

**The following annotated bibliographies include information regarding the influence of proximate factors (age, sex, parenting experience, group size, and group composition) on infant care behaviour.**

Price, E. C. (1992a). Contributions to infant care in captive cotton-top tamarins (*Saguinus oedipus*): The influence of age, sex, and reproductive status. *International Journal of Primatology*, 13(2), 125–141. <https://doi.org/10.1007/BF02547838>

#### **Article Summary:**

The reproductive strategy commonly used in the callitrichid family involves twinning and a communal rearing system. Cooperative infant care occurs in these groups where breeders and nonbreeders participate in infant rearing. Breeders may experience reduced energetic costs and increased infant survival, while helpers may gain parenting experience, develop bonds with the infant, and may increase tolerance from group members when occupying the same territory.

The purpose of the study was to test predictions regarding the amount of infant care contributed by different group members based on factors such as age and experience, sex, and reproductive status. Researchers examined captive groups of cotton-top tamarins (*Saguinus oedipus*) that included 14 litters that were observed from birth till 12 weeks. Each infant was observed for three-five 30 minute sessions a week. Carrying was recorded at each occurrence and food sharing was recorded once a week during fruit feedings.

Older siblings carried infants more than parents. During the first three weeks, mothers carried more than fathers, but contribution declined after. Fathers carried the most during weeks three-four. The effects of group size, age class and litter size were significant on carrying time ( $P < 0.0001$ ). Parents carried more than offspring and older offspring carried more than younger offspring. Infants received more food from parents compared to siblings when begging. Adult siblings shared more with infants than younger siblings. Groups with twins experienced more begging for food from infants.

Overall, evidence suggest that cooperative infant care may exist to ensure infant survival and may benefit the fitness of helpers. Helping behaviour by males can increase their fitness as groups can be polyandrous or monogamous, but cooperating may increase their chances of reproduction or defend their breeding positions. Other helpers may increase tolerance of their presence in groups by performing infant care, and can also gain parenting experience.

#### **Article Contribution:**

This study had a sufficient sample size to examine the effects of age and sex cooperative infant care. The captive study allowed for direct analysis regarding genetic relations to the infant while maintaining natural group sizes. The results regarding food sharing conflicted with previous captive studies. Other captive studies found that fathers and adult males carried more than their female counterparts. These conflicting results may result from different group sizes from each study. However, all studies demonstrate that cooperative infant care is prevalent in all groups of tamarin monkeys. Future long-term field studies are needed to resolve these conflicting results.

Price, E. C. (1992b). The benefits of helpers: Effects of group and litter size on infant care in tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 26(3), 179–190.  
<https://doi.org/10.1002/ajp.1350260304>

### **Article Summary:**

Previous studies on the callitrichid family observed helping behaviour from fathers, older offspring, and nonrelatives. Also, previous studies on moustached tamarins demonstrated a possible positive correlation between the survival of infants and their group size. However, there is a lack of evidence on the benefits of having helpers and how much help is given based on group size.

The purpose of this study was to determine the benefits of having helpers in a captive colony of cotton-top tamarins. The predictions were that infants receive more care in larger groups, the number of males in a group will affect carrying time of infants, there is a negative correlation between family size and mean amount of care, group size affects contributions made by parents, and litter size also affects parental investment.

The study subjects were 21 cotton-top tamarin infants from eight captive families. The behavioral categories measured included carrying, suckling, and food-sharing. The infants were observed from birth until 12 weeks old. Focal infants were observed for an average of 2.4 hours/week. Carrying and suckling were measured at each occurrence. Food sharing was measured once a week during fruit feedings. Results suggested that infants were carried more and received more food in larger groups, singletons were carried more than twins, and caretakers and fathers provided less care in larger groups. Authors found that group size had no effect on amount of maternal contribution to infant care, but these results conflict with other studies. Overall, the results suggest that larger group size and communal rearing behaviour is beneficial to infant survival and reduces energetic costs for individuals within the group. Future work suggested by the authors include studies on wild populations to gain a more accurate understanding of the behaviour and to resolve the conflicting result regarding the amount of maternal care.

