = 0.94, P = 0.21$ ). There was no significant effect of percent change in male initiating contact or male temperament on percent change in female initiating contact (Table 4B; LMM:  $\beta = -0.43, \text{SE} = 0.34, t = -1.28, P = 0.22$ ).

On average, females increased their frequency of initiating social proximity  $58.2 \pm \text{SE } 19.3\%$  from the control to the experimental condition. Data on female percent change in frequency of initiating proximity were normally distributed ( $W = 0.95, P = 0.43$ ). There was also no significant effect of male percent change in initiating proximity or male temperament on percent change in female initiating proximity (Table 4C; LMM:  $\beta = -0.11, \text{SE} = 0.28, t = -0.40, P = 0.70$ ).

Percent change in tail-twining was also used as a measure of affiliation for this study; however, this behavior occurred too infrequently for analyses (for more details, see Witczak et al., 2018).

**Agonistic partner-directed responses to the mirror**—We used percent change in frequency of back-arching/tail-lashing displays (arching/lashing), pair-mate restraint, and bouts of partner-directed aggression (e.g. biting, grabbing, hitting) as measures of percent change in agonistic partner-directed responses to the mirror relative to the control condition. In the presence of a threat to the pair, female percent change in arching/lashing increased by  $362.9 \pm \text{SE } 170.2\%$  compared to the control condition. Data were not normally distributed; thus, we used a log transformation. Following a log transformation, our data were normally distributed ( $W = 0.97, P = 0.76$ ). We found a significant effect of the percent change in male arching/lashing on the percent change of female arching/lashing (Table 4D; LMM:  $\beta = 0.51, \text{SE} = 0.23, t = 2.22, P = 0.04$ ), suggesting a positive correlation between the way the two members of the pair react to the social stressor through arching/lashing displays (Figure 2). With regards to effect size, percent change in male arching/lashing had a medium positive effect on percent change in female arching/lashing (Table 4D;  $D = 0.50$ ). A log likelihood ratio test showed that this model fit better than the null model (Supplementary Table 3H;  $X^2 = 4.83, \text{df} = 1, P = 0.03$ ).

Data on percent change in frequency of female restraining were not normally distributed. We performed a log transformation, a square root transformation, a reciprocal transformation, and an arcsine transformation. Following those transformations, data were not normally distributed; however, a log transformation resulted in the closest approximation of a normal distribution ( $W = 0.89, P = 0.03$ ) and resulted in non-significant skewness (skewness =  $0.55 \pm \text{SE } 0.54, P > 0.05$ ) and kurtosis (kurtosis =  $-0.58 \pm \text{SE } -0.29, P > 0.05$ ). We did not find any significant effect of percent change in male restraining or male temperament on percent change in frequency of female restraining (Table 4E; LMM:  $\beta = -0.47, \text{SE} = 0.32, t = -1.47, P = 0.16$ ).

Acts of aggression by females (e.g. biting, grabbing, hitting) occurred too infrequently for analysis. Only one female exhibited two instances of aggression in the experimental condition. Neither of these instances of aggression led to injury. We did not observe any other instances of aggression from females during testing.

### **Anxiety-related responses to the mirror**

To measure changes in anxiety-like responses from the control to the experimental conditions, we examined percent change in frequency and duration of locomotion (Capitanio et al., 2006; Ragen et al., 2015; Witczak et al., 2018) and percent change in frequency of females breaking affiliative contact with their partners (Amaral, 2002; Barros, Major, Huston, & Tomaz, 2008; Steimer, 2002; Witczak et al., 2018). In the mirror condition, saw a change in both female locomotion duration and frequency by  $64.5 \pm \text{SE } 29.0\%$  and  $48.9 \pm \text{SE } 20.8\%$ , respectively, in the mirror condition compared to the control condition. Female percent change in locomotion duration data were not normally distributed; thus, we used a square root transformation. Data were normally distributed following a square root

transformation ( $W = 0.98$ ,  $P = 0.94$ ). Female percent change in locomotion frequency was normally distributed ( $W = 0.92$ ,  $P = 0.09$ ), therefore, no transformation was necessary. Male percent change in locomotion duration and frequency had a significant effect on percent change in female locomotion. There was a positive correlation for both female percent change in locomotion duration (Table 4F; Figure 3; LMM:  $\beta = 0.19$ ,  $SE = 0.06$ ,  $t = 2.98$ ,  $P = 0.02$ ) and female percent change in locomotion frequency (Table 4G; Figure 4; LMM:  $\beta = 0.71$ ,  $SE = 0.14$ ,  $t = 5.17$ ,  $P < .001$ ). Male percent change in locomotion had a medium positive effect on female percent change in locomotion duration (Table 4F;  $D = 0.67$ ) and a large positive effect of female percent change in locomotion frequency (Table 4G;  $D = 1.16$ ). A log likelihood ratio test suggested that our models for percent change in locomotion duration (Supplementary Table 3L;  $X^2 = 7.05$ ,  $df = 1$ ,  $P = 0.008$ ) and percent change in locomotion frequency (Supplementary Table 3N;  $X^2 = 17.96$ ,  $df = 1$ ,  $P < .001$ ) fit better than their respective null models.

Female breaking affiliation increased by  $48.6 \pm SE 23.9\%$  in the mirror condition compared to the control. A log transformation was necessary to normalize the data. After a log transformation our data were normally distributed ( $W = 0.96$ ,  $P = 0.52$ ). We observed a significant effect of the percent change of male breaking affiliation on female percent change in breaking affiliative contact (Table 4H; LMM:  $\beta = 0.50$ ,  $SE = 0.19$ ,  $t = 2.68$ ,  $P = 0.02$ ), suggesting a positive correlation between male and female percent change in breaking affiliation in the presence of the social stressor (Figure 5). With regards to effect size, male percent change in breaking affiliation had a medium positive effect on female percent change in breaking affiliation (Table 4H;  $D = 0.60$ ). A log likelihood ratio test suggested that this model fits better than the null model (Supplementary Table 3P:  $X^2 = 6.71$ ,  $df = 1$ ,  $P = 0.01$ ).

