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

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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.
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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

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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 babysitting (Bock, 1995, Fig. 57; Ivey, 2000; Turke, 1988; Weisner & Gallimore, 1977), passing on important skills and knowledge (Biesele & 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 predominately 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.

Reciprocal altruism (Trivers 1971) can evolve as long as the cost of aiding another individual is outweighed by the benefit of receiving aid from that individual later, devalued by the probability that aid will be returned (Boyd, 1990). If the reciprocal exchange is profitable, individual altruists can expect payback in the future from self-interested actors who wish to continue obtaining the benefits that accrue from long-term cooperation. Such cooperation is even more likely to appear when punishment of defectors is possible (Fehr & Gächter, 2002; Ostrom, Walker, & Gardner, 1992; Yamagishi 1986). Nepotism may emerge independent of inclusive fitness benefits if individuals find their relatives more desirable as reciprocal exchange partners than nonrelatives.

1.4. Contingent reciprocity

Since reciprocal altruism provides exchange partners with the temptation to defect by accepting the benefits of their partner's altruism, without later paying any costs of altruistic acts themselves, reciprocal altruists must identify and punish or avoid free riders. For this reason, Hill and Kaplan (1993) argue that reciprocal altruism makes a central prediction of "contingency" in food exchanges. Hill & Kaplan define contingency as giving that is conditional upon expectations of future receiving, where individuals infer expectations of future receiving from prior sharing patterns. In modern societies, despite legal enforcement of reciprocity, contingency is implemented through practices such as credit checks. Only those who have met obligations to repay in the past are provided current goods and services with the expectation of repayment in the future.

Contingent reciprocity may prove difficult to detect because reciprocal altruism does not imply perfectly balanced exchanges between individuals. For an exchange to occur, reciprocal altruism theory predicts only that the average utility of the expected return outweighs the utility of the resource given up today. For example, a satiated household may pay little cost in providing (say) 2000 calories now, while benefiting greatly from (say) 500 calories at a future date when household members are ill or hungry. This may be analogous to the logic of insurance coverage in which one may pay premiums at a low utility cost for years in order to cover any high utility needs in the event of a future catastrophic shortfall. Additionally, if households engage in reciprocal exchanges that include several goods and services, an evaluation of food exchanges alone may underestimate the true contingent reciprocity occurring in the society. Despite these complications, we expect to find that the amount of food provided by any household D to any household R will correlate with the amount of food provided by household R to household D if reciprocal altruism plays a role in food transfers over the time scale of observation. Researchers studying other forager-horticulturalists populations have found dyadic correlations in food shares among the Achuar/Quichua/Zapara (Patton, 2005), Aka Pygmies (Gurven, 2004), Dolgan/Nganasan (Ziker, 2005), Hiwi (Gurven et al., 2000b), Mikea (Tucker, 2004), Pilaga (Gurven, 2004), Yanomamo (Hames, 2000), and Ye'kwana (Hames & McCabe, 2007). However, amounts of food given to all others does not correlate with amounts of food received from all others for Hadza large game (Hawkes, O'Connell, & Blurton Jones, 2001) nor Meriam turtle meat exchanges (Bliege Bird, Bird, Smith, & Kushnick, 2002).

1.5. Reciprocity among kin

Individuals may prefer close kin to distant kin and nonkin as partners for reciprocity. Relatives can make ideal candidates for reciprocal exchanges due to factors such as familiarity, trust, proximity, a high probability of future interaction, or an expectation that relatives will cooperate. When choosing among potential reciprocity partners, individuals should generally prefer partners who will provide the highest expected return benefit. Due to additive indirect fitness benefits on top of the direct benefits that collaborators gain from cooperation, reciprocal exchanges with relatives will often yield larger expected return benefits than reciprocal exchanges with nonkin.

Familiarity and emotional bonds fostered over time may make close kin easier to "read" and trust than distant kin and nonkin. Would-be transgressors likely experience more guilt from cheating victims with whom they have emotional ties (Frank, 1988). Furthermore, individuals may have good reason to trust close kin over other potential exchange partners because indirect fitness costs make cheating a close relative less profitable than cheating nonkin. If an exchange partner does fail to reciprocate due to deliberate cheating or an inability to repay (as can occur with a move, injury, or death), the loss is not complete for a slighted relative who still receives an indirect fitness benefit from their non-reciprocating relative's gain. Therefore, individuals assume less risk in initiating reciprocal exchanges with relatives than with nonrelatives.

Finally, the close proximity that kin often maintain can create more opportunities for exchange and increase the probability of future interaction, which promotes cooperation (Andreoni & Miller, 1993; Axelrod & Hamilton, 1981). At our study site, the homes of households joined by a close kinship tie tend to be nearer to each other than the homes of households not joined by a close kinship tie (Gurven et al., 2001).

The factors discussed above (familiarity, emotional bonds, trust, proximity, and indirect fitness costs and benefits) can promote an expectation among kin that a relative will cooperate, and experimental research has shown that expectations of cooperation promote and stabilize altruistic behavior (Dawes, 1980; Messick & Brewer, 1983). Thus, we might expect close kin to provide frequent goods and services in a stable arrangement of reciprocal altruism rather than simple kin-directed charity.

2. Study case: the Northern Ache

The Northern Ache are indigenous peoples of lowland northeastern Paraguay. At peaceful contact in 1971, they subsisted as nomadic hunter-gatherers. Beginning in the mid 1970s, the Northern Ache began residing in permanent horticultural settlements. Yet, they continue to utilize the forests around their settlements and spend up to half of their time on extended foraging trips (McMillian, 2001). Characteristics of Northern Ache forest life, including resource acquisition, time allocation, food sharing, life history theory, and group composition have been extensively studied over the past 25 years (Hill & Hawkes, 1983; Hill, Hawkes, Hurtado, & Kaplan, 1984; Hill & Hurtado, 1996; Hill, Kaplan, Hawkes, & Hurtado, 1985; Hurtado, Hill, Hawkes, & Kaplan, 1985; Kaplan & Hill, 1985; McMillian, 2001). Aspects of Northern Ache reservation life have been the focus of a few recent studies (Gurven et al., 2001; Gurven, Hill, & Kaplan, 2002; Hawkes, Kaplan, Hill, & Hurtado, 1987).

