

REVIEW ARTICLE

Phylogenetic Analysis of Twinning in Callitrichinae

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The callitrichines are known for twinning and for a communal rearing system in which all or most group members help care for the offspring. The origin of twinning has been the subject of much speculation. In this study predictions from earlier hypotheses are tested on the basis of two alternative phylogenetic trees. From this analysis we infer that helping behavior and male care preceded the origin of twinning, and that these traits did not coevolve with, but might have been important prerequisites for twinning in callitrichines. Small body size does not necessarily result in twinning, although it might still have been a prerequisite for its evolution. Gum feeding was an ecological change which evolved along with twinning. If nutrition was a limiting factor in the number of offspring produced, then the use of a new feeding resource could have been crucial for the origin of twinning in callitrichines. According to one of the two alternative solutions inferred by the total evidence tree, and in accordance with the morphological tree, semi-annual breeding appears in the marmosets together with specialization in gum feeding. The fact that gums are available for these monkeys all year may have facilitated semi-annual breeding. We suggest that the exploitation of gums as a feeding resource could have been the decisive factor in the increase of the reproductive rate by twinning and by semi-annual breeding. *Am. J. Primatol.* 51:135–146, 2000. © 2000 Wiley-Liss, Inc.

Key words: twinning; gum feeding; helpers; Callitrichinae; phylogeny

INTRODUCTION

Callitrichines are small-bodied New World monkeys that give birth to twins in 80% of their litters [Goldizen, 1987], an unusual trait among anthropoid primates. The group includes marmosets (*Callithrix* and *Cebuella*), tamarins (*Saguinus*), lion tamarins (*Leontopithecus*), and Goeldi's monkey (*Callimico goeldii*). Callitrichines live in small groups and have a communal breeding system in which all or most group members help care for the offspring [Goldizen, 1987]. Helpers are individuals that provide care for other individuals' young. In callitrichines, helping primarily involves carrying and transporting infants. Older

Contract grant sponsor: Swedish Natural Science Research Council.

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Received 4 August 1999; revision accepted 10 February 2000

offspring often stay in the group after reaching reproductive age, and juveniles and subadults in these groups provide a substantial amount of care [Goldizen, 1987]. Twinning involves increased costs for the females, not during pregnancy in these species, but primarily during lactation [Garber & Leigh, 1997].

Twinning in callitrichines has been the subject of much speculation [Ford & Davies, 1992; Garber, 1994; Goldizen, 1990; Leutenegger, 1979; Martin, 1992]. What factors might have led to its origin? In this paper we summarize earlier hypotheses, as well as formulate some new ones, concerning the evolution of twinning, and we derive phylogenetic predictions from these hypotheses. We then test these hypotheses by mapping character states of extant species onto phylogenetic trees, thereby inferring in which order various character transformations have occurred [Brooks & McLennan, 1991; Lindenfors & Tullberg, 1998; Sillén-Tullberg & Møller, 1993]. Because the relationships among New World monkeys have been the focus of many recent phylogenetic analyses, with partly conflicting results, we will use two main hypotheses concerning callitrichine relationships as the basis for our study.

Hypotheses

Helping and male care. This hypothesis implies that helping behavior is an important prerequisite for the evolution of twinning in callitrichines, and predicts that helping predates twinning in a phylogenetic analysis. We base this hypothesis on the reasoning of Terborgh and Goldizen [1985] that a lone reproductive pair of saddle-backed tamarin would have difficulties raising twins by themselves. Twin neonates in callitrichines weigh 15–19% of the mother's weight [Garber & Leigh, 1997], and because of the high cost of pregnancy and lactation females do relatively little infant carrying [Terborgh & Goldizen, 1985]. Thus, in a lone pair the male would have to do almost all the carrying. Because carriers seldom eat or forage (shown in the saddle-backed tamarin [Goldizen, 1987] and the cotton-top tamarin [Price, 1992]), the male would not have enough time to eat. A lone reproductive pair would therefore need helpers to carry their infants [Terborgh & Goldizen, 1985].

Goldizen [1990] suggested that twinning and helping behavior co-evolved, with an increase in the frequency of twinning selecting for helping behavior, which in turn would make more frequent twinning possible. Co-evolution by these means predicts that the origins of helping and twinning should appear on the same branch in a phylogenetic tree. Goldizen [1990] also suggested that marmosets and tamarins most likely first evolved male care, which was followed by helping together with twinning, and subsequently to variable mating patterns. Mating patterns will not be discussed here, but the prediction that male care precedes helping and twinning can be investigated in a phylogenetic analysis.

Size reduction. Leutenegger [1973] found that the ratio between neonatal litter mass and maternal body mass declines with increasing maternal body mass, i.e., smaller primates have relatively heavier litter weights than do larger primates. He argues that delivery of a large fetus is difficult, and that multiple births are a result of selective pressures against oversized fetal dimensions [Leutenegger, 1973, 1979, 1980]. According to Leutenegger, there should be a threshold in the ratio of neonatal weight to maternal weight above which twinning should evolve to eliminate problems at birth. Twinning in callitrichines should then have developed as a by-product of the decrease in adult body size, and this hypothesis predicts a phylogenetic co-occurrence of size decrease and twinning. Goldizen [1990], however, argues that there must exist benefits other than smaller fetal size, otherwise callitrichines could have evolved a single smaller fetus.

