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Understanding Cooperative Breeding and Infant Care Behavior in Callitrichine Species

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Abstract

Since Darwin (1859), scientists have been puzzled by how behaviors that incur fitness costs to helpers while benefiting their competitors could evolve through natural selection. Hamilton's (1964) theory of inclusive fitness provided an explanation by showing how cooperative behaviors could be adaptive if directed at closely related kin. Recent studies, however, have begun to question whether kin selection is sufficient to explain cooperative behavior in a number of species (Bergmüller, Johnstone, Russell, & Bshary, 2007). Many researchers have instead emphasized the importance of direct fitness benefits for helpers in the evolution of cooperative breeding systems. Furthermore, individuals can vary in who, when, and how much they help, and the factors that affect this variation are poorly understood (Cockburn, 1998, Heinsohn, 2004). Cooperative breeders thus provide excellent models for the study of evolutionary theories of cooperation and conflict (Cant, 2012).

Keywords: Allocare, Alloparental Care, Cooperative Breeding, Group Augmentation, Helping, Kin Selection, Marmosets, Parenting Experience, Pay to Stay, Provisioning, Social Prestige, Tamarins

Cooperative behaviors are widespread throughout the animal kingdom, and are perhaps most conspicuous among cooperative breeders. Cooperative breeding (*sensu strictu:* Lukas & Clutton-Brock, 2012) is a reproductive system in which one or several nonbreeding adult "helpers" (or alloparents, see glossary) assist in the care of the young of the breeding pair(s), and in doing so often delay their own breeding efforts. While alloparents can increase the survival and reproduction of breeders and their offspring, they may also suffer costs, such as lost mating opportunities, energy expenditure, and risk of injury (Le Vin, Mable, Taborsky, Heg, & Arnold, 2011).

Among mammals, cooperative breeding has evolved independently in several lineages, including primates, rodents, mongoose and canids (Lukas & Clutton-Brock, 2012). For one group of mammals, the callitrichines, cooperative breeding appears to be related to a suite of unusual reproductive biological traits. **Marmosets and tamarins always produce twins, which typically share a common placenta, through which one twin may pass stem cells into the blood, hematopoietic tissues, and possibly even the gametes of the other (Ross, French, & Ortí, 2007). Chimerism thus potentially increases relatedness among twins and may increase the inclusive fitness benefits in this system (Haig, 1999).** Furthermore, tamarins (*Leontocebus* and *Saguinus*) are particularly interesting, as social groups are typically polyandrous, representing an exceptionally rare system in which the benefits to cooperating males are largely unknown (Huck, Löttker, Böhle, & Heymann, 2005).

In all callitrichine species studied to date, all group members, including unrelated individuals, participate in a number of cooperative behaviors including infant carrying and provisioning, shared vigilance, and communal group defense (Garber, 1998). In fact, together with humans, callitrichines exhibit the strongest reliance on allocare among primates (Hrdy, 2009, Díaz-Muñoz, 2011). Recently, there has been increasing interest in the high levels of allomaternal care exhibited by humans, and the evolutionary causes and consequences of this behavior. The cooperative breeding hypothesis in particular posits that the unique cognitive abilities shared by humans and callitrichines are a result of psychological adaptations to this rare primate breeding system (see Box 1).

In most non-human primates, immature individuals receive few direct food offers from adults. This type of nutritional supplementation, called provisioning, is very rare and only routinely observed among callitrichines, owl monkeys, and humans (Rapaport & Brown, 2008, Hrdy, 2016). In callitrichines, transfers of fruit and prey items are generally initiated by immatures begging for food from adults (Rapaport & Brown, 2008). Provisioning peaks when offspring are 3-5 months old, but may continue until they are over a year in age (Rapaport & Brown, 2008). Adults may encourage provisioning by producing special food-offering vocalizations, which direct infants' attention to items in their hand (Ruiz-Miranda, Kleiman, Dietz, Moraes, Grativol, et al., 1999) or older juveniles to sites which contained hidden prey, thereby facilitating development of the juvenile prey capture techniques (Rapaport, 2011). Thus, in callitrichines provisioning provides offspring with important nutrients as well as information about food choices and foraging techniques (Rapaport & Brown, 2008).

In many callitrichine taxa, mothers allow other group members to carry their infants within a few days postpartum, whereas *Leontopithecus* and *Callimico* mothers delay allomaternal transport until 2-3 weeks postpartum (Ross, Porter, Power, & Sodaro, 2010, Tardif, Santos, Baker, Van Elsacker, Feistner, et al., 2002). Infants are usually transported all the time in the first couple of weeks postpartum, but carrying declines thereafter: by 5-10 weeks, infants are transported only 50% of the time, and carrying ceases altogether as early as 11 weeks postpartum (Snowdon, 1996). Although all callitrichine group members may help with infant transport including mothers, non-breeding adult females, and juveniles (Snowdon, 1996), several studies have shown that adult males typically provide the most infant care (Garber, 1998, Yamamoto & Box, 1997, Zahed, Kurian, & Snowdon, 2010). Many factors may contribute to variation in maternal infant transport rates, including maternal condition (Bales, French, & Dietz, 2002), maternal experience (Snowdon, 1996), litter size (Tardif et al., 2002), and the contributions of other group members (Bales et al., 2002).

