

Theories on the Evolution and Function of Allomothering in Primates

Shemi, N. R.

University of Southern California

ABSTRACT

Allomothering is a prevalent social exchange between primate mother-infant dyads and female conspecifics. Theories on the evolution and function of allomaternal behavior suggest seemingly contradicting views: while originally seen as an altruistic behavior that provides help to mothers, allomothering has been reconsidered under a Darwinian light as a selfish behavior that mainly benefits allomothers. Additionally, playmothering can sometimes result in mistreatment and either intentional or unintentional abuse of infants. In a cost-benefit analysis of potential outcomes of allomothering, the substantial selfish benefit allomothers gain by practicing maternal skills is possibly offset by the various benefits it provides to mother-infant dyads, suggesting the two views are not necessarily mutually exclusive. Furthermore, allomothering can be considered adaptive since young female primates that display maternally inclined behaviors would be inherently better mothers, and selection for the behavior could be due to physiological changes that lead to increased interest in neonates, resulting in optimal maternal disposition. Future research on the social exchanges between female primates in relation to infant-directed behavior can provide more substantial syntheses of the current theories on allomothering and its underlying evolutionary rationale.

KEYWORDS

Allomothering, Playmothering, Primate Sociality, Mutual-Altruism, Female Bonds, Social Intelligence

INTRODUCTION

Sociality has long been established as an important part of development and learning processes in primates. Many studies have investigated the crucial role of sociality in the life histories and trajectories of primate individuals and its implications on reproductive success, and research on the social behavior of non-human primates has been imperative to the understanding of the causes, benefits, as well as potential drawbacks of sociality in both nonhuman and human primates. Amongst its many

AUTHOR NOTE: Correspondence concerning this article should be addressed to Noa Raychel Shemi. Contact: shemi@alumni.usc.edu.

underlying rationales, sociality in primates is of significant evolutionary advantage, posited to have reduced predation risk by the formation of group associations (Burkart, 2017; Sorato et al., 2012). Throughout the evolution of many primate species, most likely as a result of living in relatively large groups, primates have become highly predisposed to social learning (Reviewed in Whiten & van de Waal, 2018).

Social learning is known to be an essential aspect of the successful development of primates from infancy to adulthood. Whiten and van de Waal (2018) review the hypotheses relating to the evolutionary roots of social learning and the life-long advantages it provides when exercised during the early years of infancy. In their analysis of the early phases of social learning, Whiten and van de Waal identify three main phases, the first two of which focus on the importance of mother-infant interaction as the primary source of social exposure, as well as of selective learning from an extending network of group members.

Social interaction, which is enabled and necessitated by social learning, is the primary manner by which primates acquire their distinctive behaviors. Learned behaviors are achieved through the accumulation of social interactions, from early mother-infant interaction to later juvenile and adult bonds, as well as independent observations and experimentation. For instance, social play and environmental exploration in young tufted capuchins (*Cebus apella*) have been demonstrated as critical to their locomotor and activity pattern development (Byrne & Suomi, 1995). While these are observable learned developmental landmarks, more subtle consequences of social exchanges between primate individuals may have similar evolutionary significance as they relate to life history strategies and overall reproductive success. Allomothering—the non-maternal care and handling of an infant by a female group member—represents such a social exchange. The highly nuanced nature of interactions between primate mother-infant dyads and other female conspecifics has led to a theoretical debate on the origin and ultimate function of allomothering throughout the evolution of primate intragroup social dynamics, varying both in form and possible function of its behavioral repertoire.

THE RECIPROCAL VALUE OF ALLOMOTHERING: MUTUAL ALTRUISM

Mothering a primate infant for the first time, although not an exclusively learned behavior by itself, nevertheless requires social skills that were previously demonstrated as not consistently instinctual. Maternal abuse of primate infants, for instance, was observed in multiple studies (Maestriperi et al., 1997; Maestriperi & Carroll, 2000; Nadler, 1980; Sanchez et al., 2010). Furthermore, the inherent conflict that arises between mothers and infants can restrict the mother's necessary foraging time (Reviewed in Maestriperi, 2002; Trivers, 1972).