The food transfers observed in this study occurred on the Arroyo Bandera reservation where 117 permanent residents arranged into 23 households resided during the 1998 study period. Small wooden dwellings (typically about 4×4 meters) allow Ache families to store goods, but caches of food are rare. The Ache lack technology for refrigeration, freezing, drying, or canning and customarily consume resources shortly after harvesting them. We only observed occasional caching of purchased goods (sugar, hard bread rolls, rice, and noodles) obtained from infrequent wage labor opportunities and large bundles of harvested peanuts that family members and visitors would snack on throughout the day. These infrequent caches are likely to be known throughout the community given the close proximity of dwellings situated an average of 21 meters apart and arrayed, in a circular pattern, with entries that are visible from most other households in the community.

The Ache prize food sharing and remark with pride on their culture's ethic of generosity. Traditional food sharing norms exhort group members to share with all present, to give to those in need, and to refrain from excessive personal consumption of large package resources that one produces. Nearly all food preparation and cooking is done in plain view of other community members around open fires located in front of the doorway to each family's respective house. From any given house, one can see nearly half of the other open fires in the community. An ample depth (measured as the percentage of production transferred to other households) but restricted breadth (measured as the number of other households that receive a portion) characterizes food transfers at Arroyo Bandera. A typical household at Arroyo Bandera distributes just over eight food items per day, keeps only 20–30% of the food it acquires, and shares the remaining 70–80% with two to three other households, on average (Gurven et al., 2001).

3. Research methods

3.1. Measurements

Allen-Arave and Gurven sampled food production and distribution from February to May 1998 through random 3-hour time block observations of two to three mutually visible neighboring households. We observed every household in Arroyo Bandera for a total of 51–60 h using this method. We made weight measurements of resources with spring scales whenever possible. When weighing an item proved unfeasible, we made a numeric count of the item and converted the measurement into kilograms using weight measurements we obtained from large trials of counted resources. We subsequently converted kilogram measurements into calorie equivalents using conversion estimates obtained from the *Food Composition Table for Use in Latin America* (The Institute of Central America & Panama and The Interdepartmental Institutes of Health, 1961) and from lab analyses on food samples conducted at Hill's request in the early 1980s. The sample consists of 380 complete food distributions, for which we observed the consumption of the entire food package, and 635 incomplete food distributions, for which some distribution of the resource occurred outside of the observation block.

We define households as married adults and their dependents and treat households as the unit of observation. Within a household, residents often eat from a common plate and freely pass food items back and forth. The intensity of food sharing within a household likely means that when donors send food shares to a specific household they cannot target one desired recipient but, instead, expect all members of the recipient household to consume portions (Hames, 1987; Kurland, 1979). There are 23 households in this sample constituting 253 household dyads.

We calculate the coefficients of relatedness between all individuals residing at Arroyo Bandera during the study period using genealogical data obtained by Hill & Hurtado (1996) over the past 29 years through observing pregnancies and co-habitation patterns, frequent censuses, and from retrospective interviews covering reproductive histories and family genealogies. We code kinship between any two households, D and R, as the average coefficient of relatedness of each member of household D to each member of household R. This measure takes into account the interests of all members of a household. Ache men, women, and children alike routinely distribute shares to recipient households and it is rarely clear from simple observation as to who within the donor household ultimately initiates a transfer. Adults likely have more power than children do in determining which households receive shares of their own household's production. Yet, even children as young as 5 years were often observed to share "leftovers" and "snacks" from their homes with members of other households when their parents were not home to sway the transfer. Because we are unable to

assert that any particular class of individuals is powerless in influencing which households receive shares of their own household's production, we consider the average relatedness of all members of household D to all members of household R.

With the relatedness measure employed here, the households of two full brothers who each live with an unrelated mate attain a relatedness value of 0.125. This measure remains unaffected by the addition of children to a household as long as the man of the household fathered the children. However, the presence of stepchildren may lower or increase relatedness between any two given households. The mean relatedness between dyads of households in our sample is .02±.04. Four dyads have an average relatedness of .25 between them, which is the highest average relatedness between any dyads in this sample; 152 household dyads have no genealogical kinship ties joining them. For graphic displays, we divide dyads into four groups to create the ordinal categories of "close" kin (r>.05, n=34), "near" kin (.018<r<.047, n=34), "distant" kin (0<r<.018, n=33), and nonkin (r=0, n=152).

To measure disparity in amounts of food exchanged between any two households, we follow Hames (1987) and calculate "specific imbalance" as the number of calories transferred from household D to household R minus the number of calories transferred from household R to household D over the sample period. As the inequality in exchange between two households increases, the specific imbalance measuring their exchanges attains values further from 0, achieving positive values if the imbalance favors household D and negative values if the imbalance favors household R.

We sum age-specific daily food consumption estimates across all members of a household to obtain a measure of each household's daily consumption requirement. Kaplan (1994) calculated age-specific consumption estimates from resting metabolic energy expenditure rates by age and sex for the Ache following a method used by the World Health Organization (1985) and the National Research Council (1989b). When summed across all members of a household, this measure captures both the number of individuals and the age of each individual within a household. The mean summed consumption requirement for a household in our Ache sample is 7706 cal/day with a range from 3502 cal/day (an elderly couple with no dependents) to 14,643 cal/day (a middle-aged couple supporting their five young children and two unrelated teenagers).