Gum feeding. Surely there is a benefit to producing more offspring more quickly, but why do some callitrichines give birth to twins and not others (*Callimico*), and which ecological or behavioral changes could have influenced the occurrence of twinning? Here we investigate whether there is a phylogenetic relationship between gum feeding and twinning. In addition, we study the relationship between gum specialization and reproductive rate.

Methods

Several phylogenetic analyses have been performed on platyrrhine relationships [Carnavez et al., 1999; Chaves et al., 1999; von Dornum & Ruvolo, 1999; Ford, 1986; Horovitz et al., 1998; Kay, 1990; Pastorini et al., 1998; Porter et al., 1995; Porter et al., 1997a, b; Rosenberger, 1981; Schneider et al., 1996; Shoshani et al., 1996]. Most of these studies agree on the monophyly of callitrichines (*Callimico*, *Callithrix*, *Cebuella*, *Saguinus*, *Leontopithecus*), pitheciins (*Pithecia*, *Chiropotes*, *Cajacao*) and atelines (*Ateles*, *Brachyteles*, *Lagotrix*), though there is no consensus regarding relationships within and between these groups. There are two main hypotheses concerning relationships within Callitrichinae. Most morphological studies suggest a tree with the topology *Callimico* (*Saguinus* (*Leontopithecus* (*Cebuella*+*Callithrix*))) [Ford, 1986; Horovitz et al., 1998; Kay, 1990; Rosenberger, 1981]. Most molecular studies, however, place *Callimico* as the sister group to *Callithrix* and *Cebuella* [Carnavez et al., 1999; Chaves et al., 1999; Horovitz et al., 1998; Pastorini et al., 1998; Porter et al., 1995; Porter et al., 1997a, b; Schneider et al., 1996; von Dornum & Ruvolo, 1999]. *Callithrix* is sometimes categorized as a paraphyletic group, and *Cebuella* is placed among the *Callithrix* species in some phylogenies [Carnavez et al., 1999; Porter et al., 1997a]. This possibility does not contradict any of the conclusions in this study.

We have chosen to use the total evidence tree of Horovitz et al. [1998], as it is based on the greatest number of characters. Moreover, it is based on morphological and mitochondrial data as well as on nuclear sequence data. This total evidence tree, part of which is shown in Figure 1, is well supported by the decay index values [Horovitz, 1999] (Fig. 1). Several studies have shown that molecular and morphological data give conflicting results regarding callitrichine relationships, and the molecular data dominate the total evidence tree. Therefore, we also performed our analysis on a tree based on morphological data only [Horovitz et al., 1998], which for callitrichine relationships is the same as the morphological trees of Rosenberger [1981], Ford [1986], and Kay [1990]. Some of the morphological trees are partly based on the same data, which might be one reason why they are so similar. The position of *Callimico* as the most basal of the callitrichines is well supported in this tree (decay index indicated in Fig. 2). Decay index [Bremer, 1988] analysis was carried out on the morphological tree, based on data from Horovitz et al. [1998], using Autodecay [Eriksson & Wikström, 1996].

We have defined male care as care provided by adult males that are potential fathers. Helpers are defined as individuals that are not potential parents. We include in our definition of caregiving any behaviors that appear to increase the fitness of the infant, such as carrying, feeding, and guarding. This definition includes a wide range of involvement with the infants, from occasional guarding to time-consuming carrying, but here we were interested in the origin of helping and male care specifically. Although defining a specific individual as a male caregiver or helper may sometimes be problematic, we had no difficulty in classifying a species as having male care and/or helpers.