It is expected that the benefits gained from transporting and provisioning infants must offset the costs. Infant carrying, for example, incurs especially heavy costs to helpers including lost feeding time (Price, 1992), weight loss (Achenbach & Snowdon, 2002), and possibly increased predation risk (Tardif, 1997). Food provisioning may also result in lost time and energy spent acquiring foods, which are shared with infants and juveniles (de A. Moura, Nunes, & Langguth, 2010). In fact, it is hypothesized that infant care costs alone can explain much of the variation in callitrichine social and reproductive behavior among genera (Díaz-Muñoz, 2015). **Yet, despite the importance of cooperative infant care among callitrichine species, we still have very limited understanding about how this specialized breeding system evolved and the distribution of costs and benefits maintaining it across taxa.** Further, individual contributions vary greatly, suggesting that a number of factors likely affect the participation of any given alloparent (Bales, Dietz, Baker, Miller, & Tardif, 2000). In the following review, we identify the major hypotheses concerning the evolution of cooperative breeding systems as well as the proximate factors likely affecting individuals’ decisions to help. We review the evidence for each hypothesis first in vertebrates and then more specifically in callitrichines. Our goal is to clarify the current state of understanding of callitrichine cooperative breeding systems, identify the knowledge gaps that limit our interpretations, and suggest potential areas for future fruitful investigation.

Ultimate Explanations for Cooperative Infant Care

A number of hypotheses have been proposed as to the benefits that helpers receive to offset these costly investments in cooperatively breeding species (Table I). These benefits can be indirect, accrued by the actors' relatives (i.e., kin selection), or direct, accrued by the actors themselves (i.e., parenting experience, social prestige, increased survival, future reproductive opportunities).

Kin selection

The kin selection hypothesis proposes that the costs of helping are offset by the indirect benefits accrued when helpers are related to recipients (Hamilton, 1964). For kin selection to be effective, there should be a high probability of relatedness between helpers and breeders and help should provide fitness benefits to breeders or their offspring. In long-tailed tits, for instance, although helpers incur survival costs by participating in alloparental care, they also accrue significant benefits through increased survival of related breeders and offspring (Hatchwell, Gullett, & Adams, 2014). A meta-analysis of cooperatively breeding vertebrates demonstrated a positive relationship between the amount of help given and average relatedness within a species (Griffin & West, 2003). Although a number of studies have shown that helpers tend to care for relatives, few have shown that helpers preferentially care for closer kin. A notable exception is a recent study of a bird, the bell miner (*Manorina melanophrys*), which found that helpers facultatively adjusted their provisioning rates depending on their relatedness to the brood (Wright, McDonald, te Marvelde, Kazem, & Bishop, 2010). In addition to enhanced survival, fitness gains for offspring from helpers include, for example, an earlier age at first reproduction or increased chance of attaining alpha rank (e.g., meerkats, *Suricata suricatta*, Russell, Young, Spong, Jordan, & Clutton-Brock, 2007).

Only a handful of studies have used microsatellite markers and mitochondrial haplotypes to explore patterns of relatedness within wild callitrichine groups (Nievergelt, Digby, Ramakrishnan, & Woodruff, 2000, Faulkes, Arruda, & Monteiro da Cruz, 2003, Huck et al., 2005, Díaz-Muñoz, 2011). Given that groups are polyandrous, two males may sire infants in the same litter, and twins may be chimers, kin relationships in callitrichines are genetically more complex than in most other vertebrates (Ross, 2005). In common marmosets (*Callithrix jacchus*), moustached tamarins (*Saguinus mystax*), and saddleback tamarins (*Leontocebus weddelli*) within-group relatedness was generally high, but unrelated individuals were also found in many groups (Nievergelt et al., 2000, Faulkes et al., 2003, Huck et al., 2005). Two studies have investigated the relationship between estimates of relatedness and contributions to infant carrying in wild callitrichine groups. In cottontop tamarins (*Saguinus oedipus*), there was no difference in the amount of time that related and unrelated juveniles (assessed using allozyme markers) carried infants (Savage, 1990). Because juveniles carry significantly less than subadults and adults, however, it is unclear whether a difference would be expected. Among golden lion tamarins (*Leontopithecus rosalia*), males carried siblings more than unrelated infants, but there were insufficient data to evaluate female contributions, and relatedness among males was inferred based on group composition and was not corroborated with molecular data (Baker, 1991). Furthermore, relatedness estimates among helpers and breeders were high, data involved polygynous groups only, and the presence of multiple breeders may have influenced results since subordinate breeders may be less likely to relinquish their infants (Tardif, 1997). **To date no published studies have directly examined individual relatedness estimates based on molecular data (e.g., microsatellite genotypes) combined with observations of helping in wild callitrichines**. Thus, a critical evaluation of this hypothesis for helping is still lacking (see Table I).

