

COOPERATIVE BREEDING: AN INTEGRATIVE APPROACH

*Nishant Hasmukh Shah
Department of Anthropology
Emory University*

In cooperative breeding, "members of the social group assist in rearing young that are not their own offspring (French and Solomon, 1997). The idea of cooperative breeding is anonymous with other phenomena like alloparenting and helping behavior. E.O. Wilson defined alloparenting as "An individual, other than the genetic parent, that provides care for a conspecific young (Riedman, 1982)." In addition, a helper is "An individual that performs parent-like behavior toward young that are not genetically its own offspring..." (Brown 1987). The terms cooperative breeding, alloparenting and helping will be used interchangeably throughout this paper. Helping behavior is a difficult social activity to justify because at first glance it appears to be truly altruistic. What could an individual gain from providing energy to rear offspring not directly related to it? This confusion is increased when looking at characteristics of cooperatively breeding societies. Cooperative Breeding includes three criterion: (1) delayed dispersal from the breeding group, (2) suppression of reproductive functions, (3) caring for another's offspring (Solomon and French 1997). What influences these characteristics and the potential costs and benefits of each unfold the development of cooperative breeding and its "adaptive" quality to the helping individual. The vast number of species incorporating aspects of cooperative breeding gives strong suggestion that there is some ecological development to the behavior. Observed behaviors are most represented in avian species, however, over 120 documented mammalian species have exhibited alloparenting (Riedman 1982). Mammals expressing cooperative breedings includes primates, canids, ungulates, and rodents. In addition, more mammals are split within groups, for example within primates, colobines express alloparenting and cercopithecines do not (McKenna, 1979). The diversity of species forces one to consider which ecological constraints or social environments would give rise to such "altruistic behavior?" There has been struggle with identifying what adaptive reasoning could be given for cooperative breeding. After, Hamilton's development of the inclusive fitness theory, it was clear that the ideas must be relevant to the apparent altruistic nature of cooperative

breeding. In his review of primate sociobiology, Gray (1985) finds seven possible adaptive explanations of alloparental behavior. These include the "mother relief" hypothesis, where the mother gains by increased foraging time while others care for her offspring. The "learning to mother" hypothesis suggests that the alloparent gains essential skills in how to parent. The "adoption" hypothesis identifies that the offspring's chances of adoption, if something happens to the parent, increases through alloparenting. A "group cohesion" hypothesis considers the developed social bonds as a result of helping behavior. The "selfish allomother" is a spiteful adaptation where the alloparent attempts to reduce the inclusive fitness of the helped mother and offspring. Finally, the "status elevation" hypothesis considers rank bonds formed through alloparental behavior. In addition to these hypotheses, considerations between what type of individual helps, i.e. males, females, young, breeders, or non-breeders, must be analyzed too. As one can see, who benefits, how much they benefit and in what way they benefit varies greatly. A further look identifies even more possibilities for the adaptive significance of cooperative breeding.

What are helping behaviors?

The issue of what are alloparental behavior is very speculative and until recently rarely defined for discussion. Behaviors which either assist in the survival of offspring or contribute to maternal energetics provides a basis from which to describe alloparental acts (Lee, 1989). In addition, Lee provides five subcategories to help clarify what is inclusive when describing cooperative or communal care of offspring. Protecting the young from predators is an important assistance helpers provide to maintain low infant mortality. The vulnerability of young makes this very important in societies where predatory behavior can greatly influence lifetime reproductive success (Goldizen, 1990). As young develop in a new ecological environment, certain environmental stressors can be dangerous. Assistance from alloparents against these stressors can be observed through cooperative denning and infant survivorship in extreme environments (Lee, 1989). The costs of parenting through the increased feeding required by mothers can be difficult to maintain while carrying young. Alloparents who take care of or carry young, allows time for the mother to seek out quality food sources (Terborgh and Goldizen 1985). Increased milk availability due to a larger number of lactating females, increases infant survivorship. This is seen through communal suckling which increases the amount of milk available per infant (Lee 1989). Finally, understanding learning patterns for young in socialized societies can be linked to the assistance provided by alloparents. Contact between young and other group members can increase social