Age-specific food consumption estimates are highly correlated with age-specific reproductive values[1] for nuclear families in our sample (Pearson r=.88, p<.0001). Age-specific food consumption values, however, have the advantage of not discounting postreproductive individuals as rapidly as age-specific reproductive values and thus provide a more biologically realistic measure of the positive influences an individual can have on inclusive fitness at each age (see Section 1.2).

In order to assess "need," we calculate net caloric production for each household by subtracting the household's standardized daily consumption requirement from the household's standardized observed food production over the sample period. We divided consumption and production figures by their mean responses to obtain two standardized estimates in order to contrast these two figures of different time scales in a single measure. As the observed food production of a household increases, so does the household's net caloric production value. As the number of consumers—and particularly consumers aged from their late teens to early 50s—in a household increases, the household's net caloric production value decreases.

3.2. Data analysis

Table 1 provides summary statistics and a description of the variables we use in the present study. To account for biases in variances, degrees of freedom, and significance tests that would result from ignoring the nonindependence inherent in dyadic data (Kenny, 1995; Kenny & Judd, 1986), we perform statistical analyses at the level of the dyad. The information supplied by each household in a dyad is often redundant with the information supplied by the other household in the dyad since each household is paired twice with each of the other households in the community, once as a donor and once as a recipient. For analyses in which there is a theoretically meaningful ordering of household roles (e.g., testing whether imbalances favor the household within each dyad characterized by the lower net caloric value), we assign each household within a dyad to the role of donor or recipient and consider each household dyad once in the analysis.

For analyses in which dyad members lack theoretically distinguishable roles (e.g., testing whether the number of calories transferred from household D to household R covaries with the number of calories transferred from household R to household D), we employ multilevel regression modeling to recognize the hierarchical structure of our data with households nested within dyads. The first step in multilevel data analysis entails fitting a simple two-level model without any predictors, which is often called an "unrestricted" model. This model is analogous to a one-way random analysis of variance model. Next, we add predictors to subsequent multilevel models to evaluate how well the predictors model caloric transfers. Reductions in the modeled variance of subsequent models over that in the unrestricted model indicate how well the added predictors explain variation in caloric transfers. We estimate the proportion of variance explained by a within-dyad

[1] Reproductive value, V_A, for individual A was calculated as: $V_A = \sum_{y=A}^{\infty} \frac{l_y}{l_A} m_y e^{-r(y-A+1)}$, where l_A is survivorship from age 0 to A, m_A is fertility at age A, and r is the instantaneous growth rate of the population. Estimates of l_A, m_A, and r for post-contact Ache were obtained from Hill & Hurtado (1996).

Table 1
Summary statistics and description of variables

	Value[a]	Type[b]	Description
Classification variables			
Household	23	c, w	Household ID
Dyad	253	c, b	Multiple dummies to represent dyad membership pairing each household with every other household once as the donor (*D*) household and once as the recipient (*R*) household
Dependent variables			
Specific imbalance	1636.74±(6033.3)[c]	i, b	(Calories transferred from household *D* to household *R*)−(calories transferred from household *R* to household *D*)[c]
Calories transferred	2298.85±(4874.84)	i, w	Calories transferred from household *D* to household *R*
Independent variables			
Relatedness	0.02±(0.04)	i, b	Average coefficient of relatedness of each member of household *D* to each member of household *R*
Need	0.75±(0.68)	i, w	Difference in net caloric production of household *D* and household *R*, where net caloric production=(food production−the age-specific food consumption estimate summed across all members of the household)
Kin-directed altruism	0.01±(0.04)[c]	i, w	Relatedness (as measured above)×need (as measured above) interaction term
Kin-favored reciprocity	253	c, b	Dyad (as measured above)×relatedness (as measured above) interaction term

[a] Summary value is the sample size for nominal classification variables and the mean±S.D. for interval variables.
[b] Variable type is: nominal classification (c), interval (i), within-dyad (w), between-dyad (b).
[c] For this measure, households are arrayed in dyads so that the household with the larger net caloric production value is assigned the role of donor (*D*) and the household with the smaller net caloric production value is assigned the role of recipient (*R*).

explanatory variable w and a between-dyad explanatory variable b, respectively, as:

$$\text{Pseudo}{-}R_1^2 = \left[\frac{\sigma_u^2 - \sigma_c^2}{\sigma_u^2}\right] \text{and Pseudo}{-}R_2^2 = \left[\frac{\tau_{00|u} - \tau_{00|c}}{\tau_{00|u}}\right] \quad (1.1 \text{ and } 1.2)$$

where σ_u^2 is the within-dyad variance for the unrestricted model, σ_c^2 is the within-dyad variance for the conditional model with predictor w, $\tau_{00|u}$ is the between-dyad variance for the unrestricted model, and $\tau_{00|c}$ is the between-dyad variance for the conditional model with predictor b (Raudenbush & Bryk 2002). Information-theoretic methods, such as Akaike's information criterion (AIC), allow us to compare models with different predictors to determine which potential predictors best describe the data. Lower AIC values indicate a model that better optimizes the tradeoff between underfitting and overfitting the data (Burnham & Anderson 2002). Multilevel modeling also allows computation of the intraclass correlation, which provides a measure of correspondence in the number of calories households transfer to each other. We compute the intraclass correlation as:

$$r_I = \frac{\tau_{00}}{\tau_{00} + \sigma^2} \quad (2)$$

where τ_{00} is the between-dyad variance in caloric transfers and σ^2 is the within-dyad variance in caloric transfers. To the extent that there are no other sources of nonindependence among household dyads in the amount of calories they transfer to one another, the intraclass correlation provides a measure of dyadic contingency.

4. Results

4.1. Kin selection

Average relatedness between all members of household *D* to all members of household *R* significantly predicts the amount of calories provided by household *D* to household *R* over the sample period (t_{251}=3.52, p=.0005). This nepotistic bias is consistent with kin selection theory, but it does not offer sufficient evidence to conclude that the adaptive function of these food transfers result from indirect fitness benefits. Rigorous tests of kin selection theory require that we look beyond a simple statistical tendency to share with kin and attend to the costs, benefits, and directionality of aid.