Parenting experience

In species where parenting experience is crucial to future reproductive success, helpers may gain skills that directly increase their own fitness (Lancaster, 1971). For the parenting experience hypothesis, breeders with prior experience should have greater reproductive success than inexperienced breeders and helpers that have already acquired the necessary parenting skills should decrease helping efforts. In experimental studies with cooperatively breeding rodents, individuals who remained with their families through the rearing of siblings reproduced earlier and had better quality and more surviving infants than those who were removed from natal groups (Margulis, Nabong, Alaks, Walsh, & Lacy, 2005). A recent study of prairie voles (*Microtus ochrogaster*) further demonstrated that individuals who spent more time helping as juveniles had larger surviving litters later in life (Stone, Mathieu, Griffin, & Bales, 2010), suggesting that allocare experience, and not simply exposure to younger siblings, has direct fitness benefits for helpers.

Numerous studies of captive callitrichines have shown that adults do not care for their young properly if they did not have previous experience with infant siblings (Tardif, 1997, but see Baker & Woods, 1992). However, in most studies, age was not controlled for and participation in allocare was not quantified, so benefits might have been gained simply through infant exposure rather than direct allocare. While a study of captive cottontop tamarins found no relationship between the amount of time that inexperienced and experienced subadult helpers spent carrying infants (Tardif, Carson, & Gangaware, 1992), wild naïve golden lion tamarin females (but not males) carried more than same-age females with carrying experience (Baker, 1991). Overall, tests of this hypothesis are largely restricted to captive settings, and show inconsistent and conflicting results (Table I).

Social prestige

If helping is a signal of individual quality (a handicap), helpers may gain social prestige that may increase their likelihood of future mating success (i.e., courtship strategy, cf. Tardif & Bales, 1997). In this scenario, individuals are expected to compete for helping opportunities in order to signal to potential mates, and those who signal the highest quality should enjoy greater mating success. The behavior of one bird, the Arabian babbler (*Turdoides squamiceps*), is often cited as an example that supports this hypothesis. In this species, individuals do indeed compete and interfere with each other over cooperative behaviors, such as feeding nestlings (Carlisle & Zahavi, 1986), but in actuality there is no evidence that these behaviors lead to increased mating success. In the tessellated darter fish (*Etheostoma olmstedi*), though, males who engaged in allocare did experience increased mating success, as females were more likely to deposit new eggs at nests where males were guarding young eggs (Stiver & Alonzo, 2011).

To date, support for this hypothesis in callitrichines is limited (Digby, Ferrari, & Saltzman, 2011). In an early study of captive cottontop tamarins, males were more likely to engage in sexual behavior when they were carrying infants, although the study did not differentiate between copulations during fertile and non-fertile periods (Price, 1990). In a follow-up study of captive common marmosets and cottontop tamarins, researchers found no relationship between the amount of time males carried infants and the frequency of copulations during fertile periods, and males did not attempt to retrieve infants from breeding females more than from other group members (Tardif & Bales, 1997). The only wild study to test this hypothesis found that, although dominant golden lion tamarin males appeared to sexually monopolize females during fertile periods, there was no difference in the amount of infant care they provided when compared to subordinate males (Baker, Dietz, & Kleiman, 1993). Thus far, observations are largely limited to captive studies, which have found little support for this hypothesis (Table I). A thorough test of these predictions in a wild population is thus needed to evaluate this hypothesis.

Group augmentation

If individuals survive or reproduce better in larger groups, they may benefit directly from raising new group members, even if unrelated (Kokko, Johnstone, & Clutton-Brock, 2001). Helpers benefit, for example, from decreased predation risk in larger groups or by gaining new helpers for future reproductive efforts. Group members are expected to attempt to maintain and recruit new helpers (to some upper limit), and participation in these activities is expected to vary according to individual fitness benefits. For example, members of the philopatric sex should invest more in helping, since they accrue more direct benefits. This is known as the “group augmentation” hypothesis. Among cooperative breeders, the presence of helpers (i.e., larger groups) is positively correlated with increased breeding success and survival

(Clutton-Brock, 2002). Group augmentation is thought to be operating in meerkat societies, as helpers gain direct fitness benefits from increasing group size (Clutton-Brock, Gaynor, McIlrath, MacColl, Kansky, et al., 1999).

Among callitrichines, infant survival is correlated with group size, with particular importance attributed to the number of adult males (Koenig, 1995, Garber, 1998, Bales et al., 2000, but see Savage, Soto, Medina, Emeris, & Soltis, 2009), suggesting that there are fitness benefits associated with larger groups in this taxon. Although there has been no explicit test, there is some anecdotal support for this hypothesis in callitrichines. In saddleback tamarins, for example, females may inherit the breeding position in their natal group and therefore remain in the same social group as the younger sibling helpers they had helped rear (Goldizen, 1990). Furthermore, in Wied’s black tufted-ear marmosets (*Callithrix kuhli*), females in small groups showed reduced levels of aggression during simulated intrusions, suggesting that they may have been attempting to augment group size when more helpers were needed (Schaffner & French, 1997). Although wild studies have found support for some of the predictions of this hypothesis (Table I), additional studies are needed to simultaneously test multiple predictions while considering other influencing factors, such as sex-biased dispersal.