## Discussion

For our study, we first wanted to know whether or not females would treat the reflection viewed in the mirror as an unfamiliar conspecific. We hypothesized that female titi monkeys would not recognize themselves in the mirror. We did not perform a formal mark test; however, we did score all of the potential signs of self-recognition described in other mirror studies (Bard, Todd, Bernier, Love, & Leavens, 2006; de Waal, Dindo, Freeman, & Hall, 2005; Fisher-Phelps et al., 2016). If the subject recognized itself in the mirror, then we would expect the subject to show an increase in self-directed behaviors and a decrease in social behaviors (Gallup, 1970). In the present study, we found no significant differences in self-directed behaviors between the control and mirror conditions. While there are limitations to using a mirror to simulate an intruder, two previous mirror studies conducted using titi monkeys (Fisher-Phelps et al., 2016; Witczak et al., 2018) found that behavioral changes in response to a mirror were comparable to responses to live intruders (Cubicciotti & Mason, 1978; Fernandez-Duque et al., 1997; Fernandez-Duque et al., 2000; Mendoza & Mason, 1986a; Menzel, 1986; Menzel, 1993). In the present study, females showed an increase in social behaviors ranging from approximately 50% (for percent change in locomotion frequency and leaving affiliative contact) to 360% (for percent change in back-arching/tail-lashing). Taken together, these results suggest female coppery titi monkeys do not recognize themselves in mirrors, which is in agreement with the view that self-

recognition has only been shown in great apes (Anderson & Gallup, 2011; Anderson & Gallup, 2015).

We had hypothesized that females paired with High-aggressive males would exhibit an inhibition of behaviors in response to an acute social stressor (Cordero et al., 2012; Cloven & Roloff, 1993; Kiewitz et al., 2016). Interestingly, we did not find any evidence that male temperament significantly predicted differences in females' behavioral responses to a perceived intruder. Only percent change in female lip-smacking showed a non-significant trend towards being lower when females were paired with High-aggressive males; however, the effect size was small (Table 4A). We may not be fully capturing differences in females' responses to their partner's temperament using our current ethogram. In other animal models, researchers have found conflicting results between male and female behavioral responses to acute stressors in models of abusive relationships (for a review, see: Shansky, 2015). Alternatively, it is possible that a female's temperament can buffer her from negative effects of her partner's aggressive tendencies (Poirier, Cordero, & Sandi, 2013). While males in our titi monkey colony are more likely to exhibit behaviors that we could categorize as aggressive (e.g. persistent food aggression, chasing, biting; Witczak et al., 2018), we do not see as many examples of females which we would categorize as aggressive. It would be helpful in the future to incorporate a behavioral assessment to measure other traits such as activity and emotionality (Capitano, 2017) in both males and females to better understand whether or not females paired with High-aggressive males respond differently to acute social stressors.

Our third hypothesis was that female percent change in behaviors would be positively correlated with male percent change in behaviors. While percent change in frequency of females initiating proximity and contact did not appear to be related to male percent changes in proximity and contact initiation, we found a statistically significant positive correlation between percent change in female lip-smacking and percent change in male lip-smacking. In the wild, titi monkeys show coordination of affiliative behaviors such as proximity to or contact with the partner, grooming, and tail-twining (Fernandez-Duque et al., 2000; Mason, 1966). The present study reveals a possible coordination of some affiliative behaviors in the presence of a social stressor in our captive population. This increased synchrony of affiliative behaviors may have beneficial effects for pair-mates. Human pair-mates can act as buffers for stressors and, as a result, can be behaviorally influenced by their partner (Cohen & Wills, 1985; Heinrichs et al., 2003). Indeed, the amount of time spent with one person can influence hormone activity in humans (Grewen, Girdler, Amico, & Light, 2005). One study demonstrated that levels of oxytocin increased in both partners after experiencing warm, emotional contact, particularly for partners who were highly supportive of each other (Grewen et al., 2005). These findings lend support to the idea that there is a link between coordinated hormone release and coordinated behaviors. We do find differences in proportion of time pairs spend in affiliative contact on a daily basis (Witczak et al., *in prep*). It would be interesting to compare differences in degrees of behavioral and physiological coordination between high-affiliative and low-affiliative pairs in the presence of a social threat such as a mirror.

Besides the potential link between hormone release and coordinated behaviors, high levels of behavioral synchrony can be a way for pairs to show to other individuals that their bond is strong. Regarding agonistic behaviors, we found a positive correlation between males' percent change in back-arching/tail-lashing and females' percent change in arching/lashing. In the wild, titi monkeys exhibit coordinated territorial displays (Anzenberger et al., 1986; Fuentes, 1998; Robinson et al., 1987), with arching/lashing being more prevalent in males (Cubicciotti & Mason, 1978; Fernandez-Duque et al., 2000; Mendoza & Mason, 1986a). For humans, bonded individuals often display behavioral and physiological synchrony, and the degree of synchrony has previously been shown to be predictive of bonding strength (Feldman 2007; Feldman 2012a; Feldman 2012b). For titi monkeys, coordinated arching/lashing in conjunction with coordinated affiliative behaviors may visually display the strength of a pair bond. Having strong bonds may also result in protective effects and may buffer partners from the potentially harmful influences of stress-induced behavioral decisions and related physiological changes (Mikulincer & Shaver, 2019; Shaver et al., 2018; Uchino, 2006). While percent change in restraining was not correlated between males and females, we saw an increase in restraining of the partner for both males (107%; Witczak et al., 2018) and females (85%) in response to a perceived intruder. This mate-guarding behavior may be used both to maintain pair bonds and ensure reproductive success (Mason, 1966; Spence-Aizenberg, Di Fiore, & Fernandez-Duque, 2016; Porter, 2001; Setchell, Charpentier, & Wickings, 2005; Van Belle, Fernandez-Duque, & Di Fiore, 2016).

