Articles

MULTIPLE SIMULTANEOUS BREEDING FEMALES IN A PYGMY MARMOSET GROUP (*CEBUELLA PYGMAEA*)

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Callitrichids form polygynandrous social units and have communal breeding systems. In natural groups there are one or more adult individuals of both sexes, as well as subadults, juveniles and infants. The sizes of the groups vary inter- and intragenerically, and inter- and intraspecifically, as well as between different populations, probably depending principally on the resources of the habitat, population density, predator pressure, or the filling of niches by other species. Nonetheless, there are specific tendencies evident in the distinct genera. The *Callithrix* species tend to have larger groups (7-8 members on average) than *Saguinus* and *Leontopithecus* which have 5-6 members on average; this seen especially in the *Callithrix* forms of the Atlantic forest region. They feed to a large extent on tree exudates such as gums, a food source available year-round and concentrated on just a few trees, with enough to feed the group. The main foods of *Saguinus* and *Leontopithecus* are the more dispersed, more seasonally available, fruit and nectar, as well as small animals, as is found with all callitrichids. *Cebuella* is an exception to this trend, feeding principally on tree exudates, and fruit plays a minor role in its diet. The groups, however, are generally smaller (averaging 6 to 7 animals: Hernández-Camacho and Cooper, 1976; Soini, 1988, 1993) than those typical of *Callithrix*, but larger than in the tamarins and lion tamarins. Ranging behavior, which is singular in callitrichids, is evidently correlated (Ferrari and Lopes Ferrari, 1989; Soini, 1993). The home ranges used at any one time are extremely small (sometimes only 0.1 acre; Soini, 1988), and are often ephemeral. When the available exudate trees are insufficient, the groups split or move to a new area. This is possible because the home ranges of different *Cebuella* groups are isolated and distant from each other.

A general characteristic of all callitrichids is the restriction of reproductive activity to just one adult female in the group. The other group members, especially the father but also other adult and subadult individuals, take part in the rearing of the offspring, especially by carrying them (communal breeding system). The causes for this altruistic behavior by the group members in their rearing the young of the reproductive female have not yet been clarified completely, although this phenomenon has been widely discussed in the literature. Callitrichid females usually give birth to twins, which combined comprise about 20% of the mother's weight. Help in carrying the infants is, therefore, seen as a necessity because of the energetic constraints on the mother during lactation (Eisenberg, 1977; Leutenegger, 1980; Garber *et al.*, 1984; Goldizen and Terborgh, 1989). There are, however, examples from the wild and from the captivity which show that mothers can rear their young by themselves (Soini, 1982a; König and Siess, 1986; Rothe and Darms, 1993). The sociobiological explanations of communal in tearing vary (increase of the inclusive fitness, gaining experience for the rearing of own offspring, submissive behavior for securing group membership, etc.) (Epple, 1975b; Rylands, 1989; Cleveland and Snowdon, 1984; Ferrari and Lopes Ferrari, 1989).

Monogamy is considered to be another characteristic of reproductive strategies in callitrichid societies (Hampton *et al.*, 1966; Epple, 1967, 1970; Kleiman, 1977). Reproduction limited to the dominant pair in a group is seen as the basic pattern. There are proven divergences from monogamy, but at a very low percentage in the wild as well as in captivity. Possible deviations from sexual monogamy in wild *Cebuella* and *Callithrix* groups have been found in about 3% of the cases studied. There are even fewer cases of non-monogamous reproduction in captivity (Rothe and Darms, 1993). Reports of polyandrous matings are most frequent, especially in tamarins in the wild. In general, however, closer investigation has shown that only one male in the group has access to the reproductive female in the estrus periods. This does not contradict the observation of polyandrous copulation out of the conceptive periods of the female, but it has often led to the interpretation of a polyandrous reproductive strategy. In principle, functional monogamy is maintained (Ferrari and Lopes Ferrari, 1989). On the other hand, polyandrous reproductive patterns are hard to prove or deny. Theoretically, the dizygotic twins might have different fathers, but genetic finger-printing techniques have failed to answer this question either way because of germ cell chimerism in the early fetal stage (Dixson, 1993).