In such instances, allomothering can potentially benefit both mothers and infants. In cases of neglecting or abusive mothers, allomothering can offset neglect or maltreatment and benefit the infant through added supervision and care, as well as increase the likelihood of infant adoption by other females in the event of a mother's death (Horwich & Manski, 1975; Lancaster, 1971; Struhsaker, 1967). When infants are being handled by other group members, mothers can allocate time for their

own physiological needs, and infants can benefit from the social exposure itself (Horwich & Manski, 1975; Hrdy, 1976). In wild capped langurs (*Presbytis pileata*), it was observed that a mother's average feeding time increases when her infant is in an allomother's care (Stanford, 1992). Pig-tailed macaque (*Macaca nemestrina*) mothers were observed to be significantly less social throughout pregnancy and for months after parturition (Maestriperi, 1999) enabling them to allocate a greater amount of energetic resources to care for themselves and their infants rather than to socializing.

The possible benefits of allomothering to mothers and their infants can explain why mothers would allow such behavior in the first place, yet the initiation of infant handling mostly originates in the caretakers themselves. Allomaternal behavior therefore poses another evolutionary question: why would allomothers dedicate time and resources to provide help and care for infants other than their own? (Mitani & Watts, 1997).

Searching for deeper evolutionary explanations for this seemingly altruistic behavior, researchers have investigated the social interactions between infants and female conspecifics with the attempt to distinguish the benefits playmothering provides to individuals who show an inclination for it. Infant handling was found to be a social priority for juvenile to adult female blue monkeys (*Cercopithecus mitis*) and suggested to reflect the benefit of practicing mothering skills from a young age (Cords et al., 2010). Similar instances of allomothering have been observed across the primate taxa and shown to result in greater offspring reproductive success, as mothers who have practiced motherhood before having their own infants, by playing with and/or being in close proximity to other mother-infant dyads, would likely become better mothers themselves (Hrdy, 1976; Lancaster, 1971; Quiatt, 1979). With similar correlation, Silk et al. first demonstrated the fitness benefits of female social relationships among a group of free-ranging chacma baboons (*Papio ursinus*), with an increase in offspring survival attributed to strong female bonds (Silk et al., 2009). Such observations suggest that allomothering is not entirely altruistic, as it provides adaptive benefits to allomothers by enabling them to practice mothering skills which can benefit their future offspring.

Allomothering is therefore thought to have adaptive merit as a reciprocally altruistic behavior. Female baboons (*Papio anubis*), for instance, were observed to groom mothers for longer periods of time when handling their infants as an exchange, and mothers themselves were more tolerant to allomothering if groomed first (Henzi & Barrett, 2002). Given this potentially mutualistic nature of allomothering, it was suggested that the biological market model—trading “social currencies” with individuals who can offer fitness benefits in return—can explain such an exchange between mothers and non-mothers (Frank & Silk, 2009).

THE DARWINIAN PERSPECTIVE: A SELFISH ACT

Originally seen as an entirely altruistic behavior that provides help to mothers, allomothering has been reconsidered under a Darwinian light which presents a counterargument to altruism-suggestive views. Following a classic Darwinian

interpretation, allomaternal behavior is seen as an entirely selfish behavior that benefits young nulliparous females who exploit infants that are not their own and use them to practice their underdeveloped mothering skills without risking their own progeny in the process (Hrdy, 1976; Lancaster, 1971; Trivers, 1972; Wasser & Barash, 1981). In this manner, it is the allomother's future infants that mainly benefit—and therefore her own reproductive success—by receiving better care and a reduced risk of suffering any unintentional mistreatment that could result from inexperience, due to the practice they have gained while handling others' infants as young allomothers.