To investigate whether the likely fitness costs and benefits of aid determine the direction of imbalances, we array households within dyads so that specific imbalance values reflect the net caloric transfer surplus (or deficit) affecting the household in the dyad with the lower net caloric production value. With this assignment of household roles, the slope of the regression of specific imbalance by net caloric production should be positive if food transfers favor households according to need. Table 2 shows the results of a multiple

Table 2
Multiple regression analysis of specific imbalance in caloric transfers from household *D* to household *R*

	Parameter estimate[a]
Independent variable	
Relatedness	−0.1298
Need	0.2882 *
Kin-directed altruism	0.1310

[a] Parameter estimates are partial standardized estimates.
* Significant at the .01 level.

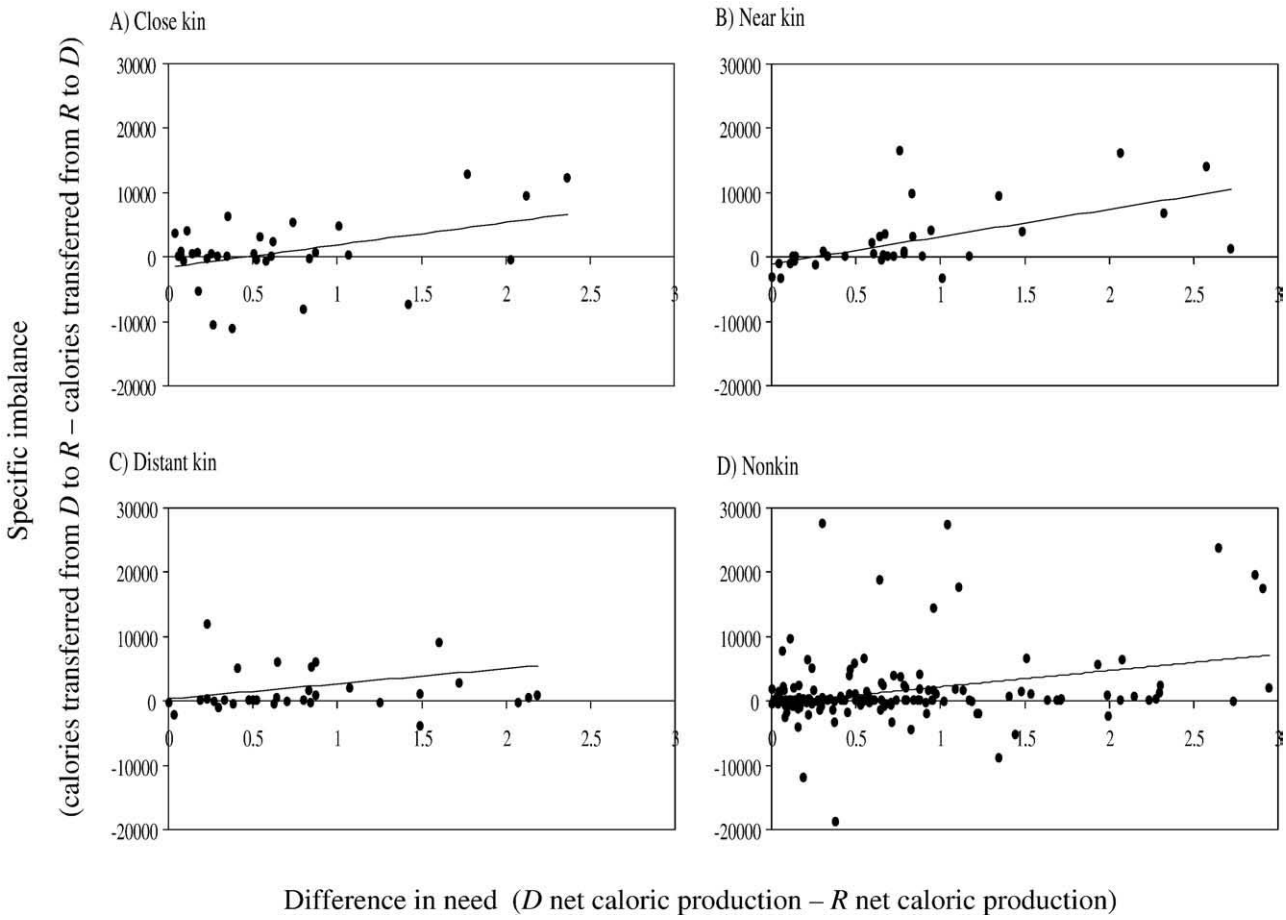

Fig. 1. Linear regression of the relationship between the difference in net caloric production between dyads of households and specific imbalance in their food transfers (arrayed so that positive specific imbalance values are attained when an imbalance favors the household with the lower net caloric value). Plots for (a) close kin (r>.05), (b) near kin (.018<r<.047), (c) distant kin (0<r<.018), and (d) unrelated dyads (r=0).

regression model of the association between relatedness, need (D net caloric production−R net caloric production), and specific imbalance in caloric transfers. The model also includes a term for the interaction of relatedness and difference in net caloric production (kin altruism). This interaction term should have a strong positive association with imbalances in food transfers if food distributions serve the function of increasing indirect fitness contributions. Under kin selection theory, neither relatedness alone nor difference in net caloric value alone should significantly predict specific imbalances in food transfers when the interaction term is included in the model. We would expect no food transfers among even very close relatives (high r) when the disparity in utility they each gain from the same unit of food is limited (low difference in net caloric production). Likewise, kin selection does not favor transfers among nonkin (low r) even when a very large disparity in food value is present (large difference in net caloric production).