Pay-to-stay

Under the pay-to-stay hypothesis, cooperative behaviors are viewed as a form of payment to dominant breeders for the right to remain in the group while waiting for future breeding opportunities (Gaston, 1978). This hypothesis assumes that the presence of helpers comes at some cost to breeders, such as increased feeding or reproductive competition (Emlen, 1982), and that subordinates offset these costs by participating in cooperative behaviors. By helping, they experience increased tolerance from breeders and increase their chance of inheriting the territory and breeding position. Experimental studies with superb fairy wrens (*Malurus cyaneus*) revealed that dominant males aggressively harassed helpers that defected from their duties (Mulder & Langmore, 1993). Acorn woodpecker (*Melanerpes formicivorus*) males who provisioned chicks more often remained as helpers longer and were more likely to inherit their natal territory and become breeders, but these differences were likely due to differences in dispersal behavior and not a consequence of helping per se (Koenig & Walters, 2011).

Few studies have explicitly tested the pay-to-stay hypothesis for callitrichines, and thus far evidence is mixed (Digby et al., 2011). Evictions of both male and female helpers have been observed in the wild (Savage, Giraldo, Soto, & Snowdon, 1996, Snowdon & Pickhard, 1999), suggesting that animals are competing for group membership. In golden lion tamarins, helpers retrieved infants from the breeding female (compared to other group members) more often than expected (Baker, 1991) and buffy-headed marmoset helpers (*Callithrix flaviceps*) provisioned infants more often when the breeding female was present (Ferrari, 1992). In both cases, subordinates may have used helping in order to avoid aggression or eviction from the dominant female. Anecdotal evidence from wild moustached tamarins suggests that helpers that carry and provision the least are more likely to be evicted than those who helped less (Huck, Löttker, & Heymann, 2004). But studies of captive cottontop tamarins found that the helpers who spent more time carrying received more aggression from the breeding female or were evicted (Tardif, 1997, Sánchez, Peláez, & Gil-Bürmann, 2002). Thus, infant carrying does not appear to be a form of payment in this species, but may instead be a way of decreasing aggression in the short term, since helpers were less likely to receive aggression while carrying infants than when alone (Sánchez et al., 2002). While several studies have documented the inheritance of the breeding position upon the death or disappearance of the breeder (Goldizen & Terborgh, 1989, Baker et al., 1993), none have demonstrated that participation in infant care influences an individual’s chance of remaining in the natal territory or inheriting the breeding position. Overall, few of the predictions for this hypothesis have been tested, and results are mixed (Table I).

Table I summarizes the results from callitrichine studies that have tested the predictions for the hypotheses outlined above. **While infant care has been examined in numerous studies, several of the key predictions about helping have never been tested. For those that have, much of the evidence is restricted to captive studies,**

which generally eliminate variation in ecology and physical condition, and manipulate demographic composition of groups, thereby strongly limiting interpretations about the adaptive value of variation in behavior in natural settings. While some species are well represented, there is no single species for which all hypotheses have been examined. Finally, for most hypotheses, the evidence is mixed. Thus, as the results are combined across species in both wild and captive groups, it is impossible to draw any conclusions about the overall support for any of the ultimate explanations for helping in callitrichines.

Proximate Factors Influencing Cooperative Infant Care

In species or systems where cooperative behavior is adaptive, there may still be differences among group members in their degree of infant care, as individuals are expected to maximize their own fitness by adjusting their contributions according to the varying costs and benefits of cooperative behavior (Komdeur, 2006). **Callitrichines have been described as exhibiting idiosyncratic patterns of helping, in that some helpers are extensively involved in infant care, while others contribute little (Tardif et al., 1992, Bales et al., 2000, Zahed et al., 2010). Understanding the causes and consequences of these differences is important to fully understanding the adaptive significance of cooperative behavior.** Furthermore, the existence of individual differences means that averaging behavior across all helpers may obscure larger patterns and limit our understanding of the significance of other factors influencing helping (Wong & Balshine, 2011). A number of factors have been identified that influence participation both within and between individuals. Once again, we review evidence for each factor in vertebrates generally as well as callitrichines specifically.

Sex

Numerous studies have reported sex differences in cooperative behaviors. Whereas among birds, males often engage more often in infant care than females (e.g., apostlebird, *Stuthidea cinerea* Woxvold, Mulder, & Magrath, 2006, laughing kookaburra, *Dacelo novaeguineae* Legge, 2000), among mammals, it is often the opposite (e.g., meerkats Clutton-Brock, Russell, Sharpe, Young, Balmforth, et al., 2002, brown hyenas, *Hyaena brunnea Owens & Owens, 1984*). These patterns are thought to arise because of differences in the benefits accrued by each sex through their investment (Cockburn, 1998). For example, in many species, the more philopatric sex participates more in infant care, presumably because they benefit more from rearing additional group members. Furthermore, males and females are likely to differ in the benefits they derive from caring for male *versus* female infants. In meerkats, for example, females (but not males) preferred to feed female pups and participated more in the care of female-biased litters, a result explained by female philopatry in this species (Clutton-Brock et al., 2002).