We also found a positive correlation between percent changes in males' anxiety-related behaviors and percent changes in females' anxiety behaviors. In particular, percent change in female locomotion (duration and frequency) and breaking affiliative contact was positively correlated with male percent change in those behaviors. A coordinated increase in anxiety-like behaviors may be due to partners' ability to affect each other both positively and negatively (Jones & Fletcher, 1996; Ferrer & Nesselroade, 2003; Mikulincer & Shaver, 2019; Shaver et al., 2018). Because pair-mates can act as buffers for stressors, one interesting question could be: Does the female react to the presence of a same-sex stranger, or does she react because her partner exhibits anxiety-like behaviors? A future study could measure females' behaviors when only giving the male access to the mirror (and vice versa). In other testing paradigms, we have observed aggressive behaviors performed by the female toward an unfamiliar male (Cubicciotti and Mason, 1978; Fernandez-Duque et al., 2000). This additional test could be a way to show if changes in females' behaviors are linked to the partner's response to the mirror or the presence of a perceived intruder.

Future studies could also examine females' behavioral responses to the presence of a stranger male without her partner, identifying females that have strong bonds with their partner and comparing them to females with weaker bonds. While monogamous prairie vole (*Microtus ochrogaster*) pairs show high aggressive behaviors in the presence of a stranger, regardless of the stranger's sex, if female prairie voles are tested alone in the presence of a male stranger, they are less aggressive and will sometimes copulate with the unfamiliar male (Solomon, Keane, Knoch, & Hogan, 2004). In a sequential preference testing paradigm where male titi monkeys were given access to either their partner, a stranger, or an empty cage, if they were treated with saline, males contacted the stranger female more frequently than their partner (Jarcho, Mendoza, Mason, Yang, & Bales, 2011). Similarly allowing

female titi monkeys to interact with an unfamiliar male in the absence of her partner could be a way to confirm whether or not female titi monkeys see a male stranger as a potential social threat and test whether or not relationship quality predicts reactions to unfamiliar conspecifics, even when their partner is not present.

One question we were unable to answer with our present methods is who is driving the observed changes in behavioral responses to the mirror. Males did show a greater increase in all behaviors except for back-arching/tail-lashing (Supplementary Table 4). However, a greater change in behavior does not confirm that males are driving changes in behaviors in response to a simulated intruder. With our current paradigm, we are unable to assess what exactly our subjects are responding to. Because the mirror is placed where the entire cage can be viewed from the mirror, it is possible that our subjects are responding to any combination of the following: 1) their own partner in the home cage, 2) their own reflection (representing an unfamiliar same-sex intruder), 3) their partner's reflection (representing an unfamiliar opposite-sex intruder), and 4) both their reflection and their partner's reflections (representing an unfamiliar pair of titi monkeys). Our video recordings do not allow us to assess who the subject is looking at when performing a behavior; therefore, we are unable to reliably discern whether the subject is initiating a behavior or responding to a behavior seen either in the mirror or in their home cage. Future studies using eye tracking in conjunction with video stimuli may be able to help identify both who the subject is responding to and whether the subject is reacting to the action of the stimulus or initiating the behavior on their own. The video stimuli could include individual males and females as well as pairs of titi monkeys. Videos would also give us more control over what the stimulus is doing. In the current paradigm, subjects are viewing simulated intruders who are behaving the same way that they are. A video stimulus would allow us to control what the simulated intruder is doing and assess the subjects' response to various behavioral displays.

Another limitation of the mirror is that the subjects can only use visual cues to determine the sex of the simulated unfamiliar conspecific. It is likely that titi monkeys do use odor (Moynihan, 1966) and vocal cues (Adret et al., 2019) to differentiate between sexes; however, these hypotheses have not yet been empirically tested. This paradigm cannot simulate the olfactory and auditory cues that a live intruder could, and so we are unable to answer the question of how our subjects identify the sex of the simulated intruder using a mirror paradigm. Future studies could use video stimuli of individual male or female titi monkeys in conjunction with olfactory and auditory stimuli to determine whether titi monkeys are using these cues to differentiate the sex of an unfamiliar conspecific. Regardless of this limitation, both males and females responded robustly to the front of the mirror and did not show evidence of self-recognition in the mirror; therefore, we can be reasonably certain that our subjects were responding to the reflections in the mirror as if they were live intruders.

