



## **A Comparative Perspective on the Evolution of Tamarin and Marmoset Social Systems**

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*Received July 6, 1988; revised April 11, 1989*

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*Tamarins and marmosets (callitrichids) present an unusual opportunity for study of the determinants of primate social systems, because both the mating and infant care patterns of callitrichids are variable, even within individual populations. In this paper, I briefly describe three characteristics of callitrichid social systems that distinguish them from most other primates: extensive male parental care, helping by nonreproductive individuals, and variable mating patterns. I then discuss the evolution of these characteristics and of the frequent twinning exhibited by callitrichids. I suggest that an ancestor of modern callitrichids gave birth to a single offspring at a time, mated monogamously, and had significant paternal care. The idea that males of this ancestral form must have provided paternal care, even though only single infants were born, derives from a comparison of litter/mother weight ratios in modern primate species. Twinning perhaps then evolved because of a combination of dwarfing in the callitrichid lineage, leading to higher litter/mother weight ratios, and a high infant mortality rate, and because the extensive paternal care already present facilitated the raising of twins. I propose that the helping behavior of older offspring may have coevolved with twinning, because helpers would have increased the chances of survival of twins, and the presence of twins would have increased the benefits of helping. Finally, the high costs of raising twins and the variability of group compositions, especially the fact that some groups would not have had older offspring to serve as helpers, may have selected for facultative polyandry in saddle-back tamarins (*Saguinus fuscicollis*) and perhaps in other callitrichid species. Both help-*

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*ing and cooperative polyandry have been extensively studied in bird species, and I apply some of the conclusions of these studies to the discussion of the evolution of callitrichid social systems.*

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**KEY WORDS:** callitrichids; polyandry; helping; twinning; paternal care.

## INTRODUCTION

It is generally accepted that most intraspecific variation in social systems is neither random nor maladaptive but is, in fact, adaptive. Indeed, the possible adaptive significance of different mating patterns and social systems is probably best studied by intraspecific comparisons within species that exhibit a variety of reproductive strategies. In such comparisons, phylogenetic histories are less likely to complicate interpretations, and many demographic and ecological factors are controlled for.

Tamarins and marmosets (Callitrichidae) are particularly interesting for intraspecific comparisons of reproductive strategies because they have unusually variable and flexible patterns of infant care, and in some species, of mating (reviewed by Sussman and Kinzey, 1984; Goldizen, 1987a, 1988; Snowdon and Soini, in press). The social systems of callitrichids differ in three major ways from those of most or all other primate species. (1) Breeding males provide at least as much infant care, and perhaps even more, than do breeding females. (2) Nonbreeding individuals, both before and after the age of potential sexual maturity, provide substantial help with the rearing of their infant siblings. (3) Members of some callitrichid species may only mate monogamously; but, saddle-back tamarins (and possibly other species) exhibit the following mating patterns: monogamy, cooperative polyandry, and polygyny and/or polygynandry.

Unfortunately, studies of reproductive strategies in wild primates are hampered by many difficult logistical problems. (1) Most primates live at quite low population densities, often in dense forest, so that many field studies only involve between one and three social groups. (2) Primates are often difficult to habituate and to mark individually for long-term recognition. (3) For methodological, ethical, or political reasons, it is usually not possible to move individual primates around or otherwise to alter group compositions in order to test hypotheses about the causes of specific strategies or social systems. (4) It is often either not practical or illegal to trap wild primates for collection of tissue samples to test paternity or genetic relatedness.

Many of these problems are absent in studies of other taxa, such as birds, amphibians, and insects. While field studies of primate social systems and alternative reproductive strategies are indispensable, our understanding

of these aspects of primate behavior could be increased greatly by a deeper understanding of the causes of similar behaviors in animals of other taxa.

The subject of this paper, the social systems of callitrichids, illustrates the usefulness of comparing similar behaviors in different taxa. Logistical problems in studying wild callitrichids are such that, despite more than 15 to 20 total years of fieldwork, there are still very few data on the behavior of wild individuals. On the other hand, the aspects of callitrichid social systems that are of most interest to primatologists (extensive male parental care, nonreproductive helpers, monogamy, and polyandry) have been well studied in other taxa, especially birds.

In this paper, I first summarize what is known about the social systems of tamarins and marmosets. Then, I discuss the evolution of callitrichid social systems, drawing heavily on ideas derived from studies of other taxa.

### Brief Summary of Callitrichid Social Systems

The Callitrichidae consist of approximately 15 species in 4 genera, 2 of marmosets (*Cebuella* and *Callithrix*) and 2 of tamarins (*Saguinus* and *Leontopithecus*) (Hershkovitz, 1977). Callitrichids are the only anthropoid primates which regularly twin (in captivity about 80% of births consist of twins, Gengozian *et al.*, 1978).

