

## RESEARCH ARTICLE

# Male Parenting and Response to Infant Stimuli in the Common Marmoset (*Callithrix jacchus*)

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*Callithrix jacchus* infants are raised in complex family environments where most members participate in rearing the young. Many studies examining male parental behavior have focused on the carrying of infants with observations made within the family context. However, interference from family members can make it difficult to assess the father's motivation to care for infants. Our goals were to develop a testing paradigm for determining an individual's response to infant stimuli separate from family influences, compare a male's motivation to respond to an infant stimulus outside the family with his paternal behavior within the family, to compare responses to infant stimuli of parentally experienced versus inexperienced males and finally to develop a reproducible and standardized method of testing male responsiveness to infant stimulus that could serve to evaluate hormonal manipulations. Fifteen experienced common marmoset fathers were evaluated using three different measures of parental behavior: (1) instantaneous scan sampling, (2) continuous focal sampling in the family, and (3) continuous focal sampling of males presented with four infant stimuli: familiar and unfamiliar infants, familiar and unfamiliar infant vocalizations. Six parentally inexperienced males (non-fathers) served as controls. Males that carried the most in the family were typically the same males that responded most to the infant vocalization tests. Experienced fathers did not differ in their latency to enter the stimulus cage for any of the four infant stimuli response tests while inexperienced males took significantly longer to enter the stimulus cage. In addition, fathers expressed a greater frequency of infant-directed behavior than did the inexperienced males during the unfamiliar infant and unfamiliar vocalization tests. These studies show that experienced male marmosets are highly motivated to interact with infant stimuli and that there is interindividual variability in response to infant vocalizations. Testing males outside of the family allows for a clear assessment of male's interest in infant stimuli in both

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## INTRODUCTION

*Callithrix jacchus* are small-bodied Neotropical primates belonging to the family Callitrichidae (marmosets and tamarins). Almost all family members engage in parenting behavior including carrying, grooming, protecting and feeding usually twin infants [Ferrari, 1992; Rothe et al., 1993; Savage et al., 1996; Washabaugh et al., 2002]. Nonmaternal carriers may be necessary for infant survival in some species [Garber et al., 1984; Koenig, 1995; Snowdon, 1996]. Common marmoset and cotton-top tamarin (*Saguinus oedipus*) fathers will carry infants on the first day after birth and may continue carrying their offspring for more than 3 months postpartum [Cleveland & Snowdon, 1984; Mills et al., 2004; Yamamoto, 1993]. Most studies of male parental behavior in cooperatively breeding marmosets and tamarins have recorded carrying of infants within the family context. Infant carrying is an obvious and measurable indicator of infant care. Some of the first studies on common marmoset infant carrying behavior showed that fathers participated extensively in carrying the infants but that individual contribution varied greatly [Box, 1977; Ingram, 1977]. Engaging in infant care is considered costly as seen in reduced time feeding and locomotion [Price, 1992] and when carriers lose weight [Achenbach & Snowdon, 2002; Sánchez et al., 1999]. Therefore, an individual must be motivated to carry infants despite these costs.

Infants are highly attractive to all group members and siblings may compete with parents for infant care [Price, 1991; Pryce, 1988; Yamamoto & Box, 1997]. Family composition has a direct impact on individual carry time. In both common marmosets and cotton-top tamarins sibling helpers affect the amount of parental infant carrying. Increased group size reduced the amount of time fathers spent carrying infants [Garber & Leigh, 1997; Locke-Haydon & Chalmers, 1983; McGrew, 1988; Rothe et al., 1993; Santos et al., 1997; Tardif et al., 1986, 1990].

Hormones may play a role in the male's motivation to care for infants in callitrichids. Prolactin effects on parenting behavior have been examined both within the family and outside of the family context [Schradin & Anzenberger, 2002]. Dixson & George [1982] demonstrated that high levels of prolactin were associated with carrying by fathers. Mota et al. [2006] and Mota and Sousa [2000] also found that prolactin levels increased after carrying infants in both fathers and older offspring. Parentally inexperienced males and females tested outside the family context injected with bromocriptine to lower prolactin levels, exhibited slowed infant retrieval rates and decreased carry times with infant retrieval eliminated in half the subjects [Roberts et al., 2001]. However, experienced marmoset fathers tested within their family groups continued to express paternal behavior when prolactin levels were reduced with cabergoline [Almond et al., 2006]. These apparently contradictory results from lowering prolactin may be the consequence of differences in testing situations that address different components of parental care behavior or due to differences in parental experience that may reduce dependence on prolactin.

Previous experience raising young affects quality of parental behavior in marmosets and tamarins [Snowdon, 1996; Tardif, 1997; Tardif et al., 1984].

In cooperative breeding groups, older siblings may have the repeated opportunity to participate in infant care and in cotton-top tamarins this early experience may be necessary for future mothers to successfully rear their own infants [Tardif et al., 1984]. Individuals that have had extensive experience caring for their younger siblings in their natal groups display more appropriate responses to their own first set of offspring.

Male motivation to care for infants has not been extensively studied in common marmosets. However, Pryce et al. [1993] examined maternal motivation and described a two-phase system for the expression of parental behavior [Pryce, 1996]. The first part is considered the *appetitive* (or incentive motivational) response and refers to the caregiver's ability to physically increase its proximity to a goal stimulus (infant). The *consummatory* component refers to the specific sequence and pattern of behavior that the caregiver expresses upon attaining contact with the goal stimulus. In most studies of parental care within family groups only consummatory behavior is recorded. In this study, we examined male behavior using both appetitive and consummatory measures to determine his interest and motivation to respond to an infant stimulus. In the test described here, the male's behavior when first exposed to an infant stimulus including the latency to reach the source of the distress cry of infants (either a live infant or recording) represents the appetitive phase. The male's subsequent response (e.g. attempt retrieve or carry) when he has achieved contact with the infant stimulus is the consummatory segment of the test.