Table 2 reveals that contrary to the prediction from kin selection theory, the interaction term of relatedness by difference in net caloric production does not significantly predict specific imbalance in food transfers between households (t_{252}=1.38, p=.1688). Even kinship alone is not associated with imbalances in food transfers on the Ache reservation (t_{252}=−1.41, p=.1594).[2] The only significant predictor in the model is the difference in net caloric production between the households (t_{252}=4.41, p<.0001). Imbalances in food transfers tend to favor the household within each dyad characterized by the lower net caloric production value regardless of relatedness. This indicates that something other than indirect fitness impacts leads "richer" households to provide more of their production to their "poorer" exchange partners than the "richer" households receive in kind from their "poorer" exchange partners.

[2] Gurven (2006) reported finding a positive correlation between imbalance in food transfers among any two households and the closest kinship tie joining the two households. The computations Gurven (2006) reported were made without regard to the direction of transfer imbalances or by only considering positive imbalances. In contrast, the present analysis considers relative "need" so that positive specific imbalance values are attained when an imbalance favors the "poorer" household in the dyad and negative specific imbalance values are attained when an imbalance favors the "richer" household in the dyad.

Table 3
Multilevel models of caloric transfers from household *D* to household *R*

	a) Unrestricted model	b) Model with relatedness only	c) Model with need only	d) Model with kin-directed altruism	e) Model with kin-favored reciprocity	f) Full model
	Parameter estimate [a]	Parameter estimate [a]	Parameter estimate [a]	Parameter estimate [a]	Parameter estimate [a]	Parameter estimate [a]
Fixed effects						
Intercept	2298.16 **	1910.41 **	2298.16 **	1910.41 **	20,057 **	20,057 **
Relatedness	–	19,568 **	–	19,568 **	561,348	561,348
Need	–	–	1255.28 **	1222.05 **	–	1222.05 **
Kin-directed altruism	–	–	–	1931.71	–	1931.71
Kin-favored reciprocity [b]	–	–	–	–	284,097.26 **	284,097.26 **
Covariance Components						
Within-dyad variation	19,467,855 **	19,467,855 **	16,328,912 **	16,381,350 **	19,467,855 **	16,381,350 **
Between-dyad variation	5,291,654 **	4,642,678 **	6,861,125 **	6,185,930 **	2,098,587	3,641,839 *
Intraclass correlation	0.21 **	0.19 **	0.30 **	0.27 **	.10	0.18 **
Fit statistics						
AIC [c]	10,043.6	10,033.5	1000.2	9991.8	9859.6	9815.9

[a] Parameter estimates are restricted maximum likelihood estimates. Fixed effects represent the estimated increase in calories transferred from household *D* to household *R* due to a one-unit increase in the independent variable.
[b] Pooled parameter estimate representing the average across all dyads for this classification variable.
[c] AIC values for comparing models were obtained with full maximum likelihood estimates.
* Significant at the .05 level.
** Significant at the .01 level.

Fig. 1 provides a graphic display of these results. Under kin selection theory alone, we would have expected Fig. 1 to reveal a steep positive slope among the most closely related dyads (the top left panel), no slope among unrelated dyads (the bottom right panel), and intermediate slopes with most giving occurring among dyad pairs in the right portion of the *x*-axis for dyads in the middle ranges of relatedness. Instead, imbalances in food transfers between households tend to favor the household with the lower net caloric production value at all relatedness levels (y=3483.6x−1603.4, R^2=.18 for "close kin"; y=4262.2x–1094.3, R^2=.34 for "near" kin; y=2351.4x+325.2, R^2=.05 for "distant" kin; y=2527.1x−317.72, R^2=.08 for nonkin).

4.2. Reciprocal altruism

While we have focused thus far on determinants of imbalances in calories of food exchanged between households, transfers between any two households at Arroyo Bandera are usually not unidirectional over time. If households display contingency in food transfers, over time, the amounts two households transfer to each other will display correspondence. To examine dyadic contingency in food transfers, we pair each household with each of the other households on the reservation once as the donor (*D*) household and once as the recipient (*R*) household in a multilevel model that hierarchically nests households within dyads.

Results from our baseline unrestricted model are presented in Table 3, Column a. The between-dyad covariance component in the unrestricted model suggests that the average number of calories any household *D* transfers to any household *R* varies from dyad to dyad (z=3.32, p=.0009). We find a statistically significant and positive intraclass correlation, suggesting that across all levels of relatedness, households display dyadic contingency [r_I=.21, F(252,253)=1.54, two-tailed p=.0006].

If investments in inclusive fitness gains provide the adaptive function of food transfers, contingency should be relatively unimportant among kin. To test this prediction, we next fit a conditional multilevel model that includes a fixed effect for relatedness. The between-dyad covariance component in Table 3, Column b, reveals that when we control for relatedness, the average number of calories transferred from household *D* to household *R* still differs from dyad to dyad (z=3.00, p=.0027). The residual intraclass correlation in this model estimates the degree of correspondence in amounts households transfer to each other after parceling out the effect of relatedness. If close kin tolerate larger imbalances in exchanges than distant kin and nonkin as we might predict under the precepts of kin selection theory, we would obtain a larger intraclass correlation from the conditional model that parcels out the effect of relatedness (Table 3, Column b) than from the unrestricted model (Table 3, Column a). Surprisingly, we find just the opposite effect. When we control for relatedness, we still find a correlation in the amounts households exchange to each other [r_I=.19, F(251,252)=1.47, two-tailed p=.0023], but this correlation is smaller than that obtained from the model that did not consider relatedness [r_I=.21, F(252,253)=1.54, two-tailed p=.0006]. This suggests that dyadic contingency is stronger, not weaker, among close kin than among more distant kin and nonkin.