Although differing views on allomothering are still argued for by researchers, the Darwinian view is currently widely accepted as the most likely explanation for the evolution of allomaternal behavior, enhancing the maternal skills of nulliparous females by playmothering, and is thus seen as adaptive mostly for young female primates.

IMPLICATION OF PLAYMOTHERING

Other than socializing with and caring for infants, playmothering can sometimes result in mistreatment and either intentional or unintentional abuse (Hrdy, 1976; Maestriperi, 1994; Silk, 1980). Infant kidnapping, for instance, was demonstrated to harm infants in some cases while rescue attempts by the mother were not always successful (Quiatt, 1979).

Additionally, extreme cases of “aunting-to-death” as coined by Hrdy (1976) have been observed (Brain, 1992; Hrdy, 1976; Shopland & Altmann, 1987), highlighting a pivotal cost of allomothering to mother-infant dyads, and providing support for the selfish aspect of the behavior considering such severe outcome. In light of such observations, allomothering has been suggested as a form of reproductive competition between females (Shopland & Altmann, 1987).

Although being handled by young nonmothers poses clear risks to infants, which thereby represent subsequent costs to the mothers, the benefits of alloparenting possibly offset the costs in some situations by freeing a substantial amount of time for mothers to tend to their own needs and even produce more offspring (Mitani & Watts, 1997).

COST-BENEFIT ANALYSIS OF VIEWS ON ALLOMOTHERING

The different views on the origin and nature of allomothering presented thus far can be summarized into four main categories, which can each be analyzed for the potential costs and benefits it confers to the individuals involved in the social interaction (i.e., mother-infant dyads and allomothers). The cost-benefit analysis is also presented in Table 1 below.

1. Enhancing the Maternal Skills of Allomothers

Playmothering confers an evolutionary advantage to the allocaretakers by enabling them to practice their maternal skills without risking their own offspring, selfishly increasing their reproductive success in the process.

1.1 Cost-benefit Analysis

This view represents the greatest costs to mother-infant dyads, constantly in an evolutionary deficit while allomothers are the main beneficiaries of their allomaternal behavior, gaining experience at the expense of others.

2. Providing Socialization for Infants

The social play provided by the allomothers confers the advantage of increased socialization for infants, which provides crucial life-long skills as well as a chance to establish social networks within one's own group.

2.1 Cost-benefit Analysis

Infants gain clear adaptive benefits (as well as their mothers by virtue of the increased reproductive success of their infants), while posing costs to allomothers by decreasing their feeding time and potentially restricting travel time and range while handling infants.

3. Maximizing the Mothers' Foraging Time

While infants are socializing under an allomother's care, mothers can dedicate their time to their own needs such as foraging, maintaining social bonds with other group members, and resting.

3.1 Cost-benefit Analysis

Mothers largely benefit by gaining crucial time that they can allocate to their needs, while the cost to allomothers is forfeiting their own time (decreasing feeding and travel time).

4. Increasing the Likelihood of Adoption

The attachment formed during the social interaction between infants and caretakers can result in inclusive fitness benefits for the mother in case of death, by increasing the probability that the infant will consequently be adopted and taken care of by another female.

4.1 Cost-benefit Analysis

Allomothers risk suffering high energetic costs in case of adoption, especially of nonkin, while highly benefiting infants (and their mothers, by extension), by enabling their survival.