### Parental Care

Tamarins and marmosets provide three forms of infant care that are energetically costly – lactation, infant-carrying, and the provision of insects and fruits to infants and juveniles. Infants are weaned from both milk and carrying at around the age of three months. During the first three months, breeding females have to increase their food intake by 50 to 100% in order to produce sufficient milk for twin infants (Kirkwood and Underwood, 1984, for captive cotton-top tamarins, *Saguinus oedipus*; Goldizen, 1987b, for wild saddle-back tamarins, *Saguinus fuscicollis*). Meanwhile, infants are carried wherever the group goes; they are occasionally “parked,” but only while the other group members feed nearby. Because the daily travel distances of callitrichids are often long (averaging one to two km for many species; reviewed by Sussman and Kinzey, 1984; Goldizen, 1987a), infant-carrying must also be an energetically costly form of care.

Many studies of callitrichids have shown that adult males do as much and usually more infant-carrying than breeding females do (in the wild: Terborgh and Goldizen, 1985; Goldizen, 1987b, for *S. fuscicollis*; Rylands, 1985, for tassel-ear marmosets, *Callithrix humeralifer*; Garber, 1986, for mous-

tached tamarins, *S. mystax*; in captivity: Epple, 1975; Vogt *et al.*, 1978; Cebul and Epple, 1984, for *S. fuscicollis*; Box, 1975; Ingram, 1977; Tardif *et al.*, 1986, for common marmosets, *Callithrix jacchus*; Hoage, 1978, for golden lion tamarins, *Leontopithecus rosalia*; Tardif *et al.*, 1986, for *S. oedipus*). Both males and females also allow infants and juveniles to take fruits and prey items (insects and occasional small vertebrates) from them (in the wild: Terborgh and Goldizen, 1985; Goldizen, 1987b, for *S. fuscicollis*; in captivity: Brown and Mack, 1978, for *L. rosalia*).

### Helpers

In all of the callitrichid species in which infant care has been studied, offspring that are still in their natal groups usually help to carry their infant siblings (in the wild: Terborgh and Goldizen, 1985; Goldizen, 1987b, for *S. fuscicollis*; Rylands, 1985, for *C. humeralifer*; in captivity: Epple, 1975; Vogt *et al.*, 1978; Cebul and Epple, 1984, for *S. fuscicollis*; Box, 1975; Ingram, 1977; Tardif *et al.*, 1986, for *C. jacchus*; Hoage, 1978, for *L. rosalia*; Tardif *et al.*, 1986, for *S. oedipus*). Older offspring also provide food to younger siblings (Goldizen, 1987b, for *S. fuscicollis*).

The actual amounts of infant-carrying done by individuals of different age-sex classes are variable. However, some possible trends are beginning to emerge. First, the amount of infant-carrying done by older offspring seems to increase with age (in the wild: Rylands, 1985, for *C. humeralifer*; Goldizen, 1987b, for *S. fuscicollis*; in captivity: Vogt *et al.*, 1978, for *S. fuscicollis*; Tardif *et al.*, 1986, for *C. jacchus*). In wild *S. fuscicollis*, only some one-year old or younger juveniles carry their infant siblings; individuals of this age perhaps contribute substantially to carrying only when their group does not have enough older carriers (Terborgh and Goldizen, 1985; Goldizen, 1987b). Secondly, there may be species differences in how soon after the birth of infants individuals of different age-sex classes begin to carry the infants. For instance, in captive *L. rosalia*, mothers are usually the sole carriers during the first week of infants' lives (Hoage, 1978). In wild *S. fuscicollis* and captive *C. jacchus*, adult males and some older offspring carry infants as early as the first or second day after birth (Goldizen, unpubl. observations; Box, 1975). Thirdly, the amount of care provided by parents may be affected by the number of helpers they have. For example, McGrew (1988) showed that, in captive *S. oedipus*, the amount of parental care (including infant-carrying) performed by mothers and fathers tended to decline with increasing numbers of helpers.

### Mating Patterns

Until recently, it was thought that callitrichids always mated monogamously (e.g., Eisenberg *et al.*, 1972; Kleiman, 1977; Leutenegger, 1980). This conclusion was supported by the following observations. (1) Groups consisting of mated pairs and their offspring were the most stable type of group in captivity. (2) Groups observed in the wild never had more than one breeding female simultaneously (Dawson, 1978; Neyman, 1978, for *S. oedipus*; Izawa, 1978, for the black-mantle tamarin, *S. nigricollis*; Hubrecht, 1984, for *C. jacchus*). (3) In captivity both adult males and females were often quite hostile to adults of the same sex (other than their grown offspring) (Wolfe *et al.*, 1975; Epple, 1978). However, aggression towards unrelated adults is not universal (Epple, 1972, for *S. fuscicollis*; Coates and Poole, 1983, for red-chested tamarins, *S. labiatus*).

Studies of the mating patterns of wild callitrichids have progressed slowly because most of them did not involve animals that were both habituated and individually marked and because, even with habituated animals, copulations of tamarins and marmosets are difficult to see. They last only a few seconds and do not occur in predictable situations.

