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Room size and offspring presence impact pair-bonded primate affiliation

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Abstract

Primates live in a variety of social groupings and vary in the expression of species-typical behaviors depending upon social conditions. Coppery titi monkeys (*Plecturocebus cupreus*) are pair-bonding, territorial primates often used to study neurobiology and social behavior in captivity at the California National Primate Research Center (CNPRC). At the center, titi monkeys are housed in cages of standardized size. However, the number of cages—and thus families—per room varies based upon the room size (small or large). Anecdotal evidence suggests titi monkeys behave differently in the two different room sizes. To empirically test this, we measured rates of pair-bonding related affiliation in 23 pairs of titi monkeys. We predicted that monkeys in small rooms would show higher rates of affiliation compared to large rooms. We used a between- and within- subjects design in which all subjects moved from either small to large or large to small rooms. Affiliative behavior was recorded via bihourly instantaneous scan samples. We found that titi monkey pairs affiliated significantly more in small rooms compared to large rooms (partial $R^2 = 0.1468$, $t_{(33)} = -3.729$, p-value < .0005). We also confirmed that the presence of offspring negatively impacts pair affiliation rates (partial $R^2 = 0.2240$, $t_{(33)} = -0.181$, p-value = 0.0011). The results of this study suggest that titi monkey pair behavior is influenced by room size, and thus the number of neighboring groups. Management decisions should consider the implications that housing may have on the results of social behavior research.

Keywords

nonhuman primates; housing; management; room size; pair bond; affiliation

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Author Contribution Statement

AL, BP, and KB designed the study. BP processed and compiled archival data. AL and LW conducted data analysis. AL wrote the original draft. All authors contributed to manuscript revisions.

Competing Interests Statement

The authors declare they have no competing interests.

Introduction

The physiological and neurological similarities between nonhuman primates (NHP) and humans make NHP use in laboratory research significant both in potential impact and ethical consideration (Bales et al., 2017). NHPs are similar to humans in some aspects of their behavior and biology due to their genetic similarities and shared evolutionary history, increasing the translational validity of results from those studies (Phillips et al., 2014). Across the Primate order, species have a wide variety of social structures, ranging from solitary living to pair living to large groups (Silk, 2007); with those various social structures come suites of correlated behaviors (Bales et al., 2021). NHP model species are often housed in captivity in research facilities and primate centers (National Primate Research Centers, 2023; Phillips et al., 2014). The captive environment poses novel challenges to animals' social behaviors (Mallapur & Choudhury, 2003; Schapiro et al., 2003). Species- or social structure-specific behaviors often intersect with the captive animals' housing environments to amplify or diminish other behaviors (Simpson & Kelly, 2011).

Coppery titi monkeys (*Plecturocebus cupreus*) have been housed at the California National Primate Research Center (CNPRC) since the 1970s because they serve as an ideal comparative model for understanding the neurobiology, physiology, and behavior of pair bonding (Bales et al., 2017; Lorenz & Mason, 1971). Titi monkeys live in bonded pairs with any subadult offspring (hereafter referred to as "pairs" or "families" depending on the presence of offspring; Mason, 1966). Like many pair-bonded species, titi monkey adults form and maintain their pair bond through prolonged physical contact and affiliative interactions (Bales et al., 2021). Titi monkeys regularly engage in territorial defense through loud, coordinated calls and aggression towards unfamiliar individuals (Cubicciotti & Mason, 1976; Robinson, 1981); such territorial behaviors have been observed in both wild (Mason, 1966) and laboratory settings (Lau et al., 2020; Müller & Anzenberger, 2002; Witczak et al., 2018). Although the titi monkeys housed at the CNPRC cannot physically interact with other family groups and have minimal visual access to non-family members, there are currently many animals in acoustic and olfactory contact with each other.

In the CNPRC housing setup, titi monkeys live in consistently sized cages, but those cages are placed in two different room sizes (small or large). Titi monkeys may perceive more auditory signals from conspecifics as the number of families in a room (local population size) increases, despite occupying separate physical spaces from other families. In other words, a large room contains more families, and presumably has a greater total occurrence of intra-room, inter-family vocal interactions, compared to a small room. How this perceived increase in population size affects behavior within the family, particularly affiliative behavior between pair mates, is investigated in our study. Using archival behavioral data, we investigated affiliation behavior based on several predictors including offspring presence or absence, housing room size, and pair-bond tenure. We hypothesized that laboratory housing directly impacts titi monkey social behavior. We predicted that rates of affiliative behavior in titi monkeys would be negatively correlated with room size. We also predicted that offspring presence would negatively correlate with rates of affiliative behavior in titi monkey pairs, consistent with our previous findings in this species (Karaskiewicz et al., 2021).