Given that even parentally experienced male common marmosets show considerable variation in time spent carrying infants and that the presence of family members influences the behavior of the father, we wanted to develop a behavioral test to quantify male interest in infant stimuli separate from the influences of other group members. The aims of this study were to: (a) develop a testing paradigm for determining an individual's response to infant stimuli separate from family influences, (b) compare a male's motivation to respond to an infant stimulus outside the family with his paternal behavior within the family, (c) evaluate responses to infant stimuli by experienced fathers compared with non-fathers, (d) evaluate different types of infant stimuli, and (e) develop a standardized method of testing male responsiveness to infant stimulus that is reproducible and could serve to evaluate hormonal manipulations in both parentally experienced and inexperienced subjects.

## MATERIALS AND METHODS

### Subjects

Common marmosets were socially housed at the Wisconsin National Primate Research Center. Experienced males ( $n = 15$ ) had fathered two or three previous litters. Control males ( $n = 6$ ) were adult parentally inexperienced males that were housed with a nonpregnant female. Males were between the ages of 2.5–9 years ( $5.27 \pm 0.38$ ) at the onset of testing (mean  $\pm$  SEM). Family group size ranged from two to seven individuals, excluding infants (less than 5 months old). Family composition for experienced males were as follows: one with zero helpers, one with one helper, three with two helpers, five with three helpers, three with four helpers and two with five sibling helpers present at birth. Marmoset families were housed in cages that measure either  $122 \times 61 \times 183$  cm or  $61 \times 91 \times 183$  cm. Diets and husbandry details have been reported previously for this colony [Saltzman et al., 1997]. Lighting was regulated on a 12:12 h light/dark cycle and the humidity was maintained at approximately 40%. Housing conditions and

behavioral testing met the guidelines for nonhuman primates and were approved by the Animal Care and Use Committee (IACUC) at the University of Wisconsin.

### **Behavioral Tests**

We used three methods of behavioral sampling: (1) instantaneous scan samples, (2) continuous focal sampling within the family, and (3) continuous focal sampling outside of the family using the infant stimuli response test (see below). Observations began on the day infants were born for the parentally experienced males (Table I) from January 2005 to October 2006. Experienced males were observed using scan and focal behavioral sampling for the first 2 weeks postpartum in their family group and during weeks 3 and 4 postpartum the males were tested in the infant stimuli response cage. Inexperienced males (controls) were only tested with two of the infant stimuli response tests that did not require having offspring of their own: unfamiliar infant stimulus and unfamiliar vocalization stimulus.

#### *Instantaneous scan sampling*

Instantaneous scan samples of infant carrying behavior in families of experienced males were taken five times daily (8:00, 10:00, 12:00, 14:00 and 16:00) during the first 2 weeks postpartum. Individual family members were marked with hair dye (Redken products, Topaz Deco Color and number 91, New York, NY) before birth to ensure immediate recognition. A trained observer entered the room and recorded the identity of the carrier(s) and the number of infants being carried. These data were used to calculate the percent carrying time for each individual family member on each day [for methods and validation see, Ziegler et al., 1990, 2000].

#### *Focal sampling within the family*

Focal observations of the father were conducted on ten occasions, alternating morning and afternoon, for 20 min each during the first 2 weeks postpartum. A predefined ethogram of parental behavior (Table II) was used to record the father's behavior as well as all infant-carrying events by any family member. Trained observers used a hand held Tungsten C Palm Pilot (2005) and the "Hand Obs" observation program (Dr. Kim Wallen, Emory University).

#### *Infant stimuli response tests (outside of the family)*

By 3 weeks after birth, infants have begun to climb off carriers in their home cage and locomote independently [Tardif et al., 1993; Yamamoto, 1993]. Therefore, at 3 weeks postpartum, males were tested outside the family environment in a specially designed infant response cage. The infant response test cage consisted of two pair cages ( $0.6 \times 0.91 \times 1.83$  m) separated by a distance of 0.6 m but connected by a mesh bridge attached 1.17 m above the floor. The bridge allowed free movement between the home cage and the stimulus cage. The cage in which the male was first placed was termed the "home cage" and the adjoining cage containing the stimulus was called the "stimulus cage". The stimulus cage had a divider midway up the cage so that the only the top portion was used. In each condition, the male (either experienced father or inexperienced male) was placed in the home cage and the stimulus was placed in the stimulus cage (Fig. 1).

Parentally experienced males were removed from their family in their home nestbox and placed in the infant response cage, which was located in a separate

**TABLE I. Experimental Design**

Instantaneous scan and focal sampling (in the family)	Infant stimuli response testing (11 days)												
One and two weeks postpartum	Three and four weeks postpartum												
↑ ↑ ↑ ↑ ↑ ↑ ↑ ↑ ↑ ↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	
	Three days habituation	↑ Stim 1	Non-stim control	↑ Stim 2	Non-stim control	↑ Stim 3	Non-stim control	↑ Stim 4	Non-stim control	↑ Stim 4	Non-stim control	↑ Stim 4	Non-stim control

Timetable for behavioral observations during the first 4 weeks postpartum including the focal observations made within the family (weeks 1 and 2) and observations outside the family during the Infant Stimuli Response Tests (weeks 3 and 4). Inexperienced males were tested with only two stimuli; unfamiliar infant and unfamiliar vocalization.

