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Long-Term Study of Infant-Carrying Behavior in Captive Common Marmosets (*Callithrix jacchus*): Effect of Nonreproductive Helpers on the Parents' Carrying Performance

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Infant-carrying behavior in four families of Callithrix jacchus *was investigated over a period covering six to eight litters. We evaluated the effect of the total number of helpers and the number of adult helpers on the parents' carrying performance for the total carrying period and for three age stages of the infants. The carrying performance of the parents reached an asymptote beginning with litters 3 to 5. In two groups, the carrying performance of the parents was significantly negatively correlated with group size. However, considerable differences existed within each group and between the groups. The mother was the primary caregiver in the early weeks of the infants' lives. In this phase the helpers' contribution to carrying was less than might be expected. The relief of the parents from infant-carrying was greatest when the infants were 4 to 7 weeks old. Breeding males benefited most and from every helper, while breeding females benefited most from adult helpers, i.e., the carrying performance of the breeding female was considerably reduced until the respective group had grown to 8 to 10 members (infants not included). This group size is considered to be ideal for maximal relief of the parents from infant carrying. An increasing number of adult nonreproductive helpers (> 4 or 5) does not induce a further reduction of the parents' carrying performance. Infant-rearing experience of nonreproductive helpers seems to be more important for the parents' and, especially, the breeding female's relief from infant-carrying than the overall number of helpers is. The data also strongly evidence that a group member's*

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participation in infant-carrying is influenced by housing conditions and the demographic history of the group.

KEY WORDS: common marmoset; infant-carrying; effect of helpers; laboratory environment; long-term study.

INTRODUCTION

Parental behavior, e.g., infant-carrying, food sharing, and baby-sitting by group members other than the breeding pair/animals is a common phenomenon in callitrichids (Mittermeier *et al.,* 1988). Nonreproductive helpers also may contribute to other activities, e.g., watching for predators and territorial defense (Caine, 1992; Koenig and Rothe, 1991). Such cooperative behavior by nonreproductive helpers is explained by their contribution to their own inclusive fitness via kin selection (Hamilton, 1964), by their gain of delayed benefits through reciprocal altruism (Trivers, 1985), and/or by their gain in rearing experience (Epple, 1978; Cleveland and Snowdon, 1984). The breeding partners may benefit from helpers' cooperation in territorial defense, antipredator behavior, and infant care by saving time and energy, and helpers may increase infant survival chances (Garber *et al.,* 1984; Koenig and Rothe, 1991; Rothe *et al.,* 1992b).

Many data on infant care in callitrichids from studies in captivity have been published (Mittermeier *et al.,* 1988). Unfortunately, for the common marmoset this is mainly from groups without (Tardif *et al.,* 1986) or, at best, with two adult offspring (Ingram, 1977) and/or adult nonreproductive helpers (Stevenson and Rylands, 1988). Only limited information is available from wild groups, which indicates a situation principally similar to the captive conditions (Alonso, 1984; Stevenson and Rylands, 1988). Furthermore, long-term studies on the influence of nonreproductive helpers on the parents' investment in infant-carrying are completely lacking for common marmosets.

Principally, a benefit to the breeding animals from helpers in terms of an asymptotic decrease in their contribution to infant-carrying with increasing group size may be presumed. However, the breeding female's participation in infant-carrying might, in fact, be less variable by the presence of helpers, since because of lactation, the mother's care for the infants can be reduced only to a certain level in order not to risk infant survival [*Saguinus oedipus* (McGrew, 1988; Tardif *et al.,* 1990)]. Compared to the females, the breeding males' contribution to infant-carrying might be reduced to a definitely lower level (in the extreme to nil) by the participation of nonreproductive helpers in infant-carrying. Furthermore, since adult nonreproductive helpers may be nutritional and sexual competitors to the

breeding male and female, the parents' investment into infant care might be less minimized by an increasing number of helpers or even increased when the helpers are too numerous.