Callitrichine research to date has identified no clear pattern for sex-biased infant care. Some studies have reported that non-reproductive male helpers carry more than female helpers (e.g., common marmosets Yamamoto & Box, 1997, cottontop tamarins Zahed et al., 2010), while others have found the reverse (e.g., common marmosets Ingram, 1977, golden lion tamarins Baker, 1991). These results may be related to differential reproductive strategies in species where males and females inherit breeding positions using different tactics. For instance, in wild common marmosets, males most commonly inherit breeding positions from their fathers, whereas females uniformly immigrate into groups with breeding vacancies (Yamamoto, Araujo, Arruda, Lima, Siqueira, et al., 2014). Infant sex was found to influence helping behavior in golden lion tamarins, where young males carried litters with at least one male infant more than all-female litters (Baker, 1991). Sex differences in other cooperative behaviors also exist. In golden headed lion tamarins (*Leontopithecus chrysomelas*), for example, female helpers transferred more food to offspring than male helpers (de A. Moura et al., 2010). And adult male common marmosets had higher rates of anti-predator vigilance than females (Koenig, 1998). Although sex differences are well established, they are rarely included in studies testing ultimate hypotheses.

Age

Cooperative behaviors are likely to change with age and weight because the energetic costs of helping constitute larger fitness costs for smaller and growing individuals (Clutton-Brock, Russell, & Sharpe, 2003). Accordingly, numerous studies have found behavioral differences between younger and older individuals in cooperatively breeding species. In naked-mole-rats (*Heterocephalus glaber*), for example, larger helpers contributed more to territory defense, whereas smaller helpers contributed more to infant care and burrow maintenance (Lacey & Sherman, 1997). In apostlebirds, yearlings spent less time incubating and provisioning nestlings than older birds (Woxvold et al., 2006). In addition, younger meerkats helpers provisioned young and dug more, whereas older helpers babysat and nest guarded more (Clutton-Brock et al., 2003). Although relatively heavy subadults and juveniles helped more than lighter ones, weight-related differences had little effect on adult care, suggesting that size-related energetic costs translate into larger fitness costs for younger individuals.

Among callitrichines, a number of studies have found age-related effects in cooperative behaviors in both captive and wild settings. In particular, adult helpers engage more in infant carrying than juvenile and sometimes subadult helpers (e.g., common marmosets Yamamoto, Box, Albuquerque, & Arruda, 1996, *Leontopithecus* and *Callithrix* spp. Santos, French, & Otta, 1997, cottontop tamarins Tardif et al., 1992). In addition, studies of food transfers have found that adults provisioned infants more than subadults and juveniles did (golden lion tamarins Ruiz-Miranda et al., 1999, cottontop tamarins Feistner & Price, 1990). Recent research on captive marmosets found that whereas prosociality increased with age and experience in males, it decreased in females, highlighting the important of considering the interaction of proximate factors as well (Burkart, 2015). Helper age is clearly a potentially confounding factor for cooperative behavior, and the failure to control for it may be responsible for some of the conflicting results in previous studies.

Physical condition

If helping is costly, individuals are expected to modify their participation in cooperative behaviors relative to their own physical condition. Numerous studies have demonstrated increased participation in cooperative behaviors for individuals in better physical condition. In meerkats, for example, heavier helpers invested more in babysitting and pup feeding than lighter ones (Clutton-Brock et al., 2002). Furthermore, experimentally fed helpers fed pups more than unfed controls (Clutton-Brock, Brotherton, O'riain, Griffin, Gaynor, et al., 2001). Similarly, in white-winged choughs (*Corcorax melanorhamphos*), experimentally fed groups delivered more food to nestlings (Boland, Heinsohn, & Cockburn, 1997). To our knowledge, there has been no study of the effects of physical condition on helping behavior in callitrichines.

Group size

Besides increased survival and reproduction in larger groups (see group augmentation hypothesis), variation in group size is expected to produce differences in the amount of time animals contribute to cooperative behaviors. As the number of helpers in a group increases, the per capita costs of helping should decrease (Clutton-Brock, Gaynor, Kansky, MacColl, McIlrath, et al., 1998). Such an effect has been reported in a number of species. In meerkats, for example, members of large groups gave away a smaller proportion of food (Clutton-Brock et al., 2001). In larger groups of laughing kookaburras, breeders and helpers reduced the size of prey delivered, and helpers also reduced the number of feeding visits (Legge, 2000). Individual provisioning rates were lower in larger groups of apostlebirds, although feeding rates per nestling increased, indicating an adjustment to the increase in available help (Woxvold et al., 2006).

Studies of captive and wild callitrichines have yielded similar results. In most studies of infant carrying behavior, increasing group size has resulted in a reduction of per capita carrying by adult males (e.g., *Callithrix* and *Leontopithecus* spp. Santos et al., 1997, common marmosets Zahed et al., 2010, reviewed in Pryce, 1993). In some studies, infants were carried more in larger groups (e.g., cottontop tamarins Price, 1992, *Callithrix* spp. Santos et al., 1997), while in others, overall carrying rates were unaffected by group size (e.g., *Leontopithecus* spp. Santos et al., 1997) Individual feeding rates were lower in larger groups of cottontop tamarins and infants received more food (Feistner & Price, 1990). It is thus critical to consider the variation in helping due to group size when testing ultimate hypotheses for helping in primates.