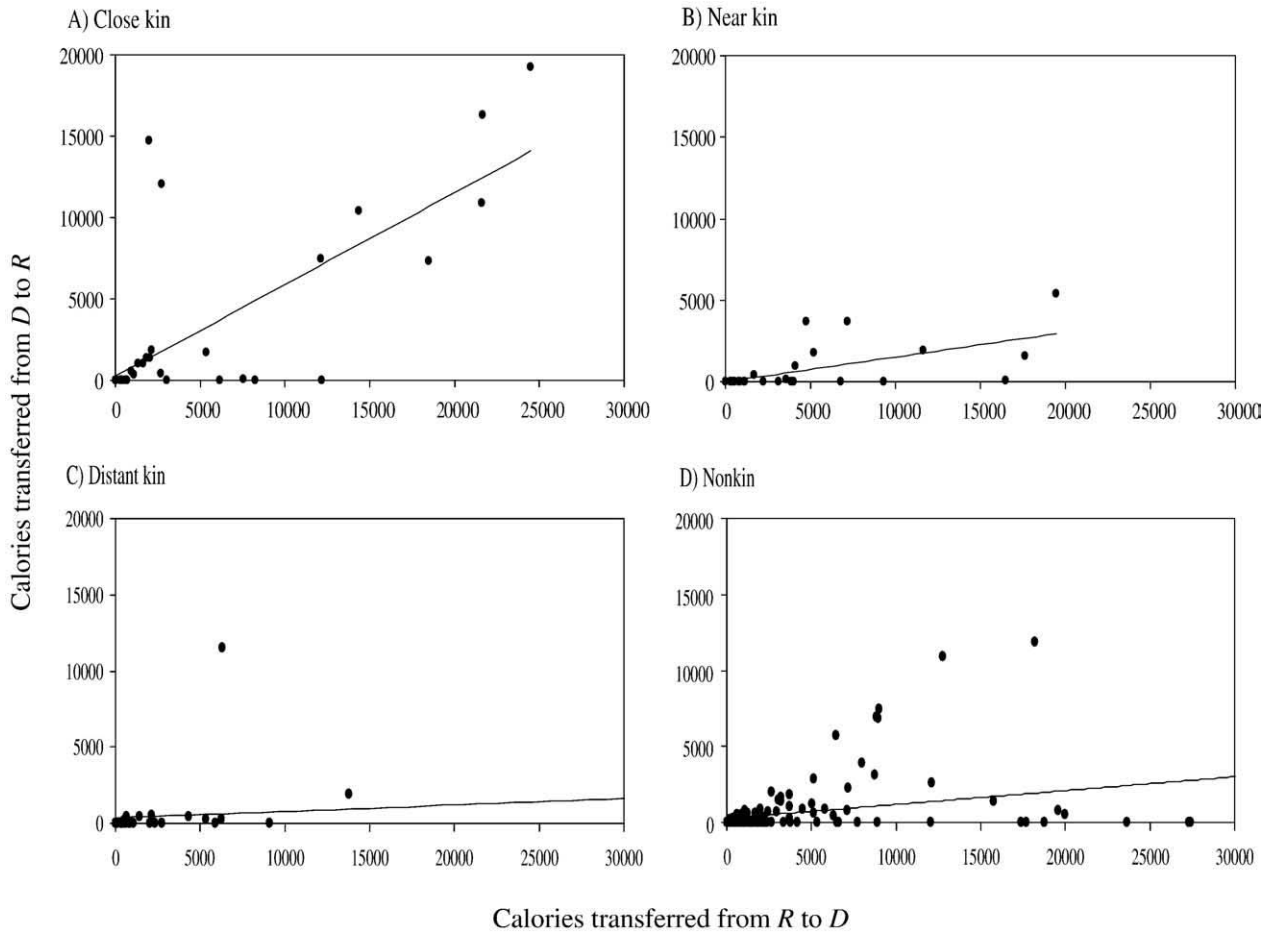

Fig. 2. Linear regression of dyadic food transfers (arrayed so the larger amount given in each household pair is plotted on the x-axis). Plots for (a) close kin ($r>.05$), (b) near kin ($.018<r<.047$), (c) distant kin ($0<r<.018$), and (d) unrelated dyads ($r=0$).

For a graphic display of these results, Fig. 2 plots the number of calories of food production household D provided to household R against the number of calories of food production household R provided to household D by kinship level. As exchanges become more equitable between households in a dyad, the slope of the linear fit in Fig. 2 increases. Interestingly, the slope for "close" kin is steeper ($y=.5648x+240.12$, $R^2=.54$) than the slopes for "near" kin ($y=.1511x-2.2553$, $R^2=.38$), "distant" kin ($y=.0423x+353.43$, $R^2=.02$), and nonkin ($y=.0911x+275.62$, $R^2=.10$).

4.3. Relatedness, need, and contingency

We have established that relatedness, need, and contingency all significantly predict the number of calories household D transfers to household R. We next fit conditional multilevel models to include need, the interaction of relatedness with difference in net caloric value (kin-directed altruism), and the interaction of relatedness with contingency (kin-favored reciprocity) as fixed effects (Table 3, Columns c–e). We also fit a conditional multilevel model incorporating all of these potential explanatory variables of food transfers (Table 3, Column f).

To eliminate confounding effects and understand how all of the predictors simultaneously influence food transfers, we discuss the results from fitting the multilevel model that includes all of the predictors (Table 3, Column f). Meanwhile, we compare each of the single-explanatory mechanism conditional models (Table 3, Column b–e) to the unrestricted model (Table 3, Column a) to estimate the explained variance of each of the individual predictors. In the full model (Table 3, Column f), the fixed-effect term for the intercept estimates that over an observation period of 102–120 h, a household transfers a mean of 2000.57 calories to an unrelated household when the donor household and recipient household do not differ in net caloric production. Increases in the amount of food any household D transfers to any household R are associated with: (1) the degree of greater net energy production of household D relative to household R ("need"), (2) the interaction of kinship with the amount of food household D transferred to household R ("kin-favored reciprocity"), and (3) dyadic contingency (indicated by the intraclass correlation).