learning and promote independence at an earlier age (Nishida, 1983). Children gaining independence earlier can allow the mother to return into estrus sooner and increase her overall reproductive success. In addition, juveniles with the opportunity to serve as alloparents can gain important knowledge and skills associated with child care. Nishida (1983) provides an interesting look at types of interactions between infants and their alloparents. Most often, older siblings serve as helpers for infants, however, Nishida also observed helping behavior from non-related immigrant females. Nishida observed four types of alloparental behaviors among the chimpanzees: invitation and enticement, detachment from mother, care and tickling, rough-and-tumble. All but the last category allowed the mother abilities to roam independent of the child. The benefits of these behaviors will be examined at the end of the paper. Elephants exhibit a very different type of alloparenting behavior. Alloparents can provide energetic benefits to the mother, elephant helpers usually provide protection and group solidarity. Infants will almost always feed from the mother and in most cases alloparents will not allow an infant to feed from them (Lee, 1987). However, the close relationship between the mothers, influences protective and learning among elephants. Young who roam too far from the group, get stuck in a hole, or make danger cries, will often be tended to by alloparents. Suckling will occur as a comforting measure. Other behaviors common between alloparents and juveniles is rubbing and greeting, mostly ways to maintain social bonds between the group members (Lee, 1987).

Ecological Constraints

A look at most cooperative breeders finds them in warm, temperate, subtropical or tropical areas (Emlen, 1982a). Within stable and predictable environments, this image became the standard ecological definition for cooperative breeding species. However, many species began to be discovered in very unpredictable environments, especially among birds in Australia (Brown, 1987). These diverse environments split scientists into two schools (Emlen, 1982a). The k-selection school believed that high investment of resources among a few offspring was the most influential factor on cooperative breeding. This would have required a stable environment where resources were readily available, however, competition was high. The variable environment school believed that variable environments with unpredictable ecologies influenced cooperative breeding. In such circumstances, extra help would be essential to maintaining populations during harsh seasons (Emlen, 1982a). How does one explain such diverse environments developing similar social and strategies? A closer look at two of the characteristics of cooperatively breeding societies, delayed dispersal and de-

layed breeding, provide explanations for the ecological and social factors which encourage cooperative breeding. Dispersal is the "process of permanently leaving the natal territory" (Koenig et al, 1992). In most species, an individual will leave the natal group when it is able to move to a new territory and establish itself as an individual breeder. It is important to note that in most species, two breeding individuals serve as the most successful reproductive pair, where cooperative breeders are the exception (Emlen, 1982a). Delayed dispersal involves juveniles staying in their natal group past the age of dependent feeding. This can be up to one or two years past weaning (Brown, 1987). Delayed dispersal and helping behavior are usually co-occurring. For most mammals, there are two choices: to disperse and breed independently or to not disperse and help in their natal group. Many different factors influence whether an individual will disperse or stay. Factors include, the cost or risk of dispersal, the probability of establishing and finding a suitable territory, the probability of finding a mate, and the likelihood of reproducing successfully after having established oneself (Emlen, 1982a). Ecological variables influence all of the above factors. The costs of dispersal include food and shelter. Also, there is the risk of predation. The group territory is usually an area of high resource yield. Food resources and shelter areas have been well established. An individual who wishes to leave the group will be independent on finding food resources. In addition, groups usually have developed strategies to deal with predators. Alone, an individual is not able to adequately defend himself, especially if the individual is young and does not have experience defending its territory (Emlen, 1982a; Koenig et al, 1992). In areas of high competition, establishing and defending a suitable territory could be difficult for a potential breeder. Also, competition for mates can present added difficulties. The level of competition for unestablished territories and mates, influenced by the population density and rates at which territories are abandoned, vary and influence how likely or unlikely a species is to disperse (Koenig et al, 1992). Finally, the likelihood of successfully reproducing after finding ones own territory and mate, is influenced by the "degree of difficulty in raising young" (Emlen 1982a). For different species and environments, the degree of difficulty varies. The measurable fitness of an individual trying to breed on its own is a combination of its ability to establish a territory with mate and its likelihood of successfully raising offspring (Emlen, 1982a). The original hypothesis to explain ecological influences only focused on the "habitat saturation" hypothesis (Koenig et al, 1992). It suggested that the inability for the lone individual to effectively compete to gain access to territory and mates most influenced its decision to stay with its natal group. A competing hypothesis was the "benefits of philopatry" reasoning (Koenig et al, 1992). It suggested

