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Commentary

Application of an integrated cooperation approach to human cooperative breeders

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In their thoughtful overview, Bergmüller et al. (2007), point out that to fully understand cooperative behavior among cooperative breeders more, it is important to consider the combined influences and interactions of direct and indirect fitness benefits. Hamilton's rule, along with its reformulation by Brown (1975), initially provided a much-needed heuristic framework to address the puzzling question of why helpers help (Brown, 1974, 1987; Emlen, 1991; Vehrencamp, 1978). The indirect fitness benefits associated with helping closely related kin are empirically supported by studies among several species, including humans. These have found correlation between the degree of genetic relatedness of the helper and the amount of allocate they provide (Denham, 1974; Hames, 1988; Ivey, 2000; Skutch, 1987; overview in Emlen, 1991; Koenig and Mumme, 1991). While historically the emphasis has been placed on indirect benefits, the focus and value of Bergmüller et al. is to turn our attention to direct fitness benefits that may account for helping behavior, and to link these explanations to general theories of cooperation. By integrating what traditionally have been the distinct approaches of cooperative breeding and cooperation into a unified framework and language, the authors provide an alternative means to look at the question of why helpers help, and to analyze diverse expressions of cooperation in a more consistent way.

Across human populations, mothers commonly rely on the help of their spouses, grandmothers, sisters, own children and other related and nonrelated individuals to raise young (Bove et al., 2002; Flinn, 1988; Hawkes et al., 1997; Hrdy, 1999, 2005; Ivey, 2000; Kramer, 2005a,b; Turke, 1988, 1989). Even though human mothers routinely depend on helpers, human mating systems are rarely placed in the context of cooperative breeding. The integrated framework proposed by the authors has particular value for resolving the challenges to

situate humans within the framework of cooperative breeding for two interrelated reasons. First, because human helpers in many cases are not sexually mature, the opportunity cost and direct benefits associated with traditional explanations focused on delayed dispersal are not applicable. Second, modeling cooperative breeding within a resource procurement strategy that involves wide spread cooperation and sharing, as is common among humans, would benefit from an integrated approach to helping behavior.

1. Sexually immature helpers; segregating staying from helping

Why help is often enmeshed in the question of why stay. Sexually mature offspring may stay in their natal territory or group if leaving incurs the risk of mortality, predation or not finding a mate. Evidence generally supports that among cooperative breeders, sexually mature offspring delay their own reproduction when constraints exist either in mating opportunities or in the availability of the resources and/or territory necessary to compete for mates and successfully reproduce (Brown, 1987; Emlen, 1982; Stacey and Koenig, 1990; Woolfenden and Fitzpatrick, 1984). Likewise among humans, the postponement of marriage and low marriage rates are associated with ecological constraints in access to resources, land or wealth necessary for reproduction (Clarke, 1993; Clarke and Low, 1992; Strassman and Clarke, 1998). Although delayed dispersal of sexually mature offspring is often attributed to being critical in setting the stage for cooperative breeding in birds and animals (Mumme, 1997), as the authors discuss, the benefits to stay do not necessarily explain why helpers help. For example, among fork-marked lemurs who live in competitive environments, offspring may remain in their natal territories following sexual maturity. The gains to offspring survival appear sufficient for parents tolerate delayed dispersal even though these individuals do not help and the increase in group size raises feeding competition and compromises the nutritional status of parents (Schülke, 2003).

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The authors make the point that since staying is not synonymous with helping, we need a more inclusive theory to explain cooperative behavior. Much of the cooperative breeding literature also makes the tacit assumption that helpers are sexually mature. Consequently, the cost that is necessary to explain from an evolutionary point of view, is why helpers forego or compromise their reproductive success to help raise young that are not their own. But, the payoff structure may be very different if helpers are not sexually mature. Importantly, depending on the helper's developmental and reproductive status, the costs and benefits of helping involve very different tradeoffs and explanations (Kramer, 2005b, Table 1.2).

Among humans, and perhaps among other cooperative breeders, juveniles are a significant, but under discussed class of helpers (Kramer, 2002, 2005a,b). As a juvenile, the expensive cost of delaying reproduction to help raise siblings is obviated. In addition, Clutton-Brock (2002) points out that the cost to help may be overstated, especially when the benefits to the helper's survival are high. This point has clear implications to humans, since juveniles often begin to help *before* they are autonomous feeders and are still dependent on others for their growth and survival. Because human juveniles fall short of where they need to be to make it on their own, they have much to gain from maintaining their dependence on others. While helping has an energetic cost, because juveniles are not yet fully grown or sexually mature, the opportunity cost for juveniles to help is attenuated since there are few competing ways to spend their time, they are not competing for mating opportunities or compromising their own reproductive success by helping.

2. Low-cost juvenile help

Even though human juveniles are sexually immature and closely related to their siblings, the cost for them to help raise their siblings is low for another reason. From a juvenile's point of view, the human feeding niche has the important characteristic of incorporating a broad diversity of resources that require variable capture and processing costs. Unlike other primates, because children's ability to support themselves falls below their consumption, human young are subsidized by others through out much of their growth and development, and in some cases even long after sexual maturity (Kaplan, 1996; Kramer, 2004). In many ecological situations, while juveniles depend on others for some of what they need to survive, they are able to produce some resources at the level of their own consumption and other resources *in excess* of their consumption. For example, among foragers living on the *llanos* of Venezuela, a Pumé boy living is successful at bringing home a catch of fish, enough fish to feed himself and his siblings. But, he also depends on shares of processed plant food and larger game from his male and female kin. In another example, among subsistence agriculturalists, an 11-year-old Maya boy spends 3% of daylight hours, or about a half an hour a day, harvesting maize—enough maize per day to meet his own consumption as well as that of his siblings. However, he does not directly consume the maize he harvests but rather after it has been shelled, leached, soaked, ground into meal, and processed as tortillas—tasks that his older sisters and

mother perform (Kramer, 2005b). In humans, although juveniles are still dependent on others, they nonetheless are net producers of some resources. This extends to other classes of helpers as well. Under these conditions, self-provisioning and helping to provision others are often incorporated into an individual's general suite of subsistence activities. This affects time allocation tradeoffs and the cost to help. The decision tree presented by the authors gives us a new way to rethink some of the assumptions commonly made about the cost to help.

Across the diversity of traditional human subsistence strategies (foraging, horticulture, pastoralism), resource procurement involves wide-spread economic cooperation and sharing (Alvard, 2002; Alvard and Nolin, 2002; Gurven et al., 2000; Hames, 1990, 2000; Hawkes, 1992; Kaplan et al., 1990; Smith and Boyd, 1990), both among closely related kin as well as across extended families and unrelated households. Adding what we know about cooperation, as the authors suggest, would greatly benefit our understanding of helping behavior. Although humans frequently are overlooked in the comparative cooperative breeding literature, anthropological samples offer a rich and challenging database to develop new models that incorporate diverse forms of cooperative behavior and a broad range of strategies to raise young.

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