Consistent individual differences

There is increasing awareness of the importance of consistent individual differences in behavioral variation (Dingemanse, Kazem, Réale, & Wright, 2010). Such differences have been found in a range of animal taxa, and a recent meta-analysis revealed that overall they explain approximately 35% of the behavioral variation among individuals within populations (Bell, Hankison, & Laskowski, 2009). Individuals often show consistent differences in the amount and type of help they are willing to provide, which may indicate the existence of different personality types (Sih, Bell, & Johnson, 2004). Female lions (*Panthera leo*), for example, showed consistent individual differences in cooperation during inter-group encounters (Heinsohn & Packer, 1995). In meerkats, contributions to babysitting and provisioning were significantly consistent within individuals despite the various short-term compensations shown in previous studies (English, Nakagawa, & Clutton-Brock, 2010). In another study, babysitting and provisioning were positively correlated within females, suggesting a helping personality may exist in meerkats (Clutton-Brock et al., 2003).

Studies of callitrichines have often reported large inter-individual differences in helping behavior (e.g., cottontop tamarins Ginther & Snowdon, 2009). At least two studies have reported that these individual differences may be consistent over time. In Goeldi's monkeys (*Callimico goeldii*) there was a strong correlation within individuals in infant carrying across two consecutive births (Schradin & Anzenberger, 2001). Cottontop tamarin males with high carrying rates in natal groups also exhibited high carrying rates when they became fathers (Zahed et al., 2010). **Although individual differences in cooperative behavior can be pronounced, no primate studies have considered this factor in tests of the ultimate hypotheses for helping.**

Conclusion and Direction for Future Research

The evolution of alloparental care within cooperatively breeding species has long posed a puzzle to evolutionary biologists. The cooperative breeding system of callitrichines represents a fascinating model for the study of the evolution and maintenance of cooperative behavior, as, together with humans, they exhibit the strongest reliance on allocare among primates (Hrdy, 2009). An evaluation of the myriad ultimate and proximate explanations for cooperative infant care have only been thoroughly evaluated in a few species of cooperatively breeding mammals, and thus our understanding is limited about the generality of those studies as well as the larger evolutionary patterns of this unique system.

Our lack of progress in thoroughly evaluating these hypotheses has been hindered by a number of factors, including the difficulty of reliably identifying, recording detailed behavioral data, and collecting genetic samples from small-bodied arboreal animals; habituating and observing dozens of individuals in several groups across multiple years; as well as conducting paternity analyses of potential genetic chimers. While captive research largely reduces these issues, it also has a number of drawbacks, in particular that it severely constrains ecological, nutritional, and demographic variation, and restricts natural migration among groups. Captive studies thus limit our understanding of costs and benefits and therefore interpretations about the adaptive value of behavior in natural settings.

We see a great need for a comprehensive evaluation of current ultimate hypotheses in primate species, in particular studies that combine individual relatedness estimates based on molecular data with behavioral observations in wild callitrichines. Multi-year studies of several groups are needed to attain the sample sizes and statistical power needed to incorporate the confounding effects of age, sex, and other proximate factors, without which, interpretations about the adaptive function of cooperative breeding systems are severely limited. Such research would significantly increase our understanding of the evolution and maintenance of cooperative breeding, relevant not only to primatologists, but to behavioral ecologists studying a wide range of taxa.

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Glossary

Alloparent / Allomother: individuals other than the genetic parents (alloparent) / mother (allomother) who assist in the care of offspring (Hrdy, 2005a)

Altruistic behavior: an act performed by an individual that benefits another individual while apparently incurring a cost to the actor (Trivers, 1971)

Cooperative behavior: acts "performed by one individual that increase the fitness of another" (Bergmüller et al., 2007: 63-64)

Cooperative breeding (sensu lato): a breeding system in which *alloparents* help rear offspring. In most studies, genetic fathers have not been identified – particularly in polyandrous groups – and so we use *allomothers* to refer to individuals of either sex who are participating in infant care (Hrdy, 2005a)

Cooperative breeding (sensu stricto): a breeding system in which a proportion of females do not breed regularly and help rear the offspring of breeding females (Lukas & Clutton-Brock, 2012)

Helper: synonym for allomother

Proactive prosociality: “spontaneous motivation that “reflects a genuine concern for the welfare of others” (Burkart & van Schaik, 2013: 212)

Prosocial behavior: acts “performed by one individual to alleviate another’s need or improve their welfare” (Cronin, 2012: 1085)

Box 1: The cooperative breeding hypothesis

The Cooperative Breeding Hypothesis (CBH) proposes that alloparents 1) provide mothers with additional energy to expend on their offspring and 2) exhibit socio-cognitive adaptations that promote helping behavior. Hrdy (1999) first introduced the CBH to explain an unusual suite of human characteristics. In 2005, she wrote, “*The cooperative breeding hypothesis presumes that mothers evolved in groups where a broader range of individuals – not just the genetic father – assisted the genetic mother in protecting, carrying, or provisioning offspring, thereby permitting her to produce and rear costlier, slower-maturing offspring than otherwise would survive*” (Hrdy, 2005b: 69). Hrdy suggested that in cooperatively breeding primates, infants who solicited attention from adults (e.g., through babbling) received more care, selecting for hyper-social behavior (Hrdy, 2005a). Since its development, several researchers have attempted to test predictions of the CBH concerning cognition and brain size in primates and other mammals.