that the benefits of staying, such as efficient foraging and protection from predation, most influenced the decision to stay. Neither one effectively explains cooperative breeding and delayed dispersal in the diverse ecological areas mentioned at the beginning of this section. For in variable environment, there may be available territory and mates, however the risks of leaving the group may not be great enough to encourage the behavior (Koenig et al, 1992). Koenig et al (1992) suggest a more inclusive theory, the delayed dispersal threshold model. Its parameters are set by five limiting factors: (1) relative population density, (2) fitness differential between dispersal and breeding vs. delayed dispersal and helping, (3) fitness of floaters (breeding individuals with no territory. most often found in birds), (4) distribution of territory quality, and (5) spatiotemporal environmental variability. This theory integrates the "habitat saturation" model and the "benefits of philopatry" hypothesis, and says that no factor is ultimately determining. In certain types of comparisons between similar groups, a single factor may predict the differences, however, all the parameters must be taken into account before an evaluation of delayed dispersal is made. Delayed dispersal is claimed to be a cause of group living in cooperative breeders (Mumme, 1997). This close relationship between group living and cooperative breeding emphasizes the evolution and maintenance of delayed dispersal. The importance of group living for cooperative breeders, makes delayed dispersal also an essential aspect of any helping society. Delayed breeding is a difficult behavior to grasp. The possible sources and influences can vary greatly. However, it has been observed in almost all cooperative breeding species. Delayed breeding appears to be very costly in terms of overall reproductive fitness of the individual (French, 1997). It is an important concept, because an individual is either limiting its ability to breed or is forcibly being prevented from breeding for the purpose of helping in its natal group. Reproductive suppression is closely linked with dispersal (Brown, 1987). Delayed dispersing groups and reproductive suppression co-occur, obviously for the reason that an individual leaves its natal group for the sole purpose of breeding. Delayed dispersal and group living can result in mating conflicts and social difficulties. Important results of suppressed reproduction include incest prevention and reduced intergroup conflict (French, 1997). Understanding how suppressed reproduction is achieved is much more difficult. There is evidence suggesting both endocrinological and behavioral influence. A look at both of these options helps evaluate which ecological constraints lead to suppressed reproduction. Cooperative breeders exhibit group breeding along a continuum from singular to plural breeding (Mumme, 1997). Singular breeders maintain one breeding pair and plural breeders have more than one pair of breeders. In singular breeding societies,

alloparents are most likely non-breeding. Plural breeders must depend on breeding alloparents. Most mammals are singular breeders and this presents a problematic situation. Mammals such as primates, have very low overall reproductive rates. Investment into individual births rather than litter births have developed over time. It would seem very detrimental to an individual of breeding capabilities to stay in the natal group and not breed. Because of this inconsistency, it is important to understand how suppressed or delayed breeding is maintained among mammals in cooperative breeding societies. Reproductive suppression is "the failure of some individuals within a social group to reproduce" (Mumme 1997). Reproductive suppression suggests that either some social or ecological factor must be limiting the individuals ability to participate in reproduction or some endocrinological or physiological limitation must be induced upon the individual. It is difficult to divide these two types of limitations into a dichotomy. Differences of suppression exist between separately ranked individuals and between the sexes. Male suppression is more commonly regulated through behavioral mechanisms, while female suppression is more commonly a mixture of both endocrinological and behavioral mechanisms (Mumme, 1997). The gray wolf, examined by Asa (1997), provides an example of behavioral suppression within group members. Especially among males, it can be found that the alpha male will intercede on subordinates attempting to copulate. If the males dominance is well established, his presence or staring can prevent reproductive behavior in subordinates, however, fighting is likely to ensue. In the gray wolf, all suppression among males and females is entirely behavioral. Male testosterone levels, testis size, and semen production is equivalent across ranks. Among females no difference is observed in estrogen, progesterone or luteinizing hormone. Because reproductive suppression is monitored by an individuals parents, it can be hypothesized that such suppression helps to prevent incest relationships. The alpha male breeder assumes the position of having fathered most of the children. Young males mating with other females will most likely be mating with close relatives, therefore reproductive suppression among the gray wolf allows close, small, genetically related groups remain together without the fear of incest. This also helps maintain a level of inclusive fitness in helping. Staying in close genetically related groups gives genetic justification to helping behavior. Primates are well studied for their reproductive suppression. Primates are extremely important to study because of their k-selection, as mentioned above, animals which give rise to few offspring, and heavily invest resources into those offspring. There are different levels of reproductive suppression. It is important to look at these different times where reproduction can be suppressed to identify their social

