American Journal of Primatology 25:185–190 (1991)

BRIEF REPORTS

Infant Carrying in a Polygynous Group of Common Marmosets (*Callithrix jacchus*)

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In a captive group of common marmosets (*Callithrix jacchus*), consisting of six group members and the three infants of the two breeding females, we analyzed participation of all group members in infant carrying, and suckling by the two breeding females. During the first two weeks of the infants' lives, the two breeding females carried their own infant(s) almost exclusively due primarily to the mutual avoidance by the two females. At the beginning of the third week of the infants' lives nearly all group members began to carry all infants to a relatively high degree and both breeding females suckled all infants. The results indicate that the greater energetic demands in rearing three infants simultaneously are compensated by an extended division of labor among group members.

All breeding animals preferred to carry and to suckle the infants according to kinship predictions. However, observed preferences of nonbreeding group members in infant carrying seemed not to be related to different degrees of genetic relatedness.

Key words: polygyny, communal suckling, kin relationships

INTRODUCTION

Recent studies on wild marmosets and tamarins have questioned the traditional view of a monogamous mating system in callitrichids [e.g., Sussman & Garber, 1987]. Surveys on captive colonies suggest that polyandry in cotton-top tamarins or polygyny in common marmosets at least may be an optional, alternative mating system [definitions according to McGrew, 1986], although its occurrence seems to be rare and dependent on specific circumstances [see Price & McGrew, in press; Rothe & Koenig, in press]. In particular, the occurrence of polygyny seems to be related to the immigration or integration of a male newcomer after the loss of the former resident breeding male [Baker, personal communication, regarding *Leontopithecus rosalia;* Goldizen, 1987 regarding *Saguinus fuscicollis;* Price & McGrew, in press, regarding *S.o. oedipus;* Rothe & Koenig, in press, regarding *C. jacchus;* Wolters, personal communication, regarding *C. geoffroyi*].

The successful rearing of the offspring of two breeding females has not been

Received for publication October 3, 1990; revision accepted December 20, 1990.

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TABLE I. Composition of the Study Group*

Name	Sex	Age (months)	Remarks
BM	M	58.5	replacement male; father of S5, J1, J2, J3
BF1	F	58.0	original breeding female; mother of BF2, S3, S4, S5, J1, J2
BF2	F	19.5	second breeding female; mother of J3; full sibling to S3, S4; unrelated to BM
S3	M	14.0	twin to S4; unrelated to BM
S4	F	14.0	see S3
S5	M	8.0	maternal half sibling to BF2, S3, S4; son of BM and BF1
J1	M	0.0	twin to J2; son of BM and BF1
J2	M	0.0	see J1
J3	F	0.0	daughter of BM and BF2

*Age at start of study.

reported in species of *Saguinus,* but has been seen in lion tamarins and marmosets [see references cited above]. In these cases, polygyny may have two implications for the cooperative breeding system of callitrichids. First, polygyny requires that the "group's resources for infant care" [Price & McGrew, in press] have to be shared between two breeding females. Second, the degree of relatedness between nonbreeding group members and the different sets of infants may differ. This suggests a need for investigating the potential influence of kin relationships on helping behavior. This paper describes the carrying and suckling of infants in a polygynous group of common marmosets.

METHODS

At the start of the present study, the group consisted of six group members: the breeding male (BM), two breeding females (BF1, BF2), and three nonbreeding group members (S3, S4, S5; see Table I). BF2 and the three nonbreeding group members were the offspring of BF1. BM had been integrated 1.5 years before and fathered only the male S5. Thus BF2, S3, and S4 were full siblings and related to S5 at F = 0.25 (maternal half siblings; F = degree of relatedness).

Fifteen days after her mother (BF1) had given birth to quadruplets (two infants survived), BF2 gave birth to twins (one dead, one alive; see Table I). Copulations had been observed between BM and both breeding females 5.5 months before the start of the present study. Since at this time S3 was still sexually immature, BM has to be the father of both sets of offspring [for a more detailed description see Rothe & Koenig, 1987].