**TABLE II. Ethogram of Positive Infant-Directed Behavior in the Family Group and Outside of the Family During the Infant Response Tests with the Four Different Stimuli (FI, UI, FV and UV)**

Instantaneous and focal family observation	Focal family observation scores	FI and UI	FV and UV
		<i>Look at infant</i> <i>Enter stimulus cage</i>	<i>Look at stimulus</i> <i>Enter stimulus cage</i>
Infant carrying	Touch Sniff  Face lick  Anogenital lick Attempt to retrieve Successful retrieve	Touch Sniff  Face lick  Anogenital lick Attempt to retrieve Successful retrieve	Search in nestbox Manipulate stimulus Attempt to retrieve

FI, familiar infant; UI, unfamiliar infant; FV, familiar vocalizations; UV, unfamiliar vocalizations. Inexperienced (non-fathers) were tested with two stimuli: unfamiliar infant and vocalization. Italicized behaviors are appetitive and the remaining behaviors are consummatory. Duration of carrying was recorded for all family observations and during FI and UI.



Fig. 1. Photograph showing the infant stimuli response cage including the “home cage”, connecting mesh bridge and the “stimulus cage”. The subject male is crossing the bridge from the home cage toward the cage containing the stimulus.

room with no auditory, visual or olfactory cues from other marmosets, other than the specific stimuli provided for the test. Each male had a 20-min habituation session for 3 consecutive days followed by 8 continuous days of testing, alternating between stimulus test and non-stimulus control tests (Table I). On control days, the male was placed in the testing cage for 10 min and his behavior was recorded without the presence of an infant stimulus. On test days, males

were presented with one of four stimuli: familiar infant (FI, the male's own offspring), UI (unrelated infant of same age), familiar vocalization (FV, recording of the male's own infant) and unfamiliar vocalization (UV recording from an unrelated infant), in randomized order without replacement. In all cases, the infants were of 21–31 days old and the recordings were of 15–17-day-old marmosets. Infant vocalization recordings were made by removing the infant from the family group on a carrier. Then the infant was lifted off the carrier and placed into an open Styrofoam sound box on a soft cotton cloth. A digital voice recorder (Olympus DS-2, Center Valley, PA) inside the box recorded cries from 2.5 to 10 min in duration (2.5 min recordings were looped to repeat for the full 10 min). The infant was then returned to the carrier in the nestbox and returned to the family group.

The test began when the nestbox door was opened and the male could move freely about the cage in response to the stimulus. Focal behaviors were recorded for 10 min, after which time the stimulus was removed from the test cage. Trained observers (90% inter-observer reliability) recorded specific infant-directed behaviors that demonstrate a male's interest in the stimulus (Table II). Latency to enter the infant cage and latency to pick-up a live infant were recorded as well as the duration of infant carrying time.

## Data Analysis

Frequencies of specific infant-directed behavior were summed for each male to provide infant response scores in both the family setting (within the family group) and for each of the four infant stimuli response tests (outside of the family). Table II lists the behaviors used in each condition. Latency to enter the stimulus cage and latency to pick-up a live infant were analyzed by time in seconds. All data were tested for normality and homogeneity of variance and as a result nonparametric statistics were used throughout. The Wilcoxon Matched-Pair Signed Rank Test was used for the instantaneous scan sampling to compare percent carrying time between weeks 1 and 2 for fathers, mothers and siblings. Mann-Whitney  $U$  was used for comparing overall carrying during the first 2 weeks between mothers and fathers. Mean duration of infant carrying of fathers in the family were compared with duration of infant carrying for the males with their own infant (FI) in the test cage by Wilcoxon Matched-Pairs Signed Rank Test. Independence of infant-directed behaviors elicited in response to stimuli compared with non-stimulus control days were determined by Friedman's analysis of variance as were the comparison of the males' behavioral response scores between the four stimuli. Fisher's exact test was used to analyze order effects for the presentation of the four stimuli. Friedman's analysis of variance was employed to determine differences between latency to enter the infant cage across each of the four infant stimuli response tests (1 male did not receive the UI test, therefore  $n = 14$ ). Mann-Whitney  $U$  was used to compare latency to enter the stimulus cage between the experienced males and inexperienced control males. All statistical tests were two tailed with a  $P < 0.05$ .

Percent time of infant carrying for the instantaneous scan samples was calculated by noting each time that an individual family member was seen to carry one, two or three infants divided by the number of opportunities to carry (five times each day). We combined the individual contributions of the siblings to provide infant carry percentages dependent on the relation to the infants (mother, father and sibling).

## RESULTS

### Instantaneous Scan Sampling of Infant Carry Behavior

Figure 2 illustrates the mean carrying time for fathers, mothers and siblings. Mean carrying time for fathers did not vary between weeks 1 and 2 (week 1:  $29.8\% \pm 5.32$ ; week 2:  $26.47\% \pm 5.96$ ;  $Z = 0.77$ ,  $n = 15$ ,  $P = 0.44$ ). However, individual variation in carrying was high between fathers (mean range for 2 weeks = 4.5–67%). Mothers, on average, carried significantly more during the first week postpartum,  $53.13\% \pm 6.22$ , than the second week declining to  $40.53\% \pm 6.07$  ( $Z = 2.36$ ,  $n = 15$ ,  $P = 0.02$ ). Differences in average carrying between the mothers and fathers were significant ( $U = 55$ ,  $n = 15$ ,  $P = 0.02$ ) with mothers carrying close to twice as much as fathers during the first 2 weeks postpartum ( $46.67\% \pm 5.6$  and  $28.33\% \pm 5.06$ , respectively). Sibling helpers carried significantly more the second week than the first (week 1:  $18.21\% \pm 5.19$ , week 2:  $34.5\% \pm 6$  [ $Z = 3.17$ ,  $n = 14$ ,  $P = 0.002$ ]). No consistent relationship between family size and the amount of infant carrying by fathers was observed during the first 2 weeks postpartum.