Methods

Subjects

Coppery titi monkeys (*Plecturocebus cupreus*) used in this study were housed at the CNPRC in Davis, California. Titi monkeys were housed in family groups, including a paired adult male and female and up to three of their offspring. The titi monkeys were provided a diet of monkey chow, sliced apples, bananas, carrots, and rice cereal twice daily, as well as various types of food enrichment. Monkeys were maintained on a 12-hour light cycle with lights on at 0600 hours and off at 1800 hours. The indoor monkey environment was maintained at 21°C. Animals were provided water ad libitum. Family groups were housed in 1.2 × 1.2 × 1.8 m or 1.2 × 1.2 × 2.1 m stainless steel cages. Cages contained four perches of varied height and texture, as well as a perch to access enrichment items mounted to the inside of the cage door (Mendoza & Mason, 1986; Tardif et al., 2006); individuals could utilize these spatial options to avoid or maintain proximity with family members.

During this study, between 2 and 23 families occupied each room. Maximum capacity was dependent on room size; throughout the study, small rooms (27.87 m^2) contained an average of 4.1 ± 0.03 cages (range 2–6) and large rooms (111.48 m^2) contained an average of 14.2 ± 0.26 cages (range 7–23). The room dimensions of small and large rooms constrained how many cages could fit in one room. From this point forward, these two population sizes/room sizes will be referred to as small and large rooms. By nature of their spatial arrangement, animals in both room sizes could hear animals living in similarly sized, adjacent rooms through the walls. Animals in small rooms could hear fewer animals through the walls than animals in large rooms. (*i.e.*, small rooms bordered other small rooms while large rooms bordered other large rooms. Small and large rooms were in different parts of the facility). Titi monkey pairs were regularly observed calling in response to animals living in other rooms.

The 23 titi monkey pairs examined in this study were housed together for at least 30 days each in both small and large rooms. Pairs moved from one room size to the other at least once. Behavioral data were collected for 30 days following 15 small-to-large room moves and 19 large-to-small room moves. Animals moved from one room size to the other based on research needs and occurred purely for colony convenience.

Behavioral Observations

Affiliative behaviors between pair mates were recorded via instantaneous scan sample every two hours, five days a week, beginning at 0630 hours and concluding at 1630 hours. The exact number of samples for each pair varied slightly depending upon personnel availability. As such, we included number of observations in our initial model. Behaviors were categorized as affiliative if pair mates engaged in “tail-twining” (male and female sitting side-by-side with tails intertwined at least one turn), “contact” (bodily touching including sitting, grooming, or copulation), or remaining in “proximity” (within one titi monkey arm’s length of each other). Failure to meet any of these criteria was marked as non-affiliative behavior, “none”. As observers approached each pair, they recorded the first identifiable behavior to minimize any possible effects of human presence. Observers were

trained to follow a long-standing protocol for collecting daily affiliation data. Data for this analysis was collected between 2008 and 2019 using the described protocol.

To capture rates of affiliation in each room size, we created daily affiliation scores for each pair. These scores were created by adding up the number of scan sample observations (hereafter referred to as "observations") in which the pair was in affiliative contact (tail-twining, contact, or proximity), divided by the total number of observations that day. Daily affiliation scores were aggregated into average scores over a thirty-day period, to ensure a comparable sample was taken for all pairs. The affiliation scores from large rooms consisted of an average of 79.4 ± 3.6 SE observations per pair (range 52–112); the total number of observations was 2,542. The affiliation scores from small rooms consisted of an average of 63.1 ± 6.3 SE observations per pair (range 28–122); the total number of observations was 1,641.

Data Analysis

We used backward model selection of a linear mixed effect model using the *nlme* package (Pinheiro, 2009) in R programming language and environment (R Core Team, 2022). We modeled affiliation as a function of room size (small or large; fixed effect), number of observations (fixed effect), offspring (absent or present, fixed effect), pair-bond tenure (in years, fixed effect), and an interaction effect between pair-bond tenure and offspring. We included pair ID as the random, repeated measures effect. The initial model included our four fixed effects, interaction effect, and random effect. As we worked through backward model selection, we compared each model using the *anova* function (R Core Team, 2022). We used the resulting log likelihood ratio and p-value to assess model fit, using a standard threshold of $P \leq .05$ as our criteria for retaining or excluding effects in our final model.