Burkart and colleagues expanded on the CBH through a series of experiments which examined proactive prosociality (Burkart, Fehr, Efferson, & van Schaik, 2007, Burkart, Allon, Amici, Fichtel, Finkenwirth, et al., 2014). They provided study subjects (potential donors) with opportunities to move a food board to within reach of genetically unrelated group mates. A donor who pulled the food board provisioned its group mates with food rewards, but received no reward itself. On the basis of tests of 15 different primate species, they concluded that, "proactive prosocial motivations … systematically arise whenever selection favours the evolution of cooperative breeding" (Burkart et al., 2014: 1).

Isler and van Schaik (2012) further explored the effects of cooperative breeding on brain size evolution. They compared helping behavior and brain size among 445 eutherian mammals, concluding that helping by allomothers was positively correlated with brain size across mammals, with the exception of primates. They proposed that primate mothers instead have allocated the energy saved from allomaternal care to increased fertility and the production of more altricial infants. Humans are exceptional in that they have increased both brain size and fertility.

These studies prompted Thornton and colleagues to re-evaluate the hypothesis that cooperative breeders show enhanced socio-cognitive abilities compared to other animals (Thornton & McAuliffe, 2015, Thornton, McAuliffe, Dall, Fernandez-Duque, Garber, et al., 2016). They critiqued the CBH on several points, including insufficient evidence of prosocial behavior across cooperative breeders and lack of an explanation for why cooperative breeders should invest "extra" energy conserved by allocare into brain tissue rather than other traits. They conclude that, "Ultimately, the absence of any compelling evidence that cooperative breeding is associated with elevated cognitive ability or large brains (indeed the opposite is true in non-human primates) cast doubt on the capacity of the CBH to explain variation in cognitive traits" (Thornton et al., 2016: 1).

Although there is now abundant evidence that cooperative breeding is an integral part of modern human reproductive strategies, there is currently no consensus as to whether the CBH can explain the origins of large brains and hyper-social behavior in our hominin ancestors or its effects in other species. Additional research should continue to explore the links between cooperative breeding and other traits in cross-species comparisons. For example, more evidence of enhanced prosocial behaviors across a variety of cooperative breeders would provide more compelling support for the CBH. In addition, cross-species comparisons should further explore the differences between care provided by fathers (for example in monogamous species) as compared to the care provided by alloparents observed among cooperative breeders.

Box 2: The ecology of helping: predicting variation among callitrichines

Callitrichines are small-bodied (90-750 g: Snowdon, 1996), arboreal primates with claw-like nails, or tegulae. Females are capable of high reproductive output, as they undergo postpartum estrus and all but *Callimico* regularly give birth to twins. All callitrichines are characterized by female reproductive skew, male-biased group composition, and alloparental care (Díaz-Muñoz, 2015). Species vary however, in the number of breeding males per group, male reproductive skew, dispersal age, and the degree of female reproductive monopolization (Díaz-Muñoz, 2015). Goldizen (2003) and Díaz-Muñoz (2015) proposed that variation in infant care costs across callitrichine genera can explain differences in their reproductive traits, including how many breeding and non-breeding group members are available to help. Díaz-Muñoz (2015) identified three main factors responsible for interspecific variation in these traits: physiology (e.g., maternal-infant mass ratio), social environment (e.g., group size and composition) and ecology (e.g., home range size).

Díaz-Muñoz (2015) proposes that if infant costs are high, a single female is expected to monopolize reproduction (in order to secure help from multiple alloparents), whereas if infant care costs are low, female reproductive skew should be reduced. In contrast, males are expected to show low reproductive skew if infant care costs are high (as males work cooperatively to raise offspring), and high skew males when costs are low. He calculates the “ecophysiological” costs of infant care across genera by multiplying relative infant weight (neonatal / adult body weight) by home range size to predict patterns of allomaternal care. Below, we summarize the foraging strategies and their impacts on home range sizes and neonatal weights of callitrichine genera to highlight the range of variation underlying this hypothesis.

Cebuella have specialized teeth for gouging trees and are able to concentrate their feeding on a small number of trees, which they repeatedly gouge to stimulate exudate production. As a result, they have very small home ranges (0.1-0.5 ha), and infants can be parked while adults forage (Goldizen, 2003). Thus, although their neonate-adult body weight ratios are the highest among callitrichines, infant care costs appear to be the lowest (Díaz-Muñoz, 2015). As a result, although *Cebuella* groups often contain only a single adult male, females often produce two litters per year (Goldizen, 2003, Díaz-Muñoz, 2015).