Table 1. A visually simplified cost-benefit analysis of the four theories of allomothering

	1. Practice	2. Socialization	3. Time	4. Adoption
Cost	Mother, infant	Allomother	Allomother	Allomother
Benefit	Allomother	Infant	Mother	Mother, infant

ALLOMOTHERING AND THE SOCIAL INTELLIGENCE THEORY

Elaborated on in *Machiavellian Intelligence: Social Expertise and the evolution of intellect in monkeys, apes, and humans* (Byrne & Whiten, 1988), the social intelligence theory posits that the evolution of intelligence depended on the increase in group size, which offered its own set of benefits (Burkart, 2017; Sorato et al., 2012; Whiten & van de Waal, 2018), and therefore on social dynamics. As social groups aggregated, a greater premium was placed on the mental capacities that seem to define intelligence, such as the ability to remember, distinguish individuals within the group and one’s relationship to them, and navigate such complex social networks while manipulating them in an individual’s own favor. The evolution of primate social dynamics seems to have evolved around this balancing act: the need to maintain large group sizes while at the same time maximize one’s own reproductive success. This presented an evolutionary need for cooperative sociality, which has introduced the potential benefits of prosociality and cooperation between conspecifics working together to achieve a shared goal which is two-fold, and seemingly dichotomous: increasing one’s own reproductive success (the selfish aspect) while increasing the reproductive success of other group members at the same time (the altruistic aspect). In such circumstances, what could be interpreted as altruism could very well be merely a byproduct of selfishly driven cooperation.

Of the large repertoire of primate intragroup dynamics, the political intrigues that arise between primate mother-infant dyads and nonmothers within a group are not often represented in the literature as such. The politics of raising and handling offspring are apparent in the data, however, whether as represented by the conflicts between mothers and allomothers, mothers and offspring, mothers and adult males, or between offspring and allomothers. As is the nature of social dynamics, neither is mutually exclusive, and together they represent the delicate net of social interactions that revolve around mother-infant dyads and hold substantial implications for all individuals involved.

With the increased ontogeny that characterizes primate life-histories, the extended period of an infant’s dependency on motherly assistance seems to have

favored the need for various forms of help in raising offspring. Unlike other mammalian mothers whose litters often become independent within weeks, primate infants rely on their mothers for an extended time period, often not becoming fully independent until a few years old. Without the gradual socialization of infants by their conspecifics, mothers would have been exhaustively restricted in their time management and allocation for the majority of the infants' developmental years. In this respect, allomothering seems to have been continuously beneficial, even necessary. Cooperative breeding and childcare in humans has been investigated for its evolutionary rationales as well, as it is thought to have had a significant contribution to the social evolution of humans, and was found to be strongly nepotistically motivated (Crittenden & Marlowe, 2008).

Whether driven by nepotism or otherwise, allomaternal behavior could have evolved as a process of cooperation by itself, introducing benefits that can be conferred by cooperative behaviors similar to cooperative hunting, foraging, and other socially collaborative processes that require manipulation of social or environmental structures in a manner which simultaneously maximizes the benefits of each individual in the group. From this perspective, allomothering in primates can be seen as an additional pivotal aspect of the evolution of prosociality, which has been continuously favored by the expansion of group size, thus contributing to the larger encephalization quotients that distinguish primates from other taxonomic groups.

SUMMARY AND CONCLUSIONS

Explanations of the function of allomothering emphasize the outcomes of the behavior, whether it is costly or beneficial to the mothers, their infants, or the allomothers. The resulting theories on allomothering suggest seemingly contradicting explanations. Certain instances of handling infants were demonstrated to be costly to mother-infant dyads and suggested to be mainly beneficial to allomothers (Hrdy, 1976; McKenna, 1979), and others were alternatively demonstrated to benefit mother-infant-dyads (Fairbanks, 1990; Frank & Silk, 2009; Silk, 1999; Stanford, 1992), while potentially limiting resources to allomothers .

It is interesting to note that combining the cost-benefit analyses of the currently accepted theories (as presented in Table 1) seems to suggest a greater overall cost to allomothers across the four views, only benefiting them under the prevalent Darwinian view. It can be suggested that the two extremes eventually offset one another over time, resulting in relatively equal averaged outcomes for all individuals involved, and therefore greater reproductive success on an individual level. Cooperative care of offspring, then, will have been beneficial enough to have been consistently adaptive, regardless of the differing nature of individual intentions leading to related behaviors. When considering the Darwinian view as inclusive of the altruistic view, it can be theorized that evolutionary mechanisms that led to the selection for allomaternal behavior have operated on the full range of behaviors that are considered under the umbrella of allomothering, which have been inclusively adaptive regardless of whether it was mostly selfishness or altruism acting as the underlying theoretical motivation for a certain behavioral category.