Group structure alone can indicate reproductive activity in more than one female. More than one reproductive female in wild groups have been observed by Soini (1982) for *Cebuella pygmaea*, by Scanlon *et al.* (1988), Digby and Barreto (1993), and Digby and Ferrari (1994) for *Callithrix jacchus*, as well as by Dietz and Baker (1992) and Dietz and Kleiman (1986) for *Leontopithecus rosalia*. There are reports of more than one reproductive female in captive groups by Abbott (1978, 1984), Rothe (1978), Jämmrich (1985), Anzenberger and Simmen (1987), and Adler and Jämmrich (1991) for *Callithrix jacchus*, as well as by Wim Mager (pers. comm. in Rothe and Darms, 1993) for *Cebuella pygmaea*.

Inhibition of reproductive activity in supernumerary adult males is probably caused by the behavior of the dominant male, although the mechanisms are still unknown. The dominant and reproductive female also inhibits reproduction in other adult females in the group, but the mechanisms differ between the genera. Physiological inhibition of ovulation of the other females occurs in *Cebuella* and *Callithrix*. Pheromones of the dominant female may prevent the secretion of gonadotropin in the hypothalamus of these females (Abbott and Hearn, 1978). Experiments involving blocking the sense of smell, however, have shown

Cover photograph by Russell A. Mittermeier: Yellow-tailed woolly monkey, *Lagothrix flavicauda*.

