



Is infant-carrying a courtship strategy in callitrichid primates?

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(Received 19 March 1996; initial acceptance 22 May 1996;

final acceptance 26 July 1996; MS. number: A7556)

Abstract. Three predictions arising from the proposal that infant-carrying serves as a form of courtship in callitrichid primates were tested, using data from captive common marmosets, *Callithrix jacchus* and cotton-top tamarins, *Saguinus oedipus*. The first prediction, that males would be more likely to successfully copulate while carrying infants than while not carrying infants, was not supported in either species. In common marmosets, males were less likely to copulate while carrying infants. This relation may reflect the lower activity levels and increased vigilance required by those individuals transporting infants. The second prediction, that the overall percentage of time that males spent carrying infants would be related to overall frequency of copulations during fertile periods, was also not supported for either species. The third prediction was that, if females selected mates relative to their infant-care ‘performance’, males should be more solicitous of the breeding female’s efforts to relinquish the infant to another carrier than to the efforts of other group members. If so, then males should retrieve harassed infants from mothers more frequently than from other group members; this prediction was not supported. The results of this study offer no support for the contention that infant care serves as a form of courtship in callitrichid primates.

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Relations between infant-care behaviours by males and mating access to females have been proposed for a wide variety of animals. In some species, male parental care may conflict with pursuit of further breeding opportunities. In some cichlid fish, for example, male investment in care of young or nests may be reduced if breeding access to other females is increased (Keenleyside 1983). In other species, males may alter their infant-care behaviours relative to previous sexual access to the breeding female. In some polyandrous birds, for example, there is evidence that the willingness of males to participate in care of nestlings is to some degree dependent upon sexual access to the breeding female (Brown 1987; Davies et al. 1992). Such relations might be expected in species in which mating behaviour precedes the period of care by a relatively short period (e.g. 10–20 days in dunnocks: Davies et al. 1992).

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Care of infants by males is less common in mammals than in either fish or birds; where it occurs, however, relations between male parental behaviour and mating access to females may also exist. One mammalian group in which male infant care is common is the primates of the family Callitrichidae (marmosets and tamarins). Because callitrichid males experience a 130–180 day delay between mating and infant care (i.e. the length of gestation), little opportunity exists for a direct causal link between mating and subsequent willingness to care for infants. Therefore, it is not surprising that callitrichid males do not appear to apportion infant care relative to previous access to mating (Cleveland & Snowdon 1984; Wambolt et al. 1988; Baker et al. 1993; Tardif 1996). A different relation between infant care by males and mating has been proposed in this taxonomic group, however. Rylands (1982, 1996), Price (1990) and Ferrari (1992) have proposed that infant-carrying by potential breeding males may function as a form of courtship, given that callitrichid primates typically ovulate 10–30 days after parturition (Hearn 1983; Ziegler et al. 1987) and are therefore fertile during the time when infants

must be nursed and carried. Price (1990) proposed that it would 'pay females to choose as mates males that are competent caretakers' (page 784) and in support of this hypothesis, reported that captive male cotton-top tamarins, *Saguinus oedipus*, were more likely to engage in sexual behaviour when they were carrying infants than when they were not. Based on this study, the conclusion that females 'actively trade sex for help with rearing' (page 1086) was cited by Dunbar (1995) as a partial explanation of why young callitrichid males might be willing to bear the cost of helping with infant care.

Issues surrounding Price's analyses, however, as well as empirical observation on other callitrichid species (Baker et al. 1993; Jurke et al. 1995) leave questions regarding the validity and the generality of this link between male infant care and mating access to the female. The present analysis was designed to further explore the relation between male infant-care behaviour and mating access to females in two callitrichid species, the common marmoset, *Callithrix jacchus*, and the cotton-top tamarin. If selection pressures have indeed led to female selection of sexual partners based upon the infant-care behaviours of those partners, a variety of relations between infant-care behaviours and sexual behaviours can be proposed. Using data collected from captive marmosets and tamarins, we tested the following three predictions regarding the relation between behavioural interactions of the breeding male and female, concentrating on the most obvious infant-care behaviour in callitrichid primates, the physical transport of infants.