### **Article Contribution:**

This article provided evidence that there are benefits for cooperative infant care behaviour in the callitrichidae family. This article outlined the predictions on what causes the cooperative behaviour on infant rearing in tamarin monkeys. Most of the findings from this article were supported by previous studies. There were also conflicting results in terms of which helper offered more help and when, as well as amount of maternal contribution in different group situations. These conflicting results require further studies, especially from wild populations as there is a lack of evidence from the natural setting.

Tardif, S. D., Carson, R. L., & Gangaware, B. L. (1992). Infant-care behaviour of non reproductive helpers in a communal-care primate, the cotton-top tamarin (*Saguinus oedipus*). *Ethology*, 92(2), 155–167. <https://doi.org/10.1111/j.1439-0310.1992.tb00956.x>

### **Article Summary:**

The callitrichid family exhibits alloparental behaviour where breeding males and non-breeding helpers participate in extensive infant care. Tamarin monkeys in the wild form monogamous or polyandrous groups where different individuals within the group participate in infant rearing. Captive study groups consist of mated pairs and older offspring who participate in infant care. Alloparental behaviour in tamarin monkeys have been found to vary between individuals. Proximate factors that influence infant care behaviour include age, gender, and experience. This study aimed to examine these factors and their interactions to understand alloparental behaviour.

This captive study examined 24 litters in 18 families of cotton-top tamarins. There were 47 potential helpers that were observed within the 24 litters. Each family was observed for 20 minutes, two-four times a week, once in the morning and once in the afternoon. Observations were recorded using a cassette recorder and stopwatch, as well as a computer program. Carrying behaviour was defined as infants clinging with at least two limbs.

Sex had no effect on frequency of carrying behaviour. Results showed that age was a contributor to variation in carrying frequency, as subadults (14-24 mo) carried more often than juveniles (6-13 mo). As infants grew older, age created less of a difference. Results suggested that infant care skills were acquired at different rate at different ages, as subadults that were exposed to infants as juveniles did not carry more frequently than those that were. It was also suggested that an increase in age, along with increase in body size, led to increased interest in infants. Overall, age is an important factor in regard to infant care behaviour as older individuals showed more interest in infants and carried more frequently. Future studies should analyze the effects of observational learning on infant care behaviour, as only anecdotal evidence exists currently.

### **Article Contribution:**

This article examined the effects of the proximate factors( age, gender, and experience) on alloparental behaviour on tamarin monkeys. The use of a captive study allowed researchers to examine the care of infants with accurate relations and age of individuals within each group. Previous studies found that experience and age were confounding factors, but this study was able to separate the effects of the two. Other studies found conflicting results in terms of gender as they found that males generally carried more than females. However, those studies included breeding males and this study did find that fathers carried more.

Zahed, S. R., Kurian, A. V., & Snowdon, C. T. (2010). Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. *American Journal of Primatology*, 72(4), 296–306. <https://doi.org/10.1002/ajp.20782>

### **Article Summary:**

Tamarin monkeys are part of the callitrichid family where infant care behaviour varies greatly between individuals within a group. Infant rearing is costly to mothers due to lactation demands and their ability to conceive again after a few weeks postpartum, therefore cooperative behaviour from other individuals is necessary. Researchers aimed to identify and characterize the factors that influence the expression of infant care.

The variables examined were related to different group conditions that may influence parental behaviour, such as presence, sex, and age of sibling helpers. Other variables examined include litter size and impact of natal helping behaviour on future parenting behaviour. Researchers used instantaneous scan sampling four times a day by recording the individual carrying and the infant being carried. Continuous focal sampling was also used to observe infant carrying, nursing, grooming, food sharing, and infant rejection.

Mothers were the main carriers for the first two weeks after birth, but fathers overall were the main carriers. Adult siblings carried more compared to juvenile siblings, where brothers carried more than sisters. Fathers began to reject infants after four weeks and mothers showed continuous rejection throughout eight weeks postpartum. Infant care varied based on group conditions. Groups with more adult siblings (helpers) resulted in less paternal care, but did not affect maternal care. Sibling males with experience carrying correlated with high levels of infant carrying when they became fathers. Prior parenting experience also influenced carrying rate as multiparous mothers carried less than primiparous mothers.