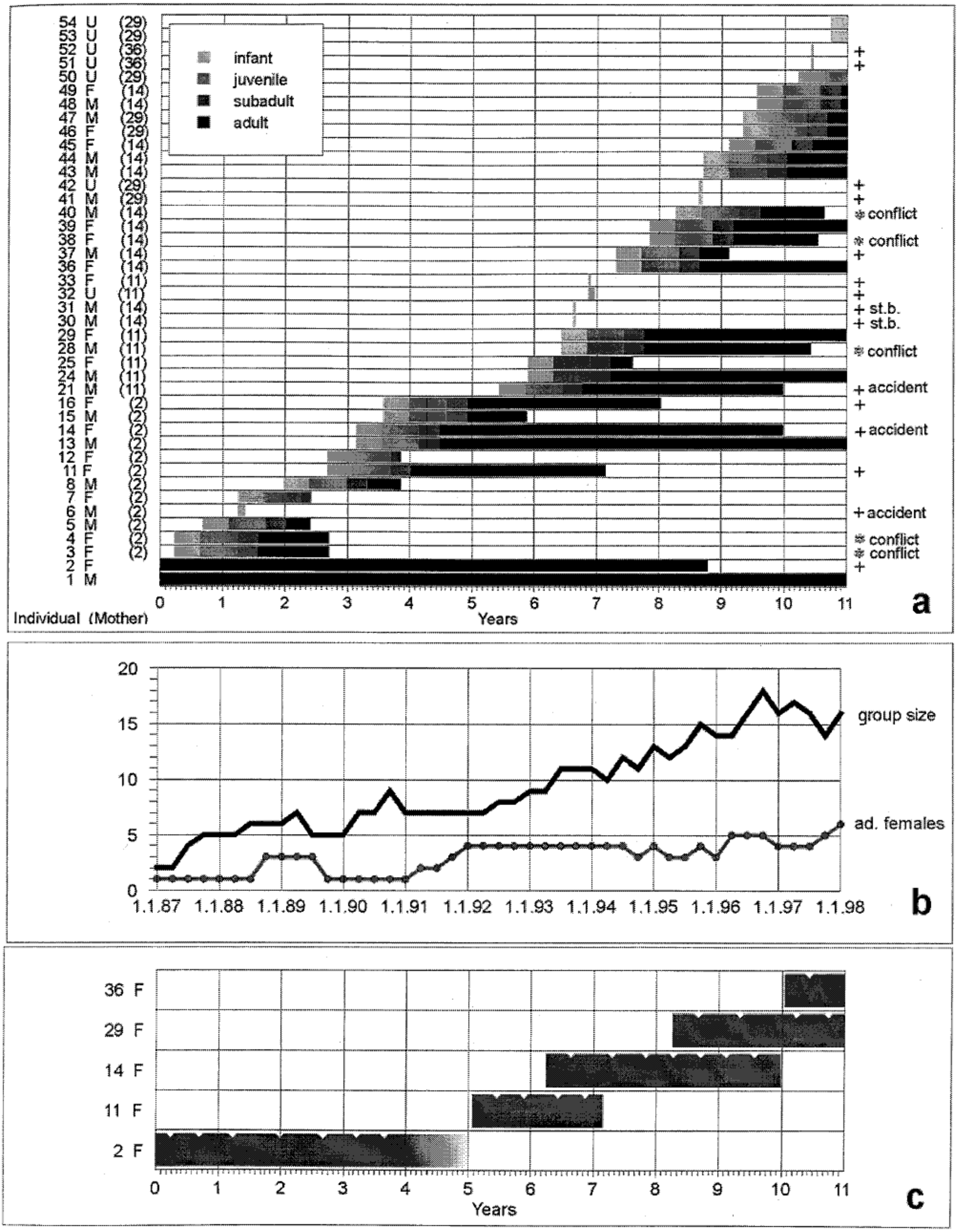

Fig. 1. a) Development and composition of a pygmy marmoset group at Magdeburg Zoo between 1987 and 1997. The left column shows the sex and identification numbers of the group members, and (in brackets) the identification number of the mother. The horizontal bars demonstrate the presence of each individual within the group at the time. The ontogenetic phases (different shades of gray of the bars) were classified following Soini (1988), and mark the infant phase (0-5 months), the juvenile phase (6-12 months), the subadult phase (13-16 months) and the adult phase (more than 16 months). All the marmosets, except M1 and F2, were born in the group. Symbols in right column: + = death; * = removal from the group after agonistic conflict. If there is no symbol at the end of the bars, the animals were separated for transfer to other zoos without intragroup conflicts. **b)** The group size during the observation period and the number of adult females in the group. **c)** The reproductive phases of the five reproductive females in the group. The notches on the barsrepresent the birth dates. Note, there are three phases of simultaneous reproduction of two females.

that the behavior of the dominant female also plays a role (Abbott *et al.*, 1993). The suppression of ovulation in subordinate females seems to be stronger in groups comprised of unrelated individuals than in family groups with mothers and daughters (Rothe and Darms, 1993). In *Callithrix jacchus* one, and only one, daughter of the reproductive female may ovulate (Abbott, 1984). This might be a sign of a forthcoming change in the reproductive and social status of the daughter in the group. Physiological inhibition has also been shown in tamarins (Epple and Katz, 1984; Ziegler *et al.*, 1989). From the diagnosis of progesterone levels in the blood, Tardif (1984) assumed that 50% of the daughters of cotton-top tamarins show ovarian cycles. There is no evidence, however, of physiological inhibition in *Leontopithecus* (see French *et al.*, 1989), although the reproductive female in a group is able to inhibit the other females from reproducing by her behavior (Abbott *et al.*, 1993). Interestingly, the ovarian cycles of all females (including the reproductive one) of a group seem to be synchronized (French and Stribley, 1987). This synchronization could also be pheromonally regulated by the dominant female, and it might give her a greater chance of monopolizing the dominant male during estrus (Abbott *et al.*, 1993).

Results

Pygmy marmosets have been kept at the Magdeburg Zoological Gardens since 1986, and have been reproducing regularly since 1987 (Schröpel, 1994). The "main group" has been stable since then and is an extended family unit. All members, with the exception of the original pair (M1 and F2), were born in the group. Temporary, smaller groups or pairs have been formed with some of the individuals from this main group, but they were disbanded or transferred to other zoological gardens. The development and the composition of this group from its beginning are shown in Figure 1.