Our aims in this investigation of *Callithrix jacchus* are to detail (a) the breeding male's and the female's relief from infant-carrying in relation to the number of nonreproductive helpers (=offspring) and (b) the breeding male's and female's relief from infant-carrying in relation to the infants' age and the number of nonreproductive helpers. The differential effect of male and female nonreproductive helpers on the parents' carrying performance and the influence of litter composition and sex of infants on the carrying performance of the parents and nonreproductive helpers will be described elsewhere (Rothe *et al.*, in preparation).

METHODS

Animals

Infant-carrying behavior was recorded in four groups of common marmosets (CO, CQ, CS, CU), starting with the second litter of each group (Table I). From CO and CS we observed eight litters; from CQ, seven litters; and from CU, six litters. Due to the small number of singletons (n = 3), we could not investigate the influence of litter size on the carrying performance of either group member. All live-born singletons (n = 3) and

Table I. Individual Data for CO, CQ, CS, and CU[a]

Group	Parents paired	Generation m/f	No. of (raised) litters[b]	No. of carrying group members[b]	Housing
CO	Feb. 1984	wc/wc	9 (9)	9	1 cage/room, no visual contact with strange group
CQ	Feb. 1984	wc/wc	8 (8)	12	As for group CO
CS	Sept. 1984	F_2/F_2, F4	10 (9)	10	7 cages, olfactory, acoustical, and visual contact with strange groups[c]
CU	Oct. 1985	F_3, F_4[d]/F_2	8 (7)	11	As for group CO

[a]m, male; f, female; wc, wild-caught.
[b]At the end of data recording.
[c]Litters 4 to 9.
[d]Father of litters 3 to 8; integrated before the birth of litter 2.

twins (n = 14) were raised to maturity, whereas from live-born triplets usually only two siblings survived (Rothe *et al.,* 1992a). The breeding animals of CU and CS were born in our marmoset colony, and they had experience in rearing at least three litters of their natal group. Those of CO and CQ were wild-caught and illegally imported by animal dealers. They were confiscated by customs and subsequently given on breeding loan to our institute by the Federal Government of Germany.

Housing

CO, CQ, and CU, were housed in separate rooms varying in size from 13.2 m^3 (for parents and first litter) to 73.5 m^3 (for groups of ≥ 10 members). The groups had no physical or visual contact either with each other or with other groups of our colony, but acoustic and olfactory contact via the central air conditioning system probably occurred. CS was housed under the same conditions when rearing litters 2, 3, and 10, but subsequently, (litters 4 to 9) the group lived in a large area, consisting of seven cages (2.0 to 19.2 m^3) interconnected by tubes made from wire mesh. CS had visual, acoustic, and olfactory contact with a neighboring family.

The cages/rooms were equipped with free-swinging and fixed climbing branches, one to four feeding boards, and one to four sleeping boxes. In addition to natural light, artificial lighting was provided by neon bulbs on a 12-hr cycle. A constant temperature of 25 to 27°C and a humidity of about 70% were maintained by means of an air-conditioning system. The animals were fed twice daily.

Data Recording and Evaluation

Data on infant-carrying were collected via the scan-sampling technique (Martin and Bateson, 1986) every 30 min, at least 10 times a day, 5 days per week for 13 weeks. $KMnO_4$ dye applied to different parts of the body was used to identify the twins, triplets, or quadruplets.

From the frequency at which each group member carried one, two, or three infants, we calculated the carrying performance as the relative contribution of each group member to the carrying of each infant as a percentage, i.e., carrying two or three infants at a time is considered the twofold/threefold carrying performance compared to carrying only one infant. Carrying one or two infants was not analyzed separately, since both followed nearly identical frequency patterns. The carrying performances of the breeding male and female were evaluated (a) for the entire 13-week period in relation to the number of nonreproductive helpers and (b) for

three age stages of the infants. The infants were grouped as follows: weeks 1 to 3 (period 1), weeks 4 to 7 (period 2), and older than 7 weeks (period 3). The end of the first period coincides with the termination of the breeding female's postpartum estrus (Hearn, 1982); the end of the second period is characterized by a substantial increase in the infants' locomotor independence resulting in a reduction of being carried (Engel, 1986; Stevenson and Rylands, 1988).