(1) During the period in which females were fertile and infants were frequently being carried, males would be more likely to successfully copulate while carrying infants than when they were not carrying infants. Such a relation between overall sexual activity and infant care during the first 8 weeks postpartum was found for captive cotton-top tamarins by Price (1990).

(2) There would be a positive correlation between overall frequency of male infant-carrying and overall frequency of copulation. Females might respond to infant care by males even if copulation was not directly associated with male infant-carrying. One test of this proposal is the comparison of frequency of copulation with frequency of male infant care. We predicted that males would be permitted relatively more copulations during the entire fertile period if they

carried infants relatively more often during that time.

(3) Males would be more responsive to the breeding female's desire to relinquish the infant to other carriers than to that of other group members. Infant carrying can be conducted only by one individual at a time. Individuals frequently harass the infants they are carrying (nipping and grabbing at them as well as rubbing them against a perch or the side of a cage) to rid themselves of the infant. A female might be expected to assess the infant-care 'performance' of a male by the extent to which she could relinquish infant-care duties when ready. For this reason, we predicted that, if infant care serves a courtship function, males would be more likely to retrieve harassed infants from breeding females than from other group members.

METHODS

Subjects of this study were 10 breeding pairs of common marmosets observed across the rearing of 18 different litters and 16 breeding pairs of cotton-top tamarins observed during the rearing of 25 different litters. When observations were made of a given breeding pair during the rearing of more than one litter, the observations from all litters were combined. The only exception to this rule was when a given pair was observed both with and without helpers present. Because helpers affect the frequency with which the breeding male carried infants (Tardif et al. 1990), these observations were treated as independent. The cotton-top tamarins were part of a captive breeding colony and were being observed as part of a longitudinal study of the factors affecting infant care and infant-survival (Tardif et al. 1990, 1992). The common marmosets were part of a longitudinal study of nutrition-reproduction interactions. All subjects were housed in similar cages (152 × 183 × 183 cm) with visual screening between groups. Groups comprised a breeding male and female, the infants, and from 0 to 7 offspring from previous litters. General details of housing and management are provided in Clapp & Tardif (1985).

Observations were conducted three times per week up to 8 weeks after delivery in cotton-top tamarin groups. Common marmoset groups were observed once or twice daily from days 1-14

postpartum and three times per week from week 3–16. During each 30-min observation, the following information was recorded, using either a hand-held tape recorder and stopwatch or a notebook computer with Observer 3.0 software: (1) identity of each individual who carried infants; (2) each transfer of an infant from one carrier to another and whether the transfer was accompanied by harassment on the part of the first carrier; (3) copulations (defined as mounts with thrusting); (4) mounts without thrusting (scored only for cotton-top tamarins). For six common marmoset groups, the time spent eating by each breeding male was also scored to determine effects of infant carrying on behaviours other than sexual behaviours.

We limited observations to the period most likely to be associated with fertile copulations and during which infants were still being carried a majority of the time. The interpretation of Price's results is confounded because data were pooled over a period during which the infants were maturing; in such a situation, the frequency with which adult males carried infants during the female's oestrus might be confounded with the relative maturity of infants. It is difficult to determine cause and effect in such a scenario.

In this study, the common marmoset females underwent a laparoscopic examination at 14 days postpartum that, in each case, provided evidence of ovulation prior to day 14. Infants were carried infrequently after 4 weeks of age. We therefore limited the observations used for this study to weeks 1–4 for the common marmosets. The occurrence of postpartum ovulation in the cotton-top tamarins used in this study was not determined. Ziegler et al. (1987), however, found that ovulations occurred most often between 13 and 29 days postpartum in this species. Infant carrying by mothers decreased substantially after week 4 and that by males after week 6 (Tardif et al. 1990). We therefore limited the observations used for this study to weeks 1–6 for this species.

