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Infant Care in Callitrichids: Cooperation and Competition

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Abstract

Yamamoto ME. Infant Care in Callitrichids: Cooperation and Competition. ARBS Ann Rev Biomed Sci 2005;7:149-60. In this paper I examine parental care in cooperative breeding callitrichid monkeys, with particular attention to *Callithrix jacchus*, considering the breeding strategies adopted by females, and comparing callitrichid communal breeders with the most extensively studied cooperative birds. Cooperative breeding describes situations in which adult individuals, in addition to the genetic parents, aid in the rearing of the young. This rearing system was first described in a few bird species and since then in many other bird and mammal species. Among these are the callitrichids, in which females exhibit energetically demanding reproduction. I examine helping patterns, potential benefits and costs to helpers, variables that influence helping behavior in callitrichids and differences between genera. Females in such cooperative systems compete for breeding opportunities, and I review published data to analyze which of the two models, the limited control or the optimal skew model, better explains this issue. Finally, I briefly compare cooperative breeding systems in birds and callitrichids.

KEYWORDS: callitrichids, cooperative care, helping, skew reproduction

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1. Introduction

Should individuals care for their offspring? Our mammal bias would suggest that we should, especially where females are concerned. But, as with any other behavior, caring for offspring has costs and benefits, and sometimes the costs can be so high that parenting is not worth the effort. Parental behavior should be selected when it makes a difference in offspring survival and success. Accordingly, parental care should be more frequent when eggs and/or infants have to cope with harsh environments, high predation pressure, high levels of parasitism, and intense competition from conspecifics (Magrath & Komdeur, 2003).

As recently as the 1960's parental care was viewed among biologists as an adaptation that benefits the species. Recognition of the costs of reproduction and individual fitness helped to understand the biological basis of parental care and investment, and its variable expression (Gross, 2005).

Two major points derived from life history theory, called the William Principle, are relevant to the issue of costs of parental care (Coleman & Gross, 1991; Gross, 2005): first, any energy allocated to one specific offspring is not available for use elsewhere, be it future mating, future offspring, energy accumulation or simple survival; second, lifetime reproductive success has two components, one achieved through the present offspring and the other through all future broods. These issues imply that parents and offspring will disagree regarding the amount of investment that one specific offspring should receive, the offspring attempting to maximize its reproductive success, which usually requires more care than the parent is willing to give (Trivers, 1974).

Another important point comes from the theory of sexual selection, that anysogamy (the dimorphism in gamete sizes) leads to a conflict of interest between the sexes (Westneat & Sargent, 1996). In anysogamous species, the sex with higher reproductive potential will pay a higher cost for parental care, in that it loses mating opportunities. There may be consequences of that conflict on care patterns, with either both parents caring for the offspring (because the costs and benefits are similar for both), neither parent caring, or one parent compensating, at least partially, for the reduced or non-existent care of the other. Variations may also be related to certainty of paternity. A number of studies have shown that males may regulate their provision of care according to the probability of having sired the offspring or part of the brood (Dixon *et al.*, 1994; Wright & Cotton, 1994). Nevertheless, complex interactions determine if and how much care each sex will dispense. The benefits that result from a particular level of care depend on the behavior of the partner and that of other members of the population, the availability of new mates and their receptivity, and the need for mate guarding (Houston *et al.*, 2005). Given these complex interactions, it is difficult to predict the level of care that will evolve, and therefore it is important to examine each species individually.

In this paper I will examine parental care in cooperative breeding callitrichid monkeys, with particular attention to *Callithrix jacchus*, considering the breeding strategies adopted by females, and comparing callitrichid communal breeders with the most extensively studied cooperative birds.

2. Cooperative Breeding Systems

Cooperative breeding describes situations in which adult individuals, in addition to the genetic parents, aid in the rearing of the young. This rearing system was first described in birds by Skutch (cited in Emlen, 1991) and since then approximately 220 bird species and 120 mammalian species have been reported as exhibiting it. This kind of cooperation represents a paradox for evolutionary theory, and a large number of investigations have been directed at the unveiling of the many questions that are associated with it. Emlen (1997) raises some of these: the first was if, in fact, helpers helped. Most studies confirmed that they did and established that in most cases cooperative breeding occurred in family groups, and helpers benefited from their behavior by increasing their inclusive fitness. But why do offspring remain in their natal group rather than disperse and start breeding on their own? Stacey (1979) provided an answer that suggests the existence of dispersal constraints; the habitat saturation hypothesis. Finally, recent data have suggested that cooperative breeders do not only cooperate, but also compete for breeding positions, even inside their own natal groups. The reproductive skew theory attempts to explain why dominant individuals monopolize reproduction and why they sometimes share it with other group members.