Observations were recorded from the first day of life of BF1's infants ("sampling all occurrences of some behaviors for all group members" [Altmann, 1974]) and lasted for a period of 65 days. Data presented here are based on 90 × 30 min observation sessions (24 before birth of BF2's infant and 66 afterwards). We analyzed in particular the carrying frequency of all group members and suckling by the two breeding females. Carrying bouts were counted with respect to the number and identity of infants and the identity of the carrier. $KMNO_4$ dye applied to different parts of the body of BF1's infants was used for identification of the infants. Thus the data refer to the contribution of each group member to the carrying frequency of each infant ("carrying performance"). Suckling frequency was examined by counting each suckling bout of each infant. To test for preferences for the different infants, a "chi-square-test for split probabilities" [Weber, 1986] was used

TABLE II. Relative Week-by-Week Percent Contribution to Carrying of All Infants

Group member	Week 1[a]	Week 2[a]	Week 3[b]	Week 4[b]	Week 5	Week 6	Week 7	Week 8	Week 9	Weeks 3 to 9
BM	20.7	22.8	21.9	10.0	12.8	19.6	27.3	14.3	18.0	17.3
BF1	79.3	76.1	25.6	28.6	29.3	34.8	29.2	28.6	42.6	29.9
BF2	0.0	1.1	46.2	34.7	19.7	7.8	9.5	19.8	19.7	24.0
S3	0.0	0.0	6.1	18.6	17.6	16.4	19.0	16.5	11.5	15.4
S4	0.0	0.0	0.3	2.9	9.3	2.9	4.0	5.5	8.2	4.3
S5	0.0	0.0	0.0	5.1	11.3	18.4	11.1	15.4	0.0	9.2

[a]Only BF1's infants present.
[b]Percent of carrying of BF2's infant during week 3 to 4 (see text).

(significance level $P < 0.05$). For both carrying performance and suckling, the expected probabilities were $P_e = 0.667$ (BF1's infants) and $P_e = 0.333$ (BF2's infant).

RESULTS

During the first two weeks, until the birth of BF2's infant, carrying was almost exclusively performed by the respective parents and in particular by the breeding female BF1 (BF1: 77%; BM: 22%; BF2: 1%; see also Table II). The same pattern followed for the first two weeks of life of BF2's infant, which was carried most often by BF2 and BM (BF2: 84%; BM: 14%; BF1: 2%). During these first weeks we observed that the breeding females sometimes "sham" attacked each other. This behavior was usually shown when BF2 approached BM, who was carrying BF1's infants, or vice versa, when BF1 approached BM, who was carrying BF2's infant. At the beginning of the third week of the infants' lives, all group members began to carry all of the infants and sham attacks between the two breeding females were no longer seen.

Table II shows the week-by-week contribution of individual group members to carrying of all infants. In particular, from week 5 onwards the percent scores of carrying became increasingly balanced across subjects. Usually five of the six group members took part with a proportion of more than 7%. In summary, the carrying of all three infants after the birth of BF2's infant was mainly performed by the two breeding females, followed by BM and the male S3. The participation of the remaining two group members S4 and S5 was less than 10% (Table II, last column).

Remarkable carrying preferences emerged (Table III). Both breeding females carried their own infant(s) significantly more often than expected. The twins S3 and S4 preferred to carry their mother's infants significantly more frequently, whereas BM showed a tendency to carry the infant of BF2 more often than expected ($P < 0.1$). Only male S5 showed no carrying preference for either infant(s).

Although both breeding females suckled all infants, they preferred to suckle their own infants (BF1: n = 49, $P_o = 0.817$ vs. $P_e = 0.667$, $\chi^2 = 5.42$; BF2: n = 40, $P_o = 0.714$ vs. $P_e = 0.333$, $\chi^2 = 38.31$). Unfortunately it was not possible to distinguish whether the breeding females, the infants, or both were responsible for these preferences.

DISCUSSION

The results of our study differ from some observations on infant carrying in monogamous families of captive common marmosets, in which usually all family members participate in infant carrying from the first day of the infant's life [e.g.,

TABLE III. Comparison of Expected (P_e) and Observed (P_o) Probabilities for Carrying Performance*

Group Member	BF1's infants (P_e = 0.667)		BF2's infant (P_e = 0.333)		
	N	P_o	N	P_o	χ^2
BM	221	0.621	135	0.379	(3.4)
BF1	507	0.822	110	0.178	66.7
BF2	194	0.393	300	0.607	166.8
S3	277	0.874	40	0.126	61.2
S4	82	0.932	6	0.068	26.7[a]
S5	121	0.637	69	0.363	(0.6)[a]
Total	1402	0.680	660	0.320	(1.6)

*Values in parentheses indicate nonsignificant deviations from the expected value.
[a]Values include the correction of Yates [Weber, 1986].