The first prediction was tested by comparing the frequency of copulations when males were or were not carrying infants. To directly compare our observations with those of Price (1990), we calculated the copulation frequency per 30 min spent carrying versus 30 min spent not carrying infants for breeding males and females. The rates of copulations when carrying versus not carrying

infants were compared with a Wilcoxon matched-pairs signed-ranks test for both males and females for the common marmosets. We observed few copulations in the cotton-top tamarin groups. Therefore, the data on copulations and the extent of infant carrying by males in the 2 weeks surrounding the observed copulation are presented without statistical analysis.

The second prediction, that there would be a positive relation between frequency of male carrying and copulations, was tested in the common marmosets by calculating a Spearman correlation coefficient between frequency of copulations per 30 min observed and percentage of time spent carrying by males. For both species, a Mann–Whitney *U*-test was used to compare the percentage of time that males carried in the groups in which copulations were observed with that of males in groups in which no copulations were observed.

To test the third prediction, that males would be more likely to retrieve harassed infants from the breeding females than from others, the ratio of male retrieval following harassment/total number of harassments by breeding females versus other group members was compared with a Wilcoxon matched-pairs signed-ranks test. In this case, only groups with members in addition to the infants and breeding pair were considered.

The percentage of time that common marmoset males spent eating when they were carrying versus not carrying infants was compared with a Wilcoxon matched-pairs signed-ranks test. All statistical analyses were performed using SPSS 6.1.

RESULTS

Prediction 1: Males Will Copulate More While Carrying Infants

Common marmosets

Eight pairs were observed to copulate during weeks 1–4. The median number of copulations per pair per litter was 1.5 (range=0–7). Males were carrying infants during 20.7% of all copulations. The frequency of copulations per 30 min carrying versus not carrying for each pair during the peri-ovulatory period differed significantly, but in the opposite direction of that found by Price: males were more likely to copulate while they were not

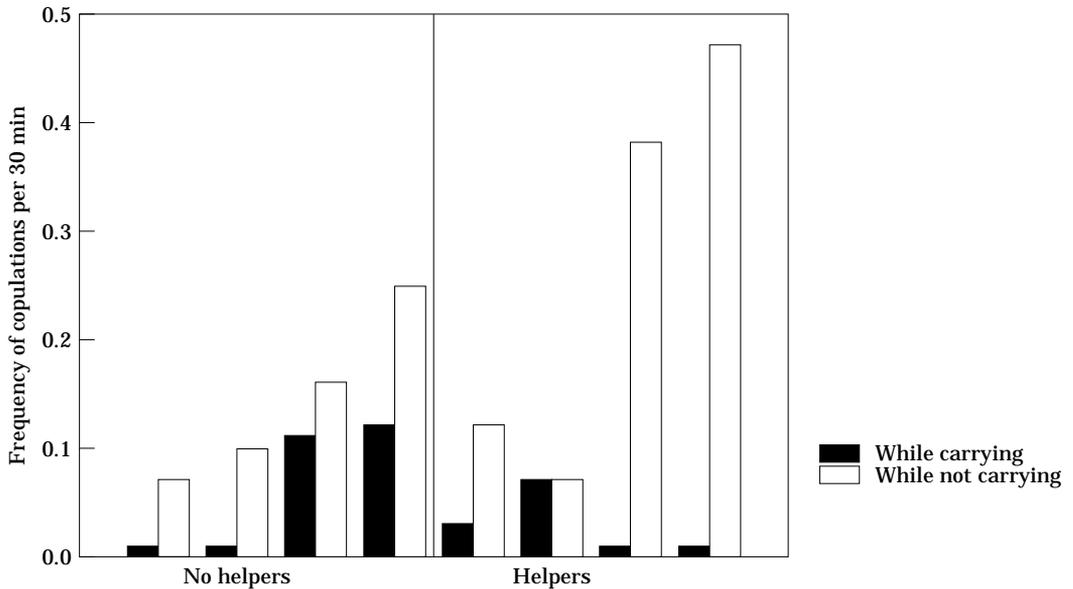


Figure 1. Number of copulations per 30 min that males were either carrying (■) or not carrying (□) infants ($N=8$ common marmoset males).