### Continuous Focal Sampling of Paternal Behavior in the Family

Comparisons of sampling methods showed that infant carrying time between the scan samples and the focal samples were highly correlated ( $r = 0.74$ ,  $n = 15$ ,  $P = 0.002$ ) for fathers during the first 2 weeks postpartum. We found no correlation between the fathers' focal family behavioral scores (based on frequencies of infant-directed behavior: Table II column 2) and the amount of fathers' carrying time in the family ( $r = 0.39$ ,  $n = 15$ ,  $P = 0.26$ ).

### Infant Stimulus Response Test

#### *Stimulus tests versus non-stimulus control tests*

Stimuli-directed behaviors (enter stimulus cage and search in nestbox) occurred at a low frequency on non-stimulus control days (habituation day 3, days

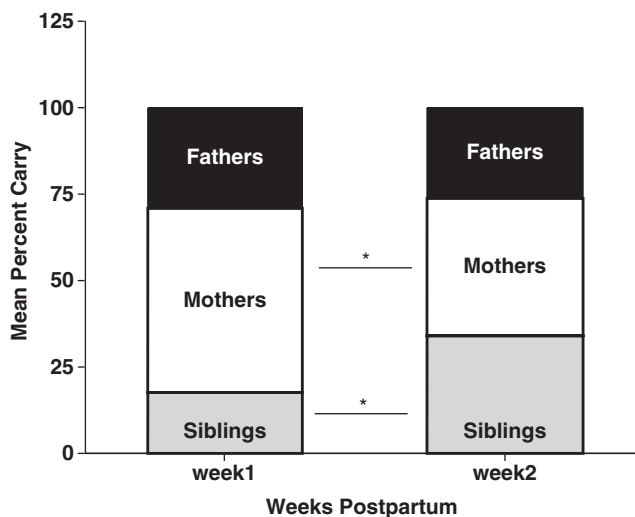


Fig. 2. Mean percent carry from instantaneous scan samples during the first 2 weeks postpartum for fathers, mothers and siblings. \*Significant differences.

2, 4, 6 and 8 of testing). There were no significant differences between the control days ( $\chi^2 = 1.61$ ,  $df = 4$ ,  $P = 0.81$ ). In addition, there was no order effect owing to the random sequence of the four stimuli tests presented to each individual male ( $P = 0.718$ ). However, when comparing between conditions the results showed that males responded significantly differently to the four different stimuli ( $\chi^2 = 16.38$ ,  $df = 3$ ,  $P = 0.001$ ).

*Familiar infant stimulus and unfamiliar infant stimulus*

Initial responses of all experienced males to UIs were comparable with their response to their own familiar offspring (Fig. 3). There was no significant difference in latency to cross the mesh bridge into the stimulus cage between the FI and UI tests ( $Z = 0.52$ ,  $n = 14$ ,  $P = 0.6$ ). For all fathers who crossed the mesh bridge and entered the stimulus cage, FI mean latency was  $10 \pm 2$  sec and UI mean latency was  $20 \pm 8$  sec. Experienced fathers showed little individual variation in their responses to the FI stimulus. In all cases except one, fathers immediately approached and retrieved their own infants and carried them for the duration of the test. On average, males who carried their infants spent  $96.76\% \pm 1.2$  of the total test time carrying their infants compared with a mean average of  $41.62\% \pm 6.21$  per family focal observation. Comparisons of mean duration of carrying between FI and the mean carrying time per focal family observation for each male were significantly different ( $Z = 3.29$ ,  $n = 15$ ,  $P = 0.001$ ). Overall, FI behavioral scores derived from frequency of positive infant-directed behaviors (Table II) for each experienced male were lower than behavioral scores for the other three infant stimuli tests and males showed little overall variation (mean =  $6.99 \pm 1.13$ ). Fathers' UI behavioral response scores varied (mean =  $46.64 \pm 6.03$ ), but seemed to be dependent on the behavior of the infant

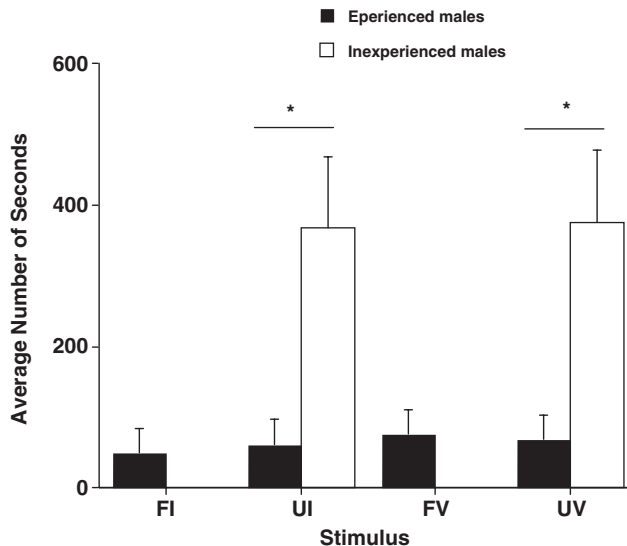


Fig. 3. Mean latency and SE to enter “stimulus” cage during the four different infant stimuli response tests for parentally experienced males versus inexperienced males. FI, familiar infant; UI, unfamiliar infant; FV, familiar vocalization; UV, unfamiliar vocalization. Mann-Whitney *U* showed no significant difference across condition for experienced males however, there was a significant difference between parentally experienced versus the inexperienced males responses ( $P < 0.05$ ).

