



Original Article

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

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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.

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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, 2000; 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 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

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60 correlated amounts of food transferred between related
61 households challenges us to disaggregate the relative
62 contributions of indirect fitness impacts and reciprocal
63 benefits in maintaining nepotistic Ache food transfers. The
64 present paper presents new analyses to (1) examine the
65 direction of imbalances in food transfers between households
66 and (2) consider the difference in net caloric production
67 between households.

68 1.1. Kin selection theory

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

88 1.2. Direction and magnitude of imbalances

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

106 The ages of household members matter as much as the
107 number of residents a household contains for determining the
108 fitness impact a transferred unit of food may have for a
109 household because energy requirements and reproductive
110 values peak in young adulthood. Resting metabolic energy
111 expenditure rates indicate that individuals aged from their
112 late teens to fifties require more energy than younger and

113 older individuals do (National Research Council, 1989a;
114 World Health Organization, 1985). Young adults also
115 possess a larger potential to translate food energy into
116 inclusive fitness gains than other age classes, owing to the
117 greater number of childbearing years likely to await young
118 sexually mature and about to mature individuals in the
119 future. Thus, individuals in the middle of the lifecourse can
120 return greater indirect fitness benefits to donor kin from large
121 amounts of food than younger and older individuals can.

122 Despite straightforward theoretical expectations that food
123 flows should favor individuals of high reproductive value,
124 application of this logic to human populations presents
125 complications. Several theorists (e.g., Charlesworth &
126 Charnov, 1981; Hamilton, 1964; Rogers, 1993; Taylor &
127 Frank, 1996; Trivers, 1971) have noted that the reproductive
128 value of donors and recipients should alter the costs and
129 benefits of giving and receiving aid. However, measures of
130 reproductive value do not provide an adequate estimate of
131 the expected inclusive fitness contribution made by indi-
132 viduals in species, such as ours, with child altriciality and
133 common allocaire. While prereproductive and postreproduc-
134 tive individuals cannot produce copies of their genes in the
135 form of offspring, they regularly assist copies of their genes
136 located in other relatives through activities such as baby-
137 sitting (Bock, 1995, Fig. 57; Ivey, 2000; Turke, 1988;
138 Weisner & Gallimore, 1977), passing on important skills and
139 knowledge (Biesele & Howell, 1981; Liederman & Liederman,
140 1977), provisioning during times of need (Hawkes,
141 O'Connell, & Blurton Jones, 1997), or offering protection
142 and support (Chagnon & Bugos, 1979). The expected fitness
143 contribution made by individuals—*especially postreproduc-*
144 *tive individuals*—is therefore underestimated by reproduc-
145 tive value measures alone because direct reproduction is not
146 the only way to increase inclusive fitness. Still, food
147 requirements and fertility measures alike indicate that food
148 transfers, which enhance inclusive fitness, should predomi-
149 nately favor households containing young reproductive-
150 aged residents over households containing other age classes,
151 when we control for the number of residents and their
152 production abilities.

153 1.3. Reciprocal altruism

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

161 Reciprocal altruism (Trivers 1971) can evolve as long as
162 the cost of aiding another individual is outweighed by the
163 benefit of receiving aid from that individual later, devalued
164 by the probability that aid will be returned (Boyd, 1990). If
165 the reciprocal exchange is profitable, individual altruists can
166 expect payback in the future from self-interested actors who

167 wish to continue obtaining the benefits that accrue from
 168 long-term cooperation. Such cooperation is even more likely
 169 to appear when punishment of defectors is possible (Fehr &
 170 Gächter, 2002; Ostrom, Walker, & Gardner, 1992; Yama-
 171 gishi 1986). Nepotism may emerge independent of inclusive
 172 fitness benefits if individuals find their relatives more
 173 desirable as reciprocal exchange partners than nonrelatives.