The characters mapped in the analyses were derived from the literature

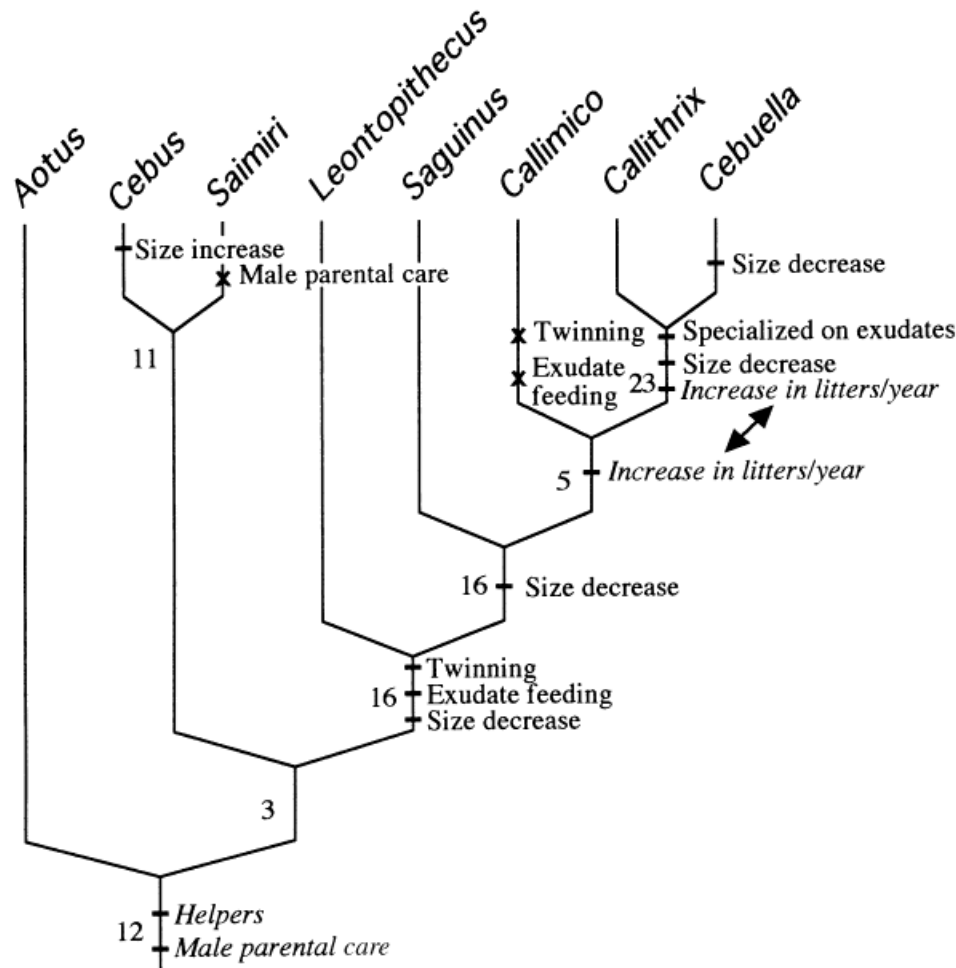


Fig. 1. Part of the total evidence tree [Horovitz et al., 1998] on which twinning, helpers, male care, body weight change, breeding rate, and plant exudate feeding have been mapped using character optimization. Bars illustrate gains, crosses show losses, and alternative solutions are shown in italics. Numbers indicate decay values for each node [Horovitz, 1999].

(Table I). There is some uncertainty as to whether *Callimico* breeds once or twice each year, because the field data are very scarce on this species [Martin, 1992; Pook & Pook, 1981]. The characters have been mapped in the trees using character optimization by parsimony methods [Brooks & McLennan, 1991] in MacClade [Maddison & Maddison, 1999]. The common logarithm of body weight has been traced as a continuous character using the linear parsimony option in MacClade. Mean weights for the genera, both sexes, are derived from Ford and Davies [1992] (Table I).

RESULTS

The analyses were conducted on trees including all platyrrhines, though only the callitrichines and their closest relatives are shown in Figures 1 and 2.

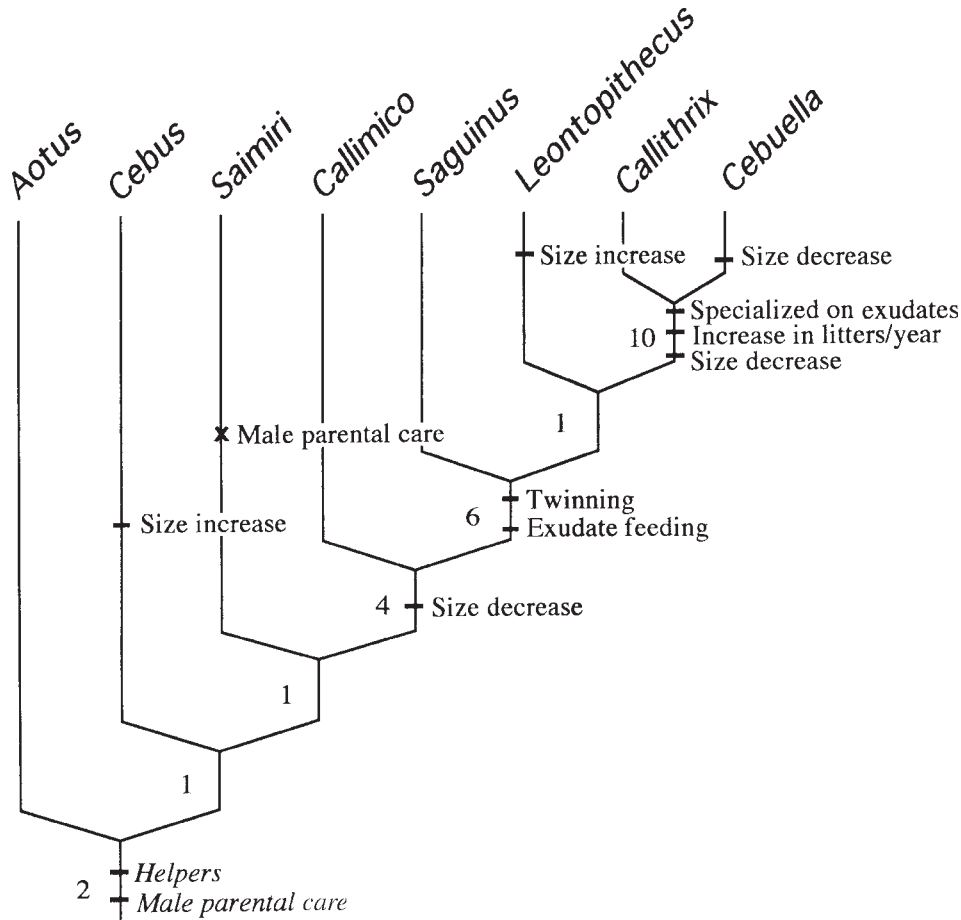


Fig. 2. Part of the morphological tree [Horovitz et al., 1998] on which twinning, helpers, male care, body weight change, breeding rate, and plant exudate feeding have been mapped using character optimization. Bars illustrate gains, crosses show losses, and alternative solutions are shown in italics. Decay values are indicated by numbers (based on data in Horovitz et al. [1998]).

Twinning

Phylogenetic analysis of the total evidence tree (Fig. 1) led us to infer that twinning evolved in the ancestor to the callitrichines and was later lost in *Callimico*. The analysis based on the morphological tree inferred the origin of twinning in the ancestor of callitrichines after *Callimico* had branched off. Twinning is thus a derived character in the callitrichines.