The statistical significance of the interaction term of relatedness with dyadic contingency in the full model (Table 3, Column f) indicates that households give

preference in their food distributions to other households that contain kin *and* provide ample food in return [$F(100,151)=1.54$, $p=.0082$], even when we control for the other explanatory variables. The model that considers only the "kin-favored reciprocity" predictors (Table 3, Column e) yields a lower AIC than the models that consider only relatedness measures, need measures, or kin-directed altruism measures (Table 3, Column b–d). This suggests that the "kin-favored reciprocity" model provides the best fit of any single-explanatory mechanism model. The pseudo-R_2^2 [Eq. (1.2)] estimates that the interaction of relatedness with dyadic contingency models 60% of the explained variance among dyad averages (compare Table 3, Column e to Column a). The predictive power of this "kin-favored reciprocity" term is consistent with a view that households mainly engage in reciprocal exchanges and prefer kin as their exchange partners.

The residual intraclass correlation in the full model (Table 3, Column f) indicates that after controlling for the effects of the other predictors, 18% of the variation in the amount of calories transferred from household *D* to household *R* is attributable to the dyad [$F(248,249)=1.44$, two-tailed $p=.0042$]. This measure of dyadic contingency conforms to the predictions of reciprocal altruism and indicates that while kin are preferred reciprocal food exchange partners, households also commonly engage in reciprocal exchanges with nonkin.

The final significant predictor in the full model is the difference in net caloric production ("need") between household *D* and household *R* [$F(1,251)=0.19$, $p<.0001$]. The pseudo-R_1^2 [Eq. (1.1)] estimates that the difference in net caloric production ("need") between household *D* and household *R* models 16% of the explained variance in food transfer amounts within dyads (compare Table 3 Column c to Column a). This result is consistent with a view that beyond their reciprocal exchanges, households also help "needy" families that produce insufficient food relative to their consumption requirement.

Relatedness retains no significant predictive power [$F(1,151)=0.11$, $p=.7430$] in any model that includes the interaction of relatedness and dyadic contingency (kin-favored reciprocity). This implies that while kin are favored with food shares, such favoritism only persists if food aid is returned. Such discrimination among kin is not consistent with models of kin selection, because the benefits of nepotism in these models accrue from indirect fitness benefits regardless of how the related recipient responds. The term for the interaction of relatedness with difference in net caloric value (kin-directed altruism) is also not significant [$F(1,251)=0.19$, $p=.6605$] and loses predictive power in any model that also includes relatedness and difference in net caloric value (need) separately. Although, the model that only considers "kin-directed altruism" as an explanatory mechanism (Table 3, Column d) yields a lower AIC than the model that only considers "need" as an explanatory mechanism (Table 3, Column c), this improvement in model fit is attributable to the combined effect of relatedness and need together, not their interaction. The interaction term of relatedness and need is the only factor in the model that truly tests the cost–benefit conditions necessary for inclusive fitness gains from altruism.

5. Discussion

Household pairs at Arroyo Bandera display correspondence in the amounts of calories they transfer to one another. While nepotistic biases are present in the data, households give preference to kin who are likely to reciprocate, rather than kin who will benefit more from the aid. Closely related households display even higher correspondence in the number of calories they provide for each other than distantly related and unrelated households, suggesting that contingent reciprocity is the norm among close kin. To the degree that exchanges between households are uneven, imbalances tend to favor households that require more calories either because they are low producers, contain many mouths to feed, or both. These food flows favoring "poorer" households over "richer" households occur irrespective of kinship distance.

5.1. The selective forces of kin selection and reciprocal altruism

The results suggest that Ache households mainly transfer food on the reservation because of fitness gains from expected food repayment rather than because of payoffs from nepotistic investment in indirect fitness benefits. This may not be surprising given that, unlike models of kin selection, the ratio of the recipient's benefit to the actor's cost need not be very great for reciprocal altruism to favor a food transfer (Kaplan & Hill, 1985). In order for kin selection to favor a food transfer among even full siblings, the average fitness impact of the transferred food should be twice as great for recipient as for the donor. Yet, for reciprocal altruism to favor the same transfer, the fitness cost of giving food now need only be less than the benefit of food received in the future devalued by the probability of future repayment. Consider Hamilton's rule (1964) for assisting kin:

$$Br>C \tag{3.1}$$

in comparison to the rule Axelrod and Hamilton (1981) derived for tit-for-tat based cooperation:

$$Bp>C \tag{3.2}$$

where *B* is the benefit to the recipient, *C* is the cost to the provider, *r* is the coefficient of genetic relatedness, and *p* is the probability of future interaction. This comparison suggests that aid will be more strongly favored by the forces of reciprocal altruism than the forces of kin selection whenever $p>r$ (Gurven et al., 2001). If siblings trust each other, interact frequently, and rarely defect on

repayment, their value of p may often greatly exceed their r value of 0.5.

5.2. Relatives as attractive partners for reciprocal altruism

A nepotistic bias along with sharing patterns consistent with the predictions of reciprocal altruism, rather than kin selection theory, supports a view that relatives are preferred exchange partners. Our finding that exchanges between close relatives display more contingency than exchanges between distant relatives and nonrelatives supports the view that close relatives are less inclined to cheat on social obligations. Meanwhile, indirect fitness payoffs, while not large enough to provide the primary adaptive function of interhousehold food transfers, may still confer additive fitness payoffs to individuals who choose their close kin as their exchange partners. It seems probable that close relatives prefer to live near each other in order to engage in reciprocal provisioning of goods and services. If true, residential proximity in a self-selected living arrangement might be better regarded as an outcome of actors' preferences for interaction rather than as an independent predictor of resource flows.