Statistical procedures included Spearman's rank correlation coefficient r_s (one-tailed) (Siegel and Castellan, 1988) to test the predicted negative correlation between carrying performance of the breeding male and female and number of nonreproductive helpers and between carrying performance and number of nonreproductive helpers in each age period of the infants and *z*-test (Haseloff and Hoffmann, 1968) for the differences in carrying performance by males, females, and nonreproductive helpers in each age period of the infants (data for all groups pooled).

RESULTS

Carrying Performance of the Breeding Male and Female in Relation to the Number of Nonreproductive Helpers

The carrying performance of the breeding males and females (data of all groups pooled) showed a significant negative correlation with the total number of nonreproductive helpers (males, $r_s = -0.79$, $P < 0.01$; females, $r_s = -0.68$, $P < 0.05$), whereas their carrying performance was differently influenced by the presence of adult offspring (males, $r_s = -0.32$, $P > 0.05$; females, $r_s = -0.93$, $P < 0.01$).

Table II. Spearman's Rank Correlations r_s Between Carrying Performance and Number of Nonreproductive Helpers During the Entire Carrying Period

Group	Parents	Breeding male	Breeding female
CO	-0.732**	-0.537*	-0.878***
CQ	-0.937***	-0.937***	-0.667*
CU	-0.812*	-0.551	-0.899**
CS	-0.381	-0.476	+0.143

*$P < 0.1$.
**$P < 0.05$.
***$P < 0.01$.

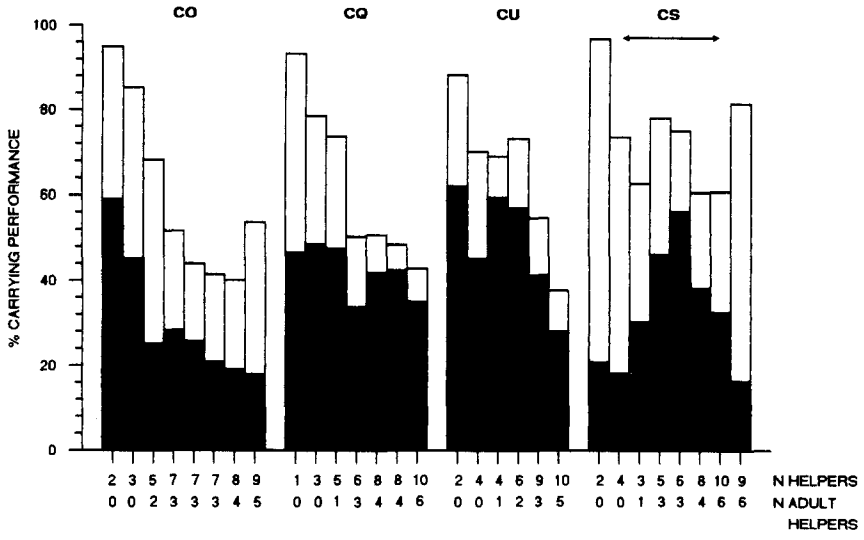

Fig. 1. Carrying performance of the breeding male (open columns) and breeding female (filled columns) of groups CO, CQ, CS, and CU. Columns represent the data for consecutive and successfully reared litters of each group. Double arrow indicates contact with neighboring group.

Figure 1 shows the carrying performance of the breeding male and female of each group and of each litter in relation to the number of nonreproductive helpers. The respective values of Spearman's rank correlation coefficient r_s are given in Table II.