Helping and Male Care

There are two equally parsimonious solutions to the optimization of helping in the platyrrhines. One solution is that helping originated separately in the ancestor to the *Aotus-Cebuella* clade (Figs. 1 and 2) and in *Callicebus*. The other solution is that helpers were already prevalent in the ancestors of all platyrrhines and were later lost in the *Alouatta-Ateles-Brachyteles-Lagothrix* clade and in the *Pithecia-Cacajao-Chiropotes* clade, but were still present in *Callicebus*.

TABLE I. Character States of Callitrichine and Related Genera*

Genus	Helpers	Male care	Offspring/ litter [5]	Litters/ year	Eat exudates	Specialized on exudates	Mean body weight (g) [5]
<i>Callithrix</i>	yes [1]	yes [1]	2	2 [5,9]	yes [6]	yes [6]	336
<i>Cebuella</i>	yes [2]	yes [2]	2	2 [5,10]	yes [6]	yes [6]	123
<i>Leontopithecus</i>	yes [1]	yes [1]	2	1 [5,11]	yes [6]	no [6]	596
<i>Saguinus</i>	yes [1]	yes [1]	2	1-1.5 [5,12]	yes [6]	no [6]	464
<i>Callimico</i>	yes [2]	yes [2]	1	1-2 [5]	no [7]	no [5]	492
<i>Cebus</i>	yes [3]	yes [3]	1	0.5-1 [5]	no [5]	no [5]	2811
<i>Saimiri</i>	yes [3]	no [3]	1	1 [5]	no [5]	no [5]	836
<i>Aotus</i>	yes [4]	yes [4]	1	1 [5]	no [5]	no [5]	902
<i>Callicebus</i>	yes [4]	yes [4]	1	1 [5]	no [5]	no [5]	1005
<i>Pithecia</i>	no [8]	no [8]	1	1 [5]	no [5]	no [5]	2094
<i>Cacajao</i>	no [8]	no [8]	1	?	no [5]	no [5]	3011
<i>Chiropotes</i>	no [8]	no [8]	1	0.3 [5]	no [5]	no [5]	2862
<i>Alouatta</i>	no [8]	no [8]	1	0.5-1 [5]	no [5]	no [5]	6415
<i>Ateles</i>	no [8]	no [8]	1	0.25-0.5 [5]	no [5]	no [5]	7835
<i>Lagothrix</i>	no [8]	no [8]	1	0.5-0.75 [5]	no [5]	no [5]	8398
<i>Brachyteles</i>	no [8]	no [8]	1	?	no [5]	no [5]	10788

*References: 1, Goldizen, 1987; 2, Garber, 1994; 3, Robinson and Janson, 1987; 4, Robinson et al., 1987; 5, Ford and Davies, 1992; 6, Sussman and Kinzey, 1984; 7, Pook and Pook, 1981; 8, Smuts et al., 1987; 9, *Callithrix jacchus* (Digby and Barreto, 1993; Hubrecht, 1984; Stevenson and Rylands, 1988), *Callithrix flaviceps* (Ferrari and Diego, 1992; Ferrari and Ferrari, 1989), *Callithrix intermedia* (Rylands, 1981), *Callithrix humeralifer* (Ferrari and Ferrari, 1989); 10, Soini, 1988; 11, Dietz et al., 1994; 12, *Saguinus oedipus* (Savage et al., 1996), *Saguinus fuscicollis* (Goldizen et al., 1996), *Saguinus nigricollis* (Izawa, 1978).

Male care was inferred to have the same two alternative solutions, but was lost in *Saimiri* (Figs. 1 and 2). These results imply that helping and male care were present long before twin births in New World monkeys, which supports the hypothesis that helping may be a prerequisite for twinning. It is not possible to infer from this study whether helping or male care came first, and therefore Goldizen's [1990] prediction that male parental care evolved before helping can be neither verified nor refuted. However, both traits occurred before twinning, which contradicts Goldizen's hypothesis of a successive co-evolution of twinning and helping behavior.

Size Reduction

Decrease in size is inferred to have occurred several times in the callitrichines (Figs. 1 and 2). In the total evidence tree a decrease in size occurs at the same time as twinning, as predicted by Leutenegger's [1973, 1979, 1980] hypothesis. Contrary to the prediction, however, no increase in size occurs simultaneously with the loss of twinning in *Callimico*. In both trees *Cebus* undergoes a size increase. In the morphological tree a decrease in size occurs in the ancestor of the callitrichines which does not coincide with twinning. There is also a size increase in *Leontopithecus*.

Gum Feeding

A change in the feeding habit (Figs. 1 and 2) does coincide with the origin of regular twinning. Those monkeys that began regular twinning also began to exploit gums as a new food resource. In the total evidence tree, *Callimico* has lost

twinning and the ability to eat gums simultaneously, which further supports the correlation between gum feeding and twinning. Moreover, changes in the exploitation of gums and breeding rate might be coupled. *Callithrix* and *Cebuella* have specialized teeth which allow them to gnaw holes in bark, causing exudate flow, and the gut is specialized to digest gums. The total evidence tree indicates two alternative explanations for the change in litters per year: 1) The increase occurred in the ancestor of *Callithrix* and *Cebuella*, and the increase in litters per year occurred together with a specialization on gum feeding. 2) The ancestor of *Callimico*, *Callithrix* and *Cebuella* had two litters per year; *Callimico* later lost twinning, and the ancestor of *Callithrix* and *Cebuella* specialized in exudate feeding thereafter. If this is the case, then the specialization in gum feeding followed rather than coincided with an increased reproductive output (a combination of twinning and semi-annual breeding). If wild *Callimico* have two litters per year, then the reproductive rate in *Callimico* does not differ from that of *Saguinus*, despite the fact that *Callimico* does not feed on gums. In any case, *Callimico* has at most two young a year, while the marmosets normally have four, and this is combined with a specialization in gum feeding. In the morphological tree, as in the first solution for the total evidence tree, an increase in litters per year and specialization in gum feeding occur at the same time.