that often rejected carrying attempts by an unfamiliar male. Although all fathers (except one) attempted to retrieve UIs, only half of the fathers ( $n = 7$ ) were able to successfully retrieve infants. Mean carrying was  $94 \pm 46$  s and carrying time ranged from 0 to 493 sec.

#### *Familiar and Unfamiliar Vocalization Stimuli*

Wide variation in behavioral response scores between fathers was expressed during both vocalization tests (FV: mean =  $44.67 \pm 11.05$ ; UV: mean =  $54.1 \pm 10.69$ ) although, father's behavior scores for FV and UV response tests were strongly correlated ( $r = 0.73$ ,  $n = 15$ ,  $P = 0.002$ ). In addition, the combined frequencies of infant-directed parenting behavior during FV and UV correlated significantly with carrying time analyzed from the instantaneous scan samples obtained in the family context ( $r = 0.73$ ,  $n = 15$ ,  $P = 0.002$ ). Therefore, the males that carried most in the family during the first 2 weeks postpartum were often the same males that responded most to the infant vocalization stimuli.

For all males that entered the stimulus cage containing FV and UV stimuli, average latencies were  $38 \pm 17$  and  $31 \pm 15$  sec, respectively. Additionally, Figure 3 shows that fathers were highly responsive to all stimuli owing to their similar latency to enter the stimulus cage with each of the four stimuli ( $\chi^2 = 3.00$ ,  $df = 3$ ,  $P = 0.39$ ). Specifically, there were no significant differences between latencies to respond to live infants FI compared with vocalizations FV ( $Z = 1.73$ ,  $n = 15$ ,  $P = 0.084$ ). Additionally, there were no significant differences in latency responses between familiar and unfamiliar vocalizations, FV versus UV ( $Z = 0.03$ ,  $n = 15$ ,  $P = 0.98$ ).

#### *Parentally Experienced Versus Inexperienced Males*

There were distinct differences between the parentally experienced fathers and the inexperienced males in response to infant stimuli. Experienced males showed significantly higher behavioral scores than inexperienced males toward the UV stimulus ( $U = 14.5$ ,  $n = 15, 6$ ,  $P = 0.02$ ) but not toward the UI ( $U = 25$ ,  $n = 14, 6$ ,  $P = 0.16$ ; Fig. 4). However, only half of the inexperienced males entered the stimulus cage to investigate the live infant during the entire UI test period.

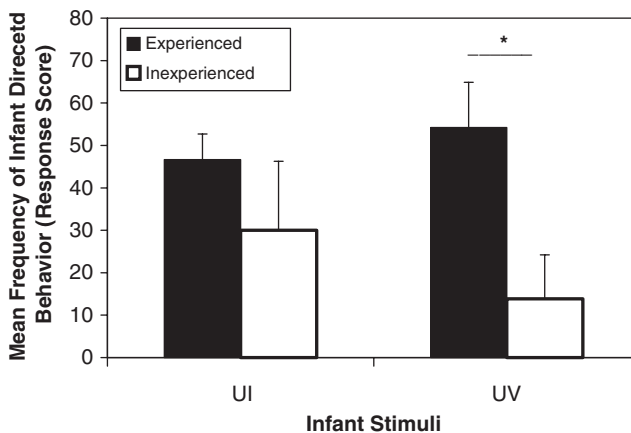


Fig. 4. Behavioral response scores (frequency of infant-directed behavior) for parentally experienced ( $n = 15$ ) versus inexperienced males ( $n = 6$ ) during the unfamiliar infant (UI) stimulus and the UI vocalization (UV) stimulus. \*A significant difference.

Latency to enter the stimulus cage for the UV test showed that non-fathers were significantly slower than fathers who crossed into the stimulus cage ( $U = 14.5, n = 15, 6, P = 0.02$ ). When placed with a live infant (UI), inexperienced controls responded significantly less quickly than did parentally experienced males ( $U = 6.5, n = 14, 6, P = 0.003$ ).

## DISCUSSION

Our results indicate several important factors that influence the expression of paternal care in common marmoset males. Infant care behavior expressed by fathers within the family does not necessarily provide information about his level of interest and responsiveness to infants. Experienced fathers responded with equal magnitude when presented with their own live infant or with an unrelated infant of the same age. Parentally experienced males also responded similarly to the recording of infant cries as they did to a live infant. However, parentally inexperienced males were not as responsive to either live infants or to infant vocalizations compared with experienced fathers.

Mother marmosets carried infants more than fathers during the first 2 weeks afterbirth. Like fathers, however, mothers can vary in the amount of time that they carry their infants [Fairbanks, 1996; Fite et al., 2005; Oliveira et al., 1999] and this may affect a male's ability to carry infants in the family. Therefore, the behavior of the mother may play a role in the variability seen in the expression of paternal care in the family. Protective marmoset mothers may carry the infants more often and thus reduce the amount of time that a father can care for his infants. In this relatively fast growing species [Tardif, 1994], nursing frequency may limit the extent to which mothers can relinquish infant carrying to others before weaning. Tardif [1994] listed two factors that affect the distribution of infant carrying in a group: the interest of non-mothers in infant care and access by non-mothers to infants. Therefore low average carry time by fathers does not necessarily indicate a reduction in the male's interest or willingness to interact or care for his offspring.