Rothe, 1978]. Carrying behavior in the polygynous group of the present study resembles more closely the situation in lion tamarins, in which the breeding female carries her infant(s) nearly exclusively during the first weeks [Baker, 1990; Hoage, 1978; Kleiman et al., 1988].

It should be noted, however, that there was some evidence that during these first weeks the breeding females each prevented the other from approaching their own infants. Observations of breeding females avoiding one another have been noted in two other polygynous groups by Jaemmrich [personal communication] and Tardif [personal communication; see also Price & McGrew, in press]. Furthermore, Alonso [1986] reported two cases of infanticide by a dominant female in a polygynous group of captive common marmosets. Thus, the restriction of infant carrying to the respective parents may be a protective strategy to prevent infanticide.

This restrictive pattern changed when the infants became more independent, and they began to move around on their own for considerable periods of time during the third week of life [see also review in Stevenson & Rylands, 1988]. The overall contribution of individual group members to infant carrying became more balanced, with nearly all group members involved to a relatively high degree. In contrast, previous studies on the carrying behavior of common marmosets have shown that in families of comparable size and age structure, often only three to four family members contributed substantially to infant carrying [Rothe et al., submitted; Tardif et al., 1986]. Hence the greater energetic demands in rearing three infants are compensated by a more extended division of labor among group members.

Although the two breeding females preferred to carry and to suckle their own infant(s), both suckled all infants. Such a communal suckling or co-nursing is rarely reported in nonhuman primates. Hrdy [1976] reported only two cases in *Colobus guereza* and *Presbytis johnii,* respectively, and Pereira et al. [1987] as well as Pereira and Izard [1989] provided evidence for co-nursing in prosimians (*Varecia variegata variegata, Lemur catta*). Information on callitrichids is only available on free-ranging polygynous groups of lion tamarins. Communal suckling was rare and may be regarded as accidental events [Baker, personal communication]. In this study the relatively high proportion of suckling infants of the other breeding female may have been facilitated by the restricted laboratory condition. Nevertheless, common marmosets may fulfill the criteria for what McGrew [1986]

called communal maternity, that is, ". . . more than one female in the group has significant probability of giving birth, after which the young are communally nursed."

Baker [1990] found a greater contribution to infant carrying by the more closely related individuals in golden lion tamarins. In accordance with his result, all breeding animals of our study group followed the expected kinship predictions. Concerning the carrying behavior of nonbreeding group members, however, our data on common marmosets differ from the expected prediction. S5, who was more closely related to his mother's infants than to BF2's infant ($F = 0.5$ vs. $F = 0.375$), showed no preference in carrying behavior. In contrast, S3 and S4, who were equally related to all infants ($F = 0.25$), preferred to carry their mother's infants significantly more often.

Interestingly, several weeks after weaning the infants, severe fights took place between BF2 and her siblings S4 and S3, respectively. S4 had to be removed permanently from the group. Thus, differential helping behavior by S3 and S4 may have been preceded or at least may have been affected by their social relationships with BF2 [see also Koenig & Rothe, in press]. However, a broader data base is needed to clarify further the potential influence of kin relationships on helping in common marmosets.

CONCLUSIONS

1. During the first two weeks of the infants' lives, the two breeding females carried their own infant(s) almost exclusively, due primarily to the mutual avoidance between the females.

2. At the beginning of the third week of the infants' lives, nearly all group members began to carry all infants to a relatively high degree and both breeding females suckled all infants.

3. The results indicate that the greater energetic demands in rearing three infants simultaneously are compensated by an extended division of labor among group members.

4. All breeding animals preferred to carry and to suckle the infants according to kinship predictions. However, observed preferences of nonbreeding group members in infant carrying seemed not to be related to different degrees of genetic relatedness.

ACKNOWLEDGMENTS

We are grateful to Jutta Kuester, Bill McGrew, Ute Radespiel, and two anonymous reviewers for their helpful comments on earlier drafts of this paper. We thank Mauvis Gore, German Primate Center, Göttingen, for her help in translating this article.

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