Overall, tamarins display variable infant care as it depends on experience and the group/helpers and resources available to them. The results demonstrated that tamarins are able to adjust their infant care behaviour according to environmental, group and social conditions.

### **Article Contribution:**

This article identified many conditions that allow tamarins to have variable levels of infant care behaviour. The cooperative aspect of infant rearing in tamarin monkeys is influenced by group size and environmental conditions. Researchers provided evidence that tamarin monkeys adjust their level of care based on their living conditions. With increased group sizes, infant care can be distributed and the overall energetic costs for participating individuals can be reduced. The large database collected from this study allowed for the development of general trends regarding infant care in tamarin monkeys.

Piper, L.A.H., Dietz, J. M., & Raboy, B. E. (2017). Multi-male groups positively linked to infant survival and growth in a cooperatively breeding primate. *Behavioral Ecology and Sociobiology*, 71(12), 1–12. <https://doi.org/10.1007/s00265-017-2404-3>

### **Article Summary:**

Previous studies on primates found that the callitrichid family exhibits a cooperative breeding system where non-breeders participate in infant rearing for breeding individuals. Typically, male callitrichids contribute more to infant care than non-breeding females. Also, the presence of multiple males in a group is attributed to infant survival. Larger groups reduced infant survival, possibly because of increased resource competition. Reproduction is energetically costly for callitrichids because the birth of twins is common, and infants typically are large at birth compared to adults. The participation of non-breeders in infant care suggests that group composition may influence the survival of infants. Researchers aimed to understand the influence of group composition, specifically the number of males, on the success of infant survival in *Leontopithecus chrysomelas* (golden-headed lion tamarins).

Eight breeding groups of *L. chrysomelas* were studied for 2-12 years between 1991-2007. These groups were habituated then followed for 2-10 days/month year-round. Behavioral scans were conducted in 20 minute intervals and behaviours from focal animals were recorded at each occurrence.

Results found that the presence of multiple adult males had a positive effect on infant survival. Infant survival was greater because of the extensive parental care displayed by fathers and non-breeding males. Contrasting previous studies, this study found that a larger group size is beneficial to infant survival (infants grew faster and larger), as long as the proportion of adult males remained high. Overall, this evidence suggests that male presence contributed to infant survival and growth. Future studies should investigate the lifetime reproductive success of infants with high adult body mass due to male care. Also, the effects of potential shared paternity on extensive infant care in male callitrichids should be examined further.

### **Article Contribution:**

This study contained the largest sample size of wild *L. chrysomelas* infants, which provided more information regarding group composition and infant success. This article provided evidence that the presence of male helpers contributed to infant survival and may influence the reproductive success of these infants in the future. Other studies suggest that inclusive fitness may explain participation by male helpers in infant rearing, as infant survival may benefit their fitness depending on relatedness, but there are conflicting results from this study that requires further examination. Overall, this article provided new insight regarding the effects of group composition on infant care.

Erb, W. M., & Porter, L. M. (2020). Variable infant care contributions in cooperatively breeding groups of wild saddleback tamarins. *American Journal of Primatology*, 82(12), e23190. <https://doi.org/10.1002/ajp.23190>

### **Article Summary:**

Callitrichids experience extensive alloparental care as a result of their cooperative breeding system. Social groups usually consist of one breeding female, two or more adult males, one or more non-breeding females, and juveniles. Helpers participate in grooming, food sharing, protection, and infant carrying behaviours. The objective of this paper was to examine the forms of infant care provided (by who and when), how helpers adjust their behaviour while caring for infants, and whether contributions by helpers differ between individuals.

Four wild groups of saddleback tamarins in Bolivia were studied, and each member was marked with identification collars. Each group was observed for an average of 7.6 hours/day for 4.5 days/month. Behaviour sampling was used to record infant-directed behaviours such as infant carrying, retrieval, refusal to carry, and food sharing. Instantaneous sampling at five-minute intervals was used to record behaviours such as feeding, resting, foraging, traveling, and vigilance.