The largest group size obtained was 18 individuals (five adult females, six adult males, two subadult males, two juvenile females, one juvenile male, and two infants) between September and December, 1996. The first exclusions due to agonistic behavior in the group did not occur when the group was at its largest but in the early years (1989), when it consisted of one adult male, three adult females, one juvenile male, and two neonate females. Perhaps the exclusion of the two non-reproductive females (F3 and F4) was influenced by the mother's giving birth to twins (F11 and F12) a few days previously. Possible hints concerning the reasons for this agonistic behavior can be found in observations of wild *Callithrix jacchus* groups by Digby and Barreto (1993).

For most of the births of the female "Caqueta" (F2) there were no other adult females living in the group. In 1990, however, at the age of 5½ years, this female gave birth for the last time. She stayed in the group up to her death (October 1995, at the age of 10 years and nine months) together with other females (daughters) without agonistic clashes. There were further expulsions through agonistic conflicts in 1997 (two males, four and two years old, and one nonreproductive female, two years old).

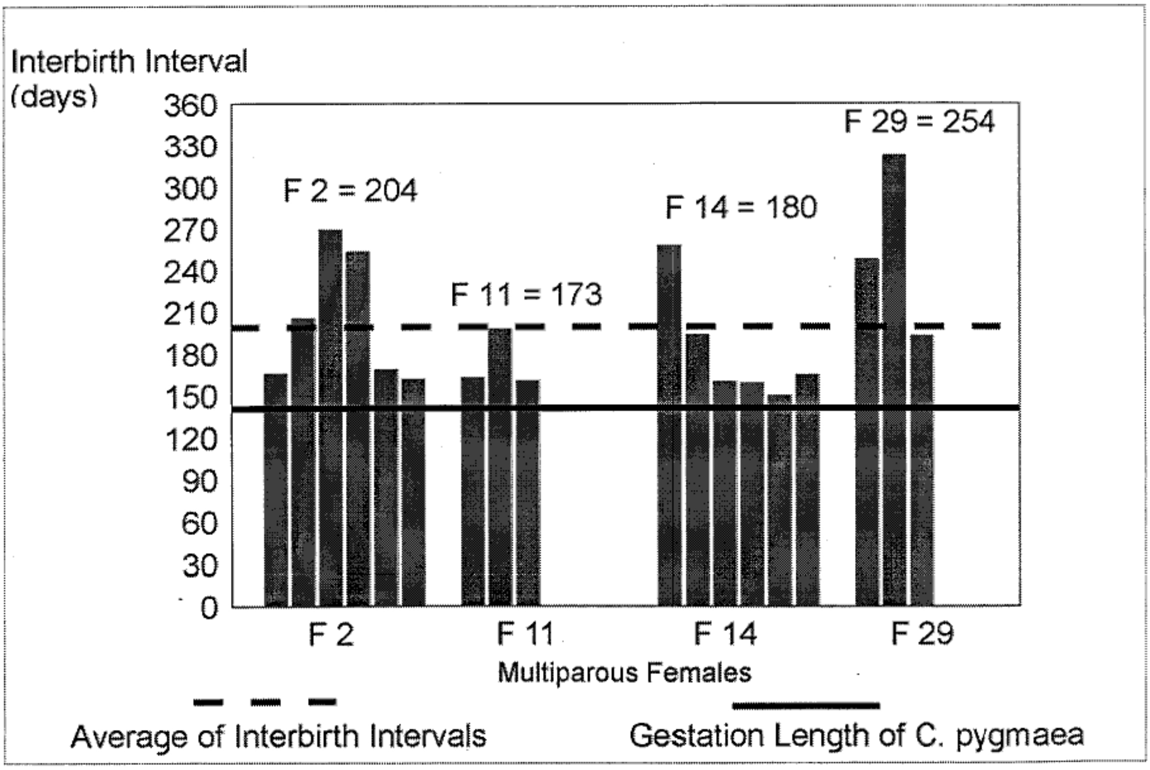

Fig. 2. Interbirth intervals of the multiparous females of the pygmy marmoset group. The last birth of F11 occurred during the first, very long interval (247 days) of F14, 86 days after the first birth and 161 days before the second birth of F14. The *Cebuella pygmaea* gestation length of 137 or 138 days was taken from Soini (1988). Soini (1993) found interbirth intervals of between 5 and 7 months for wild pygmy marmosets.

