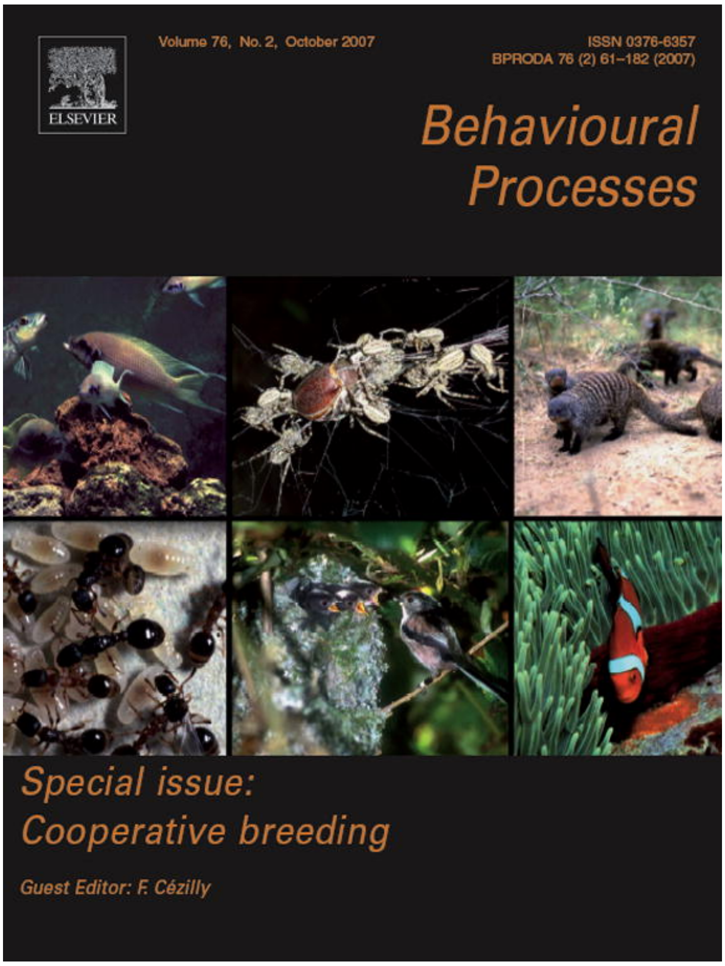
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Commentary

Cooperative breeders do cooperate

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Bergmüller et al. (2007) make an important contribution to studies of cooperative breeding and provide a theoretical basis for linking the evolution of cooperative breeding with cooperative behavior. We have long been involved in empirical research on the only family of nonhuman primates to exhibit cooperative breeding, the Callitrichidae, which includes marmosets and tamarins, with studies in both field and captive contexts. In this paper we expand on three themes from Bergmüller et al. (2007) with empirical data. First we provide data in support of the importance of helpers and the specific benefits that helpers can gain in terms of fitness. Second, we suggest that mechanisms of rewarding helpers are more common and more effective in maintaining cooperative breeding than punishments. Third, we present a summary of our own research on cooperative behavior in cotton-top tamarins (*Saguinus oedipus*) where we find greater success in cooperative problem solving than has been reported for non-cooperatively breeding species.

1. Fitness benefits of helping

A major issue in studies of cooperative breeding is whether helpers are really necessary for reproductive success. In both moustached tamarins (*Saguinus mystax*) and cotton-top tamarins, the number of non-breeding helpers is directly related to infant survival in the wild (Garber et al., 1984; Savage et al., 1996b) with parents plus three additional helpers being optimal for cotton-top tamarins. Even in our captive colony where food is readily available and predator pressures are absent, the same effect is present (Snowdon, 1996). Competition over helpers can lead to infanticide in wild populations of common marmosets (*Callithrix jacchus*) when two females in a group give birth close in time and one female kills the infants of the other (Digby, 1995; Lazaro-Perea et al., 2000). When females give birth asynchronously and helpers can be time-shared across litters, aggression toward infants is not observed (Digby, 1995). Helpers are critical resources for successful reproduction in marmosets and tamarins.

Infant care is costly with infant carriers losing up to 10% of their body weight in the 3 months of intensive infant care (Sanchez et al., 1999; Achenbach and Snowdon, 2002). The latter study also reported an inverse linear relationship between number of helpers and weight loss; the more helpers present, the less weight an individual loses. Others (e.g. Price, 1992) have reported reduced locomotion and feeding by those carrying infants. Both parents and helpers share food with infants at the time of weaning, increasing energetic costs to caregivers. Thus, there are significant costs to both biological parents and helpers.