The experienced males' appetitive responses showed that males were interested and motivated to respond to all infant stimuli and displayed short latencies to enter the stimulus cage. Moreover, experienced fathers were equally as responsive to infant vocalizations as they were to a live infant indicating that vocal stimuli of infants are as salient a signal as the live infant. Male consummatory behavior expressed once in contact with the infant vocalization stimuli showed a wide individual variation. Some males seemed determined to seek and to find the infant stimuli, looking under the recorder and inside the nestbox, attempting to find the "infant" and thus achieved high behavioral scores, whereas other males would slow or quit their search early. This variability allows us to examine differences between males and how these differences might be affected by other factors such as hormone levels and gene expression.

The use of a vocal stimulus compared with a live infant has many advantages. For example, removing an infant from its family and using it as a stimulus could be stressful to the infant [Pryce et al., 2002]. In addition, vocal recordings can be used repeatedly serving as novel stimuli for multiple males. Our study showed that males did not harm UIs and no aggressive behaviors were expressed toward any UI. However, no tests have been performed to determine the effects on the infant of being removed from its family and placed in an unfamiliar setting. Infants over the age of 21 days often expressed rejection behaviors toward the unfamiliar male. Infants avoided and/or rejected a male's attempt to retrieve the

infant. However, many adult males continued to approach and attempted to retrieve infants despite cuffing behavior by the infant. Even though all fathers (except one) attempted to retrieve UIs, only half succeeded. Studies in the wild and in captivity have not shown breeding males to differentiate between genetic offspring and other infants.

It is not clear whether fathers can distinguish the vocal sounds of his own infant from that of a novel infant. Adult common marmosets have structurally different and unique vocalizations [Jones et al., 1993], but it is not known whether infants have individually distinct features in their calls. In this study, experienced males showed equal latency responses to both familiar and unfamiliar vocalizations. Responses to recordings of infant cries have also been studied in humans. Fleming et al. [2002] found that human fathers displayed a strong and immediate response (on a questionnaire) to infant cries from an (unfamiliar) unrelated infant. Furthermore, experienced fathers responded with a greater “need to respond” than first-time fathers and experienced fathers compared with non-fathers were more alerted by and more sympathetic to the playback of infant cries. Thus, parental experience seemed to contribute to the variance in males’ affective responses to infant cries.

Parentally inexperienced marmoset males were not as responsive as experienced fathers to either the unfamiliar infant or unfamiliar vocalization tests. Experience seems to have a major influence on infant care behaviors in callitrichids [Nunes et al., 2001]. Interestingly, Nunes et al. [2000, 2001] reported that males with considerable earlier experience caring for infants tended to have lower testosterone and estradiol levels than males with little or no experience. The influence of parental experience on both behavior and hormone levels raises the possibility that experience affects certain components of parenting behavior via modulation of hormone levels. Yet, some elements of parental behavior likely become increasingly independent of hormones as parents gain experience caring for their young [Fleming et al., 1996].

We initially hypothesized that the live infant tests (FI and UI) would elicit the most robust response from adult males and provide the greatest degree of variation. However, the results showed that the recordings of a distressed infant provoked equally dynamic responses from the males, and furthermore that the responses to FIs did not provide the variation we had expected. Fathers released from the competition of other family members had the opportunity to immediately retrieve and carry their infants without disruption. In a study of rhesus macaques (*Macaca mulatta*) males tested alone with an infant (outside of the normal social context) expressed otherwise unapparent parental behavior [Gibber & Goy, 1985; Redican & Mitchell, 1973]. In a case where a mother disappeared, four male macaques initially adopted the 11-week-old orphan and provided food, warmth, transport and protection from conspecifics [Berman, 1982], exhibiting skilled and immediate parental care. But, how might a cooperative breeding male marmoset that is needed for successful infant rearing express his motivation to care for infants when released from competing family members? We found that he immediately approached and attempted to retrieve infants and if allowed, carried throughout the test period. We also found that experienced fathers were just as responsive to cues from unrelated infants as they were to cues from their own infants.

Experienced males expressed variability in their involvement in infant care in the family and in their responsiveness to infant stimuli. The obvious paternal behavior expressed is infant carrying but more subtle behaviors might also be important to infant survival such as anogenital licking that stimulates excretion

of waste and has been linked to greater exploratory behavior later in life [Kaplan & Rogers, 1999, 2006]. This example illustrates the potential importance of other parenting behaviors in addition to carrying infants. Clearly both types of behavior indicate some level of male interest in the infant. Yet, males that received high focal family observation scores (based on frequencies of positive infant-directed behavior) were not necessarily the same that carried the most. Those fathers that were not carrying infants often, perhaps because a mother would not relinquish the infant(s) or because an older sibling was highly competitive, or because the father was less motivated to carry his offspring, might still lick or touch the infants while on another carrier. Thus, the breeding male can score high for frequencies of positive infant-directed behavior without spending much time carrying his young. Yet there was no clear pattern linking the number of sibling helpers to amount of infant carrying by fathers within the family. Therefore, it is unclear what are the determining factors within the family regulating expression of paternal behaviors.