We retained the random effect of PairID in our final model despite it not contributing significantly to the overall model variance. We examined a quantile-quantile plot of the residuals of the final model to assess goodness of fit. Our figure was created in R programming language and environment (R Core Team, 2022) using the *ggplot2* (Wickham, 2011) and *cowplot* (Wilke et al., 2019) packages.

Ethical Note

This study was approved by the Institutional Animal Care and Use Committee of the University of California, Davis. This study met all legal requirements of the United States as well as guidelines set by the American Society of Primatologists for the ethical treatment of non-human primates.

Results

Results from our backward model selection indicated the model which best explains pair affiliation included room size (small or large) and offspring presence or absence (Table 1). In each location, room size significantly predicted affiliation scores in that pairs in small rooms affiliated more compared to pairs in large rooms (partial $R^2 = 0.1468$, $t_{(33)} = -3.729$, P value < .0005; Table 1). Similarly, offspring absence or presence significantly predicted affiliation scores such that pairs without offspring affiliated more than pairs with offspring

(partial $R^2 = 0.2240$, $t_{(33)} = -0.181$, P value = 0.0011). The proportion of observations pairs spent affiliating was greater in small rooms (mean 0.49 ± 0.05 SE) than in large rooms (0.34 ± 0.03; Figure 1A). The proportion of observation pairs spent affiliating was greater when the pair did not have offspring (0.49 ± 0.04) compared to when they did have offspring (0.31 ± 0.04; Figure 1B).

Discussion

We predicted that titi pairs would display more affiliation in small rooms compared to large rooms. Our behavioral observations support this prediction, with pairs exhibiting significantly higher levels of affiliation in small rooms compared to large rooms. Furthermore, we found that titi monkey pairs that did not have offspring displayed more affiliation than titi monkey pairs that did have offspring. This effect of offspring remained regardless of room size. The negative impact of offspring behavior has been established in this species (Karaskiewicz et al., 2021; Witczak et al., 2022). Our study confirms this finding in an additional sample.

Our results for titi monkey affiliation may be due to pairs engaging with their acoustic environment. In large rooms, the perception of more vocalizing titi monkeys may draw the attention of pair mates away from each other and to outside the cage. In titi monkeys, vocal communication, specifically vocal duetting, is a known form of intergroup communication that conveys information about caller territory (Robinson, 1981), age (Clink et al., 2019), pairing tenure (Clink et al., 2019), identity (Lau et al., 2020), and heritability (Clink et al., 2022). Therefore, it is possible that titi monkeys in large rooms spend more time attending to these socially relevant caller cues compared to titi monkeys in small rooms.

The continued utilization of titi monkeys in studies at the CNPRC and display in zoos worldwide warrants further investigation regarding ideal housing practices. Further research regarding the behavioral effects of the auditory environment may elucidate if sound dampening is effective in achieving similar behavioral results as small rooms. Acoustic communication is the most likely indicator of population size to titi monkeys, especially considering the restriction of other sensory cues. Future studies should also investigate the impacts of room size on other, non-affiliative behaviors such as mate-guarding, territorial calling, and aggression. Beyond observable behavior, there are likely physiological mechanisms underlying the behavioral changes observed in titi monkey affiliative behaviors in response to their housing environment. It is a worthwhile goal to holistically understand the physiological mechanisms underlying widespread behavioral changes such as those reported here.

Of current application, the affiliation data used in this study are often used in other studies to provide a longitudinal measure of pair-bond quality (Karaskiewicz et al., 2021; Witczak et al., 2022). Consideration of the effects of room size on affiliation is crucial in properly interpreting these data for use in future research, especially experiments using affiliative behavior as a response variable. Further, the behavioral differences observed based on housing environment should be taken into consideration for all studies involving captive animals, as the home environment likely impacts other animal outcome measures.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Data Availability

Data and code to reproduce the analyses are available in the electronic supplementary material.