174 1.4. Contingent reciprocity

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

190 Contingent reciprocity may prove difficult to detect
 191 because reciprocal altruism does not imply perfectly
 192 balanced exchanges between individuals. For an exchange
 193 to occur, reciprocal altruism theory predicts only that the
 194 average utility of the expected return outweigh the utility of
 195 the resource given up today. For example, a satiated
 196 household may pay little cost in providing (say) 2000
 197 calories now, while benefiting greatly from (say) 500
 198 calories at a future date when household members are ill or
 199 hungry. This may be analogous to the logic of insurance
 200 coverage in which one may pay premiums at a low utility
 201 cost for years in order to cover any high utility needs in the
 202 event of a future catastrophic shortfall. Additionally, if
 203 households engage in reciprocal exchanges that include
 204 several goods and services, an evaluation of food exchanges
 205 alone may underestimate the true contingent reciprocity
 206 occurring in the society. Despite these complications, we
 207 expect to find that the amount of food provided by any
 208 household *D* to any household *R* will correlate with the
 209 amount of food provided by household *R* to household *D* if
 210 reciprocal altruism plays a role in food transfers over the time
 211 scale of observation. Researchers studying other forager-
 212 horticulturalists populations have found dyadic correlations
 213 in food shares among the Achuar/Quichua/Zapara (Patton,
 214 2005), Aka Pygmies (Gurven, 2004), Dolgan/Nganasan
 215 (Ziker, 2005), Hiwi (Gurven et al., 2000), Mikea (Tucker,
 216 2004), Pilaga (Gurven, 2004), Yanomamo (Hames, 2000),
 217 and Ye'kwana (Hames & McCabe, 2007). However,
 218 amounts of food given to all others does not correlate with
 219 amounts of food received from all others for Hadza large
 220 game (Hawkes, O'Connell, & Blurton Jones, 2001) nor

Meriam turtle meat exchanges (Bliege Bird, Bird, Smith, & 221
 Kushnick, 2002). 222

1.5. Reciprocity among kin 223

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

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

251 Finally, the close proximity that kin often maintain can
 252 create more opportunities for exchange and increase the
 253 probability of future interaction, which promotes coopera-
 254 tion (Andreoni & Miller, 1993; Axelrod & Hamilton, 1981).
 255 At our study site, the homes of households joined by a close
 256 kinship tie tend to be nearer to each other than the homes of
 257 households not joined by a close kinship tie (Gurven et al.,
 258 2001).

259 The factors discussed above (familiarity, emotional
 260 bonds, trust, proximity, and indirect fitness costs and
 261 benefits) can promote an expectation among kin that a
 262 relative will cooperate, and experimental research has shown
 263 that expectations of cooperation promote and stabilize
 264 altruistic behavior (Dawes, 1980; Messick & Brewer,
 265 1983). Thus, we might expect close kin to provide frequent
 266 goods and services in a stable arrangement of reciprocal
 267 altruism rather than simple kin-directed charity.

268 2. Study case: the Northern Ache

269 The Northern Ache are indigenous peoples of lowland
 270 northeastern Paraguay. At peaceful contact in 1971, they
 271 subsisted as nomadic hunter-gatherers. Beginning in the mid
 272 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 they acquire, 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 lab analyses for food samples Hill sent out in the early 1980s and the *Food Composition Table for Use in Latin America* (The Institute of Central America & Panama and The Interdepartmental Institutes of Health, 1961). 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 (Hill & Hurtado (1996) have obtained 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 $.02 \pm .04$. 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 imbalance 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 values¹ 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 house-

hold’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

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 (Table 1).

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

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

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

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).