Almost exactly two years after the last birth of the female "Caqueta" (F2), the daughter of two years and nine months "Cali" (F11) gave birth for the first time to a single young. At that time, she was the oldest female after her mother, who had ceased reproduction. There were then two other adult females in the group, aged 2½ years and 2 years. There were no agonistic interactions evident. This female (F11) gave birth to twins three times, at intervals of 162, 197 and 160 days (see Fig. 2). The twins of the last birth died at the ages of five days and 34 days. Tension in the group was obviously responsible for this, probably affecting the care given to the neonates, although this was difficult to ascertain exactly. The mother "Cali" died of an unknown cause three months after her last birth, at the age of 4½ years.

Between the penultimate and last birth by the female "Cali", her younger (3½ year-old) sister "Sela" (F14) gave birth for the first time. The twins were stillborn. This was 74 days after the previous birth by "Cali", who gave birth again 86 days after her sister "Sela". After the death of "Cali", the female "Sela" was the only reproductive female of the group, but with two other resident adult sisters. Up to June 1996, "Sela" had given birth to twins on a further four occasions and twice to a single offspring. All of these young survived. The birth interval after the first stillbirth of "Sela" was 247 days, and subsequently 193, 159, 143, 158 and 149 days. "Sela" died in an accident at the end of 1996.

Another female of the group (F29) gave birth to twins between the fourth and the fifth births of "Sela". The female F29 was aged two years and three months, and there was only one other female in the group, F36 aged one year and four months. On the third day after parturition, we found one of the neonate twins abandoned and suffering from hypothermia in the bottom of the enclosure. On the fourth day, the second infant was found with severe bites, and died. The individuals involved in the attack were not identified and it was not possible to say for sure if this was a case of infanticide. F29 again produced twins after an interval of 247 days; 83 days after the penultimate birth by the female "Sela" (F14). This time the young grew up without any problems. Sixty-six days after the birth of the twins of F29, "Sela" gave birth for the last time. F29 continued reproducing, giving birth to a singleton after an interval of 322 days and to twins after a further 192 days. Another female, almost certainly F36, gave birth to twins for the first time between the penultimate and the last birth of F29. The neonates, however, died on the first and second day, respectively.

Five females, therefore, have reproduced in this pygmy marmoset group, with three phases of polygynous reproduction when two females were breeding simultaneously. It is certain that "Napo" (M1) was the father of all the offspring of the original female "Caqueta" (F2), but the paternity of the other offspring was impossible to ascertain. Currently, "Napo" is living in the group together with five other adult males of different ages.

Discussion

The size of the pygmy marmoset group at the Magdeburg Zoo exceeds, by far, the average group size given for this species in the wild, although up to 11 (Soini, 1988, 1993) or 15 individuals (Hernández-Camacho and Cooper, 1976) have been reported occasionally. Soini (1988), however, argued that these larger troops were temporary aggregations of two social units, and indicated that the reproductive male or female of one group may have been the offspring of the reproductive pair of the other. Very large groups, at least when they are extended families, can be stable for a long time under captive conditions (Rothe and Darms, 1993). There is currently a group of golden-headed lion tamarins (*Leontopithecus chrysomelas*) with 13 individuals at the Magdeburg Zoo. In the wild, golden-headed lion tamarin groups are comprised of 5 to 8 (Rylands, 1989), or 3 to 9 individuals (Dietz *et al.*, 1994). The home range for a captive group is always considerably smaller when compared to the wild, but there are certainly no restricting factors for the group size up to a minimum range for normal locomotion and other behavioral functions. Food competition between group members is not an important factor in captive colonies. Dawson (1977) reported that *Saguinus geoffroyi* groups in habitats with stable food resources ("survival habitats") were relatively stable, but in areas with strong seasonal differences in food resources ("colonization habitats") they were unstable. The extent to which social and socio-sexual parameters have an influence on the group size in captivity is not yet known.