## Conclusions

We have demonstrated that this mirror technique is a valuable tool for mimicking the presence of an unfamiliar intruder to measure female behavioral responses. We did not find any evidence that females recognized themselves in the mirror. Surprisingly, we also found

no significant effect of male temperament on changes in female behaviors in response to the mirror. We observed positive correlations between percent change in male and female affiliative (lip-smacking), agonistic (arching/tail-lashing), and anxiety-related behaviors (locomotion and breaking affiliation). This coordination of behavioral responses to a simulated intruder between pair-bonded males and females may be a way to display the strength of the pair's relationship and ensure their reproductive success by avoiding the intrusion of a same-sex stranger. Additionally, greater synchrony of behaviors may have protective buffering effects on pair-mates and reduce the risk of adverse health outcomes. To our knowledge, this is the first empirical study to investigate the effects of partners' aggressive temperament on females' behaviors in a pair-bonding New World monkey. Future studies should examine the effects of female temperament and the strength of a pair's bond on partner's responses to acute social stressors. Studies should also investigate which member of the dyad is driving changes in behavior in species that exhibit coordination of behaviors.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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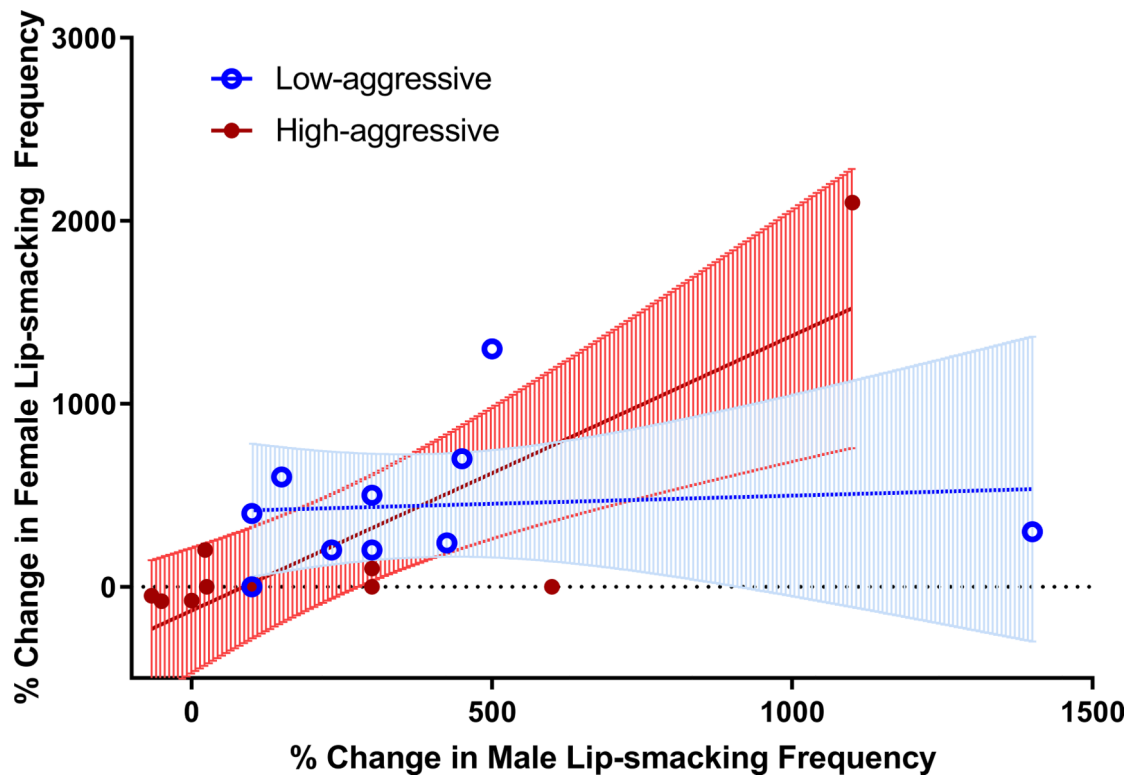
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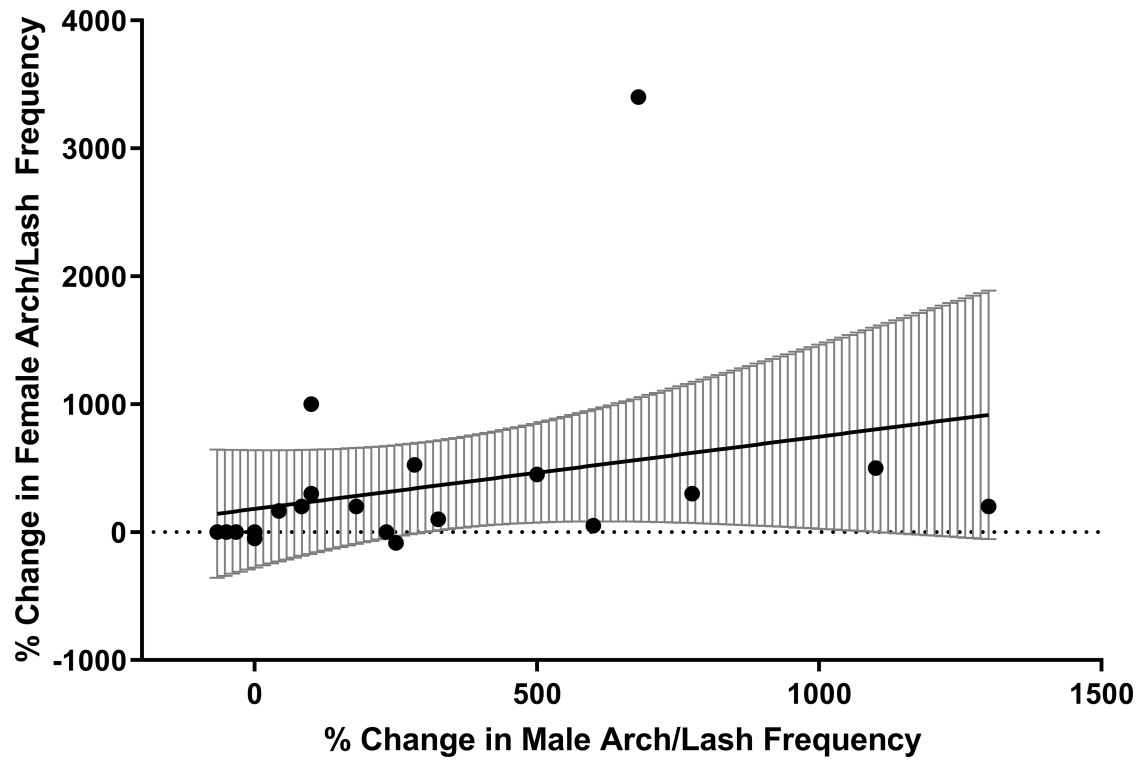
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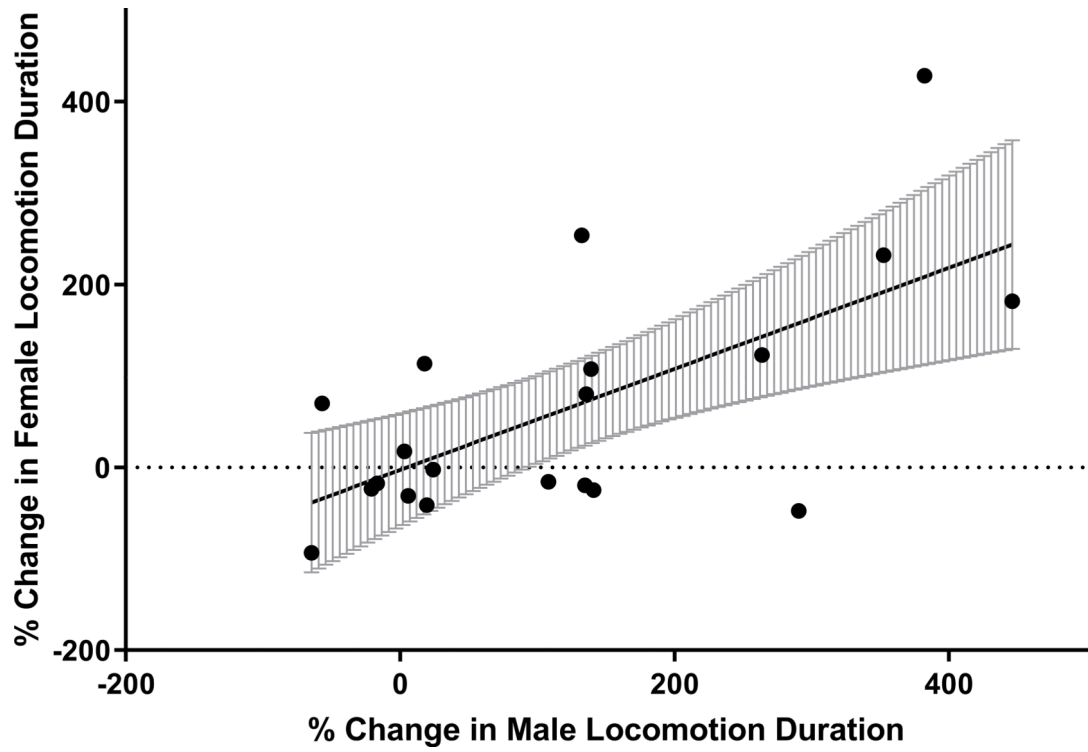