t1.1 Table 1

t1.2 Summary statistics and description of variables

t1.3	Value ^a	Type ^b	Description
t1.4	Classification variables		
t1.5	Household	23	c, w Household ID
t1.6	Dyad	253	c, b Multiple dummies to represent dyad membership pairing each household with every other household once as the donor (<i>D</i>) household and once as the recipient (<i>R</i>) household
t1.7	Dependent variables		
t1.8	Specific imbalance	1636.74±(6033.3) ^c	i, b (Calories transferred from household <i>D</i> to household <i>R</i>)–(calories transferred from household <i>R</i> to household <i>D</i>) ^c
t1.9	Calories transferred	2298.85±(4874.84)	i, w Calories transferred from household <i>D</i> to household <i>R</i>
t1.10	Independent variables		
t1.11	Relatedness	0.02±(0.04)	i, b Average coefficient of relatedness of each member of household <i>D</i> to each member of household <i>R</i>
t1.12	Need	0.75±(0.68)	i, w Difference in net caloric production of household <i>D</i> and household <i>R</i> , where net caloric production=(food production–the age-specific food consumption estimate summed across all members of the household)
t1.13	Kin-directed altruism	0.01±(0.04) ^c	i, w Relatedness (as measured above)×need (as measured above) interaction term
t1.14	Kin-favored reciprocity	253	c, b Dyad (as measured above)×relatedness (as measured above) interaction term

t1.15 ^a Summary value is the sample size for nominal classification variables and the mean±S.D. for interval variables.t1.16 ^b Variable type is: nominal classification (c), interval (i), within-dyad (w), between-dyad (b).t1.17 ^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*).

482 variance for the conditional model with predictor *b* (Rauden-
 483 bush & Bryk 2002). Information-theoretic methods (such as
 484 AIC) allow us to compare models with different predictors to
 485 determine which potential predictors best describe the data.
 486 Lower AIC values indicate a model that better optimizes the
 487 tradeoff between underfitting and overfitting the data
 488 (Burnham & Anderson 2002). Multilevel modeling also
 489 allows computation of the intraclass correlation, which
 490 provides a measure of correspondence in the number of
 491 calories households transfer to each other. We compute the
 492 intraclass correlation as:

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

493 where τ_{00} is the between-dyad variance in caloric transfers
 494 and σ^2 is the within-dyad variance in caloric transfers. To the
 495 extent that there are no other sources of nonindependence
 496 among household dyads in the amount of calories they
 497 transfer to one another, the intraclass correlation provides a
 498 measure of dyadic contingency.
 499

500 4. Results

501 4.1. Kin selection

502 Average relatedness between all members of household *D*
 503 to all members of household *R* significantly predicts the
 504 amount of calories provided by household *D* to household *R*
 505 over the sample period ($t_{251}=3.52, p=.0005$). This nepotistic
 506 bias is consistent with kin selection theory, but it does not
 507 offer sufficient evidence to conclude that the adaptive
 508 function of these food transfers result from indirect fitness
 509 benefits. Rigorous tests of kin selection theory require that
 510 we look beyond a simple statistical tendency to share with
 511 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
 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

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

Multiple regression model showing the effect of relatedness and difference
 in net caloric production in influencing the specific imbalance in calories
 exchanged between household *D* and household *R*.

^a Parameter estimates are partial standardized estimates.

* Significant at the .01 level.

