

Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an Ache reservation[☆]

Wesley Allen-Arave^{a,*}, Michael Gurven^b, Kim Hill^c

^aDepartment of Anthropology, University of New Mexico, Albuquerque, NM 87131, USA

^bDepartment of Anthropology, University of California Santa Barbara, Santa Barbara, CA 93106, USA

^cSchool of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA

Initial receipt 9 December 2006; final revision received 24 March 2008

Abstract

Cooperation among relatives is often regarded as evidence of kin selection. Yet altruism not requiring shared genes can also evolve among relatives. If characteristics of relatives (such as proximity, familiarity, or trust) make kin preferred social partners, the primary causes of nepotistic biases may reside principally in direct fitness payoffs from cooperation rather than indirect fitness payoffs acquired from aiding collateral kin. We consider the roles of kin selection and reciprocal altruism in maintaining nepotistic food transfers on an Ache reservation in northeastern Paraguay. Households do not primarily direct aid to related households that receive larger comparative marginal gains from food intake as we would predict under kin selection theory. Instead, (1) food transfers favor households characterized by lower relative net energy production values irrespective of kinship ties, (2) households display significant positive correlations in amounts exchanged with each other, suggesting contingency in food transfers, and (3) kinship interacts with these positive correlations in amounts households exchange with each other, indicating even stronger contingency in sharing among related households than among unrelated households. While kin are preferred recipients of food aid, food distributions favor kin that have given more to the distributing household in the past rather than kin that would benefit more from the aid. Such discrimination among kin accords better with reciprocal altruism theory than with kin selection theory. © 2008 Elsevier Inc. All rights reserved.

Keywords: Nepotism; Kin selection; Reciprocal altruism; Resource sharing; Human behavioral ecology; Ache

1. Introduction

Behavioral studies demonstrate that individuals in small-scale societies preferentially aid close kin over more distant kin and nonkin (e.g., Betzig, 1988; Betzig & Turke, 1986; Chagnon, 1981; Chagnon & Bugos, 1979; Flinn, 1988; Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000b; Hames, 1987; Hawkes, 1983; Patton, 2005). Such nepotistic biases are often cited as evidence that indirect fitness payoffs (Hamilton, 1964; Maynard Smith, 1964) have shaped human social interactions. Kin selection theory is so elegant and appealing that theorists often attribute instances of nepotism

to inclusive fitness benefits without a careful consideration of alternatives. However, pathways to altruism not requiring shared genes can lead to increased levels of cooperation among relatives over nonrelatives if kin possess characteristics that are preferred in social partners.

We examine the roles of indirect fitness impacts and reciprocal exchanges in maintaining nepotistic food transfers among reservation-living Ache forager-horticulturists of northeastern Paraguay. We previously reported that Ache households give preference in food distributions to recipient households that contain at least one close relative (Gurven, Allen-Arave, Hill, & Hurtado, 2001). This nepotistic bias in food transfers follows lines of genealogical relatedness rather than lines of Ache social kinship terminology (Allen-Arave, Gurven, Hill, & Hurtado, 1999). Theorists have used similar results from other populations to argue for the importance of indirect fitness payoffs in patterning human social interactions. Yet, our previous report also reveals that even among households linked by a close kinship tie, the amount of food

[☆] The National Science Foundation (grant no. 9617692), L. S. B. Leakey Foundation, University of New Mexico Student Research Allocations Committee, and University of New Mexico Office of Graduate Studies Research Project and Travel grants provided support for this research and its dissemination.

* Corresponding author.

E-mail address: allenara@unm.edu (W. Allen-Arave).

any household D (donor) transfers to any household R (recipient) is correlated with the amount household D receives from household R (Gurven et al., 2001). We expect such a result if returns from reciprocation provide the adaptive payoffs of the transfers but not if nepotistic investments in indirect fitness benefits provide the adaptive payoffs of the transfers. The presence of both nepotism and correlated amounts of food transferred between related households challenges us to disaggregate the relative contributions of indirect fitness impacts and reciprocal benefits in maintaining nepotistic Ache food transfers. The present paper presents new analyses to (1) examine the direction of imbalances in food transfers between households and (2) consider the difference in net caloric production between households.