significance. Table 1 lists many of the different strategies of suppression (French, 1997). An examination of Callitrichid primates, including marmosets and tamarins, summarizes some of the behaviors found in Table 1. Among callitrichids, delayed breeding among subordinates is very common. French (1997) found that among callitrichids, delays in puberty served as a physiological mechanism delaying breeding. There is much evidence for the social control of such delays. It has been found that cotton-top tamarin females housed away from the natal group entered ovulation much earlier than females housed with the native group (Tardif in French, 1997). However, isolation was not enough to return females to normal ovulation patterns. Only when housed in isolation with unfamiliar males, did females regain normal ovulatory patterns. It appears that female delayed puberty is under social constraints depending on a females rank, and the males around her (French, 1997). These restraints help maintain cooperative breeding and prevent incest and conflict over mating. In the common marmoset, ovulatory suppression has been observed to be regulated by olfactory cues. It is important to note that the individual cues must come from the females natal dominant female (Barret et al., 1993). Such a method is important in understanding the development of singular breeding. A dominant female would have to be able to limit the breeding ability of other females (French, 1997). Postconception methods of suppression are not nearly as common as preconception. Examples of stress or aggression induced abortions are very rare but can have impacts on the overall fitness of the individual. These may serve as mechanisms to prevent females from attempting to breed rather than ways of maintaining cooperative breeding (French, 1997). Targeted aggression is the most common type of behavioral preconception mechanism among callitrichids. Targeted aggression can be more abusive between females than males, however, the number of aggressive encounters between males and between females are observed to be equal. Aggression is also used as a tactic in preventing unrelated females from entering the social group. This behavior may help maintain singular breeding by keeping the natal group closely related and increasing inclusive benefits to staying and helping (French, 1997). Finally, behavioral mechanisms of postconception suppression are an unlikely method for maintaining singular breeding. Behaviors such as infanticide are not observed among wild callitrichids and thus are not considered to be effective methods by dominant individuals to maintain breeding status among groups (French, 1997). Again, it is important to emphasize that cooperative breeding societies exist among a continuum of singular to plural breeders. No society is strictly singular or plural, often times exceptions are found within these societies. It is a careful balance defining how singular breeding is maintained. Many of

the factors described above contribute to that maintenance, but a complete understanding of such behaviors is dependent on more conclusive studies of delayed breeding patterns in mammals. Defining ecological factors which may contribute to delayed breeding is difficult. Some relationships can be inferred to delayed dispersal, for often times, delayed breeding and delayed dispersal co-exist. However, it would be important to conduct field studies examining habitat quality and suppressive mechanisms (French, 1997).

The previous discussions have worked to emphasize the social and ecological influences that help establish cooperative breeding among certain societies. Small groups of closely related individuals provide inclusive benefits for cooperative breeding. Measuring fitness between the options to stay in one's natal group and help versus dispersing to breed establishes the criterion for cooperative breeding. Mechanisms for delayed breeding serve to maintain cooperative breedings by keeping individuals within their natal group. It is important to note that cooperative breeding is the exception to the rule. It is more common to find species leaving their natal group to establish their own territories, but this just emphasizes the importance of looking at both ecological and social conditions which maintain cooperative breeding.

Adaptive Significance

The introduction provides a brief summary of possible adaptive strategies for cooperative breeding. An important question to ask is "who is benefiting?" There are three main players in cooperative breeders, the helper, the mother, and the infant. How does each one gain in relation to the behaviors? A look at each individual will help explain exactly where the advantages of helping can be identified. The infant has much to gain, being the object of help. Protection from predators, protection from environmental stresses, adoptive advantages, social learning, and nutritional gains are the main benefits for infants involved in cooperative breeding. Protection from predators is an important benefit. An underlying theme for benefits of all individuals is infant survival. As seen, for reasons of reproductive success and inclusive fitness, protecting infants is an important part of helping. In chimpanzees, protection by family when the mother is not near the infant is common (Nishida, 1983). Along the same lines, elephants have been observed helping young walk and bringing young back to the group if it happens to wander too far. Elephant societies are made up of mostly related females. If the mother is absent, another female will look after the infant and make sure it does not jeopardize itself (Lee 1987). In certain circumstances, an infant's mother may be killed. In these instances, helpers provide possible adoptive individuals. Adoption of orphaned infants by helpers has been observed in the common

langur after the infants mother was killed by dogs (McKenna, 1979). This data supports the "adoption" hypothesis proposed by Gray (1985), referred to in the introduction. Growing up in a group provides important opportunities for social learning. Interaction with more adults and other group members teaches the infant about social behavior and group dynamics.