Table I. Copulations and infant-carrying in five cotton-top tamarin groups

Helpers present?	Who carried infant during copulation	% Time spent carrying by		
		Breeding male	Breeding female	Neither
No	Breeding female	18.3	67.9	13.8
Yes	Neither	27.9	15.7	56.4
Yes	Both breeding female and male	29.6	14.8	55.6
Yes	Neither	24.2	29.7	46.1
Yes	Breeding female	43.2	53.1	3.7

carrying infants (Wilcoxon matched-pairs signed-ranks test: $Z = -2.366$, $P = 0.018$; Fig. 1). There was no apparent effect of helper presence on this relation, that is, males copulated more often while not carrying both in pairs and in family groups. There was no relation between infant-carrying by females and copulations (data not shown), a result similar to that found by Price (1990) for captive cotton-top tamarins.

Cotton-top tamarins

Completed copulations were observed in only five breeding pairs (Table I). The male was carrying the infant during the copulation in 1/5 cases. In 4/5 cases the animal carrying the

infant during copulations was the animal that most frequently carried the infant during the 2-week period surrounding the observed copulation, suggesting that copulations did little to alter who carried the infant. In addition to these completed copulations, mounts with no thrusting (i.e. incomplete copulations) were observed in five breeding pairs. Total copulations (complete and incomplete) were evenly divided between males who were carrying and not carrying infants, but there was an apparent relation between carrying and success: 1/5 males who successfully copulated were carrying infants while 4/5 males who unsuccessfully copulated were carrying infants.

Copulations might be less frequent when males were carrying infants because most activities are generally less frequent during infant transport. To determine whether this might be the case in the common marmosets, we compared the frequency with which males displayed a different behaviour (eating) while they were carrying versus not carrying infants ($N=6$). These results are similar to those for copulations, with males tending to eat less often while carrying (median=2.0%) than while not carrying (median=6.8%; $Z = -1.782$, $P=0.075$).

Prediction 2: Males Who Carry More Often Will Copulate More Often

Common marmoset

The correlation between percentage of time males carried infants and frequency of copulations was not significant (0.424, $P=0.170$). Time spent carrying by males that were never observed copulating (median=24.0%, range=3.1–68.1%) was not significantly different from those males which were observed to copulate (median=52.0%, range=23.3–74.3%, $U=9.0$, $N_1=8$, $N_2=4$, $P=0.234$).

Cotton-top tamarin

Time spent carrying by males which were never observed copulating (median=33.3%, range=11–60%) was not significantly different from those males which were observed to copulate (47.1%, range=12–87%, $U=29.0$, $N_1=5$, $N_2=19$, $P=0.188$).

Prediction 3: Males Will Be More Likely to Retrieve Harassed Infants from the Mother than from Other Group Members

Males were not more likely to retrieve infants from breeding females than from other carriers in either species (common marmoset: $Z = -0.314$, $P=0.753$; cotton-top tamarin: $Z = -0.902$, $P=0.367$; Table II).

DISCUSSION

The results of this study provide no support for the contention that infant-carrying may serve as a

Table II. Ratio of male retrievals to number of harassments of infants relative to identity of harasser

Species (N)	No. male retrievals/ No. harassments by:	
	Breeding female	Others
Common marmoset (6)		
Median	0.33	0.35
Range	0.0–1.0	0.12–0.53
Cotton-top tamarin (13)		
Median	0.28	0.25
Range	0.0–0.67	0.0–1.0

form of courtship in callitrichid primates. There are a number of possible reasons why the results of this study differ so dramatically from those found by Price (1990). First, analyses of copulations per carrying time were limited to the time during which ovulation was likely and infants were still being transported a majority of the time. If males carried infants less frequently during later weeks, owing to increasing maturity of the infants and also copulated less during this period because the females were not ovulating, then the pooling of data over periods longer than 6 weeks postpartum may have suggested a causal relation that does not really exist. Second, we separated completed copulations, defined as those that included a mount followed by pelvic thrusting, from incomplete copulations. Price (1990) included both completed and attempted mounts and did not indicate what percentage of the total mounting attempts were completed. This factor may be important because a growing body of evidence suggests that many complex behaviour patterns are incompatible with infant carrying in callitrichids.