Only two published studies have yielded data on both parental care and mating patterns. In the *S. fuscicollis* population living in Peru's Manu National Park, some groups consisted of monogamous pairs with offspring, while others were polyandrously mated individuals (one female with more than one male) with or without offspring. In addition, one group appeared to be polygynous (two females were pregnant at the same time) and another was either polygynous or polygynandrous (more than one male mated to more than one female) (Terborgh and Goldizen, 1985; Goldizen, 1987b). The form of polyandry exhibited by these tamarins, in which the female has a single set of offspring at a time that are cared for by all of the adults, is called cooperative polyandry (Faaborg and Patterson, 1981). In the best-studied polyandrous group, the two males mated with equal frequency, and did equal amounts of infant-carrying (Goldizen, 1987b). Accurate data on the frequency of these different mating patterns in the Manu population are not yet available, but preliminary observations suggest that polyandry may be the most common, followed by monogamy, with other patterns quite rare. In Ryland's study group of *C. humeralifer* on the Rio Aripuana in Brazil, all three adult males mated with the same female, and all carried infants, though one male did much less infant-carrying than the other two did (Rylands, 1985).

Cooperative polyandry is also suspected to occur (based on group compositions) in *S. mystax* (Garber *et al.*, 1984) and emperor tamarins (*S. im-*

*perator*) (Goldizen, unpubl. data), and in *L. rosalia* (based on observations of two males mating with the same female; Dietz and Kleiman, 1986). Observations of matings among wild individuals have been published for only two other species. Hubrecht (1985) observed four matings between a young female *C. jacchus* of one group and one or more males of a neighboring group. Such intergroup matings have not been recorded for other callitrichid species, and do not yet have a clear explanation. Soini (1987) described a six-day postpartum estrous period in a group of wild pygmy marmosets (*Cebuella pygmaea*) consisting of two adult males, one adult female, and offspring. During this period both males attempted to mate with the female, but the alpha male was more aggressive and was the only one to mate successfully with the female, suggesting that this group was not polyandrous in the way that some groups of *S. fuscicollis* and the group of *C. humeralifer* described before were. Much more data are needed on the mating patterns of wild callitrichids before we can know whether all species are facultatively polyandrous, or whether some are indeed obligately monogamous.

## EVOLUTION OF CALLITRICHID SOCIAL SYSTEMS

In this section I will discuss the following aspects of tamarin and marmoset physiology and social systems in the order in which I think that they are most likely to have evolved: male parental care, helping and twinning, and then variable mating patterns (Figure 1). I assume that these are most likely to have evolved after monogamy in callitrichid ancestors, but I will not discuss the evolution of monogamy here. It is possible, but seems less likely, that monogamy could have evolved in a polygynous ancestor that already exhibited significant paternal care.

### Male Parental Care

It is believed by some researchers that callitrichid ancestors were larger than present-day forms and, therefore, that the evolution of callitrichids has involved dwarfing (Leutenegger, 1973, 1979, 1980; Ford, 1980). However, Sussman and Kinzey (1984) are skeptical about the dwarfism hypothesis; they suggest instead that all the features that Leutenegger and Ford consider to be evidence of dwarfing could have other explanations. A decrease in body size could have been selected for because it allowed the callitrichid ancestors to shift to foods, such as insects, gum and nectar, that were not heavily used by competing primate species. Before dwarfing occurred, callitrichid ances-