It is widely accepted that there is no clear hierarchical structure in callitrichid social units except for the dominant and reproductive pair (Epple, 1975a; Stevenson and Rylands, 1988; Caine,1993; but see Rothe, 1978). If a hierarchy becomes evident, it is generally related to age and sex. Dawson (1977) refers to this as "age-related, male-female groups" in *Saguinus geoffroyi*. In wild (Soini, 1988) and captive (Christen, 1974) pygmy marmoset groups, the older offspring of the dominant pair are dominant over their younger siblings. However, according to Soini (1988), the younger siblings, during the weaning period especially but also when benefiting from parental protection, are responsible for the peripheralization of their older siblings and their subsequent expulsion from the group. This rarely happens through overt aggression, but is more of a gradual process, involving, for example, exclusion of the individuals from the prime exudate gnawing-sites. The starting point for this may be the reproductive status of the dominant female at the time. She is often intolerant with other group members in the third month of pregnancy. This coincides with the weaning period of the last-born young (see also Kleiman, 1986, for *Leontopithecus rosalia*). Under captive conditions this behavior may subside and offspring stay much longer in the group as a result (see Rothe, 1978, for *Callithrix jacchus*). In captivity, the gradual expulsion process, involving mainly social peripheralization, is difficult to detect (Rothe *et al.*, 1986).

It is only when there is overt aggression that the keepers remove the animals, corresponding to emigration in the wild.

In the *Cebuella* group described here, there was at first a matrilineal transmission of the reproductive position. When the initial reproductive female "Caqueta" (F2) stopped giving birth, her oldest daughter "Cali" (F11), took over after two years. This conforms with the reproductive strategy described by Ferrari and Diego (1992) for marmosets in the wild. When the fertility of a reproductive female is reduced or lost, her daughter takes over. Especially in areas with a high population density and stable social groups, this is a more promising alternative for the young female than emigrating and starting a new group, or taking over the reproductive position of another established group. Ferrari and Diego (1992) did not record any immigrations of females into existing groups of *Callithrix flaviceps*. The possibility of matrilineal transmission is also supported by the results of physiological suppression of the ovulation of the adult female group members by the reproductive female in marmosets (Abbott, 1984). Besides the mother, the oldest daughter is the only female showing ovarian cycles. In the case of the pygmy marmosets discussed here, it is possible that the reproductive decline of the old female was accompanied by a loss in her ability to physiologically inhibit reproduction in her daughter.

After three births by the new reproductive female "Cali" (F11) and a time span of one year, there were two reproductive females in the group, with her younger, primiparous sister "Sela" (F14) also breeding. The neonate twins of "Sela" were, however, stillborn. Digby and Ferrari (1994) argued for a correlation of high population density and the presence of two reproductive females in wild *Callithrix jacchus*. However, they were referring to mother and daughter, while the two reproductive females in this pygmy marmoset group were sisters. Since emigration, as explained above, is not necessarily the best alternative, permitting reproduction by a second female may be an effective solution, if the reproductive success of the female is not compromised (i.e., enough helpers are available for infant care, there is sufficient food, etc.). Multiple reproduction may also increase the inclusive fitness of both females in cases where they are close relatives (Digby and Ferrari, 1994). These factors still apply even though population density is not a factor in captive groups.

The female "Cali" died a short time after her subsequent birth, and again there was only one reproductive female, "Sela". All her offspring from the six following births survived. Shortly before the fifth birth by the female "Sela", another female began reproducing; the female F29, a daughter of "Cali" (F11). This gave rise to the same situation as before between "Cali" and "Sela". The liveborn offspring were neglected and abandoned. Unfortunately it was not possible to observe which group members were responsible for the deaths of the offspring (the mother and/or others). One of the young animals was bitten to death, and infanticide was possible. About eight months later, and 83 days after the birth of a singleton by "Sela", the female F29 again gave birth to twins, which she reared normally. At the time of writing this, they are already adult. There were, as such, therefore, two reproductive females breeding successfully in the group. The older reproductive female "Sela" (F14) later gave birth for the last time, but died in an accident at the end of 1996. Immediately after her death, another female (F36) became reproductive and gave birth to twins, between the births of F29. The neonates did not survive, however. Both the females (F29 and F36) were alive at the end of 1997.