The key question is how do unrelated helpers benefit from infant care? One important finding from studies of Callitrichids is that helpers that have cared for other infants have greater reproductive success when they become parents than individuals that do not have previous infant care experience. In common marmosets, saddleback tamarins (*Saguinus fuscicollis*), and cotton-top tamarins infant mortality is high among parents without previous infant care experience (Epple, 1978; Tardif et al., 1984; Johnson et al., 1991). All individuals regardless of experience or relatedness appear interested in and attracted to infants with even the youngest siblings competing with other group members for access to infants (Price, 1991; Achenbach and Snowdon, 1998). We have found that all tamarins, regardless of prior experience as parents or helpers or neither are attracted to visual and vocal cues from unrelated infants (Almond, Pieper, Ziegler and Snowdon, in preparation). Despite the universal attraction of infants, those without prior care-taking experience appear discomforted by infants on their back and repeatedly bite and push off infants. Inexperienced females appear clumsy in positioning infants for nursing. Theoretical accounts of cooperative breeding rarely discuss the importance of learning infant care skills and yet, based on data from marmosets and tamarins, these skills may be critical to individual fitness.

A second category of potential benefits to unrelated helpers is the benefits derived from group living given that there are rel-

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atively few breeding vacancies in the wild. This is true for both the endangered cotton-top tamarin and the abundant common marmoset. In field studies on both species we have been able to monitor dispersing animals, and find that none have gained breeding positions until the death of a breeding adult of the same sex (Savage et al., 1996a; Lazaro-Perea et al., 2000). If formation of new breeding groups is limited by habitat availability and if breeding vacancies within groups occur infrequently, then unrelated helpers can gain the benefits of living in a social group (communal foraging or protection against predators) by assisting in the care of infants and constantly monitoring neighboring groups until a vacancy occurs. In common marmosets we have found that what initially appeared to be daily territorial encounters with adjacent groups could also be interpreted as assessing the status of neighboring animals (Lazaro-Perea, 2001). In the real world opportunities for breeding are rare in Callitrichids and therefore they may be benefiting by making the best of a current situation.

A third potential benefit for unrelated helpers was proposed by Smuts and Gubernick (1992) for male interest in infants in all mammals, not just cooperative breeders. They argued that care of infants should be seen as mating effort. Males are not necessarily involved in the care of their own genetic offspring, but males that display involvement with infants are more likely to obtain subsequent mating with the female they assist. An expansion of this idea can apply to both male and female unrelated helpers. Infant care can be seen as a mating strategy for both sexes that may increase the probability of becoming a parent within that group.

There are several by-product effects by which helpers may benefit directly. Protection against predators has already been mentioned. Specific food related vocalizations attract other group members to sources of food (Elowson et al., 1991). Marmosets have specialized dentition and gouge holes in trees to collect exudate on which they feed. Communal effort to gouge and extract exudates may benefit all group members. We have also seen trade-offs between infant carrying and vigilance in wild tamarins (Savage et al., 1996b) with larger groups allowing some individuals to rest or forage while one individual carries an infant and another maintains vigilance. All group members nest together at night and data from captive groups indicate that basal metabolic rate is lowered at night as a likely energy conservation measure for these small-bodied animals that are inactive 13 h a day. Larger sleeping groups can provide thermal benefits to minimize individual metabolism and conserve energy for all group members.

Finally, it is likely that proximate mechanisms selected to increase the inclusive fitness of helpers in their natal groups will be brought with them as the join a group of unrelated animals. Thus, infant care by unrelated helpers may be a result of mechanisms selected to assist with related infants.

2. Social mechanisms maintaining helpers

Bergmüller et al. (2007) stress punishment as an enforcement of helper's participation in infant care. From our experience observing marmosets and tamarins, we see social reward as much more important than punishment in maintaining helpers. Direct conflict is generally rare in these species especially between parents and helpers (Ginther et al., 2001; Ginther and Snowdon, in preparation). However, there are some important exceptions. As noted above field studies of common marmosets have reported female infanticide when more than one female gives birth in close temporal proximity, but this infanticide appears to be a conflict between mothers over access to caretakers. Also as noted above there is conflict within a group over obtaining access to infants. There is also occasional severe aggression within group that leads to expulsion of group members, but this aggression is typically between brothers as a result of conflict over access to infants, or between mothers and daughters when daughters begin to escape reproductive suppression (Snowdon and Pickhard, 1999). We have never observed punishment (i.e. group expulsion) over not caring for infants.

Instead affiliative behavior serves to reward helpers. In a field study Lazaro-Perea et al. (2004) reported that common marmosets groom down the hierarchy with breeding adults grooming helpers significantly more than the reverse. Since grooming behavior releases beta-endorphins (Keverne et al., 1989) and oxytocin (Carter, 1998), both of which provide reinforcing effects, high levels of grooming of helpers by breeding adults can be seen as providing direct physiological reinforcement to helpers.