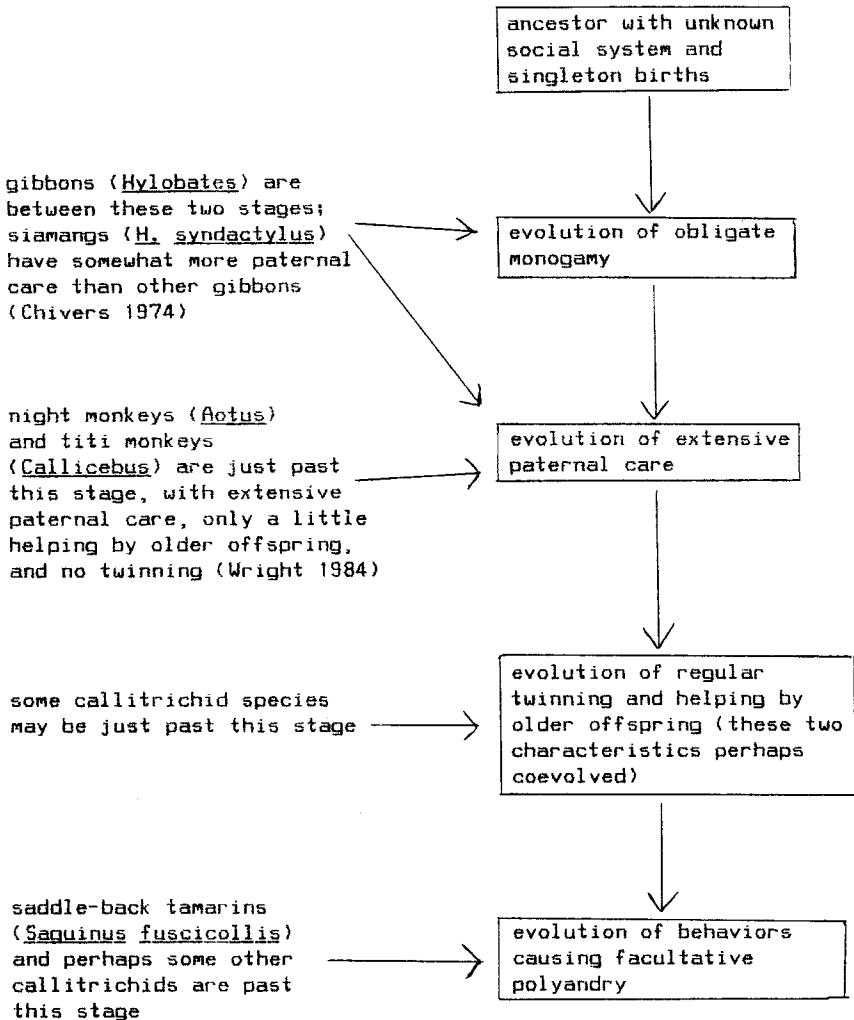


Fig. 1. Hypothesized chain of events in the evolution of the social systems of callitrichids and other monogamous primate species. This does not imply that the other monogamous species noted on this figure will necessarily continue through this entire evolutionary sequence.

tors may have been about 1 kg, the size of the smaller modern species of *Cebidae*. It is also believed that, like cebids, ancestral callitrichids gave birth to singletons (Leutenegger, 1973). Modern callitrichids show the tell-tale signs of this ancestry in their unicornate uterus and single pair of nipples.

Since the mating patterns of modern callitrichids are either monogamous or an extension of monogamy (cooperative polyandry can be viewed

as an outgrowth of monogamy because it involves more than one male being paired to a single female), it is probably reasonable to assume that the most recent pre-dwarfing ancestor of callitrichids was also monogamous, and that this species exhibited fairly extensive male parental care. This last conclusion derives from a comparison of maternal-fetal weight ratios in modern primates.

In modern callitrichids litter birth weight/mother weight ratios range from 0.14 to 0.23 (Table I). Kleiman (1977) suggested that, when a primate mother's litter grows to more than 20 to 25% of her weight, the mother is no longer able to carry the young without help. In fact, among primates in general there seems to be a threshold at a litter birth weight/mother weight ratio of approximately 0.10 above which mothers might not be capable of carrying their infant(s) constantly throughout their period of dependency, as do most female primates. Leutenegger (1973) and Kleiman (1977) list only a few primates other than callitrichids that have ratios above 0.10: the western gray mouse lemur (*Microcebus murinus*), the lesser and dwarf bushbabies (*Galago senegalensis* and *G. demidovii*), the Philippine tarsier (*Tarsius syrichta*), the common squirrel monkey (*Saimiri sciureus*), and the night monkey (*Aotus trivirgatus*).

In none of these species, with the possible exception of *Saimiri*, do mothers carry their infants constantly (Table I). *M. murinus*, two *Galago* species, and *T. syrichta* all leave their newborns in tree holes or nests, although it is not clear how long the infants remain in these nests (Richard, 1987; Bearder, 1987). *Aotus* are monogamous, and males do most of the infant-carrying (Wright, 1984). Female *S. sciureus* are often helped with infant-carrying by other females, sometimes extensively (Carol Mitchell, pers. comm.). However, some female *S. sciureus* seem to carry their young without help, but the fact that most females only have infants every other year, even though infant-carrying only lasts about four months, suggests that infant care is very draining energetically to females (C. Mitchell, pers. comm.).

Because the callitrichid ancestor had single young, it perhaps had litter/mother weight ratios lower than modern callitrichids do, but these were nonetheless probably over 0.10. Together with the likelihood that this ancestral species was monogamous, this suggests that the ancestor exhibited significant paternal care.

### Twining and Helping

It is not clear in what order twinning and the helping behavior of older offspring are likely to have evolved. In fact, it is perhaps most likely that the two coevolved, with an increased frequency of twinning selecting for helping behavior by older offspring and, at the same time, an increased frequency of helping making even more frequent twinning possible.