2.1. Alloparental Care in Callitrichids: Why do Helpers Help?

To what extent is cooperative breeding in callitrichids similar to that displayed by other species, particularly birds, the most studied group with respect to this topic?

Reproduction is energetically very demanding for callitrichid females, since they give birth to twins with high birth weights, and may become pregnant again in a short time, while still nursing the previous set of infants. The father and other non-reproductive individuals may act as helpers, assisting the females in carrying the infants, sharing food with them, being vigilant and defending the territory, and protecting the infants from predators (Snowdon, 1996).

But, do helpers help or, in other words, do they significantly increase infant survival? There are many studies that report that this assertion is true for different callitrichid species (Sussman & Garber, 1987, for *Saguinus midas;* Baker *et al.*, 1993, and Bales *et al.*, 2000, for *Leontopithecus rosalia*; and Koenig, 1995, reviewing data for *Callithrix jacchus*). In all but one case increased infant survival is related to the presence of adult males, suggesting that reproductive females benefit from an increasing number of adult males in the group. Data from our wild population suggest that neither group size nor the number of adult males affected the percentage of surviving offspring. As all groups had at least 5 potential helpers, this may surpass the minimum necessary number of helpers. There is also evidence that a few non-reproductive helpers provided the better part of the care (Albuquerque, 1994) and that these were mostly males. Moreover, females were sometimes prevented from carrying infants (Albuquerque, 1999), suggesting that their help was neither necessary nor wanted.

In the same vein as Emlen (1997), my next question is why do (some) helpers help and why do they remain in the group without breeding? Postponing reproduction can bring heavy costs to helpers and even prevent them from breeding at all if they remain long enough in the group as helpers. Besides, infant care also has costs in callitrichids, as caregivers have less time to forage, are more susceptible to predators and have decreased mobility while carrying infants (Price, 1992; Tardif, 1997). These costs may be particularly heavy when resources are low. Consequently, there must be benefits to individuals that care for infants.

Emlen (1991) lists four potential benefits for helpers:

(i) enhanced survivorship through both increased group size and access to the physical and social resources of the natal group;

(ii) enhanced future probability of breeding through the budding off of natal territory, or the taking over of a vacancy when a breeder dies or leaves the group;

(iii) increased fecundity as a breeder through previous exposure to parental skills and by recruiting helpers from among the animals that it helped to raise;

(iv) increased production of non-descendant kin, thereby enhancing its inclusive fitness.

There is evidence to support all four of these hypotheses among callitrichids (Baker *et al.*, 1993; Digby, 1994; Epple, 1978; Garber *et al.*, 1984; Tardif *et al.*, 1984). However, Tardif (1997) argues that the evidence is, at best, insufficient. She argues that the correlation between characteristic or behavior and proposed benefits does not prove a causal relationship. For instance, benefits accrued to experience, which would improve reproductive performance, may reflect the lessening of a neophobic response to infants (Pryce, 1992) and may be gained by simple exposure to infants as opposed to actual participation in infant care (Tardif *et al.*, 1992). Experimental studies are essential for a better understanding of this topic.

Not all helpers help. I will examine two variables that influence helping behavior: differences among genera and characteristics of helpers.

Differences among four of the Callitrichidae family genera { *Callithrix*, *Saguinus*, *Leontopithecus* and *Cebuella* (Rylands *et al.*, 2000) } are apparent. *Callithrix* carry and provision infants for a shorter period than do *Saguinus* species, and *Leontopithecus* displays an intermediate intensity of care. These differences are mainly correlated with ranging patterns in wild environments (Tardif *et al.*, 1993). *Callithrix* species use small home ranges (mean varying between 4 and 10 ha) that have clumped resources, resulting in a daily path length between 704 to 974 m.day^{-1} (Hubrecht, 1985; Rylands, 1989). Both *Saguinus* (Garber, 1988; Tardif *et al.*, 1993) and *Leontopithecus* (Rylands, 1989; Dietz *et al.*, 1996) species use much larger home ranges (between 9 and 40 ha for the former and 36 to 117 ha for the latter). Feeding resources are scattered, both spatially and temporally in *Saguinus*, but there is no detailed information on *Leontopithecus*. Tardif *et al.* (1993) suggest that *Callithrix* infants have an earlier independence because food is clumped and the foraging path length is shorter than it is in *Saguinus* and *Leontopithecus*.