Results showed that helpers participated in vigilance while carrying and food sharing when infants were weaned from mothers. Further, results demonstrated variation in infant care among individuals within the group. As infants grew, mothers refused to carry more often than adult males due to the increased energetic costs from infant weight and lactation demands. Rates of infant carrying varied based on group size and composition, as groups with more adults resulted in more carrying. Further, resident males contributed more to infant care than immigrant males. Overall, evidence showed that helpers suffered increased energetic costs and decreased mating opportunities when helping. The results may suggest that variation in infant care by alloparents results from the balancing act between the costs and benefits of helping. Future studies should analyze the indirect benefits like inclusive fitness and the direct benefits like parenting experience as factors influencing the evolution of cooperative behaviour.

### **Article Contribution:**

This article provided quantitative data on infant care behaviour in wild populations of saddleback tamarins. The authors identified different forms of infant care behaviour as well as alloparental care by group members. They identified causes for variation in infant care by different group members that result from variability in group and environmental conditions. Authors examined the findings with the underlying idea that the variation in infant care result from the balancing act between costs and benefits of helping in order to create an adaptive advantage to be an alloparent.

**The following annotated bibliography examines factors including group composition, group size, and parenting experience that may influence infant survival.**

Savage, A., Snowdon, C., Soto, L., Medina, F., Emeris, G., & Guillen, R. (2021). Factors influencing the survival of wild cotton-top tamarin (*Saguinus oedipus*) infants. *American Journal of Primatology*, 83(7), e23262. <https://doi.org/10.1002/ajp.23262>

**Article Summary:**

Previous studies showed that callitrichid primates have a cooperative breeding system where helpers participate in infant care, which provides them with parenting experience while increasing infant survival. Twin births are common, and the weight of infants at birth can be 15-20% of the mother's weight, resulting in the need for helpers to raise infants. Younger callitrichids who participate in infant care gain experience and are more successful with their future offspring than inexperienced individuals.

This study examined factors such as reproductive experience of females, group and litter size, number of adults, and effects of adult immigration to determine their impact on infant survival. Researchers observed 126 litters of cotton-top tamarins over a long-term study from 1999-2008. Data was collected using instantaneous two-minute sampling and all-occurrence sampling.

Results demonstrated that infant survival was not related to group size or the number of either sex in the group. However, groups with only one male had decreased infant survival. Also, first-time mothers had lower infant survival rates. In terms of litter size, twins had higher survival than triplets as they had higher birth weights and lower energetic costs for care. Group disruptions such as breeding female eviction influenced infant survival as it caused multiple females to compete for the breeding position. Further, it was rare for groups to contain more than one actively breeding female because it resulted in lower infant survival. First-time mothers without prior parenting experience were found to be as successful as those with prior experience. This lack of difference contradicts findings from captive studies but likely resulted because of how groups form in the wild. In the wild, individuals can immigrate and form new groups, therefore experienced infant caretakers contribute to the success of infant survival. Overall, the results suggest that group composition may influence the survival of infants.

**Article Contribution:**

This article provided overall context regarding the influences of group structure on infant survival in wild groups of cotton-top tamarins. Researchers examined factors that influence survival of infants over a 20 year field study to provide a greater understanding on wild groups. Examining the variables that influence infant survival offers a better perspective on how cooperative infant care arises. The results regarding group size and number of males conflicted with previous captive and field studies on different species of tamarins. The differing results were thought to arise because group structures and formation differs in the wild compared to captive groups.

**The following annotated bibliographies include evolutionary theories regarding the behaviour.**

Secondary Article (Review)

Díaz-Muñoz, S. L. (2016). Complex cooperative breeders: Using infant care costs to explain variability in callitrichine social and reproductive behavior. *American Journal of Primatology*, 78(3), 372–387. <https://doi.org/10.1002/ajp.22431>

**Article Summary:**

The callitrichid family are one of many group-living taxa where social mating and caregiving behaviours are common. Callitrichids also exhibit high variation in reproductive and social behaviours. A common view for these behaviours emerges from the idea that individuals within these groups are attempting to balance cooperation while maximizing their reproductive success.