**Table I.** Litter/Mother Weight Ratios and Type of Infant Transport for a Sample of Primate Species<sup>a</sup>

Species	Litter/mother weight ratio	Type of infant transport	Reference
<b>Prosimians:</b>			
ring-tailed lemur ( <i>Lemur catta</i> )	0.04	mother?	
potto ( <i>Perodicticus potto</i> )	0.04	mother	in Bearder, 1987
western gray mouse lemur ( <i>Microcebus murinus</i> )	0.14	mother, also stored in nests	in Richard, 1987
lesser bushbaby ( <i>Galago senegalensis</i> )	0.10	mother, also stored in nests	in Bearder, 1987
dwarf bushbaby ( <i>Galago demidovii</i> )	0.13	mother, also stored in nests	in Bearder, 1987
Philippine tarsier ( <i>Tarsius syrichta</i> )	0.22	mother, also stored in nests	in Bearder, 1987
<b>Callitrichids:</b>			
common marmoset ( <i>Callithrix jacchus</i> )	0.21–0.27	parents and older siblings	Box, 1975
pygmy marmoset ( <i>Cebuella pygmaea</i> )	0.22–0.23	parents and older siblings?	
cotton-top tamarin ( <i>Saguinus oedipus</i> )	0.14–0.18	parents and older siblings	Tardif <i>et al.</i> , 1986
golden lion tamarin ( <i>Leontopithecus rosalia</i> )	0.19	parents and older siblings	Hoage, 1978
<b>Cebids:</b>			
night monkey ( <i>Aotus trivirgatus</i> )	0.12–0.14	mother and father	Wright, 1984
spider monkey ( <i>Ateles fusciceps</i> and <i>A. geoffroyi</i> )	0.06–0.07	mother (for <i>A. paniscus</i> )	Symington, 1987
common squirrel monkey ( <i>Saimiri sciureus</i> )	0.12–0.16	mother and allomothers	Carol Mitchell, pers. comm.
<b>Cercopithecid:</b>			
rhesus monkey ( <i>Macaca mulatta</i> )	0.03–0.14	primarily mother	in Nicolson, 1987
gelada baboon ( <i>Theropithecus gelada</i> )	0.07 (different study) 0.05	primarily mother	Dunbar, 1984
<b>Apes:</b>			
siamang ( <i>Symphalangus syndactylus</i> )	0.05–0.06	mother and father	Chivers, 1974
orangutan ( <i>Pongo pygmaeus</i> )	0.04	mother	in Rodman and Mitani, 1987
gorilla ( <i>Gorilla gorilla</i> )	0.02–0.04	mother	Fossey, 1983
common chimpanzee ( <i>Pan troglodytes</i> )	0.04	primarily mother	Nishida, 1983

<sup>a</sup>References for litter/mother weight ratios are in Leutenegger (1973) and Kleiman (1977).

### *Twinning*

Leutenegger (1973, 1979) suggested that callitrichid ancestors evolved an increased frequency of twinning as dwarfing occurred, because the heads of their singleton offspring became too large for easy delivery through the mothers' pelvic canals. He showed that among primates, both neonatal/maternal body weight ratios and neonatal brain/body size ratios are negative allometric relationships, so that the smaller a primate species the larger the neonates' heads relative to their mothers' pelvic canals. He then noted that in *Saimiri*, in which females weigh about 0.6–0.7 kg and the litter/mother weight ratio is 0.14, deliveries are very difficult and often unsuccessful (from Goss *et al.*, 1968). According to Leutenegger, ancestral callitrichids evolved twinning because this allowed them to produce the same litter weight as they had before, but as two infants with smaller heads instead of one with too large a head.

This argument seems insufficient; it seems that there would have had to be additional benefits to twinning in order to outweigh the high costs of rearing twins. Leutenegger did not explain why ancestral callitrichids did not simply evolve to produce one infant at a time that was small enough to be born easily. The negative allometric relationship of litter/mother weight ratios in primates suggests only that smaller primates are somehow able to produce larger litter weights. Leutenegger's argument implies, conversely, that smaller primates must, for some reason, have larger litter weights, but he does not explain why.

Given that callitrichids' small size allowed them to produce twins, a high predation rate on the young may have been the factor that made twinning beneficial. Infant mortality during the first year for *S. fuscicollis* in Peru's Manu National Park is 30 to 50% (about 70% of young survived to 6–12 months of age; Goldizen and Terborgh, 1989). Most of this mortality is probably due to predation occurring soon after the young begin to travel independently; such mortality would not be tied closely to the infants' size or to the parents' ability to raise young. This suggests that a young callitrichid with a twin would not have been twice as likely to fall victim to a predator than would an infant without a twin.

Seasonal breeding could also have helped to make twinning adaptive. Although most callitrichids are able to breed twice per year in captivity (e.g., Gengozian *et al.*, 1978, for *S. fuscicollis* and *S. oedipus*), in all tamarin species studied in the wild births showed a nonrandom seasonal distribution, and individual females did not have more than one litter per year on average (reviewed by Goldizen *et al.*, 1988). If callitrichid ancestors were also seasonal breeders, and often lost their single infants to predators, they could not have immediately conceived replacements. Thus, those that had twins

and lost one infant to a predator would still have had another to invest in that year. However, callitrichid ancestors may not have been seasonal breeders, since some marmoset species are not (e.g., *C. humeralifer*; Rylands, 1985).

### Helping

In the biological literature, helpers are individuals which provide care for other individuals' young (Skutch, 1935). Helping behavior (also called alloparental behavior) is widespread among birds and mammals; it has been observed in over 222 bird species (Brown, 1987) and 120 mammal species (Riedman, 1982). Helpers are sometimes individuals which are not breeders, though they may be sexually mature; at other times helpers are reproductive and may even have infants of their own while they help raise those of others. The details of helping behavior vary in different species; Table II presents some information on helping in six well-studied species of cooperatively breeding birds.