t2.1

t2.2

t2.3

t2.4

t2.5

t2.6

t2.7

t2.8

t2.9

t2.10

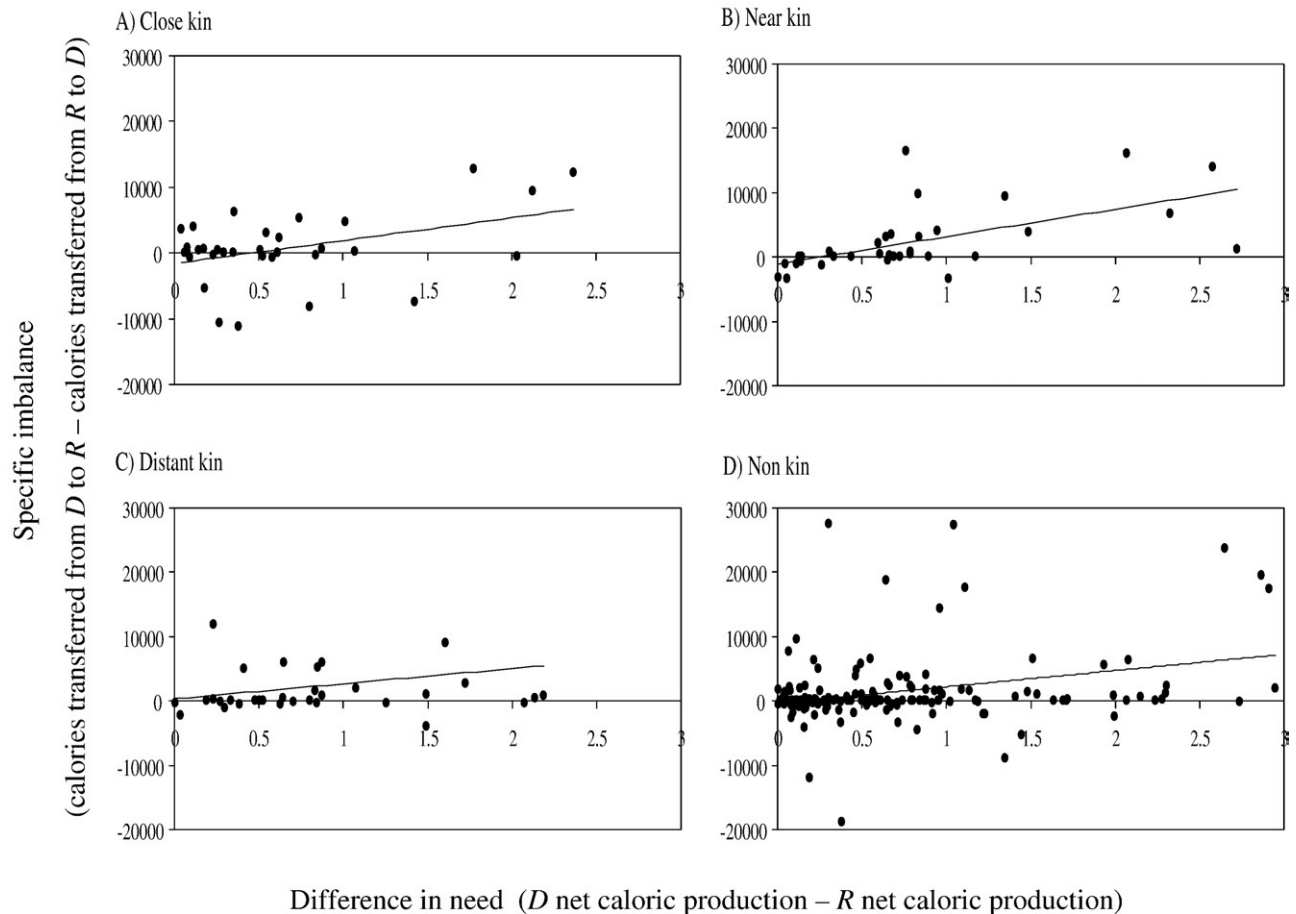


Fig. 1. Linear regression of the relationship between the difference in net caloric production between dyads of households and specific imbalance in their food transfers (arrayed so that positive specific imbalance values are attained when an imbalance favors the household with the lower net caloric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

533 no food transfers among even very close relatives (high r)
 534 when the disparity in utility they each gain from the same unit
 535 of food is limited (low difference in net caloric production).
 536 Likewise, kin selection does not favor transfers among
 537 nonkin (low r) even when a very large disparity in food value
 538 is present (large difference in net caloric production).

539 Table 2 reveals that contrary to the prediction from kin
 540 selection theory, the interaction term of relatedness by
 541 difference in net caloric production does not significantly
 542 predict specific imbalance in food transfers between house-
 543 holds ($t_{252}=1.38$, $p=.1688$). Even kinship alone is not
 544 associated with imbalances in food transfers on the Ache
 545 reservation ($t_{252}=-1.41$, $p=.1594$).² The only significant

546 predictor in the model is the difference in net caloric
 547 production between the households ($t_{252}=4.41$, $p<.0001$).
 548 Imbalances in food transfers tend to favor the household
 549 within each dyad characterized by the lower net caloric
 550 production value regardless of relatedness. This indicates
 551 that something other than indirect fitness impacts leads
 552 “richer” households to provide more of their production to
 553 their “poorer” exchange partners than the “richer” house-
 554 holds receive in kind from their “poorer” exchange partners.