The simultaneous reproduction by two females in one group succeeded, therefore, in only one case. The question arises whether the simultaneous fertility of two females can be considered a reproductive strategy at all. There is the possibility that it is merely a failure of the physiological inhibition of ovulation of the subordinate females by the reproductive female. Other mechanisms, probably behavioral, then prevent the survival of the offspring of the second female. The breeding pattern remains monogynous. Price and McGrew (1991) found some cases of simultaneous reproduction by mother and daughter in captive *Saguinus oedipus*. The offspring of the daughter, however, did not survive. In one of the cases, it involved infanticide of the offspring of the daughter by her mother. Evaluation of the one success in simultaneous reproduction of the two females in the pygmy marmoset group is dependent on further data. The premises for multiple reproduction as an effective alternative to emigration (the participating females being close relatives, enough helpers in the group, a large supply of food) among wild *Callithrix jacchus* as assumed by Digby and Ferrari (1994) apply to the present case. But there are, however, other factors considering the captive conditions, in this large group particularly, which perhaps may play a role, and referring to it as a reproductive strategy as such may be unwarranted. The helpers would often sit with the dependent young of both mothers in close contact, and there was no obvious agonistic behavior between the mothers.

Nothing can be said concerning the paternity of the offspring except that incest was involved, with the exception of the original pair "Napo" (M1) and "Caqueta" (F2). So far, there have been no adverse consequences. There are several reports of incest among callitrichids in captivity (Epple, 1970; Abbott, 1984; Jämmrich, 1985; Anzenberger and Simmen, 1987; Price and McGrew, 1991; Rothe and Darms, 1993), but no information from wild groups, because the family relationships are mostly unknown. Considering, however, the stability of wild callitrichid groups, incestuous reproduction cannot be completely ruled out. Immigrations in groups are often re-immigrations. For example, out of 18 immigrants in *Saguinus geoffroyi*, 13 had formerly emigrated from the group, and were, therefore, closely related (Dawson, 1977). Few immigrations have been recorded for *Cebuella* and *Callithrix* (Soini, 1988; Rylands, 1982; Ferrari and Diego, 1992; Digby and Barreto, 1993). New members mostly result from births. Perhaps in callitrichids inbreeding resulting from long-term stable groups may have contributed to genetic drift and be responsible, therefore, for at least part of the enormous variety of forms of this primate group, in a similar fashion to island populations. Such a hypothesis is very speculative, but requires consideration. In captive management there is always a conflict between the problem of avoiding incest, available space, and the usually undesirable measure of breaking up stable social groups by excessive manipulation.

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THE EFFECT OF RAINFALL SEASONALITY ON THE GEOGRAPHIC DISTRIBUTION OF NEOTROPICAL PRIMATES

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Introduction

Studies carried out on the geographic distribution and ecology of New World Primates (for example, Pagel *et al.*, 1991; Ross, 1992; Rosenberger, 1992; Strier, 1992; Ford, 1994) all find that environmental variables such as temperature and rainfall have an important effect on the morphological adaptations and behavioral ecology of the platyrrhine primates.

There is a general relationship between overall body size and ecological, behavioral and physiological traits in mammals (for example, Calder, 1984; Clutton-Brock and Harvey, 1983; Eisenberg, 1981; McNab, 1987; Peters, 1983; Schmidt-Nielsen, 1984). In primates there is a consistent relationship between body size and feeding ecology (Ford and Davis, 1992). Body size by itself, therefore, is a useful predictor of a species' adaptations (Damuth and McFadden, 1990), and appears to be related to numerous life-history variables (Clutton-Brock and Harvey, 1983; Harvey and Clutton-Brock, 1985).

Platyrrhines are thought ideal for examining morphological adaptations to diet, because of their monophyletic origin, universal arboreality, and variation in food prefer-