The author used a systematic review method to examine the hypothesis that the variation in reproductive traits can be explained by the differences in infant care cost. Physiological influences on infant care costs involve infant size. Ecological influences include home range size. It was predicted that traits among callitrichids vary along a continuum. At one end, groups with greater costs will contain multiple males mating and providing infant care, high suppression of breeding in subordinate females, fewer individuals delaying natal dispersal, and increased reproduction by the dominant female. At the other end of the spectrum, the predictions are the opposite for low infant costs.

Collective findings showed that tamarin monkeys fit the predictions for high infant care cost and two other callitrichid species fit the predictions for low infant costs. However, results for species with intermediate costs contradicted the predictions. Proximate factors that may increase infant care cost in tamarin monkeys include large home range sizes as they must travel further for resources. Evidence from field research also showed female reproductive skew as it was rare for two females to breed successfully. Shared paternity was found in field studies where multiple non-natal males mated with the dominant female, which increased infant care costs for the males as they may be mating without actually reproducing. Breeding opportunities were also reduced as evidence showed that both sexes regularly dispersed from their natal groups. Overall, results may suggest that variation in infant care costs leads to variation in infant care behaviour.

**Article Contribution:**

This study provided a means to generate predictions regarding infant care behaviour in callitrichids. Further, it provided suggestions and future directions regarding the study of callitrichine social and reproductive behaviour. The factors that result from infant care costs can be used as predictions to examine the level of alloparental care exhibited by callitrichids in future studies. Understanding factors that influence the social and reproductive behaviour will allow for a greater understanding for the development of alloparental and helping behaviour as a strategy for reproduction.



Secondary Article (Review)

Erb, W. M., & Porter, L. M. (2017). Mother's little helpers: What we know (and don't know) about cooperative infant care in callitrichines. *Evolutionary Anthropology*, 26(1), 25–37. <https://doi.org/10.1002/evan.21516>

### **Article Summary:**

This article reviews the major hypotheses regarding the evolution of cooperative breeding systems in callitrichids and examined the ultimate and proximate factors that may contribute to an individual's helping behaviour. The cooperative breeding hypothesis (CBH) states that alloparents (non-genetic individuals participating in infant care) provide relief in terms of energetic costs to mothers and causes selection for hypersocial behaviour (an infant's ability to gain attention from an adult). CBH examines the cognitive and psychological adaptations for cooperative behaviour. The infant care hypothesis states that increased costs of infant care cause mothers to monopolize reproduction and secure help from group members. The variation in infant care costs is based on the relative weight of infants and home range sizes, as larger home range sizes and infants are more costly, resulting in females having greater reproductive skew.

The ultimate explanations outlined include kin selection, parenting experience, social prestige, group augmentation, and pay-to-stay (future reproductive opportunities). The authors examined available studies for each explanation and combined results from wild and captive studies but determined that with mixed and limited results, no conclusions could be drawn. The proximate factors include sex, age, physical condition, group size, and consistent individual differences. Age was determined as a confounding variable as helping behaviour varies with age. Group size influences helping behaviour as the larger the group, the less costly it is for helpers and the more beneficial it is for infants with increased care.

Although the authors found limited evidence to significantly support the hypotheses for cooperative infant care, they outlined possibilities for these behaviours. The authors stated that the understanding of the evolution of allocare in callitrichids is limited because the research done so far is too general. The lack of supporting evidence can be mediated by more focused studies on each hypothesis and explanation.

### **Article Contribution:**

This review article outlined the predictions regarding the evolution of helping behaviour in infant rearing in callitrichine species. Multiple primary studies were included in this article that focused on specific helping behaviours for different species of tamarin monkeys. The authors examined the cooperative behaviour in several species along with callitrichines. The studies examined by the authors for each hypotheses or proximate factors have lacked supporting results or had anecdotal evidence. However, this review article was important for outlining the predictions for the evolution of helping behaviour in infant rearing and suggests further in depth studies that directly analyzes the predictions.