DISCUSSION

Twinning

Twinning is inferred to have originated within the callitrichine clade, either in the ancestor of all callitrichines as inferred from the total evidence tree, or after the ancestor of *Callimico* had branched off from the ancestor of the other callitrichines, as indicated in the morphological tree.

Helping and Male Care

Parsimony analysis results in an inferred early origin of helping behavior and male care in the evolution of New World monkeys. These results support the hypothesis that helping was a prerequisite for the evolution of twinning. At the same time, they contradict the co-evolutionary hypothesis of helping and twinning proposed by Goldizen [1990]. In *Saimiri*, only females care for infants [Baldwin & Baldwin, 1981], thus male care has been lost in this species. Helping and male care both may have been likely prerequisites for the origin of twinning in callitrichines.

Size Reduction

The total evidence tree indicates that there was a reduction in body size at the same time as twinning occurred, which supports Leutenegger's hypothesis that twinning is a result of the decrease in body size [Leutenegger, 1973, 1979, 1980]. However, contrary to the hypothesis, *Callimico* has later lost twinning without an increase in body size. The morphological tree, on the other hand, implies that the decrease in body size does not coincide with twinning. In this case, small body size does not immediately lead to twinning, as *Callimico* is small but does not give birth to twins. Thus, small size is not closely correlated with twinning, but might still have been a necessary prerequisite for the evolution of twinning.

Kay [1994] conducted a study of callitrichine phylogeny that included a fossil platyrrhine, *Loganimico*, the inferred body mass of which is 1200 g. Parsimony analysis placed *Loganimico* as the next-most basal species after *Callimico*. This implies that there was either a decrease in body size in the callitrichine ancestor and that *Loganimico* thereafter increased in size, or that *Callimico* and the other callitrichines evolved smaller body size separately. Furthermore, we do not know where *Loganimico* would be placed in a total evidence tree. The smallest platyrrhine fossil known is *Micodon kiotensis*, whose teeth are about the size of *Callithrix*, and whose relationship to other callitrichines is unknown [Rosenberger, 1992].

A decline in body size of callitrichines, which probably led to a shorter period of infant dependency (three weaning months for callitrichines versus six to eight for *Saimiri* [Garber & Leigh, 1997]), may have been a prerequisite for semi-annual breeding. Larger platyrrhines would be unable to breed twice a year because they would then have several litters of infants dependent on parental care at the same time. Callitrichines are also able to conceive soon after giving birth [Garber & Leigh, 1997], unlike other primates in which ovulation is suppressed during lactation.

Gum Feeding

At the same time as twinning is inferred to have originated in callitrichines, they began to feed on gum. Could gum feeding have had an impact on the occurrence of twinning? Gum is an important substitute for fruit in *Saguinus fuscicollis* when fruit is scarce [Snowdon & Soini, 1988], and the use of exudates probably enables *Callithrix* to colonize relatively dry habitats [Stevenson & Rylands, 1988]. This indicates that the use of plant exudates involved an extension of available food resources in the callitrichine lineage. But could opportunistic feeding on gums really have such an impact on reproduction? In one study, wild *Saguinus oedipus* fed on gums during the wet season only, when fruits and insects were relatively abundant. This suggests that gums are not just a substitute for fruits, but also provide additional nutrients which are otherwise scarce in their diet [Garber, 1984]. Garber [1984] proposed that the high calcium/phosphorus ratio of gum is important, because insects have a low digestible calcium/phosphorus ratio. This has also been suggested for gum feeding in galagos [Bearder & Martin, 1980]. In choice experiments common marmosets generally preferred a calcium solution to water [Power et al., 1999]. Calcium is especially important for females during the latter part of pregnancy and lactation, and lactating females also ingested the greatest amount of calcium solutions in the same experiment. In a group of wild *Saguinus fuscicollis*, the breeding female was the individual which fed on gums most frequently [Garber, 1993]. If nutrition was the limiting factor for the breeding output of the ancestors of the callitrichines, then the exploitation of this new feeding resource could have made it possible for them to increase their breeding output by twinning.

Callimico does not twin, nor does it feed on gums [Pook & Pook, 1981]. In the total evidence tree this implies that *Callimico* has lost both twinning and the ability to utilize gums, which further supports the correlation between gum feeding and twinning.

There is some uncertainty as to whether *Callimico* gives birth to one or to two litters per year. Izawa [1979] argues that groups as large as eight individuals must be a result of *Callimico* giving birth twice a year. Pook and Pook [1981], on the other hand, found one newborn infant and two 12-month-old juveniles in

their study group, which suggests an inter-birth interval of one year, and that there was more than one breeding female in the group. Furthermore, subordinate *Callimico* females (in common with *Leontopithecus*) do not experience ovulatory suppression as do *Callithrix*, *Cebuella* and *Saguinus* females [Dettling & Pryce, 1999]. The absence of ovulatory suppression leads to earlier sexual maturation, although it is unclear what impact this has on the onset of reproduction in *Callimico* [Dettling & Pryce, 1999].