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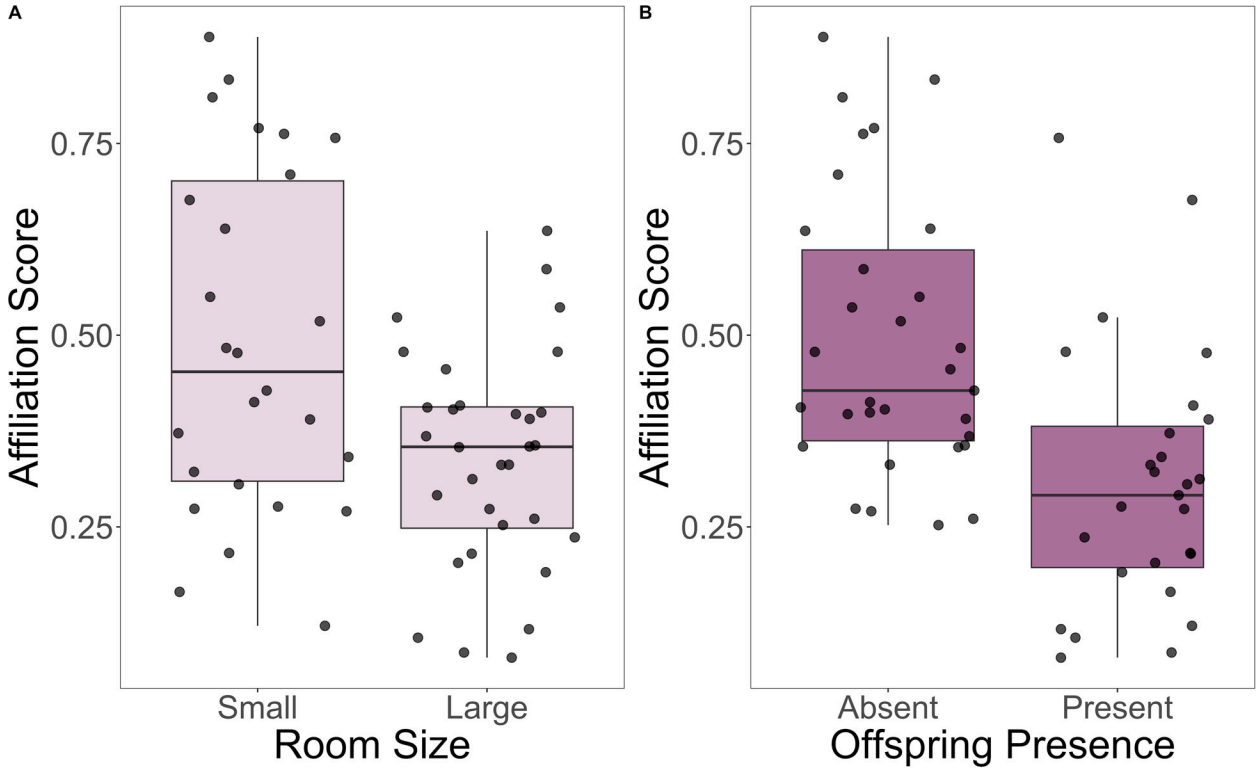

Figure 1.

Affiliation scores (proportion of observations for which affiliative behavior was observed) for 23 pairs. A) Pairs affiliated more in small rooms compared to large rooms. B) Pairs also affiliated more when they did not have offspring, compared to those pairs who did have offspring. For descriptive statistics, see text. For model results, see Table 1.

Table 1.

Results of the linear mixed-effects model assessing pair affiliation. The Model column indicates the statistical model tested (written in the form of independent variable ~ dependent variables). Bolded values indicate the *p* value was significant at $p < 0.05$. The model included PairID as a random effect. For this table, s.e. indicates the standard error of the corresponding parameter estimate. df indicates the degrees of freedom. LLR indicates the log-likelihood ratio. The adjusted repeatability of the random effect represents the proportion of variance due to random effects over the total variance not explained by fixed effects. A smaller value of adjusted repeatability represents higher overall repeatability and thus higher reliability.

Model	Estimate	s.e.	df	t-value	LLR	P value	Partial R2	Marginal R2	Conditional R2
PairAffiliation ~ RoomSize + Offspring									
Intercept	0.575	0.038	33	15.234					
RoomSize	−0.154	0.041	33	−3.729	12.250	**<.0005**	0.1468	0.3731	0.4067
Offspring	−0.181	0.044	33	−4.136	10.689	**0.0011**	0.2240		
Random Effects (adjusted repeatability of PairID = 0.0566)									
PairID	0.0381				0.0252	0.8738			
Residual	0.1556								