**Figure 1.**

Percent change in female lip-smacking in response to the front of the mirror (experimental condition) relative to responses to the back of the mirror (control condition). Percent change in female lip-smacking was positively correlated with male percent change in lip-smacking (LMM:  $\beta = 0.74$ ,  $SE = 0.22$ ,  $t = 3.39$ ,  $P = 0.004$ ), and was trending towards being lower for females paired with High-aggressive males (LMM:  $\beta = -0.80$ ,  $SE = 0.41$ ,  $t = -1.92$ ,  $P = 0.07$ ).

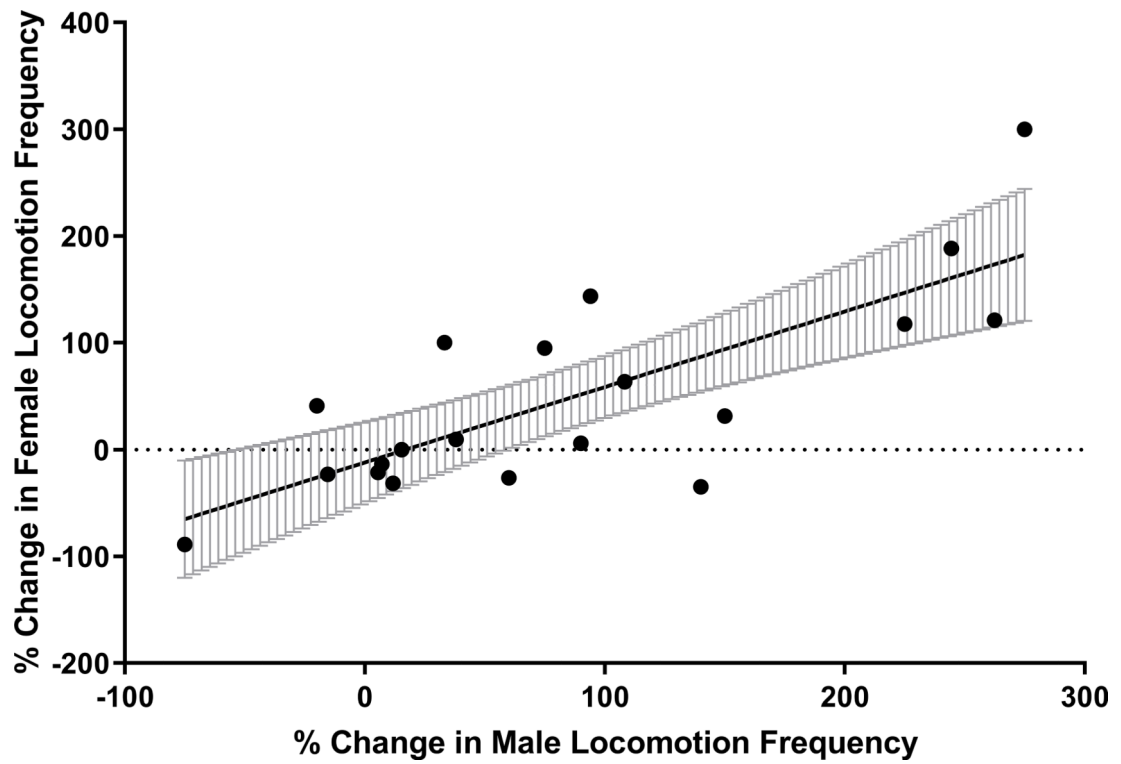


**Figure 2.** Percent change in female back-arching/tail-lashing in response to the front of the mirror (experimental condition) relative to responses to the back of the mirror (control condition). Percent change in female arching/lashing was positively correlated with male percent change in arching/lashing (LMM:  $\beta = 0.51$ ,  $SE = 0.23$ ,  $t = 2.22$ ,  $P = 0.04$ ).

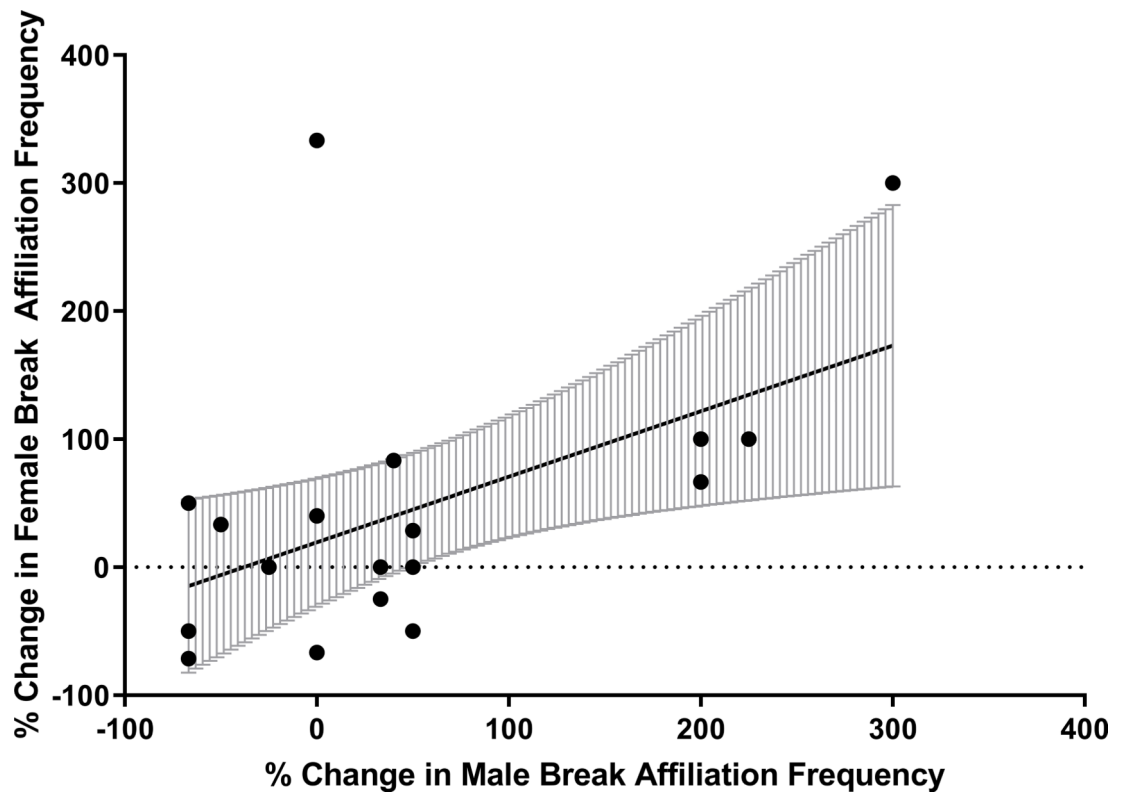


**Figure 3.** Percent change in female locomotion duration in response to the front of the mirror (experimental condition) relative to responses to the back of the mirror (control condition). Percent change in female locomotion duration was positively correlated with male percent change in locomotion duration (LMM:  $\beta = 0.19$ ,  $SE = 0.06$ ,  $t = 2.98$ ,  $P = 0.02$ ).





**Figure 4.** Percent change in female locomotion frequency in response to the front of the mirror (experimental condition) relative to responses to the back of the mirror (control condition). Percent change in female locomotion frequency was positively correlated with male percent change in locomotion frequency (LMM:  $\beta = 0.71$ ,  $SE = 0.14$ ,  $t = 5.17$ ,  $P < .001$ ).



**Figure 5.** Percent change in female break affiliative contact in response to the front of the mirror (experimental condition) relative to responses to the back of the mirror (control condition). Percent change in female breaking affiliation was positively correlated with male percent change in breaking affiliation (LMM:  $\beta = 0.50$ ,  $SE = 0.19$ ,  $t = 2.68$ ,  $P = 0.015$ ).