There are several other primates which also feed on gum, including *Galago senegalensis*, *Galago crassicaudatus* [Bearder, 1987], and *Cheirogaleus medius* [Richard, 1987]. During shortages of fruits and insects, *G. senegalensis* and *G. crassicaudatus* are able to subsist on gum alone [Bearder, 1987]. These two *Galago* species have a modal litter size of two infants [Bearder, 1987], in contrast to other species in the genus, which also do not eat gums. Several cheirogaleid species often have twins and triplets in captivity, but the frequency of multiple births in the wild is unknown [Richard, 1987]. We therefore speculate that gum feeding may have influenced the reproductive output in these species. This speculation, of course, should be tested in a phylogenetic analysis.

Garber [1992] proposed that the evolution of claws in callitrichines is an adaptation for a large-trunk foraging niche. It is possible that the evolution of exudate feeding evolved concomitant with claws (inferred from the total evidence tree, but not from the morphological tree), which enables a clinging position on large trunks. Claws would facilitate the exploitation of gums. However, since *Callimico* does not eat gums, their claws might be better correlated with foraging on large trunks than gum feeding. Garber [1992] also points out that, "For example, *Daubentonia madagascariensis*, *Euoticus elegantulus*, *Phaner furcifer*, and *Mizra coquereli* are small-bodied species possessing clawed or modified nails that aid in the exploitation of a large-branch feeding niche." All of these primates except *Daubentonia* also eat gums [Rowe, 1996], which suggests a correlation between gum feeding and claws.

Another indication of the importance of feeding habits to the breeding rate is that marmosets (*Callithrix* and *Cebuella*), according to one of the two alternative solutions inferred by the total evidence tree, and in accordance with the morphological tree, became specialized in exudate feeding and at the same time started to regularly breed twice each year. Their teeth are specialized for gnawing holes in trees, causing exudate flow, and when fruits are scarce they feed on gums. They have a food resource available throughout the year, which could have enabled them to reproduce twice each year instead of once. Tamarins, however, cannot gnaw holes themselves but are dependent on exudates from trees that are injured by insect borings or other damage [Snowdon & Soini, 1988]. They live primarily on fruits and insects, and during the dry season they spend much of their time licking nectar from flowers. In this season nectar seems to be the only plant material available, and they have to compete for it with birds and other monkey species. They may lose up to 15% of their body mass during that part of the year [Terborgh & Stern, 1987]. However, there is some evidence that tamarins also increase their ingestion of gums during the dry season [Egler, 1992; Snowdon & Soini, 1988]. Goldizen et al. [1988] found that saddle-backed tamarins gave birth so that lactation occurred when food was abundant. The fact that all callitrichines breeding in captivity appear able to reproduce twice each year [Goldizen, 1987] suggests that the available amount of food determines the reproductive rate in these monkeys, which was also proposed by Ferrari and Ferrari [1989].

Tardif et al. [1993] studied differences in infant care among callitrichids and found that *Callithrix* carry and provision their infants for a shorter period than

do *Saguinus* and *Leontopithecus* [Harrison & Tardif, 1994]. *Callithrix*, because of their use of exudates (which is a clumped and temporally continuous feeding resource), have shorter foraging paths, and therefore Tardif et al. [1993] hypothesized that their infants may forage independently at a younger age. If this is true, the specialization on gum feeding not only provided a continuous substitute for fruits, but also decreased both the cost of carrying (since they have shorter day ranges) and the infant dependency period. Harrison and Tardif [1994] found that obligate gummivory in marmosets increases the proportion of non-adults in groups, while the group size remains constant. Territorial behavior and aggression also differs between the marmosets and *Saguinus* [Harrison & Tardif, 1994], which indicates that gummivory has further implications for social behavior.

In conclusion, helping, male care, small body size and gum feeding were all probably important for the evolution of twinning, although each trait by itself might have been insufficient. Furthermore, the close coupling of changes in the two characters, exudate feeding and number of offspring produced, suggests that exudate feeding has made it possible for these monkeys to increase their reproductive rate. Firstly, gum feeding occurs in the same branch as twinning, which suggest that it might have been a decisive factor for twinning, possibly by increasing the amount of calcium available to breeding females. Secondly, specialization of gum feeding, by providing a continuous feeding resource, is suggested to have made semi-annual breeding possible.

ACKNOWLEDGMENTS

We thank Inés Horovitz for providing us with support values from her tree and the matrix for the morphological tree; Patrik Lindenfors, Lars Werdelin, and three anonymous referees for valuable suggestions and comments on the manuscript; and Klas Nyblom for help with the decay analysis.