Except for CS and CU (trend), the carrying performance of the parents of CO and CQ was significantly negatively correlated with the number of helpers. However, as can be seen from Fig. 1, considerable differences exist between the groups in the effect of increasing group size on the decrease in the parents' carrying performance. A considerable relief of the parents from infant-carrying is achieved only when the group contains five or six helpers. This condition is reached when at least one offspring has reached adulthood [> 15 months; age classification according to Stevenson and Rylands (1988)], assuming regular breeding of the parents and an interbirth interval of about 150 days (Koenig *et al.*, 1990) (lower abscissa in Fig. 1). This dynamic development of infant-carrying was most pronounced in CO and CQ, delayed in CU, and highly variable, as well as apparently related to the housing condition, in CS. CS and CU differed from CO and CQ in the lack of a continuous reduction in the parents' carrying perform-

ance with increasing group size (CS), a rather high variation from litter to litter, and the apparent dependence of the reduction in the parents' carrying performance on a greater number of adult nonreproductive helpers (CU) as opposed to group CO and CQ. Both CS and CU are "special groups" with respect to housing and demographic history (Table I).

When evaluating the infant-carrying behavior of the breeding male and female separately, only in CQ was the male's carrying performance significantly negatively correlated with an increasing number of nonreproductive helpers. This male showed the most conspicuous reduction in the carrying performance of all males (down to 6%). Although a substantial decrease in infant-carrying was also seen in the CO male from litter 3 to litter 4, this was only a slight and nonsignificant correlation (trend) if all litters are taken into consideration. The males of CS and CU were not significantly affected by the increasing number of nonreproductive helpers. Their carrying performance varied considerably. As a whole, the male of CS showed the highest carrying performance of all males. This behavior was apparently strongly influenced by the housing conditions, as evidenced by the high contribution when no contact with strange conspecifics was possible but the low carrying performance when CS was housed in the neighborhood of a strange group. The male of CU contributed little from the beginning, subsequently showing a still further gradual, but nevertheless substantial, reduction in his carrying performance.

The greatest overall reduction in the carrying performance, and a significant correlation between the carrying performance of the breeding female and the number of nonreproductive helpers, was observed in CO. The carrying performance of the CU female also showed a significant correlation with the group size, but the decrease was delayed compared to CO. The infant-carrying of the breeding female in CQ was only slightly (trend) affected by the number of nonreproductive helpers. The carrying performance of the CS female was positively correlated (nonsignificant) with the number of nonreproductive helpers. Additionally, this female showed a rather pronounced tendency to compensate for the decrease in the male's carrying performance and vice versa.

Carrying Performance of the Breeding Male and Female in Relation to the Number of Nonreproductive Helpers and Age of the Infants

In Fig. 2 the carrying performance of the breeding male and female is shown during each age period of the infants in relation to the number of nonreproductive helpers. The respective values of Spearman's rank correlation coefficient r_s are listed in Table III.