Including the theory of reciprocal altruism in relation to allomothering (Fairbanks, 1990) and the biological market model (Frank & Silk, 2009) as complementary to the Darwinian explanation can therefore explain the overall payoffs of the sum of all interactions between females and infants in group-living primates. Such a hypothesis is consistent with evolutionary theory, as it is the process of natural selection which “calculates” the value conferred by either selfishly or reciprocally driven behaviors and “translates” them into reproductive success, thereby propagating behaviors that are ultimately adaptive to individuals. Individuals involved in each interaction do not necessarily have to be acting with either a selfish or altruistic ethos, as they may very well be unaware of any reasoning underlying their behavior, and are otherwise driven by immediate instincts or physiological urges. In this respect, it is important to acknowledge both selfishness and altruism as the metaphors that they represent, and while effective in describing evolutionary theories and processes of selection, they can sometimes eclipse the actual underlying mechanisms of natural selection (Quiatt, 1979).

While gaining the experience necessary for handling one’s own infant at the expense of another’s is seen as fundamentally selfish, whether the intention that precedes allomaternal behavior is selfish or altruistic is challenging to assess empirically and therefore often ignored. Yet the two are not necessarily mutually exclusive either: if the intention to help mothers is the main motivation, experience will nonetheless be gained in the process. Similarly, if the intention is to handle infants for one’s own benefit (most likely driven by physiological changes), helping their mothers can result as an unintentional yet still beneficial byproduct. Both instances will eventually benefit both the allomother and the mother-infant dyad involved, regardless of intentionality, which is therefore difficult to establish.

In cases of kidnapping or abuse of infants during handling, mother-infant dyads can suffer relatively high costs as a result of the exchange. In such circumstances, forced handling of infants is most likely selfishly driven, resulting from interest in handling infants for the sake of the behavior itself. The interpretation of such behavior as well as behaviors of other group members that actively intervene in such interactions, trying to chase away the kidnapper or otherwise assist the mother in efforts to retrieve the infant, can be more correctly described as altruistic, directly aiming to provide help. It is in these circumstances therefore that intentionality can be more accurately assessed.

Furthermore, a relatively simpler explanation of the adaptive benefit acquired by the interest in infants is that young female primates that demonstrate such interest would be better mothers than those who show less interest in caring for and handling infants to begin with (Silk, 1999). The selection for the behaviors related to allomothering, therefore, could have been strongly driven by the selection for the physiological changes that specifically lead the increased interest in caring for infants that adolescent female primates demonstrate. These physiological changes lead to a range of infant-directed behaviors with an array of possible outcomes: some interpreted as more altruistic as they seem to be cordial and helpful to mother-infant dyads, while others are thought of as selfish as they pose risks to mother-infant dyads and enable allomothers to handle infants as they wish and gain respective experience. All of these, however, can be driven by the same hormonal pathways that increase interest in neonates, resulting in increased behavioral engagement with

infants which will be crucial to the females' future offspring as it represents an adequately optimal maternal disposition.

The possibility of altruism remains, however, just as does that of selfish nepotism, and the amalgamation thereof: do primate allomothers, other than proximately and ultimately enjoying the value of maternal experience, also intend to provide some of the help that they seem to bestow? Indeed, such questions are notoriously challenging to answer since the nuances of behavior, such as its underlying intention, cannot be definitively extrapolated from empirical research. Nonetheless, future research on the social exchanges between female primates in relation to infant-directed behavior should aim to provide a synthesis of current theories to show that they are not mutually exclusive, and attempt to shed light on any immediate, proximate intentionality that precedes behavior.

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