In chimpanzees, a helper was seen preventing a child from eating a food which was not part of their diet. Therefore, through the helpers the infant learned which foods were edible and which foods were not (Nishida, 1983). Advanced social learning can help a child become independent more quickly, giving it reproductive advantages. Finally, the infant may achieve nutritional gains through alloparenting. Communal suckling is one form of increased milk available for infants. Goldizen observed adult helpers providing food to infants in saddle-backed tamarins. Often times infants would steal food long past their dependence on helpers and their mother (1987). The potential benefits for infants are clear. It is important to note that many times alloparenting can have ill effects on infants. Other breeding mothers have been observed abusing unrelated infants. This can in extreme cases result in the death of the infant. Infants have no energetic consequences with alloparenting, therefore any helpful behavior is entirely beneficial for the infant. As a result, it is difficult to justify the evolution of helping behavior through the benefits of infants. The mother is an important player in analyzing costs and benefits of cooperative breeding. Gray (1985) mentions the "mother relief" hypothesis as a possible adaptive explanation for alloparental behavior. This is probably the most common cited benefit for mothers. Extra feeding time and leisure time is important for mothers in many ways. The cost of increased nutrition when a mother has dependent young is expressed through the infants nutritional needs, requirements to maintain lactation, and energy requirements for foraging for high quality foods can be increased if an infant must be looked after or carried at the same time. (Lee 1989). Among elephant societies, the mother is the key provider of milk. Rarely will other females allow young to feed from them. Therefore it is important that the mother meet nutritional requirements to maintain lactation (Lee 1987). Possibly the most important selective factor comes if the mothers inter-birth interval can be reduced to increase her lifetime reproductive fitness (Lee 1989). Helpers maintain growth levels while the mother does not have to exert as much energy. As a result, the mother can energetically recover faster and return to estrous or reproductive capability sooner. Describing the adaptive benefits for the helper takes a step towards the more complicated. Who is the helper is the first question to be asked. The helper can vary from nulliparous (non breeding) females, to parous (breeding) females, to males. Each has a different adaptive reason to partici-

pate in cooperative breeding, all in attempts to increase their lifetime reproductive success. In most cases, helping females will be nulliparous. The energetic requirements for breeding females to take care of their own young, in addition to helping other infants is rare. The exception lies in species that have very crowded breeding groups and allow communal raising, such as in seals. Referring again to Gray's list of adaptive hypotheses, nulliparous females serve to gain through "learning to mother" and the "status elevation" hypothesis (1985). Gaining experience in mothering is an important result of allomothering. The allomother is allowed to carry, raise, and play with the offspring. Through this interaction, allomothers learn efficient methods for raising young. Among chimpanzees, Nishida noticed that parous females, would rarely contact or interact with infants. On the otherhand nulliparous females could gain important maternal experience through handling the infants, experience already possessed by the parous females (1983). Goldizen noticed that in wild callitrichids, mothers were better at rearing their own young if they had had experience carrying when they were younger (1990). Riedman points out that learning to mother can be extremely important among k-selected individuals. Parent quality would be important in such species, therefore, anything to enhance future parenting behavior would be beneficial to lifetime reproductive success (Riedman, 1982). There are some exceptions to the learning to mother hypothesis. Among vervet monkeys, older, experienced, adult mothers are often the ones seen allomothering. Their involvement in allomothering would have to be for some reason other than maternal experience. From a selective point of view, learning to mother could be an important characteristic. Societies where such a behavior was present, could reach greater future reproductive successes. Experience would allow young females to enhance their long-term reproductive fitness (Terborgh and Goldizen, 1985). "Status elevation" can be a strong benefit for allomothering. In wild callitrichids, the death of the dominant, breeding female, will result in a helper inheriting that position. In addition, the individual inherits potential helpers through offspring she had helped rear (Goldizen, 1990). Status elevation does not require inheriting a breeding position. Bond formation and coalition forming against the dominant female can be a possible result of helping, too. Status elevation is difficult to address evolutionarily. Because cooperative breeders live in environments with highly competitive breeding schemes, staying at home waiting to inherit one's natal territory can serve as the most successful method of reproduction. However, it is difficult to judge and the quantitative evidence does not exist. Adult, parous, females have much less to gain through helping. However, Emlen proposes an entirely different hypothesis which may have contributed to the selection for alloparenting behavior. He analyzed the role of group