1.1. Kin selection theory

Researchers commonly predict from kin selection theory that altruistic aid will positively correlate with the degree of relatedness between interactants. Yet, kin selection theory does not presume that individuals should *always* act altruistically toward all relatives, nor should they necessarily share mainly with close relatives. Mathematical models illuminate that natural selection can favor nepotistic acts when the benefit to the recipient, B , discounted by the coefficient of genetic relatedness, r , is greater than the cost to the provider, C : $Br > C$ (Hamilton 1964). Whenever a household can obtain higher inclusive fitness payoffs by hoarding resources rather than providing them to relatives, kin selection theory suggests that no transfer will occur. Likewise, when distant relatives obtain a much larger positive fitness impact than close kin from assistance, kin selection theory predicts higher rates of transfer to distant kin than to close kin. Thus, an evaluation of kin selection theory must consider not only relatedness, but also the costs and benefits of aid.

1.2. Direction and magnitude of imbalances

If nepotistic transfers constitute investment in indirect fitness, the direction and magnitude of imbalances within dyads of related households should attend to (1) the capability of household members to produce food calories, (2) the number of hungry mouths a household contains, and (3) the ages of household residents. All of these factors affect the marginal gains of food intake on household summed reproductive value (Fisher, 1958). Given the reasonable assumption that the curve relating food intake to fitness is negatively accelerated, kin selection theory implies that imbalances in food transfers between related households should favor households that produce less food over households that produce more food, when we hold other factors constant. Holding all else constant, kin selection theory also implies that imbalances between related households should favor households with more mouths to feed over households with fewer mouths to feed.

The ages of household members matter as much as the number of residents a household contains for determining the fitness impact a transferred unit of food may have for a household because energy requirements and reproductive values peak in young adulthood. Resting metabolic energy expenditure rates indicate that individuals aged from their late teens to fifties require more energy than younger and older individuals do (National Research Council, 1989a; World Health Organization, 1985). Young adults also possess a larger potential to translate food energy into inclusive fitness gains than other age classes, owing to the greater number of childbearing years likely to await young sexually mature and about-to-mature individuals in the future. Thus, individuals in the middle of the lifecourse can return greater indirect fitness benefits to donor kin from large amounts of food than younger and older individuals can.

Despite straightforward theoretical expectations that food flows should favor individuals of high reproductive value, application of this logic to human populations presents complications. Several theorists (e.g., Charlesworth & Charnov, 1981; Hamilton, 1964; Rogers, 1993; Taylor & Frank, 1996; Trivers, 1971) have noted that the reproductive value of donors and recipients should alter the costs and benefits of giving and receiving aid. However, measures of reproductive value do not provide an adequate estimate of the expected inclusive fitness contribution made by individuals in species, such as ours, with child altriciality and common allocare. While prereproductive and postreproductive individuals cannot produce copies of their genes in the form of offspring, they regularly assist copies of their genes located in other relatives through activities such as baby-sitting (Bock, 1995, Fig. 57; Ivey, 2000; Turke, 1988; Weisner & Gallimore, 1977), passing on important skills and knowledge (Bieseke & Howell, 1981; Liederman & Liederman, 1977), provisioning during times of need (Hawkes, O'Connell, & Blurton Jones, 1997), or offering protection and support (Chagnon & Bugos, 1979). The expected fitness contribution made by individuals—*especially postreproductive individuals*—is therefore underestimated by reproductive value measures alone because direct reproduction is not the only way to increase inclusive fitness. Still, food requirements and fertility measures alike indicate that food transfers, which enhance inclusive fitness, should predominantly favor households containing young reproductive-aged residents over households containing other age classes, when we control for the number of residents and their production abilities.

1.3. Reciprocal altruism

Any valid evolutionary explanation accounting for exchanges between nonkin may also apply to economic interactions between kin. Thus, we should never a priori assume that cooperation among kin results from inclusive fitness benefits to the exclusion of other pathways to cooperation. We now consider the role reciprocal altruism may play in food exchanges among relatives.

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