5.3. Aiding the "needy"

In addition to favoring households that return aid, food transfers on the Ache reservation favor households with low net caloric production values, regardless of kinship. The salience of "need" in determining the direction of food flows is not unique to the present study. Kaplan and Hill (1985) found among the Ache in the forest that families received food in accord to their number of consumers. Similar patterns of food distributions favoring "needier" households have been documented among the Batak (Cadelina, 1982), G/wi (Silberbauer, 1981), Hiwi (Gurven et al., 2000b), and Maimande (Aspelin, 1979) but have not been found among the Ye'kwana (Hames & McCabe, 2007) or Yanomamö (Hames, 2000).

This pattern initially strikes us as congruent with food sharing models based on tolerated scrounging (Blurton Jones, 1983; Hawkes, 1993; Winterhalder, 1996). However, the fact that Ache producers willingly pay the costs of harvesting and transporting excess food portions rather than leaving recipients to bear these costs suggests that producers anticipate a benefit from providing food and are not simply relinquishing food they cannot defend. Further, if the demands of others determined transfers of excess food portions as postulated by tolerated scrounging, we would not expect households to transfer food portions to only a small and stable breadth of recipient households through time with a preference given to reciprocating partners and close kin. Reciprocation with nonfood items and reputational benefits offer more likely explanations than tolerated scrounging for the provisioning observed on the Ache reservation.

Given that Ache households engage in exchanges of multiple goods and services, our examination of food transfers alone may miss channels used by lower net producing households to repay higher net producing households. Households that receive food provisioning may repay their benefactors with nonfood goods (such as tools, raw materials for tool manufacture, firewood, and valuable Western goods) and labor inputs (such as childcare, tool manufacture, garden labor, and house construction).

Ache provisioners may also earn social utility. Economic experiments reveal the willingness of individuals in this culture to conform to socially prescribed patterns of generosity. Ache bystanders to economic experiments verbally encourage players to cooperate and Ache players make larger mean contributions when economic experiments are played in public than when they are played in private (Hill and Gurven 2004). A reputation for generosity in Ache society may bestow tangible benefits such as political support, deference, allies in disputes, or caretaking during illness and injury. One tangible benefit has been confirmed; those who produce an abundance of food and generously share the excess receive more food aid than less generous individuals do when they fall ill and require others to provision them (Gurven, Allen-Arave, Hill, & Hurtado, 2000a). Finally, generous individuals may attract a larger and healthier social support group (Wiessner 2002), which may provide more opportunities for cooperation and advantage in competitive interactions with other groups. Because Ache provisioning of the "needy" may be a cooperative behavior backed by third party punishment (Hill and Gurven 2004), we must consider the possibility that this cultural convention has evolved through cultural group selection (see Bowles 2006; Boyd, Gintis, Bowles, & Richerson, 2003; and Henrich 2004).

5.4. Implications for previous kin selection studies

Among the Ache at Arroyo Bandera, relatedness is a statistically significant predictor of food transfers only until we control for the interaction of relatedness with dyadic contingency. Early empirical tests of kin selection theory commonly measured only relatedness and neglected to investigate the ratio of benefit of aid for the recipient to the cost of providing aid for the actor (Kurland, 1980). Researchers commonly attributed cooperation among kin to the process of kin selection without considering processes such as reciprocal altruism that may occur among kin. The conclusions from such studies warrant reconsideration.

If nepotism in social interactions sometimes results from factors such as proximity, familiarity, trust, or higher expectations of cooperation, then indirect fitness benefits may play a smaller role in shaping cooperation among kin than evolutionary researchers have previously assumed. In an early introductory sociobiology text, Barash (1982, p. 74) proclaims, "… inclusive fitness provides a coherent theory for the biology of nepotism among living things." The empirical body of evidence to back this up, however, is heavily biased by studies in which juveniles obtain adult provisioning. Evidence presented in this paper suggests that nepotistic aid to adults may sometimes represent investment in direct

fitness benefits. Even if nepotism in social interactions involves additive inclusive fitness payoffs on top of larger direct fitness payoffs from cooperation then claims that genetic ties provide the "social glue" for these partnerships may overstate the role of kin selection. Primatologists have also recently begun to question whether direct fitness benefits, rather than indirect fitness benefits, are responsible for some nepotistic interactions in non-human primate societies (Chapais 2001).

Understanding the contexts in which the gains from nepotistic aid come primarily from reciprocal benefits and those in which they come primarily in indirect fitness impacts requires consideration of the adaptive problem that each specific instance of aid solves (Hames 2004). On the Ache reservation, turn-taking in food production and sharing is likely an adaptive response to an economy of scale (Gurven et al., 2001). In such turn-taking systems of exchange, the payback from reciprocation likely provides a larger payoff from cooperation than indirect fitness benefits [i.e., p in Eq. (3.2) is likely larger than r in Eq. (3.1)]. Paralleling our findings, Hames and McCabe (2007) suggest that Ye'kwana meal sharing is also an adaptive response to an economy of scale, and they find no significant correlation between relatedness and imbalance. By contrast, Hames (1987) found a significant correlation between relatedness and short-term imbalances in Ye'kwana garden labor exchange. Hames suspects that Ye'kwana garden labor exchange is an adaptive response to unpredictable garden failures as labor expended in someone else's garden can bolster a laborer's claim on the fruits of that garden should the laborer's own garden fail. In this instance, the expectation of direct repayment (p in equation 3.2) is low and so we expect nepotistic investment in indirect fitness to play a larger role in shaping this cooperative behavior.

While we caution that the role of kin selection may be overstated in many instances of cooperation among adult kin, we suspect that kin selection plays a prominent role in some cases. Where there is little expectation of future repayment, where the ratio of the recipient's benefit of aid to the actor's cost of providing aid is very high, or where the recipient has much higher reproductive value than the donor does, indirect fitness benefits are likely to provide the adaptive function of cooperation. Where there is a high expectation of future repayment relative to the disparity in the fitness impact of aid for the recipient over the donor, direct fitness benefits from cooperation may dominate the adaptive payoffs from cooperation, even when performed among close kin.

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