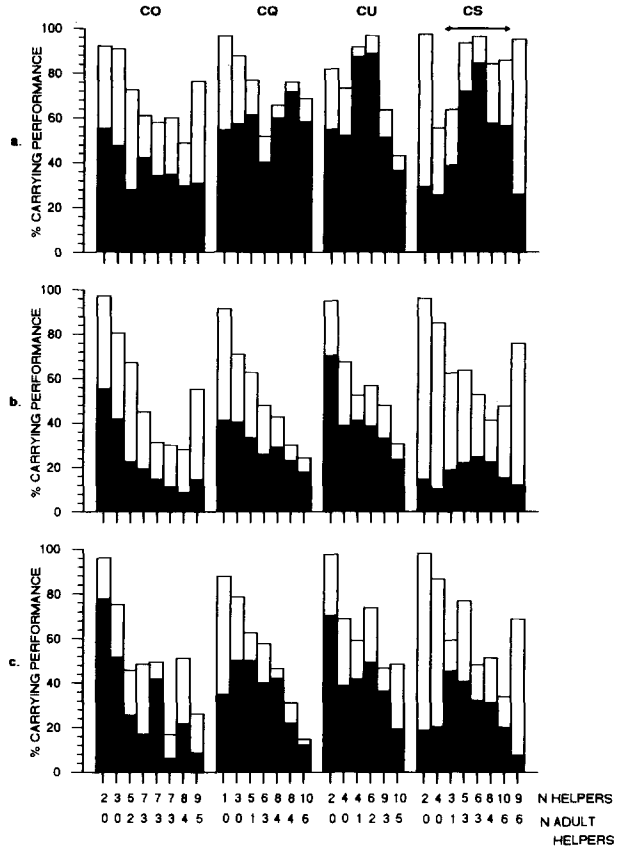

Fig. 2. Carrying performance of the breeding male (open columns) and breeding female (filled columns) of groups CO, CQ, CS, and CU during age period 1 (a), age period 2 (b), and age period 3 (c) of the infants. For further details see Fig. 1.

A significant negative correlation between the carrying performance of the parents and the number of nonreproductive helpers could be revealed only for CQ during the first 3 weeks of the infants' lives (period 1, Fig. 2a). In CO the correlation just failed to reach statistical significance, whereas in CS and CU no significant correlation was found. The high correlation for CQ apparently resulted mainly from the male's reduction in infant-carrying (< 10% in litters 6, 7, and 8), whereas the carrying performance of the remaining three breeding males was highly variable and not significantly correlated with the number of nonreproductive helpers. The breeding females were even less affected. Only in CO was a weak

Table III. Spearman's Rank Correlations r_s Between Carrying Performance and Number of Nonreproductive Helpers During Age Periods 1 to 3

	Period 1			Period 2			Period 3		
Group	Parents	Breeding male	Breeding female	Parents	Breeding male	Breeding female	Parents	Breeding male	Breeding female
CO	-0.610*	-0.146	-0.586*	-0.712**	-0.415	-0.805**	-0.561*	-0.073	-0.756**
CQ	-0.721**	-0.883**	+0.432	-0.991***	-0.991***	-0.937***	-0.991***	-0.955***	-0.545
CU	-0.551	-0.493	-0.551	-0.899**	-0.667*	-0.899**	-0.754*	-0.145	-0.812*
CS	0.0	+0.048	+0.238	-0.619*	-0.595*	+0.143	-0.595*	-0.333	-0.143

*$P < 0.1$.
**$P < 0.05$.
***$P < 0.01$.

negative correlation (trend) observed. Conversely, the carrying performance of the breeding female of CQ and CS showed a positive but nonsignificant correlation with the number of nonreproductive helpers.

During period 2 the relief of the parents from carrying was greatest. Except for CS (trend), there was a significant negative correlation between the parents' carrying performance and the number of nonreproductive helpers. A similar result was obtained when evaluating the male's and female's infant-carrying separately. However, the correlations were higher in females than in males. If all groups were pooled, the nonreproductive helpers' contribution to infant-carrying increased from 24.63% (period 1) to 43.65% (period 2) ($z = 36.58$, $P < 0.03$), whereas the breeding females reduced their carrying performance from 52.03% (period 1) to 27.35% (period 2) ($z = 44.67$, $P < 0.03$). Thus, the nonreproductive helpers and, to some extent, also the breeding males (23.34% in period 1, as opposed to 29.00% in period 2; $z = 11.32$, $P < 0.03$) compensate for the reduction in the females' carrying performance.