**Table 1.**

Ethogram for Self-directed and Mirror-Guided behaviors. All behaviors scored as frequency (count).

| <b>Behavior</b>                    | <b>Definition</b>   |
|------------------------------------|---|
| Looking behind the mirror          | Subject tries to look behind the mirror. Subject has to be in front of the mirror or from the side of the mirror but close to the bars. Does not count if they are on the side of the mirror on a perch (they can't look behind the mirror) or if they are looking behind the structure holding the mirror. |
| Double Take                        | Subject looks at the mirror then looks quickly at something in particular behind itself than goes back to the mirror. Does not count if the subject is just looking around then goes back to the mirror.  |
| Touches/ Tries to touch the mirror | Subject touches or tries to touch the mirror or the structure.  |
| Touches body                       | Subject touches part of its body. Scratching counts as "touches body". Touching a different part of the body with the same hand/foot counts as a new behavior. Touching the same part of the body with another hand/foot counts as a new behavior.  |
| Self-grooming                      | Subject makes sweeping motions with their hands across their body. Can grab at and pull fur when grooming, but has to be in conjunction with a sweeping motion.   |
| Adjust                             | Subject uses the mirror to adjust movements of the body.  |
| Examine                            | Subject uses the mirror to examine parts of the body that are not normally visible. Subject seems to hold on to the bars of the cage to examine those parts of their body. Does not count if subject is back-arching.   |
| Tool                               | Subject uses the mirror to look at the environment.   |

**Table 2.**

## Ethogram for Social Behaviors.

| <b>Behavior</b>                           | <b>Definition</b>  |
|---|--|
| <i>Affiliative Social Interactions</i>    |  |
| Female Lip-smack <sup>‡</sup>             | Female makes rapid lip movement accompanied by smacking sound.   |
| Passive Contact <sup>‡, †</sup>           | Male and female's bodies are in physical contact that does not include tail-twining.   |
| Social Proximity <sup>‡, †</sup>          | Animal's body (excluding the tail) is within arm's length (approximately 6 inches) of another animal (excluding the tail).   |
| Tail-twine <sup>‡, †</sup>                | Male and female tails are intertwined least one full turn.   |
| <i>Aggressive Social Interactions</i>     |  |
| Female Back-arch / Tail-lash <sup>‡</sup> | Female raises dorsal surface of the back. The subject may also have her arm and trunk lifted off the perch. Female repetitively swings whole tail from side to side (area greater than 40°). The two can co-occur or occur separately. May be accompanied by piloerection. |
| Female restraining <sup>‡</sup>           | Female reaches for, holds and/or pulls their mate to forcibly restrain him.  |
| Female aggression <sup>‡</sup>            | Female grabs, hits, or bites the male as a low intensity display of aggression.  |
| <i>Anxiety-related Interactions</i>       |  |
| Female Locomotion <sup>‡, †</sup>         | Female has moved at least one body length and lasts until immobile for 1 second.   |
| Female Break Affiliation <sup>‡</sup>     | Female withdraws from contact/proximity of male.   |

<sup>‡</sup>Scored as frequency behavior (count)

<sup>†</sup>Scored as duration behavior (seconds)

**Table 3.**

Parameter estimates from general linear mixed models (LMM) and effect sizes (Cohen's D) for self-directed and mirror-guided behaviors. For all behaviors, models included mirror condition (back of the mirror or front of the mirror) and female ID (random effect).

|  | $\beta$ | SE    | t     | P     | D     |
|--|---------|-------|-------|-------|-------|
| 3A: Looking behind the mirror          |         |       |       |       |       |
| Intercept                              | 1.07    | 0.34  | 3.18  | 0.004 | 0.70  |
| Mirror                                 | -0.5    | 0.29  | -1.72 | 0.10  | -0.39 |
| 3B: Double Take                        |         |       |       |       |       |
| Intercept                              | 0.05    | 0.07  | 0.74  | 0.47  | 0.16  |
| Mirror                                 | 0.10    | 0.10  | 1.04  | 0.30  | 0.22  |
| 3C: Try / Touch the mirror / Structure |         |       |       |       |       |
| Intercept                              | 0.51    | 0.2   | 2.53  | 0.02  | 0.57  |
| Mirror                                 | -0.45   | 0.25  | -1.79 | 0.09  | -0.40 |
| 3D: All touches to body parts          |         |       |       |       |       |
| Intercept                              | 3.09    | 0.52  | 6.04  | <.001 | 1.33  |
| Mirror                                 | -0.75   | 0.67  | -1.12 | 0.28  | -0.25 |
| 3E: Touch hand                         |         |       |       |       |       |
| Intercept                              | <.001   | 0.005 | 0.002 | 1.00  | 0.00  |
| Mirror                                 | 0.01    | 0.007 | 1.43  | 0.17  | 0.32  |
| 3F: Touch foot                         |         |       |       |       |       |
| Intercept                              | <.001   | 0.005 | 0.00  | 1.00  | 0.00  |
| Mirror                                 | 0.01    | 0.007 | 1.45  | 0.15  | 0.32  |
| 3G: Touch chest                        |         |       |       |       |       |
| Intercept                              | 0.14    | 0.12  | 1.16  | 0.25  | 0.26  |
| Mirror                                 | 0.00    | 0.16  | 0.00  | 1.00  | 0.00  |
| 3H: Touch belly                        |         |       |       |       |       |
| Intercept                              | 0.09    | 0.06  | 1.53  | 0.14  | 0.34  |
| Mirror                                 | -0.05   | 0.08  | -0.64 | 0.529 | -0.14 |
| 3I: Touch back                         |         |       |       |       |       |
| Intercept                              | 0.05    | 0.08  | 0.63  | 0.53  | 0.14  |
| Mirror                                 | 0.05    | 0.11  | 0.45  | 0.66  | 0.10  |
| 3J: Touch arm                          |         |       |       |       |       |
| Intercept                              | 0.10    | 0.06  | 1.66  | 0.11  | 0.37  |
| Mirror                                 | -0.05   | 0.09  | -0.59 | 0.56  | -0.12 |
| 3K: Touch flank                        |         |       |       |       |       |
| Intercept                              | 0.60    | 0.26  | 2.32  | 0.03  | 0.52  |
| Mirror                                 | 0.10    | 0.37  | 0.27  | 0.79  | 0.06  |
| 3L: Touch head                         |         |       |       |       |       |
| Intercept                              | 0.03    | 0.01  | 1.75  | 0.09  | 0.67  |
| Mirror                                 | <.001   | 0.02  | 0.00  | 1.00  | 0.00  |
| 3M: Touch neck                         |         |       |       |       |       |