Callithrix and *Mico* can also gouge trees to stimulate exudate production throughout the year. *Callithrix* species vary in their degree of exduativory and home ranges are smaller for the more exudativorous species and larger for the mycophagous species (range 14-138 ha, Díaz-Muñoz, 2015). Due to their small home ranges and reliance on replenishable resources, infant care costs are predicted to be lower in *Callithrix* than in tamarins or lion tamarins. As predicted by the model, *Callithrix* groups are large, groups may contain two breeding females, and a single male may attempt to monopolize breeding; unfortunately, little is known of the social behavior of *Mico* groups (Goldizen, 2003, Díaz-Muñoz, 2015).

Callimico feed on fruits, insects and fungi, and lacks specialized dentition for exudate feeding. *Callimico* have relatively large home ranges (50 -150 ha); however, as they produce singletons rather than twin offspring, their infant care costs are expected to be lower than the tamarins' (Díaz-Muñoz, 2015). As predicted, some groups contain two breeding females, biannual birth seasons are possible, and a single male may attempt to monopolize reproduction (Díaz-Muñoz, 2015).

Saguinus and *Leontocebus* focus their feeding on fruits, insects, flowers and exudates. Unlike the marmosets, they do not have specialized dentition for gouging holes to stimulate exudate flow. As a result, their home ranges are larger than for marmosets (20-120 ha), and neonate-adult body weight ratios are relatively high. Thus, their infant transport costs are estimated to be high (Goldizen, 2003). As predicted, groups generally contain a single breeding female, males exhibit little reproductive skew, and males provide essential care for infants (Goldizen, 2003, Díaz-Muñoz, 2015).

Leontopithecus forage on fruits, insects and exudates. Like other tamarins, they do not have specialized dentition for gouging trees. Lion tamarins have the largest home ranges (20-300 ha) and neonates are relatively large, leading to the prediction that infant transport costs should be high (Díaz-Muñoz, 2015). However, contrary to prediction, groups often contain two breeding females, and a single male often attempts to monopolize breeding (Díaz-Muñoz, 2015). Thus, additional research is needed to understand why this genus does not support the "infant cost hypothesis". For other genera, evidence generally supports the hypothesis, and additional studies should continue to test its strength at predicting variation in alloparental care across genera, among species, and even among groups with different home range sizes in the same population.

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Table I. Predictions for each of the ultimate hypotheses for helping

Hypothesis		Prediction	Species	Setting	Support	Ref
Kin selection	1	Reproductive success is positively related to help received	not tested	--	--	--
	2	Within-group relatedness is greater than between-group relatedness	*C. jacchus, S. mystax, S. geoffroyi, S. weddelli*	Wild	Pos	Huck et al., 2005, Nievergelt et al., 2000, Faulkes et al., 2003, Garber, Porter, Spross, & Fiore, 2015
	3	Helpers provide more help to closely related than to more distantly related individuals	not tested	--	--	--
Parenting experience	1	Helping experience improves reproductive success	*Callithrix, Leontopithecus, Saguinus* spp.	Captive	Pos	Tardif, 1997 [r]
	2	Allocare behavior improves with experience	*L. oedipus*	Captive	Neg	Tardif et al., 1992
	3	Experienced helpers carry less than inexperienced helpers	*L. rosalia, L. oedipus*	Mixed	Mixed	Baker, 1991, Tardif et al., 1992
Social prestige	1	Helping is positively related to mating success during fertile periods	*C. jacchus, L. oedipus*	Captive	Neg	Tardif & Bales, 1997
	2	Helping occurs more in the presence of opposite-sex individuals	*C. jacchus, L. oedipus*	Captive	Neg	Tardif & Bales, 1997
	3	Individuals compete for helping	not tested	--	--	

		opportunities				
Group augmentation	1	Individuals survive and reproduce better in larger groups	*C. jacchus, L. rosalia, L. fuscicollis, S. mystax*	Wild	Pos	Sussman & Garber, 1987, Koenig, 1995, Bales et al., 2000
	2	If dispersal is sex-biased, the more philopatric sex helps more	not tested	--	--	--
	3	Individuals attempt to recruit and maintain helpers	*C. kuhli*	Wild	Pos	Schaffner & French, 1997 [a]
Pay-to-stay	1	Helpers are costly to breeders	not tested	--	--	--
	2	Helping is positively related to an individual's group tenure	*S. mystax*	Wild	Pos	Huck et al., 2004 [a]
	3	Helping is positively related to inheritance of the territory/breeding position	not tested	--	--	--
	4	Helping is negatively related to aggression received from breeders	*L. oedipus*	Captive	Mixed	Tardif, 1997, Sánchez et al., 2002 [a]
	5	Helping occurs more in the presence of same-sex breeders	*C. flaviceps, L. rosalia*	Wild	Pos	Baker, 1991, Ferrari, 1992 [a]
	6	Older non-breeding females help more than other non-breeding group members	not tested	--	--	--

* References limited to the 3 most relevant with emphasis on wild studies, r = review of other studies, a = anecdote or non-significant result. Note that we determined support for each prediction using results directly reported in the referenced studies, even though in some cases, the studies were not designed explicitly to test the specified hypotheses