555 Fig. 1 provides a graphic display of these results. Under
 556 kin selection theory alone, we would have expected Fig. 1
 557 to reveal a steep positive slope among the most closely related
 558 dyads (the top left panel), no slope among unrelated dyads
 559 (the bottom right panel), and intermediate slopes with most
 560 giving occurring among dyad pairs in the right portion of the
 561 x -axis for dyads in the middle ranges of relatedness. Instead,
 562 imbalances in food transfers between households tend to
 563 favor the household with the lower net caloric production
 564 value at all relatedness levels ($y=3483.6x-1603.4$, $R^2=.18$
 565 for “close kin”; $y=4262.2x-1094.3$, $R^2=.34$ for “near” kin;
 566 $y=2351.4x+325.2$, $R^2=.05$ for “distant” kin; $y=2527.1x-$
 567 317.72 , $R^2=.08$ for nonkin).

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.

t3.1 Table 3

t3.2 Multilevel models of caloric transfers from household *D* to household *R*

t3.3	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
t3.4	Parameter estimate ^a	Parameter estimate ^a	Parameter estimate ^a	Parameter estimate ^a	Parameter estimate ^a	Parameter estimate ^a
t3.5	Fixed effects					
t3.6	Intercept	2298.16 **	1910.41 **	2298.16 **	1910.41 **	20,057 **
t3.7	Relatedness	–	19,568 **	–	19,568 **	561,348
t3.8	Need	–	–	1255.28 **	1222.05 **	–
t3.9	Kin-directed altruism	–	–	–	1931.71	–
t3.10	Kin-favored reciprocity ^b	–	–	–	–	284,097.26 **
t3.11	Covariance Components					
t3.12	Within-dyad variation	19,467,855 **	19,467,855 **	16,328,912 **	16,381,350 **	19,467,855 **
t3.13	Between-dyad variation	5,291,654 **	4,642,678 **	6,861,125 **	6,185,930 **	2,098,587
t3.14	Intraclass correlation	0.21 **	0.19 **	0.30 **	0.27 **	.10
t3.15	Fit statistics					
t3.16	AIC ^c	10,043.6	10,033.5	1000.2	9991.8	9859.6

t3.17 Multilevel models showing the effect of relatedness, difference in net caloric production, and the number of calories received by household *D* from household *R* in influencing the number of calories transferred from household *D* to household *R*.

t3.18 ^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.

t3.19 ^b Pooled parameter estimate representing the average across all dyads for this classification variable.

t3.20 ^c AIC values for comparing models were obtained with full maximum likelihood estimates.

t3.21 * Significant at the .05 level.

t3.22 ** Significant at the .01 level.

568 4.2. Reciprocal altruism

569

570 While we have focused thus far on determinants of
 571 imbalances in calories of food exchanged between house-
 572 holds, transfers between any two households at Arroyo
 573 Bandera are usually not unidirectional over time. If
 574 households display contingency in food transfers, over
 575 time, the amounts two households transfer to each other
 576 will display correspondence. To examine dyadic contin-
 577 gency in food transfers, we pair each household with each
 578 of the other households on the reservation once as the
 579 donor (*D*) household and once as the recipient (*R*)
 580 household in a multilevel model that hierarchically nests
 581 households within dyads.

582 Results from our baseline unrestricted model are
 583 presented in Table 3, Column a. The between-dyad
 584 covariance component in the unrestricted model suggests
 585 that the average number of calories any household *D*
 586 transfers to any household *R* varies from dyad to dyad
 587 ($z=3.32$, $p=.0009$). We find a statistically significant and
 588 positive intraclass correlation, suggesting that across all
 589 levels of relatedness, households display dyadic contingency
 590 [$r_1=.21$, $F(252,253)=1.54$, two-tailed $p=.0006$].