Allomaternal care has been observed in a number of primate species, including ring-tailed lemurs (*Lemur catta*), howler monkeys (*Alouatta seniculus*), gray langurs (*Presbytis entellus*), black-and-white colobus (*Colobus guereza*), vervet monkeys (*Cercopithecus aethiops*), patas monkeys (*Erythrocebus patas*), Japanese macaques (*Macaca fuscata*), rhesus macaques (*M. mulatta*), savanna baboons (*Papio cynocephalus*), gelada baboons (*Theropithecus gelada*), gorillas (*Gorilla gorilla*), and chimpanzees (*Pan troglodytes*)—reviewed by Riedman, 1982; Nicolson, 1987. Some of these allomothers were nonreproductive females; others were females with young of their own. In primates other than callitrichids, significant helping behavior by nonreproductive males is not very common, while allopaternal care by reproductive males is hard to measure because of the difficulty of assigning paternity in many species.

The helping behavior of young callitrichids can probably be better understood through comparisons with nonprimates instead of primates for several reasons. (1) The helping exhibited by many young tamarins and marmosets is probably substantially more frequent and energetically costly than is the alloparental behavior of most other primates. (2) In callitrichids, young of both sexes seem to give approximately equal amounts of help, as occurs in many cooperatively breeding bird species (Table II), but unlike most other primates. (3) There have been few systematic studies of patterns of helping in primates, while there have been dozens of such studies on birds (Emlen, 1984; Brown, 1987).

To understand why sexually immature individuals serve as helpers we need to ask two questions. (1) How do these helpers gain in inclusive fitness

**Table II.** Information on Age and Reproductive Status of Helpers, Tasks Performed by Helpers, and the Possible Benefits of Helping to Helpers for Six Well Studied Species of Cooperatively Breeding Birds

Species	Sex of helpers	Reproductive <sup>e</sup> status of helpers	Main tasks performed by helpers	Suggested benefits to helpers
pied kingfisher <sup>b</sup> ( <i>Ceryle rudis</i> )	M	R, NR	feed young, feed breeders, mob predators	indirect fitness gains, access to future mates, experience
Florida scrub jay <sup>c</sup> ( <i>Aphelocoma coerulescens</i> )	M, F	NR	feed young, mob predators	territory inheritance (males), experience
stripe-backed wren <sup>d</sup> ( <i>Campylorhynchus nuchalis</i> )	M, F	NR	feed young, defend nests	indirect fitness gains, raising helpers who will then help them (mostly for males)
white-fronted bee-eater <sup>e</sup> ( <i>Merops bullockoides</i> )	M, F	R, NR	construct and defend nests, incubate eggs, feed young	indirect fitness gains, reciprocity (help raise young that might later return the help)
Galapagos mockingbird <sup>f</sup> ( <i>Nesomimus parvulus</i> )	mostly M	R, NR	feed young	indirect fitness gains
green woodhoopoe <sup>g</sup> ( <i>Phoeniculus purpureus</i> )	M, F	NR	feed young	indirect fitness gains, reciprocity (help to raise young that might later reciprocate)

<sup>a</sup>R = individuals who had bred, N = individuals who had never bred.

<sup>b</sup>Reyer, 1980.

<sup>c</sup>Woodfenden and Fitzpatrick, 1984.

<sup>d</sup>Rabenold, 1985.

<sup>e</sup>Emlen, 1981, 1984; Emlen, in Brown, 1987.

<sup>f</sup>Curry, 1988.

<sup>g</sup>Ligen, 1981.

(Hamilton, 1964) from their helping behavior? (2) How do parents gain from being helped? To understand why sexually mature, yet nonreproductive, individuals help, we need to ask two additional questions. (3) Why do these individuals postpone their own breeding? (4) Given that these individuals have postponed breeding, why are they living in a territory (usually their natal territory) with breeding individuals, instead of dispersing in search of a territory and/or mate for themselves?

I will begin with the last two questions. Research on cooperatively breeding birds has suggested a number of reasons why individuals might not breed as soon as they are physiologically capable of reproduction. These hypotheses propose that delayed breeding might be due to (1) severe environmental conditions that reduce the chance of successful breeding (Emlen, 1982), (2) dangers of dispersal, (3) saturation of suitable breeding habitat (Selander, 1964; Stacey, 1979a), (4) lack of potential mates, (5) insufficient foraging skills for successful breeding (Ashmole, 1963; Heinsohn *et al.*, 1988), or (6) inclusive fitness benefits of helping to rear siblings (reviewed in Brown, 1987). The study of wild *S. fuscicollis* in Peru's Manu National Park suggests that dispersal dangers, habitat saturation and inclusive fitness benefits, as well as a shortage of potential helpers, are possible causes of delayed breeding in this species (Goldizen and Terborgh, 1989).

There are various reasons why an individual that delays breeding might benefit from remaining in its natal territory, if permitted to do so (reviewed by Brown, 1987). (1) There may be no vacant habitat into which such individuals can move. (2) Undirected dispersal may be too risky because of the dangers of predation and the difficulty of finding food in unknown areas. Individuals remaining in their natal territories would have access to known food patches and might suffer reduced predation risks because of being in a group. (3) Individuals remaining in their natal groups might eventually be able to breed in that territory. (4) Individuals which remain in their natal territories might be able to increase their inclusive fitness by helping to rear siblings, and increasing those siblings' chances of survival. Wild tamarins often remain in their natal territories for one or more years past the time when they could potentially be breeding on their own (Goldizen and Terborgh, 1989). Unfortunately, there is not enough information on wild callitrichids to evaluate the four possible explanations for delayed dispersal listed above, although all seem to be reasonable for tamarins.