conflict and looks at the role of the breeding helper. Emlen came to the conclusion that because the helper has much to gain from group living (at least in environments which have extreme constraints to breeding independently), the helping breeder will try to minimize the possibility of being expelled from the group through helping (1982b). Individuals could be selected for such a characteristic and abilities to avoid group conflict. A spiteful mechanism is referred to by Gray as the "selfish allomother" hypothesis. Nishida's observations with chimpanzees, provide a case in point. Abuse toward young was common from parous females. This included pushing and pulling young out of trees and shrubs, or striking another infant with her knuckles. This sort of abusive relationship has never been observed to produce serious physical injury, however, the existence of "abuse" is still present. Finally, the helping male as a beneficiary to alloparenting. The most important involvement of male help is in the polyandrous behaviors observed among tamarins. Usually in trios, two males will assist one female. Each male will copulate with the female, and after giving birth, both males will remain to help. For a female, carrying offspring can be extremely energy consuming. Having a helper, especially male, can greatly increase the mother's ability to forage and feed effectively. However, it is unlikely that one male will assume this responsibility because of the individual costs to his fitness, two males can share the roles of carrying and foraging effectively, preventing any major compromises in fitness (Terborgh and Goldizen, 1985). This system is probably a compromise for males to mutually enhance their reproductive success (Goldizen, 1990). Especially among callitrichids, where twinning is common, females could rarely raise the offspring without help. Two male helpers can successfully raise more offspring than a single male mate (Goldizen, 1990). Maintaining anonymous paternity by the female maintains that both males who have equal mating opportunities will maintain helping strategies. Among callitrichids, ovulation and physical sign of estrus are concealed so that males are unable to detect when the female is ovulating. It is not known if other indicators exist, but concealed ovulation may have been an important strategy in maintaining the polyandrous trio (Goldizen, 1987). There is one final set of benefits which may be incurred through cooperative breeding. Group benefits serve to help all of the individuals in a society. Among cooperative breeders, group living is observed to be a result of delayed dispersal (Mumme, 1997). This close relationship between delayed dispersal and the benefits of group breeding serve as an important advantage for group living cooperative breeders. All the advantages of group living, increased foraging efficiency, protection from predators, etc., will serve as benefits for cooperative breeders. Gray also suggests the "group cohesion" hypothesis, that the construction of social bonds through helping

maintains the structure of the group.

Fitness and Natural Selection

A genetic link to group and individuals must be established to evaluate whether there is an selective advantage of cooperative breeders. A look at total fitness through its four components; current direct fitness, current indirect fitness, future direct fitness, and future indirect fitness; provides reasoning for the selective advantages of cooperative breeding (Lucas et al, 1997). Current direct fitness can be measured as the number of offspring an individual can have. For the breeder, cooperative breeding is definitely advantageous. As seen in elephants and callitrichids, help provided to the individual increases infant survivorship and the direct fitness of the breeder. Current direct fitness does not benefit the helper because more often than not, the helper has non-breeding status. Future direct fitness is evaluated by the individuals lifetime reproductive success. This would be overall survivorship of young and increased fecundity over a lifetime for helpers (Lucas et al, 1997). Benefits inclusive of future direct fitness are parental experience for helpers and inheritance of breeding positions and potential alloparents (Mumme, 1997). All of these factors promote survivorship and the lifetime reproductive success of an individual. Indirect fitness gains may be the most important influence on cooperative breeding. Mumme cites seven extensive studies on the indirect fitness gains of alloparental behavior and five of the seven presented significant evidence for benefits of reproduction. More and more evidence is also being presented that alloparental care is preferentially directed towards kin versus non-kin (1997). The effect of helpers on breeders is a decrease in energetic costs for the breeders. The decrease in work increases the survivorship and future reproduction of those who are helped. As most cooperative breeding societies consist of closely related individuals, most benefits of helping will be toward kin and therefore increase the future indirect fitness of the helper. In the end, most of the energetic and reproductive benefits of cooperative breeding is speculative. Much more research concerning the measured individuals benefits must be conducted if final answers concerning the evolution of cooperative breeding is to be assessed (Lucas et al, 1997).