591 If investments in inclusive fitness gains provide the
 592 adaptive function of food transfers, contingency should be
 593 relatively unimportant among kin. To test this prediction,
 594 we next fit a conditional multilevel model that includes a
 595 fixed effect for relatedness. The between-dyad covariance
 596 component in Table 3, Column b, reveals that when we
 597 control for relatedness, the average number of calories

598 transferred from household *D* to household *R* still differs 598
 599 from dyad to dyad ($z=3.00$, $p=.0027$). The residual 599
 600 intraclass correlation in this model estimates the degree of 600
 601 correspondence in amounts households transfer to each 601
 602 other after parceling out the effect of relatedness. If close 602
 603 kin tolerate larger imbalances in exchanges than distant kin 603
 604 and nonkin as we might predict under the precepts of kin 604
 605 selection theory, we would obtain a larger intraclass 605
 606 correlation from the conditional model that parcels out the 606
 607 effect of relatedness (Table 3, Column b) than from the 607
 608 unrestricted model (Table 3, Column a). Surprisingly, we 608
 609 find just the opposite effect. When we control for 609
 610 relatedness, we still find a correlation in the amounts 610
 611 households exchange to each other [$r_1=.19$, $F(251,252)=$ 611
 612 1.47 , two-tailed $p=.0023$], but this correlation is smaller 612
 613 than that obtained from the model that did not consider 613
 614 relatedness [$r_1=.21$, $F(252,253)=1.54$, two-tailed $p=.0006$]. 614
 615 This suggests that dyadic contingency is stronger, not 615
 616 weaker, among close kin than among more distant kin 616
 617 and nonkin. 617

618 For a graphic display of these results, Fig. 2 plots the 618
 619 number of calories of food production household *D* provided 619
 620 to household *R* against the number of calories of food 620
 621 production household *R* provided to household *D* by kinship 621
 622 level. As exchanges become more equitable between 622
 623 households in a dyad, the slope of the linear fit in Fig. 2 623
 624 increases. Interestingly, the slope for “close” kin is steeper 624
 625 ($y=.5648x+240.12$, $R^2=.54$) than the slopes for “near” kin 625
 626 ($y=.1511x-2.2553$, $R^2=.38$), “distant” kin ($y=.0423x+$ 626
 627 353.43 , $R^2=.02$), and nonkin ($y=.0911x+275.62$, $R^2=.10$). 627