We have also observed high levels of tolerance of breeders for helpers. For example, adult male helpers in captive family groups engage in as much mounting behavior as they do when they become breeders (Ginther et al., 2001). Although much of this behavior is directed toward other group members, we also observe mounting attempts to the dam at times when she is not fertile. We have observed no aggressive behavior between helpers and breeding males during or following mounting attempts. In some case sires show affiliative behavior with helpers immediately after the helper has mounted the dam (Ginther and Snowdon, in preparation). We hypothesize that affiliative behavior and even tolerance of mounts may serve to reward helpers and may be a mechanism maintaining the presence of helpers and that social rewards by breeders may be much more common than punishments (Ginther and Snowdon in preparation).

3. Cooperative behavior and reciprocity

We have previously argued that species with social systems characterized by a high degree of within group cooperation, such as cooperative breeders, should be skilled at cooperating in other domains as well. Specifically, cooperative breeders should demonstrate behavioral coordination and attentiveness to social cues in novel contexts, as these skills have been selected to coordinate infant care among multiple group members. Results from cooperative problem solving experiments with captive cotton-top tamarins support this hypothesis.

We presented unrelated, pair-bonded cotton-top tamarins with a cooperative task that required simultaneous extension of two handles located too far apart from one another for a single tamarin to access both, and found that tamarins demonstrated extremely high success on this task, solving an average of 97% of trials (Cronin et al., 2005). The tamarins also demonstrated an understanding of the role of the partner in the cooperative task, as evidenced by their reduced rate of pulling when their partner was removed. This effect was observed without an accompanying decrease in time spent in contact with the apparatus. Skills from the cooperative breeding context, such as coordination of actions with conspecifics and concentrated attention to social cues, were necessary to succeed at the cooperative problem-solving task. The percent success demonstrated by tamarins on this task met or exceeded that of all cooperative problem solving studies with non-cooperatively breeding primate species (Chimpanzees: Brosnan et al., 2006; Chalmeau, 1994; Melis et al., 2006; Orangutans: Chalmeau et al., 1997; Capuchins: de Waal and Berger, 2000; de Waal and Davis, 2003; Hattori et al., 2005; Mendres and de Waal, 2000). However, we note that different apparatuses and reward schemes have been used in nearly every species examined.

In our first study both individuals obtained immediate rewards from the cooperative act. Recently, we presented the same tamarins with a scenario in which only one tamarin obtained the majority of benefits upon completion of the cooperative act across all trials in a session. In the following session the other tamarin obtained the majority of the rewards. Although their performance decreased slightly over the 10 sessions, the tamarins continued to demonstrate high success in this reciprocal reward payoff condition. The unrewarded animal exhibited no signs of aggression toward its mate (Cronin and Snowdon, in press). As noted by Bergmüller et al. (2007), asymmetries between individuals have not been fully addressed in cooperation theory. Pair-bonded cotton-top tamarins lack the dominance asymmetries that occur in most dyads of unrelated primates. The symmetrical nature of their relationships may have contributed to their cooperative success and lack of observable aggravation in response to temporary inequity.

The tamarins in this study had been paired with their partners for at least 5 years at the time of this reciprocal reward experiment. Their tolerance of the temporarily inequitable reward distribution may be due not only to the cooperative skills of Callitrichids generally, but also specifically to the quality of the relationship between partners. Bergmüller et al. (2007) remark that partner choice is a key component of cooperative interactions, and that an individual's choices in a cooperative encounter may be influenced by their social relationships. Specifically, if the dyad were in a lasting relationship we would expect that the costs and benefits of interactions would be evaluated over a longer period of time rather than a brief interaction. Others have demonstrated the effects of varying relationships on cooperative success and inequity tolerance within a species (Beck, 1973; Brosnan et al., 2005; Werdenich and Huber, 2002; Melis et al., 2006). The effects of various relationships among individuals on their cooperative performance is a intriguing topic worthy of future research.

4. Conclusion

We have shown that helpers are essential for infant survival in tamarins and that helpers incur considerable costs. Compensating for these costs are the important benefits of learning parental care skills, using infant care as a passport to be part of a groups and having a greater probability of becoming the breeder upon the death of the same sex parent. Helpers also gain the benefits of group living. Proximate mechanisms selected by inclusive fitness benefits in one's natal group may simply be carried over to care for unrelated infants. We have argued that parents provide social rewards for helpers through grooming and toleration of mounting and that aggression rates by parents toward helpers are lower than between any other animals in the group. Finally, we have concrete evidence that cooperative problem solving occurs readily with high success even when only one animal is rewarded at a time. These cooperative problem-solving skills may also be due to the same proximate mechanisms initially selected for infant care through inclusive fitness. Bergmüller et al.'s (2007) theoretical point is supported by empirical results. Cooperative breeders do cooperate.

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