REFERENCES

- Baldwin JD, Baldwin JI. 1981. The squirrel monkeys, genus *Saimiri*. In: Coimbra-Filho AF, Mittermeier RA, editors. Ecology and behavior of neotropical primates. Rio de Janeiro: Academia Brasileira de Ciências. p 277–330.
- Bearder SK. 1987. Lorises, bushabies, and tarsiers: diverse societies in solitary foragers. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 11–24.
- Bearder SK, Martin RD. 1980. *Acacia* gum and its use by bushabies, *Galago senegalensis* (Primates: Lorisidae). *Int J Primatol* 1(2):103–128.
- Bremer K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42:795–803.
- Brooks DR, McLennan DA. 1991. Phylogeny, ecology and behavior. Chicago: The University of Chicago Press, 434 p.
- Carnavez FC, Moreira MAM, Ladasky JJ, Pissinatti A, Parham P, Seuánez HN. 1999. Molecular phylogeny of New World primates (Platyrrhini) based on β_2 -microglobulin DNA sequences. *Mol Phylogenet Evol* 12(1):74–82.
- Chaves R, Sampaio I, Schneider MP, Schneider H, Page SL, Goodman M. 1999. The place of *Callimico goeldii* in the Callitrichine phylogenetic tree: evidence from von Willebrand factor gene intron II sequences. *Mol Phylogenet Evol* 13(2):392–404.
- Dettling A, Pryce CR. 1999. Hormonal monitoring of age at sexual maturation in female Goeldi's monkeys (*Callimico goeldii*) in their family groups. *Am J Primatol* 48:77–83.
- Dietz JM, Baker AJ, Miglioretti D. 1994. Seasonal variation in reproduction, juvenile growth, and adult body mass in Golden lion tamarins (*Leontopithecus rosalia*). *Am J Primatol* 34:115–132.
- Digby LJ, Barreto CE. 1993. Social organization in a wild population of *Callithrix jacchus*. 1. Group composition and dynamics. *Folia Primatol* 61:123–134.
- Egler SG. 1992. Feeding ecology of *Saguinus*

- bicolor bicolor* (Callitrichidae: Primates) in a relict forest in Manaus, Brazilian amazonia. *Folia Primatol* 59:61–76.
- Eriksson T, Wikström N. 1996. Autodecay 3.0.3. (program distributed by the authors) Dept. of Botany, Stockholm University, Stockholm.
- Ferrari SF, Diego VH. 1992. Long-term changes in a wild marmoset group. *Folia Primatol* 58:215–218.
- Ferrari SF, Ferrari MAL. 1989. A re-evaluation of the social organisation of the Callitrichidae, with reference to the ecological differences between genera. *Folia Primatol* 52:132–147.
- Ford SM. 1986. Systematics of the New World monkeys. In: Swindler DR, Erwins J, editors. Systematics, evolution and anatomy. New York: Alan R. Liss. p 73–135.
- Ford SM, Davies LC. 1992. Systematics and body size: implication for feeding adaptations in New World monkeys. *Am J Phys Anthropol* 88:415–468.
- Garber PA. 1984. Proposed nutritional importance of plant exudates in the diet of the Panamanian tamarin, *Saguinus oedipus geoffroyi*. *Int J Primatol* 5(1):1–15.
- Garber PA. 1992. Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichinae. *Am J Phys Anthropol* 88:469–482.
- Garber PA. 1993. Feeding ecology and behaviour of the genus *Saguinus*. In: Rylands AB, editor. Marmosets and tamarins. Oxford: Oxford University Press. p 273–295.
- Garber PA. 1994. Phylogenetic approach to the study of tamarin and marmoset social systems. *Am J Primatol* 34:199–219.
- 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.
- Goldizen AW. 1987. Tamarins and marmosets: communal care of offspring. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 34–43.
- Goldizen AW. 1990. A comparative perspective on the evolution of tamarin and marmoset social systems. *Int J Primatol* 11: 63–83.
- Goldizen AW, Mendelson J, Vlaardingen MV, Terborgh J. 1996. Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: Evidence from a thirteen-year study of a marked population. *Am J Primatol* 38(1):57–83.
- Goldizen AW, Terborgh J, Cornejo F, Porras DT, Evans R. 1988. Seasonal food shortage, weight loss, and the timing of births in saddle-back tamarins (*Saguinus fuscicollis*). *J Anim Ecol* 57:893–901.
- Harrison ML, Tardif SD. 1994. Social implications of gummivory in marmosets. *Am J Primatol* 95:399–408.
- Horovitz I. 1999. A phylogenetic study of living and fossil platyrrhines. American Museum Novitates (in press).
- Horovitz I, Zardoya R, Meyer A. 1998. Platyrrhine systematics: a simultaneous analysis of molecular and morphological data. *Am J Phys Anthropol* 106:261–281.
- Hubrecht RC. 1984. Field observations on group size and composition of the common marmoset (*Callithrix jacchus jacchus*), at Tapacura, Brazil. *Primates* 25(1):13–21.
- Izawa K. 1978. A field study of the ecology and behavior of the black-mantle tamarin (*Saguinus nigricollis*). *Primates* 19(2):241–274.
- Izawa K. 1979. Studies on peculiar distribution pattern of *Callimico*. Overseas Research Reports of New World Monkeys. p 1–19.
- Kay R. 1990. The phyletic relationships of extant and fossil Pitheciinae (Platyrrhini, Anthropeoidea). *J Hum Evol* 19:175–208.
- Kay RF. 1994. “Giant” tamarin from the Miocene of Colombia. *Am J Phys Anthropol* 95:333–353.
- Leutenegger W. 1973. Maternal-fetal weight relationships in primates. *Folia Primatol* 20:280–293.
- Leutenegger W. 1979. Evolution of litter size in primates. *Am Nat* 114:525–531.
- Leutenegger W. 1980. Monogamy in callitrichids: a consequence of phyletic dwarfism? *Int J Primatol* 1:95–98.
- Lindenfors P, Tullberg BS. 1998. Phylogenetic analyses of primate size evolution: the consequences of sexual selection. *Biol J Linn Soc* 64:413–447.
- Maddison WP, Maddison DR. 1999. MacClade. 3.08. Sunderland, Massachusetts: Sinauer Associates.
- Martin RD. 1992. Goeldi and the dwarfs: the evolutionary biology of the small New World monkeys. *J Hum Evol* 22:367–393.
- Pastorini J, Forstner MRJ, Martin RD, Melnick DJ. 1998. A reexamination of the phylogenetic position of *Callimico* (Primates) incorporating new mitochondrial DNA sequence data. *J Mol Evol* 47:32–41.
- Pook AG, Pook G. 1981. A field study of the socio-ecology of the Goeldi’s monkey (*Callimico goeldii*) in northern Bolivia. *Folia Primatol* 35:288–312.
- Porter CA, Czelusniak J, Schneider H, Schneider MPC, Sampaio I, Goodman M. 1997a. Sequences of the primate e-globin gene: implications for systematics of the marmosets and other New World primates. *Gene* 205:59–71.
- Porter CA, Page SL, Czelusniak J, Schneider H, Schneider MPC, Sampaio I, Goodman M. 1997b. Phylogeny and evolution of selected