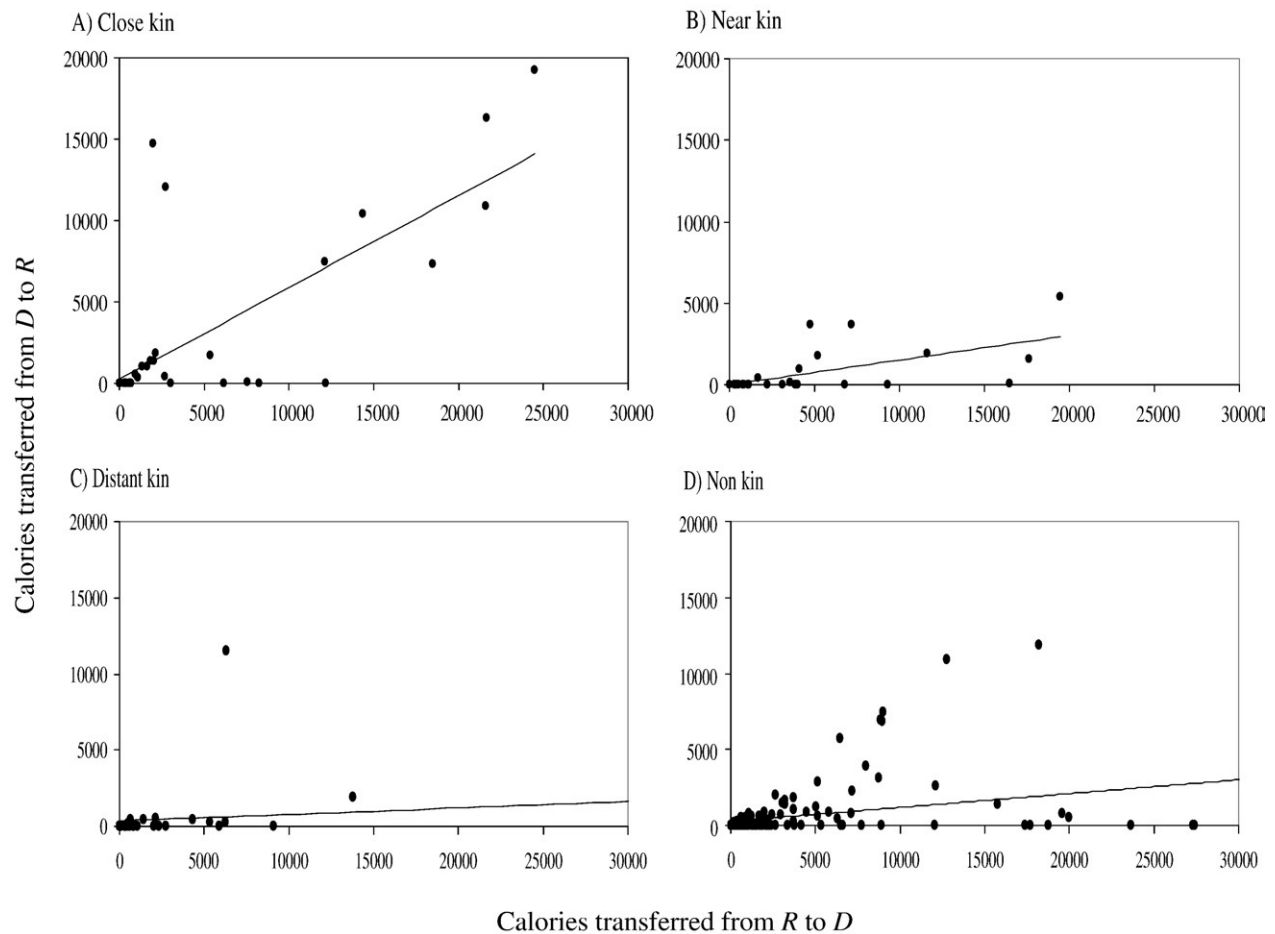


Fig. 2. Linear regression of dyadic food transfers (arrayed so the larger amount given in each household pair is plotted on the x -axis). Plots for (a) close kin ($r > .05$), (b) near kin ($.018 < r < .047$), (c) distant kin ($0 < r < .018$), and (d) unrelated dyads ($r = 0$).

628 4.3. Relatedness, need, and contingency 629

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

640 To eliminate confounding effects and understand how all
 641 of the predictors simultaneously influence food transfers, we
 642 discuss the results from fitting the multilevel model that
 643 includes all of the predictors (Table 3, Column f). Mean-
 644 while, we compare each of the single explanatory mechan-
 645 ism conditional models (Table 3, Column b–e) to the
 646 unrestricted model (Table 3, Column a) to estimate the
 647 explained variance of each of the individual predictors. In
 648 the full model (Table 3, Column f), the fixed-effect term for
 649 the intercept estimates that over an observation period of
 650 102–120 h, a household transfers a mean of 2000.57 calories

651 to an unrelated household when the donor household and
 652 recipient household do not differ in net caloric production.
 653 Increases in the amount of food any household D transfers to
 654 any household R are associated with: (1) the degree of
 655 greater net energy production of household D relative to
 656 household R (“need”), (2) the interaction of kinship with the
 657 amount of food household D transferred to household R
 658 (“kin-favored reciprocity”), and (3) dyadic contingency
 659 (indicated by the intraclass correlation).