In summary, we have developed a method that allows us to test a male's interest in infants without the need to use live infants. Experienced fathers showed great interest in infant stimuli and responded quickly to both live infants and vocalizations. This method will allow us to further examine the factors of experience, genetics and hormonal regulation on the proximate mechanisms of paternal care. Experienced fathers can be tested without competing influences of other group members and the method can be used to evaluate parentally inexperienced males as well.

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## REFERENCES

- Achenbach GG, Snowdon CT. 2002. Costs of caregiving: weight loss in captive adult male cotton top tamarins (*Saguinus oedipus*). *Int J Primatol* 23:179–189.
- Almond REA, Brown GR, Keverne EB. 2006. Suppression of prolactin does not reduce infant care by parentally experienced male common marmosets (*Callithrix jacchus*). *Horm Behav* 49: 637–680.
- Berman CM. 1982. The social development of an orphaned rhesus infant on Cayo-Santiago: male care, foster mother-orphan interaction and peer interaction. *Am J Primatol* 3:131–141.
- Box HO. 1977. Quantitative data on carrying of young captive monkeys (*Callithrix jacchus*) by other members of their family groups. *Primates* 18:475–484.
- Cleveland J, Snowdon CT. 1984. Social development during the first twenty weeks in the cotton-top tamarin (*Saguinus oedipus*). *Anim Behav* 32:432–444.
- Dixon AF, George L. 1982. Prolactin and paternal behavior in a male New World primate. *Nature* 299:551–553.

- Fairbanks LA. 1996. Individual differences in maternal style: causes and consequences for mothers and offspring. In: Rosenblatt JS, Snowdon CT, editors. Parental care: evolution mechanisms and adaptive significance. Advances in the study of behavior. San Diego: Academic Press. p 579–611.
- Ferrari S. 1992. The care of infants in wild marmoset (*Callithrix flaviceps*) group. Am J Primatol 26:109–118.
- Fite JE, Patera KJ, French JA, Rukstalis M, Hopkins EC, Ross CN. 2005. Opportunistic mothers: female marmosets (*Callithrix kuhlii*) reduce their investment in offspring when they have to, and when they can. J Hum Evol 49:122–142.
- Fleming AS, Morgan HD, Walsh C. 1996. Experiential factors in postpartum regulation of maternal care. In: Rosenblatt JS, Snowdon CT, editors. Parental care: evolution mechanisms and adaptive significance. Advances in the study of behavior. San Diego: Academic Press. p 295–326.
- Fleming AS, Corter C, Stallings J, Steiner M. 2002. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. Horm Behav 42: 399–413.
- Garber PA, Leigh SR. 1997. Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. Folia Primatol 68:1–22.
- Garber PA, Moya L, Malaga C. 1984. A preliminary field study of moustached tamarin monkey (*Saguinus mystax*) in North-eastern Peru: questions concerned with the evolution of communal breeding system. Folia Primatol 42:17–32.
- Gibber JR, Goy RW. 1985. Infant-directed behavior in young Rhesus monkeys: sex differences and effects of prenatal androgens. Am J Primatol 8:225–237.
- Ingram JC. 1977. Interactions between parents and infants and the development of independence in the common marmoset (*Callithrix jacchus*). Anim Behav 25: 811–827.
- Jones BS, Harris DHR, Catchpole CK. 1993. The stability of the vocal signature in phee calls of the common marmoset, (*Callithrix jacchus*). Am J Primatol 31:67–75.
- Kaplan G, Rogers LJ. 1999. Parental care in the common marmoset: anogenital licking and effect on exploration. J Comp Psych 113: 76–92.
- Kaplan G, Rogers LJ. 2006. Head-cocking as a form of exploration in the common marmoset and its development. Dev Psychobiol 48:551–560.
- Koenig A. 1995. Group size, composition and reproductive success in wild common marmosets (*Callithrix jacchus*). Am J Primatol 35:311–317.
- Locke-Haydon J, Chalmers NR. 1983. The development of infant-caregiver relationships in captive common marmosets (*Callithrix jacchus*). Int J Primatol 4:63–81.
- McGrew WC. 1988. Parental division of parental caretaking varies with the family composition in cotton-top tamarins. Anim Behav 36:285–286.
- Mills BA, Windle CP, Baker HF, Ridley RM. 2004. Analysis of infant carrying in large, well-established family group of captive marmosets (*Callithrix jacchus*). Primates 45:259–265.
- Mota MT, Sousa MBC. 2000. Prolactin levels of fathers and helpers related to alloparental care in common marmosets, *Callithrix jacchus*. Folia Primatol 7:22–26.
- Mota MT, Franci CR, Sousa MBC. 2006. Hormonal changes related to paternal and alloparental care in common marmosets (*Callithrix jacchus*). Horm Behav 49: 293–302.
- Nunes S, Fite JE, French JA. 2000. Variation in steroid hormones associated with infant-care behavior and experience in male marmosets (*Callithrix kuhlii*). Anim Behav 60:857–865.
- Nunes S, Fite JE, Patera KJ, French JA. 2001. Interactions among paternal behavior, steroid hormones, and parental experience in the male marmosets (*Callithrix kuhlii*). Horm Behav 39:70–82.
- Oliveira MS, Lopes FA, Alonso C, Yamamoto ME. 1999. The mother's participation in infant carrying in captive groups of *Leontopithecus chrysomelas* and *Callithrix jacchus*. Folia Primatol 70:146–153.
- Price EC. 1991. Competition to carry infants in captive families of cotton-top tamarins (*Saguinus oedipus*). Behavior 118: 66–88.
- Price EC. 1992. The costs of carrying in captive cotton-top tamarins. Am J Primatol 26:23–33.
- Pryce CR. 1988. Individual and group effects on early caregiver-infant relationships in red-bellied tamarin monkeys. Anim Behav 36:1455–1464.
- Pryce CR. 1996. Socialization, hormones and the regulation of maternal behavior in nonhuman simian primates. In: Rosenblatt JS, Snowdon CT, editors. Parental care: evolution mechanisms and adaptive significance. Advances in the study of behavior. San Diego: Academic Press. p 643–689.
- Pryce CR, Döbeli M, Martin RD. 1993. Effects of sex steroids on maternal motivation in the common marmoset (*Callithrix jacchus*): development and application of an operant system with maternal reinforcement. J Comp Psych 1:99–115.