We compared infant carrying in *C. jacchus* and *L. chrysomelas*, which exhibit marked behavioral and ecological differences (Oliveira *et al.*, 1999). *C. jacchus* groups have very small home ranges because they depend heavily on plant exudates, which are available all year round. Consequently, infants become independent earlier and are able to forage on their own. *L. chrysomelas*, on the other hand, feeds mainly on fruits and insects that are more disperse and therefore uses larger home ranges, probably associated with a longer period of infant dependence. Our comparison showed no differences between the two genera as to total carrying time for the first 8 weeks of infant life and time that mothers, fathers and helpers carried the infants. However, there were differences regarding the total duration of care and the onset of carrying by each caregiver. In *C. jacchus*, the father and non-reproductive helpers carried infants from the first day; and by the fourth day of life, non-reproductive helpers were carrying infants as much as the father was. In *L. chrysomelas*, only the mother carried the infants during the first two days, only the mother and the father for the next two days, and non-reproductive helpers only started carrying infants when they were 5 days old. These results are in line with Tardif *et al.*'s (1993) suggestions, reinforcing the importance of features such as resource type, foraging pattern, and the display and sharing of infant care in callitrichids.

A joint study between the *Universidade Federal do Rio Grande do Norte* and the University of Reading investigated the influence of individual helper characteristics such as age (juveniles, subadults and adults), gender (male and female), presence of older siblings and social status (singleton and twin) on carrying behavior in captive *C. jacchus* (Yamamoto & Box, 1997). All showed significant differences among categories, except for gender (Table 1). Helpers with the following characteristics displayed more infant carrying: adults, the oldest siblings in the group and singletons as compared to twins. Similar effects were found in measures of interest in infants, such as transfers and retrieval of infants from other carriers. A further result suggests that, although without statistical significance, adult females are less involved in infant carrying than adult males. This, together with wild group data showing that adult females are sometimes prevented from carrying infants (Albuquerque, 1999), suggest that individuals may not be able to display as much care as they are willing to give. And that leads us to female-female competition.

Table 1 – Mean percentage (± SE) of carrying infants by 48 non-reproductive helpers in 15 captive *Callithrix jacchus* families as to age, gender, presence of older siblings and status.

Female Characteristic	Category	% of infant carrying
Age	Juvenile	4.8 ± 1.9
	Subadult	11.5 ± 1.9
	Adult	18.3 ± 1.9*
Gender	Male	12.5 ± 1.4
	Female	10.1 ± 1.9
Older siblings	Absent	17.3 ± 1.9*
	Present	7.2 ± 2.4
Social status	Singleton	16.3 ± 2.9*
	Twin	8.7 ± 1.4

Adapted from Yamamoto & Box (1997).
* Significantly different from the other categories for a same characteristic (MANCOVA: age, $F_{2,47} = 11.44$, $p = 0.0001$; gender, $F_{1,47} = 1.43$, $p = 0.238$; older siblings, $F_{1,47} = 6.65$, $p = 0.0137$; social status, $F_{1,47} = 6.19$, $p = 0.0171$).

2.2. Female-female Competition in Callitrichids: Concession or Limited Control?

To understand female-female competition in callitrichids, it is important to briefly discuss the reproductive suppression of subordinate females. Suppression of ovulation in subordinate females was first demonstrated in *C. jacchus* by David Abbott (Abbott, 1984; Abbott *et al.*, 1981). There are, however, important differences among genera: in *Saguinus fuscicollis* (Epple & Katz, 1984) and *S. oedipus* (Ziegler *et al.*, 1987), subordinate females experience total ovulation suppression; *Leontopithecus rosalia* females, on the other hand, show no sign of suppression in the presence of their mothers (French & Stribley, 1987). In captive *C. jacchus*, up to half of the daughters escape from suppression, but only one female will ovulate in peer groups (Abbott, 1984; Saltzman *et al.*, 1997a,b). Recent hormonal data from wild common marmoset groups suggest that there is usually more than one ovulating female in every group (Albuquerque *et al.*, 2004).

Escape from suppression suggests that subordinate females are attempting to breed against the best interests of the dominant female. Two models were presented to explain such "insubordination": the "limited control" or "incomplete control" model (ICM) holds that power struggles between the dominant female and the subordinates determine the frequency at which the subordinates breed (Clutton-Brock, 1998). In contrast, the "optimal skew" model (OSM) posits that the dominant female fully controls subordinate female breeding, allowing them to breed only insofar as it entices them to stay with the group and to assist in rearing her own litters (Emlen *et al.*, 1998).