Conclusion

This paper has tried to objectively study cooperative breeding among various mammalian species. Though the data concerning mammals is more limited than that of avian societies, it is clear that many mammalian societies have strong expressions of cooperative breeding. It is important to return to the original question. "Are primates really unique?" The existence of cooperative

breeding across extremely diverse taxa tends one to answer "no". On the other hand, primate groups like the tamarins and marmosets exemplify very complex methods of breeding. Examples such as concealed ovulation which also exist in humans calls into question our understanding of the ability of primate groups to maintain cooperative breeding. It may be that primates are able to integrate and conform their social behavior to maintain cooperative breeding, while other species are more susceptible to ecological constraints. The evidence does not exist to say that primates are particularly "unique" when studying cooperative breeding. On the other hand, primates express a high level of variability among behavioral patterns, and added benefits and costs related to cooperative breeding. This suggests that primates may have further integrated cooperative breeding as more than just a social reproductive mechanism. Until an integrative approach is taken with cooperative breeding, studying breeding against both social hierarchy and group dynamics, it is impossible to speculate on the inherent attributes of our fellow relatives—the primates.

References Cited

- Asa, C. S. (1997). Hormonal and Experiential Factors in the Expression of Social and Parental Behavior in Canids. In Solomon, N. G., & French, J. A. (Eds.), *Cooperative Breeding in Mammals* (pp. 129-149). New York: Cambridge University Press.
- Brown, J. L. (1987). *Helping and Communal Breeding in Birds*. Princeton: Princeton University Press.
- Emlen, S. T. (1982a). The Evolution of Helping. I. An Ecological Constraints Model. *American Naturalist*, 119, 29-39.
- Emlen, S. T. (1982b). The Evolution of Helping. II. The Role of Behavioral Conflict. *American Naturalist*, 119, 40-53.
- French, J. A. (1997). Proximate Regulation of Singular Breeding in Callitrichid Primates. In Solomon, N. G., & French, J. A. (Eds.), *Cooperative Breeding in Mammals* (pp. 34-75). New York: Cambridge University Press.
- Goldizen, A. W. (1990). A Comparative Perspective on the Evolution of Tamarin and Marmoset Social Systems. *International Journal of Primatology*, 11, 63-83.
- Goldizen, A. W. (1987). Tamarins and Marmosets: Communal Care of Offspring. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (Eds.), *Primate Societies* (pp. 34-43). Chicago: Chicago University Press.
- Gray, J. P. (1985). *Primate Sociobiology*. New Haven: HRAF Press.

Koenig, K. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L., & Stanback, M. T. (1992). The Evolution of Delayed Dispersal in Cooperative Breeders. *The Quarterly Review of Biology*, 67, 111-150.

Lee, P. C. (1989). Family Structure, Communal Care, and Female Reproductive Effort. In Standen, V., & Foley, R. A. (Eds.), *Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals* (pp. 323-340). Oxford: Blackwell Scientific Publications.

Lee, P. C. (1987). Allomothering Among African Elephants. *Animal Behavior*, 35, 278-291.

Lucas, J. R., Creel, S. R., & Waser, P. M. (1997). Dynamic Optimization and Cooperative Breeding: An Evaluation of Future Fitness Effects. In Solomon, N. G., & French, J. A. (Eds.), *Cooperative Breeding in Mammals* (pp. 171-198). New York: Cambridge University Press.

McKenna, J. J. (1979). The Evolution of Allomothering Behavior Among Colobine Monkeys: Function and Opportunism in Evolution. *American Anthropologist*, 81, 818-840.

Mumme, R. L. (1997). A Bird's-Eye View of Mammalian Cooperative Breeding. In Solomon, N. G., & French, J. A. (Eds.), *Cooperative Breeding in Mammals* (pp. 364-388). New York: Cambridge University Press.

Nishida, T. (1983). Alloparental Behavior in Wild Chimpanzees of the Mahale Mountains, Tanzania. *Folia primatologica*, 41, 1-33.

Riedman, M. L. (1982). The Evolution of Alloparental Care and Adoption in Mammals and Birds. *The Quarterly Review of Biology*, 57, 405-435.

Solomon, N. G., & French, J. A. (1997). The Study of Mammalian Cooperative Breeding. In Solomon, N. G., & French, J. A. (Eds.), *Cooperative Breeding in Mammals* (pp. 1-10). New York: Cambridge University Press.

Terborgh, J., & Goldizen, A. W. (1985). On the Mating System of the Cooperatively Breeding Saddle-Backed Tamarin (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, 16, 293-299.