When an individual is in its natal group, how might helping to rear its siblings increase its inclusive fitness? Again, work on cooperatively breeding birds has suggested several possibilities. (1) If helpers increase the survival chances of their siblings, they would increase the indirect fitness component of their own inclusive fitness (e.g., Rabenold, 1985; Curry, 1988). (2) The help that helpers give might be reciprocated in the future (Trivers,

1971; Axelrod and Hamilton, 1981). (3) Helpers might increase their own future reproductive success by gaining experience with infant care (Gartlan, 1969; Lancaster, 1971). (4) Helping might increase a helper's chances of obtaining a territory or a mate (Woolfenden and Fitzpatrick, 1978, 1984). (5) Helpers might help as a form of payment for being allowed to stay in the safety of their natal territory (Gaston, 1978).

Again, there are too few data on helpers in wild callitrichids to do more than speculate on possible benefits of helping to helpers. (1) Since three or more caretakers seem important for the successful raising of offspring (see below), helpers probably often gain inclusive fitness benefits from increasing the survival of their siblings. (2) We have so far observed one case of possible reciprocity in helping among the *S. fuscicollis* at Manu; one female, which inherited the breeding position in her natal territory, also inherited potential helpers in the younger siblings that she herself had helped to rear. (3) At least three captive studies have suggested that adult callitrichids are much better at rearing their own young if they had experience carrying their siblings (Epple, 1975, on *S. fuscicollis*; Hoage, 1978, on *L. rosalia*; Tardif *et al.*, 1984, on *C. jacchus* and *S. oedipus*). However, to know whether callitrichids require the actual experience of carrying young, one would need to compare the reproductive success of first-time breeders that had been allowed to carry younger siblings with the reproductive success of first-time breeders that had watched others carry young but had not been allowed to carry any themselves. This has not yet been done. (4) In two cases at Manu, female *S. fuscicollis* that served as helpers in their natal territories eventually inherited both the territories and their mothers' mates upon the deaths of the mothers (Goldizen, unpubl. observ.).

The last of the questions regarding helping pertains to the benefits to the parents. It has been shown for many cooperatively breeding bird species that pairs with helpers raise more young than pairs without helpers (Florida scrub jays, *Aphelocoma coerulescens*, Woolfenden and Fitzpatrick, 1984; gray-crowned babblers, *Pomatostomus temporalis*, Brown *et al.*, 1982; reviewed by Emlen, 1978, pp. 252-253; Brown, 1987, p. 171). In callitrichids too, helpers are almost certainly beneficial. In fact, in *S. fuscicollis*, it appears that a pair without at least one helper would have a poor chance of raising offspring (see below). However, studies of callitrichids will never involve sample sizes as large as those in studies of birds, and this will make it hard to evaluate the relationship between reproductive success and number of helpers in callitrichids.

### Variable Mating Patterns

The evolution of twinning (which increased the costs of infant care) and of helping by nonreproductive offspring probably set the stage for the

evolution of flexible mating patterns in some or all callitrichid species. To explain the unusually variable mating patterns of *S. fuscicollis*, Goldizen and Terborgh (1986) and Goldizen (1987b) suggested that lone pairs would have a poor chance of raising offspring, and thus, if a pair did not have older offspring which could serve as helpers, both members of the pair would benefit from mating as a polyandrous trio with another male. Data on the costs of lactation and infant-carrying suggest that lone pairs would not be able to accomplish both of these tasks and still get enough to eat (Goldizen, 1987b). In fact, lone pairs have been very rare in Manu, and none conceived offspring during our study (Goldizen, 1987b). There are still not enough data on the compositions of monogamous and polyandrous groups to test adequately the suggestion that groups without helpers should be polyandrous, while those with helpers should be monogamous.

If the callitrichid species with variable mating patterns have indeed evolved the ability to adjust their mating patterns in response to the number of potential helpers present in their groups, it is not surprising that most captive individuals would show a preference for monogamous pairing. Rearing infants is much less energetically costly in captivity than in the wild, since captive animals do not have to carry their infants long distances, and are provided with more than adequate food supplies. Therefore, captive pairs should not need extra help, and while captive females might still benefit somewhat from mating polyandrously, males presumably would not. By similar reasoning, the costs of infant care probably vary for different species in the wild, or even for different populations of the same species (e.g., because of different daily travel distances), and this might affect the frequencies of polyandrous groups.

The sequence of evolutionary events undergone by saddle-back tamarins may have put males of the species in an awkward situation. I have suggested that male *S. fuscicollis* presented with a high probability of twin infants and no older offspring to serve as helpers, on average, would increase their fitness by being polyandrous rather than monogamous (Goldizen, 1987b). But would not the best solution for these males have been to be mated to monogamous females which had single instead of twin infants? This was perhaps simply not an evolutionary possibility for male tamarins. Any negative effects of twinning on males would have been of far less importance for the evolution of twinning than would its benefits to females. Thus, for male tamarins, a less than ideal mating system may have been the best response to evolution in the other sex.