The influence of the number of helpers on the parents' contribution to carrying became less pronounced with increasing age of the infants. Despite an overall decrease in the parents' carrying performance, only in CQ did a significant negative correlation result, whereas for the remaining groups the correlation just failed to reach statistical significance. Again, the breeding females were slightly more affected than the breeding males. When the data for all groups are pooled, only minor differences exist in the carrying performance of the breeding males and females and of the nonreproductive helpers between age period 2 and age period 3 (males, reduction from 29.01 to 28.36%, $z = 0.79$, $P > 0.52$; females, increase from 27.35 to 31.56%, $z = 5.26$, $P < 0.03$; nonreproductive helpers, reduction from 43.65 to 40.09%, $z = 4.0$, $P < 0.03$).

When the four groups are compared it is obvious that CS differed considerably from the others. The carrying performance of the CS parents as a whole, and of the individual breeding male and female, was either generally lower or not correlated with the number of nonreproductive helpers during the three age periods.

DISCUSSION

The carrying performances of the breeding males and females varied considerably across the groups (Box, 1977; Ingram, 1977; Stevenson and Rylands, 1988; Tardif *et al.*, 1986), but, as expected, it reached an asymptote in three of the groups, beginning with litters 3–5, when at least one or two adult nonreproductive helpers were present. This corroborates the assump-

tion that the qualification of helpers by their age-related increase in infant rearing experience is more important than the mere number of helpers (Cleveland and Snowdon, 1984; Epple, 1975, 1978; Hoage, 1982; Ingram, 1977). Only occasional observations are reported on exceptional paternal care of male marmosets which had no experience with infants during most of their juvenile lives (Box, 1977).

In the common marmoset, groups of 8–10 members (last infants not included), among which are 2–4 adults, are ideal in size with respect to maximum relief for the parents from infant-carrying [*C. humeralifer* (Rylands, 1986)]. Box (1977) observed a considerable reduction in the breeding female's infant-carrying with increasing number of group members. However, this result is based on carrying twins of only one family during their first 4 weeks of life. Our observations agree with results on the relationship of infant survival and group size in captive *C. jacchus* (Rothe *et al.,* 1992b), comparable results in tamarin species [*S. oe. oedipus* (Price and McGrew, 1990)], and observations on the group size and structure of free-living marmosets [genus *Callithrix* (Stevenson and Rylands, 1988)].

The presence of more than two to four adult nonreproductive helpers did not induce a further reduction in the parents' carrying performance. This result corresponds to observations by Rylands (1986) on carrying of four sets of infants in a free-living group of *C. humeralifer.* This might be explained by the parents' obligation to provide a certain amount of care, especially by the female (Tardif *et al.,* 1990). The parents may benefit from more than four adult offspring by their contribution to other activities, such as territorial defense, watching for predators, and others. However, this aspect needs clarification (Caine, 1992; Koenig and Rothe, 1991).

As expected, the breeding male and female differ in their relief from infant-carrying by helpers (Box, 1977; Ingram, 1977). Females were generally most affected by the presence of nonreproductive helpers, in particular by adult ones, in period 2 and less so in period 3. Hence, during the most critical phase of the infants' extrauterine life (period 1), the helpers' contribution to carrying is less than might be expected. This is true even in large groups with several adult offspring, in which the mother has the main burden, even when considering an increasing contribution to infant-carrying by nonreproductive helpers, as has been shown by Box (1977) and Ingram (1977). The breeding female is the primary caregiver in the early weeks of the infants' lives. This result is in accordance with reports on other colonies of *C. jacchus* (Box, 1977; Ingram, 1977; Locke-Haydon and Chalmers, 1983) and callitrichid species [*L. rosalia* (Hoage, 1982); *C. goeldii* (Heltne *et al.,* 1973; Masataka, 1981)], but it apparently contrasts in several aspects with results obtained from species of *Saguinus* (Epple, 1975; Hampton *et al.,*

1966; Vogt *et al.*, 1978). However, Tardif *et al.* (1986) did not find differences in the percentage of time that *C. jacchus* and *S. oedipus* mothers carried their infants during weeks 1 to 8. The high carrying performance of the females during the first 3 weeks might be explained by their pronounced protective behavior toward the infants in order to minimize the risk of perinatal mortality (Rothe *et al.*, 1992a) and by their frequent and long suckling bouts. For example, Ingram (1977) noted the most considerable shortening of the median suckling bout length from week 1 to week 2 (20 to 6 min) and a further gradual reduction down to 3 min in week 9.