- primates as determined by sequences of the e-globin locus and 5' flanking regions. *Int J Primatol* 18(2):261–295.
- Porter CA, Sampaio I, Schneider H, Schneider MPC, Czelusniak J. 1995. Evidence on primate phylogeny from e-globin gene sequences and flanking regions. *J Mol Evol* 40:30–55.
- Power ML, Tardif SD, Layne DG, Schulkin J. 1999. Ingestion of calcium solutions by common marmosets (*Callithrix jacchus*). *Am J Primatol* 47(3):255–261.
- Price EC. 1992. The cost of infant carrying in captive cotton-top tamarins. *Am J Primatol* 26:23–33.
- Richard AF. 1987. Malagasy prosimians: female dominance. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 25–33.
- Robinson JG, Janson CH. 1987. Capuchins, squirrel monkeys and atelines: socioecological convergence with Old World primates. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 69–82.
- Robinson JG, Wright PC, Kinzey WG. 1987. Monogamous cebids and their relatives: Intergroup calls and spacing. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 44–53.
- Rosenberger AL. 1981. Systematics: the higher taxa. In: Coimbra-Filho AF, Mittermeier RA, editors. *Ecology and behaviour of neotropical primates*. Rio de Janeiro: Academia Brasileira de Ciencias. p 9–27.
- Rosenberger AL. 1992. Evolution of feeding niches in New World monkeys. *Am J Phys Anthropol* 88:525–562.
- Rowe N. 1996. *The pictorial guide to the living primates*. East Hampton, New York: Pogonias Press, p 263.
- Rylands AB. 1981. Preliminary field observations on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Tio Aripuana, Mato Grosso. *Primates* 22(1):46–59.
- Savage A, Giraldo LH, Soto LH, Snowdon CT. 1996. Demography, group composition, and dispersal in wild cotton-top tamarin (*Saguinus oedipus*) groups. *Am J Primatol* 38:85–100.
- Schneider H, Sampaio I, Harada ML, Barros CML, Schneider MPC, Czelusniak J, Goodman M. 1996. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP Intron 1 and e-globin sequences. *Am J Phys Anthropol* 100:153–179.
- Shoshani J, Groves CP, Simons EL, Gunnels GF. 1996. Primate phylogeny: morphological vs. molecular results. *Mol Phylogenet Evol* 5(1):102–154.
- Sillén-Tullberg B, Møller AP. 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. *Am Nat* 141:1–25.
- Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT. 1987. Editors. *Primate societies*. Chicago: University of Chicago Press.
- Snowdon CT, Soini P. 1988. The tamarins, genus *Saguinus*. In: Mittermeier RA, Rylands AB, Coimbra-Filho AF, Fonseca GAB, editors. *Ecology and behavior of neotropical primates*. Washington DC: World Wildlife Fund. p 223–298.
- Soini P. 1988. The Pygmy marmoset, genus *Cebuella*. In: Mittermeier RA, Rylands AB, Coimbra-Filho AF, Fonseca GAB, editors. *Ecology and behavior of neotropical primates*. Washington DC: World Wildlife Fund. p 79–129.
- Stevenson MF, Rylands AB. 1988. The marmosets, genus *Callithrix*. In: Mittermeier RA, Rylands AB, Coimbra-Filho AF, Fonseca GAB, editors. *Ecology and behavior of neotropical primates*. Washington DC: World Wildlife Fund. p 131–222.
- Sussman RW, Kinzey WG. 1984. The ecological role of the Callitrichidae: a review. *Am J Phys Anthropol* 64:419–449.
- Tardif SD, Harrison ML, Simek MA. 1993. Communal infant care in marmosets and tamarins: relation to energetics, ecology, and social organization. In: Rylands AB, editors. *Marmosets and tamarins, systematics, behaviour and ecology*. Oxford: Oxford University Press. p 220–234.
- Terborgh J, Goldizen AW. 1985. On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behav Ecol Sociobiol* 16:293–299.
- Terborgh J, Stern M. 1987. The surreptitious life of the saddle-backed tamarin (*Saguinus fuscicollis*). *Am Sci* 75:260–269.
- von Dornum M, Ruvolo M. 1999. Phylogenetic relationships of the New World monkeys (Primates, Platyrrhini) based on nuclear G6PD DNA sequences. *Mol Phylogenet Evol* 11(3):459–476.