|                              | $\beta$ | SE   | t     | P    | D     |
|------------------------------|---------|------|-------|------|-------|
| Intercept                    | 0.05    | 0.04 | 1.41  | 0.17 | 0.28  |
| Mirror                       | -0.05   | 0.05 | -1.00 | 0.32 | -0.22 |
| 3N: Touch body (other parts) |         |      |       |      |       |
| Intercept                    | 0.20    | 0.11 | 1.78  | 0.09 | 0.41  |
| Mirror                       | -0.10   | 0.13 | -0.79 | 0.44 | -0.17 |

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**Table 4.**

Parameter estimates from general linear mixed models (LMM) and effect sizes (Cohen's D) for percent change in females' behavioral measures (lip-smacking, female-initiated contact, female-initiated proximity, back-arching/tail-lashing, restraining, movement duration, movement frequency, and breaking affiliation) from control to mirror condition. Each percent change in female behavior was predicted by male temperament (High-aggressive and Low-aggressive), male percent change in behavior, and an interaction between male temperament and male percent change in behavior. Parameter estimates from the best fitting models are reported here; Interpretation of results for models where male percent change in behavior significantly predicted percent change in female behavior is as follows: 4A) Because both percent change in male lip-smacking and percent change in female lip-smacking were log transformed, we can interpret percent changes in female lip-smacking as  $43.3 \pm SE 41.3\% + 74.3 \pm SE 21.9\%$  per every one-unit increase in percent change male lip-smacking; 4D) Both male and female percent change in arching/lashing were log transformed; therefore, percent change in female arching/lashing is interpreted as  $34.5 \pm SE 32.9\% + 51.5 \pm SE 23.2\%$  per every one-unit increase in percent change male arching/lashing; 4F) Unfortunately, because we needed to use a square root transformation to achieve normality for percent change in female locomotion duration, our results for the regression coefficients are virtually uninterpretable (Gelman & Hill, 2006; Pek, Wong, & Wong, 2017); 4G) Percent change in male and female frequency of locomotion bouts did not need to be transformed; therefore, female percent change in frequency of locomotion is interpreted as  $-11.8 \pm SE 19.2\% + 71.1 \pm SE 13.8\%$  per every one-unit increase in percent change male locomotion frequency; 4H) Both male and female percent change in breaking affiliative contact were log transformed; therefore, changes in female breaking affiliation can be interpreted as  $6.5 \pm SE 14.5\% + 50.1 \pm SE 18.7\%$  per every one-unit increase in male percent change in breaking affiliative contact.

|                                 | $\beta$ | SE    | t      | P     | D      |
|---------------------------------|---------|-------|--------|-------|--------|
| 4A: Lip-smacking                |         |       |        |       |        |
| Intercept                       | 0.433   | 0.413 | 1.047  | 0.324 | 0.234  |
| Male Temperament                | -0.799  | 0.416 | -1.919 | 0.072 | -0.429 |
| Male Behavior                   | 0.743   | 0.219 | 3.392  | 0.004 | 0.759  |
| 4B: Female-initiated contact    |         |       |        |       |        |
| Intercept                       | 0.339   | 0.282 | 1.200  | 0.349 | 0.268  |
| Male Temperament                | -0.431  | 0.339 | -1.272 | 0.220 | -0.284 |
| 4C: Female-initiated proximity  |         |       |        |       |        |
| Intercept                       | 0.614   | 0.213 | 2.879  | 0.010 | 0.644  |
| Male Behavior                   | -0.112  | 0.281 | -0.397 | 0.696 | -0.089 |
| 4D: Back-arching / Tail-lashing |         |       |        |       |        |
| Intercept                       | 0.345   | 0.329 | 1.048  | 0.309 | 0.234  |
| Male Behavior                   | 0.515   | 0.232 | 2.218  | 0.040 | 0.496  |
| 4E: Restraining                 |         |       |        |       |        |
| Intercept                       | 0.564   | 0.227 | 2.487  | 0.023 | 0.556  |
| Male Temperament                | -0.472  | 0.321 | -1.472 | 0.158 | -0.329 |
| 4F: Locomotion (duration)       |         |       |        |       |        |
| Intercept                       | 0.865   | 0.184 | 4.712  | 0.037 | 1.054  |
| Male Behavior                   | 0.191   | 0.064 | 2.977  | 0.021 | 0.666  |

|                            | $\beta$ | SE    | t      | P     | D      |
|----------------------------|---------|-------|--------|-------|--------|
| 4G: Locomotion (frequency) |         |       |        |       |        |
| Intercept                  | -0.118  | 0.192 | -0.616 | 0.593 | -0.138 |
| Male Behavior              | 0.711   | 0.138 | 5.169  | <.001 | 1.155  |
| 4H: Beak Affiliation       |         |       |        |       |        |
| Intercept                  | 0.065   | 0.145 | 0.449  | 0.659 | 0.100  |
| Male Behavior              | 0.501   | 0.187 | 2.679  | 0.015 | 0.599  |

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