A 10-year monitoring of a wild *C. jacchus* population suggests that ICM explains this species behavior better than OSM does (Arruda *et al.*, 2005; Yamamoto *et al.*, in press). These data suggest that females benefit from the monopolization of reproduction, since monogamous females have lower interbirth intervals, have relatively more surviving offspring, and require less time to produce a surviving infant. There are other costs for females associated with polygyny, derived from preventing subordinate females from breeding. Dominant females were reported to have higher cortisol levels than did subordinate females (Abbott *et al.*, 2003). Moreover, data from captive pairs of adult *C. jacchus* females (Alencar *et al.*, in press) suggested that the establishment and maintenance of dominance is based on agonism and may sometimes involve overt aggression.

Different strategies are open to a *C. jacchus* female and opting for one of them probably depends on her status (dominant or subordinate), her kinship and social relation with the other females in the groups, the existence of potential mates, and the availability of breeding vacancies.

A dominant female has to choose between the following: (i) maintaining breeding exclusivity, which allows her to monopolize resources and helpers, increasing the probability of infant survival. On the other hand, in order to monopolize reproduction, dominant females have to cope with the costs of physiological and/or behavioral suppression of subordinate females; (ii) sharing reproduction with a secondary female, which may benefit the dominant female when her subordinate is kin, increasing her inclusive fitness. However, the presence of another breeding female decreases the survival of her own offspring, as shown before.

A subordinate female, on the other hand, faces the following alternatives: (i) to wait for a breeding vacancy in a neighboring group or to emigrate to an incipient group, which will allow her to become an exclusive breeder, or a primary breeder in a polygynous arrangement. This option, however, requires waiting for such opportunities, which are rare and unpredictable, as stated in Stacey's (1979) habitat saturation hypothesis; (ii) to breed as a secondary female, which, although allowing for earlier reproductive activity, exposes this female to harassment and even to the infanticide of her offspring by the dominant female; (iii) to engage in copulations with extra-group males, which allows the females to escape harassment from dominants, to have access to an unrelated male and to scan neighboring groups for breeding vacancies. Although this strategy has proved successful on a few occasions, nearly all the females that became pregnant from these copulations did not find adequate conditions for offspring survival, and lost their infants (Yamamoto *et al.*, in press; Arruda *et al.*, 2005; Lazaro-Perea *et al.*, 2000).

3. Concluding Remarks - Comparing Birds and Marmosets: Different Life Styles, Similar Solutions

Birds and mammals exhibit very important differences in their physiology, reproduction and life style. Nonetheless, these differences are not so substantive as to lead to fundamentally different cooperative breeding systems. In fact, three issues have guided research on avian and mammalian systems: group living, reproductive skew and alloparental care (Mumme, 1997).

A critical feature of group living and the formation of families is delayed dispersal. Both in birds and in callitrichids, delayed dispersal is favored by the scarcity of high-quality territories, the habitat saturation hypothesis (Stacey, 1979), which was initially proposed to explain the behavior of a bird species, the acorn woodpecker (*Melanerpes formicivorous*). In callitrichids, particularly in *C. jacchus*, lack of territories is not the only constraint on dispersal; so is shortage of suitable partners and scarcity of breeding vacancies. The same is true for a number of cooperative breeding bird species (Komdeur, 1992; Pruett-Jones & Lewis, 1990).

Reproductive skew is described nowadays as the eusociality continuum (Lacey & Sherman, 1997; Mumme, 1997), with its extremes represented by singular breeding systems (complete suppression of subordinates, high reproductive skew) and plural breeding systems (no suppression of subordinates, low reproductive skew). A considerable variation in the degree of reproductive skew has been reported both among populations, in birds (Mumme, 1997), and within populations, in callithrichids (Dietz & Baker, 1993; Digby, 1995; Goldizen *et al.*, 1996; Yamamoto *et al.*, in press). In mammals, this variation has been attributed to concession (Emlen *et al.*, 1998) or, alternatively, to lack of control of dominant individuals over subordinates (Clutton-Brock, 1998). More research is necessary to better understand this issue both in mammals and in birds.

Finally, alloparental care is a pervasive pattern in cooperative birds and mammals. There is presently strong evidence that helpers help and that they are critical for offspring survival. Research on cooperative breeding birds has shown that helpers can benefit from alloparental care by increasing survival, future mating opportunities, future reproductive success and/or their indirect fitness (Lucas *et al.*, 1997; Riedman, 1982; Woolfenden, 1975; Woolfenden & Fitzpatrick, 1978). This pattern is not as well established in mammals, and many questions remain regarding the relation between helping and obtaining benefits. The measure of helper and non-helper fitness in mammals should certainly, be a topic of future research.

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