Cooperative polyandry has not been found to occur regularly in any other species of mammal except for humans (e.g., Goldstein, 1971), but it occurs in some birds: dunnocks (*Prunella modularis*) (Davies, 1983, 1985; Davies and Lundberg, 1984), Tasmanian native hens (*Tribonyx mortierii*) (Ridpath, 1972b; Maynard Smith and Ridpath, 1972), acorn woodpeckers (*Melanerpes formicivorus*) (Stacey, 1979b; Koenig and Mumme, 1987),

dusky moorhens (*Gallinula tenebrosa*) (Garnett, 1978, 1980), pukekos (*Porphyrio porphyrio*) (Craig, 1980a; Jamieson and Craig, 1987), and Galapagos hawks (*Buteo galapagensis*) (Faaborg *et al.*, 1980; Faaborg, 1986). The causes of cooperative polyandry appear to be somewhat different in each of these species and in *S. fuscicollis*. For example, in dunnocks, males usually would have higher inclusive fitness by mating monogamously or polygynously, but sometimes they cannot prevent other males from copulating with their females; thus, they are forced into cooperative polyandry (Davies and Lundberg, 1984; Davies, 1986). In Tasmanian native hens, a male-biased sex ratio and the fact that polyandrous males are usually closely related may make polyandry beneficial to at least some males (Maynard Smith and Ridpath, 1972).

In many of these cooperatively polyandrous species, trios successfully raise more offspring, on average, than pairs do (Ridpath, 1982b, for Tasmanian native hens; Koenig *et al.*, 1983, for acorn woodpeckers; Davies, 1986, for dunnocks; Faaborg, 1986, for Galapagos hawks; but see Craig, 1980b, for opposite finding for pukekos). However, the need for extra help with offspring care has probably not been as important in the evolution of cooperative polyandry in these species as in *S. fuscicollis*.

Despite the differences between these birds and callitrichids, an understanding of the dynamics of polyandry in birds can help us to understand better the evolution of polyandry in callitrichids. For example, males in species that exhibit facultative cooperative polyandry face two problems. First, should they only accept polyandrous status without a struggle if their inclusive fitness is likely to be increased by mating polyandrously? Secondly, should males in polyandrous groups only care for the young produced by their females if they have at least a good chance of having fathered those young?

Tasmanian native hens and dunnocks shed some light on the first question. Dominant male dunnocks do not seem to benefit from being polyandrous (Davies and Lundberg, 1984; Davies, 1986), and they try hard to keep other males from mating with their females (Davies, 1985). On the other hand, Tasmanian native hen males appear to benefit often from polyandry (Maynard Smith and Ridpath, 1972) and aggression among adult group members is very rare (Ridpath, 1972a). It has not been shown that males of a single species can show these two opposite types of reactions, but it seems a reasonable possibility. One pair of polyandrous male *S. fuscicollis* was surprisingly unaggressive to each other (Goldizen, 1989); perhaps this was because both of them were benefiting from being polyandrous.

The relationship between probability of paternity and male parental care has been investigated in dunnocks and pukekos. In dunnock trios, in



which the subordinate males were prevented from mating by the dominant males, they did not help to feed the young (Davies, 1986). In pukekos, the results were less clear. In groups with multiple males, those males with the highest probability of paternity performed less incubation of eggs but spent more time in chick care than did the other males (Craig and Jamieson, 1985).

## CONCLUSIONS

Saddle-back tamarins apparently evolved the ability to vary their mating and infant care behaviors according to the particular demographic and ecological conditions in which they find themselves. However, at least in Peru's Manu National Park, their decisions about mating patterns appear to be more directly affected by demographic factors, especially the number of older offspring in the group, than by ecological conditions. This is quite different from dunnocks, in which males whose females have large territories are usually polyandrous, while the mates of females with small territories are more often monogamous (Davies and Lundberg, 1984). Of course, ecological factors affect tamarin mating patterns indirectly by determining the energetic costs of infant care (e.g., through food availability and daily travel lengths).

In fact, while mating patterns within tamarin populations may be determined by demographic factors, differences between the mating patterns of different populations or different callitrichid species may be ecologically determined. Although little is known about the mating patterns of most species, there are indications that major differences in social systems exist between species. For example, group compositions seem more fluid in some species (*S. oedipus*, Dawson, 1978; Neyman, 1978) than others (*S. fuscicollis*, Goldizen, 1988; Goldizen and Terborgh, 1989). If the mating patterns of callitrichids turn out to vary between species we will have an excellent opportunity to understand how ecological differences affect social structure, since they are very close phylogenetically but vary substantially in their feeding and ranging patterns (Sussman and Kinzey, 1984; Goldizen, 1987a).

## ACKNOWLEDGMENTS

I thank M. McFarland Symington, D. Watts, and two reviewers for comments on an earlier version of the manuscript, and I. DeVore and K. Strier for the opportunity to participate in the symposium from which this paper developed.

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