With growing age and body weight of the infants, the helper system clearly became more effective. Growing locomotor activity of the infants in age period 2, either occurring spontaneously or initiated by the mother/carrier by rubbing them off, and diminishing protective behavior and lactating activity of the mother and the onset of and steady increase in solid food consumption by the infants might be factors which promote the reduction in female carrying performance and the concomitant increase in the nonreproductive helpers' contribution to infant care.

After the seventh week, the absolute carrying frequency decreases steadily and substantially; finally, infant-carrying by the females is inevitably linked to the suckling periods (Darms, 1983; Stevenson and Rylands, 1988). Thus, the relatively weak effect of the increasing number of nonreproductive helpers on mother's carrying performance may be explained by the necessity to suckle the infants.

Although only weakly correlated with the number of helpers, all breeding males (except CS) considerably reduced their contributions to infant-carrying compared to the first recorded litters. Hence, the breeding male seems to benefit generally from the presence of nonreproductive helpers, irrespective of his/her age and total group size, whereas the breeding female is not relieved substantially in her carrying performance until at least one of her litters has reached adulthood, i.e., not before the birth of her fourth litter [after approximately 20 months from pairing, taking a regular interbirth interval of 5 months (Koenig *et al.*, 1990)]. This result is more or less conformed by observations by Box (1977) and Ingram (1977) which indicate a relief of the mother from infant-carrying with increasing group size but, additionally, reveal that the greatest relative decrease in infant-carrying is shown by the breeding male, irrespective of group size and age of infants. Unfortunately, comparative data from large groups in other colonies of *C. jacchus* are lacking. In contrast, Price (1992) found no significant correlation between the mother's carrying and group size but a significant negative correlation for fathers in the cotton-top tamarin.

The fact that the breeding male in the investigated groups is definitely less often the predominant carrier than expected (Stevenson and Rylands,

1988) and compared to captive tamarins (Cleveland and Snowdon, 1984; Snowdon and Soini, 1988; but for free-living groups see Savage, 1990) especially during the infants' early ontogeny, requires us to reflect upon the postulated evolution of parental care in marmosets. The breeding female requires assistance from the breeding male(s) because of the infants' high weight in relation to the mother's size as well as the frequent twinning (Sussman and Garber, 1987). However, one should recognize that infant care may be the by-product of quite different male/female strategies [courtship strategy; *S. oedipus* (Price, 1990)] or endocrinological characteristics or both. For example, the high prolactin levels of infant-carrying males may serve as an infant care stimulating mechanism (Dixson and George, 1982), which, admittedly, could be essential for reproductive success and infant survival under specific mating systems but must not necessarily be a *conditio sine qua non* in all circumstances.

Finally, the high variability in the group members' participation and the division of labor in carrying infants of different litters, as well as the differences within and between groups, apparently reflect the group's reaction to the specific circumstances and extrinsic factors (Koenig and Rothe, 1991). The breeding male of CS and his adult sons were very often engaged in monitoring the neighboring group, showing sexual behavior toward the females or agonistic activities toward the males, but less infant-carrying than expected (Darms, 1987; Radespiel, 1990). Similarly, under free-ranging conditions environmental constraints, such as watching for predators and defense of home range, may influence the participation of group members in infant care [*C. humeralifer intermedius* (Rylands, personal communication); *S. oedipus* (Savage, 1990)]. For example, Savage (1990) observed definitely less infant-carrying by free-living cotton-top males compared to their captive counterparts. Thus, our data indicate the further need for long-term studies on infant-carrying in wild marmosets to test the validity of results from captive environments.

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