- Pryce CR, Ruedi-Bettschen D, Dettling AC, Feldon J. 2002. Early life stress: long-term physiological impact in rodents and primates. *Physiology* 17:150–155.
- Redican WK, Mitchell G. 1973. The social behaviour of adult male-infant pairs of rhesus macaques in a laboratory environment. *Am J Phys Anthropol* 38:523–526.
- Roberts LR, Jenkins KT, Lawler T Jr, Wegner FH, Newman JD. 2001. Bromocriptine administration lowers serum prolactin and disrupts parental responsiveness in common marmosets (*Callithrix jacchus*). *Horm Behav* 39:106–112.
- Rothe H, Darms K, Koenig A, Radespiel U, Juenemann B. 1993. Long-term study of infant-carrying behavior in captive common marmosets (*Callithrix jacchus*): effects of nonreproductive helpers on the parents' carrying performance. *Int J Primatol* 14: 79–93.
- Santos CV, French FA, Otta E. 1997. Infant carrying behavior in callitrichid primates: *Callithrix* and *Leontopithecus*. *Int J Primatol* 18:889–907.
- Saltzman W, Schultz-Darken NJ, Abbott DH. 1997. Familial influences on ovulatory function in common marmosets (*Callithrix jacchus*). *Am J Primatol* 41:159–177.
- Sánchez S, Peláez R, Gil-Bürman C, Kaufmann W. 1999. Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *Am J Primatol* 48:99–111.
- Savage A, Snowdon CT, Giraldo H, Soto LH. 1996. Parental care patterns and vigilance in wild cotton-top tamarins (*Saguinus oedipus*). In: Norconk MA, Rosenberger AL, Garber PA, editors. *Adaptive radiation of Neotropical primates*. New York: Plenum Press. p187–199.
- Schradin C, Anzenberger G. 2002. Why do New World monkey fathers have enhanced prolactin levels? *Evol Anthro Supp* 1: 122–125.
- Snowdon CT. 1996. Infant care in cooperatively breeding species. In: Rosenblatt JS, Snowdon CT, editors. *Parental care: evolution mechanisms and adaptive significance*. Advances in the study of behavior. San Diego: Academic Press. p 643–689.
- Tardif SD. 1994. Relative energetic cost of infant care in small-bodied Neotropical primates and its relation to infant-care patterns. *Am J Primatol* 34:133–143.
- Tardif SD. 1997. The bioenergetics of paternal behavior and the evolution of alloparental care in marmosets and tamarins. In: Solomon NG, French JA, editors. *Cooperative breeding in mammals*. Cambridge England: Cambridge University Press. p 11–33.
- Tardif SD, Richter CB, Carson RL. 1984. Effects of sibling-rearing experience on future reproductive success in two species of Callitrichidae. *Am J Primatol* 6:377–380.
- Tardif SD, Carson RL, Gangaware BL. 1986. Comparisons of infant care in family groups of the common marmoset (*Callithrix jacchus*) and the cotton-top tamarin (*Saguinus oedipus*). *Am J Primatol* 11:103–111.
- Tardif SD, Carson RL, Gangaware BL. 1990. Infant-care behavior of mothers and fathers in communal-care primate, the cotton-top tamarin (*Saguinus oedipus*). *Am J Primatol* 22:73–85.
- Tardif SD, Harrison ML, Simek MA. 1993. Communal infant care in marmosets and tamarins: relation of energetics, ecology, and social organization. In: Rylands AB, editor. *Marmosets and tamarins: systematics, behaviour, and ecology*. Oxford, England: Oxford University Press. p 220–234.
- Washabaugh KF, Snowdon CT, Ziegler TE. 2002. Variations in care for cottontop tamarin, *Saguinus oedipus*, infants as a function of group size. *Anim Behav* 6: 1163–1174.
- Yamamoto EM, Box HO. 1997. The role of non-reproductive helpers in infant care in captive *Callithrix jacchus*. *Ethology* 103: 760–771.
- Yamamoto ME. 1993. From dependence to sexual maturity: the behavioural ontogeny of Callitrichidae. In: Rylands AB, editor. *Marmosets and tamarins: systematics, behaviour, and ecology*. Oxford: Oxford University Press. p 220–234.
- Ziegler TE, Widowski TM, Larson ML, Snowdon CT. 1990. Nursing does affect the duration post-partum ovulation interval in cotton-top tamarins (*Saguinus oedipus*). *J Reprod Fertil* 90:563–571.
- Ziegler TE, Wegner FH, Carlson AA, Lazaro-Perea C, Snowdon CT. 2000. Prolactin levels during the periparturitional period in the biparental cotton-top tamarin (*Saguinus oedipus*): interactions with gender androgen levels and parenting. *Horm Behav* 38:111–122.