Recent studies, including this one, suggest that infant-care behaviours in both captive and free-ranging callitrichid primates are not compatible with other activities such as foraging and frequent locomotion (Goldizen 1987; Price 1992; Digby & Barreto, in press). This incompatibility probably stems not only from the relatively large weight burden of the infants, but also from the extremely high levels of vigilance displayed by these small primates (Caine 1993; Tardif 1994). Vigilance and crypticity are proposed to be the primary means of protection against predators in this group (Terborgh 1983; Caine 1993). Given these

relations, it is not surprising that sexual activity resulting in completed copulations may be less likely for those individuals who are carrying infants.

These results do suggest, then, that selection pressures on females are unlikely to be reflected in a simple or straightforward relation between the presence of infants on the male and successful copulation. This result does not preclude the possibility, as Price (1990) suggested, that it would 'pay females to choose as mates males that are competent caretakers' (page 784). Predictions 2 and 3 were designed to test less specific relations that might arise from such selection pressures on breeding males and females. In neither case was support found for a relation between male infant-care behaviour and access to breeding females. Prediction 2 tested the possibility that, even if males are precluded from copulating while carrying infants, a relation might still exist between the general amount of investment in infant care provided by the male and copulation frequency. Such a relation was not found. Because all of the groups observed in this study contained only one potential breeding male, a female might still choose to mate with a male that carried more often, if she was given a choice between potential breeding males. Because multiple breeding males are often found in free-ranging callitrichid groups, a relation between infant care and mating access might occur in such a setting. The only relevant results from free-ranging callitrichids do not support such a contention, however. Baker et al. (1993) compared the extent of infant care by dominant and subordinate males in free-ranging two-male-one-female trios of golden lion tamarins, *Leontopithecus rosalia*. They found no difference in the percentage of time that dominant and subordinate males carried infants, although dominant males appeared able to sexually monopolize the female during probable oestrus periods.

Prediction 3 tested the possibility that, if females were making the selection, then males might be expected to be more solicitous of the female's desire to relinquish the infant than to such desires of others. No support was found for this hypothesis. It is possible, however, that in a free-ranging setting, where the costs associated with infant-care behaviours would be higher, males might be more selective as to the conditions under which they retrieve an infant from another carrier. Perhaps in this case, some differential

response towards breeding females versus others might be seen.

Attraction to infants is widespread and evolutionarily conservative in primates. Within the platyrrhines (New World primates), infant transport by males is routinely observed in at least seven different genera, including *Aotus*, *Callicebus*, *Pithecia* and the Callitrichidae (Wright 1984; Vogt 1984). With no agreement on the phylogenetic relations between these groups, it is difficult to assess whether care arose separately for these genera, raising the possibility that infant care by males is a conserved trait among these species. In such a situation, strong selection for infant care, by itself, may form the basis for the infant-care behaviours displayed by animals that are not mothers or parents, as has been proposed for some communally breeding species of birds (Jamieson 1989). Emlen et al. (1989) proposed that subsequent adaptive modifications of these behaviours will be revealed in who participates in such behaviours and under what circumstances, and provided convincing evidence of such adaptive modifications in a number of vertebrate and invertebrate species. Such evidence linking male infant-care behaviours to mating opportunities in callitrichid primates was initially presented by Price (1990). The present study and that of Baker et al. (1993), however, suggest that it is premature to presume that infant care by callitrichid males is a courtship strategy resulting from selection pressure on females to choose mates based on their infant-care abilities.

ACKNOWLEDGMENTS

We thank Donna Layne, Barbara Gangaware and Robert Carson for their assistance in data collection. This research was supported by NIH grant R01-RR02022 to S. Tardif; K. Bales was supported by an NSF predoctoral fellowship.

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