660 The statistical significance of the interaction term of
 661 relatedness with dyadic contingency in the full model
 662 (Table 3, Column f) indicates that households give
 663 preference in their food distributions to other households
 664 that contain kin and provide ample food in return
 665 [$F(100,151)=1.54$, $p=.0082$], even when we control for
 666 the other explanatory variables. The model that considers
 667 only the “kin-favored reciprocity” predictors (Table 3,
 668 Column e) yields a lower AIC than the models that consider
 669 only relatedness measures, need measures, or kin-directed
 670 altruism measures (Table 3, Column b–d). This suggests
 671 that the “kin-favored reciprocity” model provides the best
 672 fit of any single explanatory mechanism model. The
 673 pseudo- R^2 [Eq. (1.2)] estimates that the interaction of

674 relatedness with dyadic contingency models 60% of the
675 explained variance among dyad averages (compare Table 3,
676 Column e to Column a). The predictive power of this “kin-
677 favored reciprocity” term is consistent with a view that
678 households mainly engage in reciprocal exchanges and
679 prefer kin as their exchange partners.

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

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

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

724 5. Discussion

725 Household pairs at Arroyo Bandera display correspon-
726 dence in the amounts of calories they transfer to one another.

727 While nepotistic biases are present in the data, households
728 give preference to kin who are likely to reciprocate, rather
729 than kin who will benefit more from the aid. Closely related
730 households display even higher correspondence in the
731 number of calories they provide for each other than distantly
732 related and unrelated households, suggesting that contingent
733 reciprocity is the norm among close kin. To the degree that
734 exchanges between households are uneven, imbalances tend
735 to favor households that require more calories either because
736 they are low producers, contain many mouths to feed, or
737 both. These food flows favoring “poorer” households over
738 “richer” households occur irrespective of kinship distance.

739 5.1. The selective forces of kin selection and 740 reciprocal altruism

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

$$756 Br > C \quad (3.1)$$

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

$$759 Bp > C \quad (3.2)$$

760 where *B* is the benefit to the recipient, *C* is the cost to the
761 provider, *r* is the coefficient of genetic relatedness, and *p* is
762 the probability of future interaction. This comparison
763 suggests that aid will be more strongly favored by the forces
764 of reciprocal altruism than the forces of kin selection
765 whenever $p > r$ (Gurven et al., 2001). If siblings trust each
766 other, interact frequently, and rarely defect on repayment,
767 their value of *p* may often greatly exceed their *r* value of 0.5.

768 5.2. Relatives as attractive partners for reciprocal altruism

769 A nepotistic bias along with sharing patterns consistent
770 with the predictions of reciprocal altruism, rather than kin
771 selection theory, supports a view that relatives are preferred
772 exchange partners. Our finding that exchanges between close
773 relatives display more contingency than exchanges between
774 distant relatives and nonrelatives supports the view that close
775 relatives are less inclined to cheat on social obligations.
776 Meanwhile, indirect fitness payoffs, while not large enough
777

777 to provide the primary adaptive function of interhousehold
778 food transfers, may still confer additive fitness payoffs to
779 individuals who choose their close kin as their exchange
780 partners. It seems probable that close relatives prefer to live
781 near each other in order to engage in reciprocal provisioning
782 of goods and services. If true, residential proximity in a self-
783 selected living arrangement might be better regarded as an
784 outcome of actors' preferences for interaction rather than as
785 an independent predictor of resource flows.

786 5.3. Aiding the "needy"

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

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

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

825 Ache provisioners may also earn social utility. Economic
826 experiments reveal the willingness of individuals in this
827 culture to conform to socially prescribed patterns of
828 generosity. Ache bystanders to economic experiments
829 verbally encourage players to cooperate and Ache players
830 make larger mean contributions when economic experiments

are played in public than when they are played in private 831
(Hill and Gurven 2004). A reputation for generosity in Ache 832
society may bestow tangible benefits such as political 833
support, deference, allies in disputes, or caretaking during 834
illness and injury. One tangible benefit has been confirmed; 835
those who produce an abundance of food and generously 836
share the excess receive more food aid than less generous 837
individuals do when they fall ill and require others to 838
provision them (Gurven, Allen-Arave, Hill, & Hurtado, 839
2000). Finally, generous individuals may attract a larger and 840
healthier social support group (Wiessner 2002), which may 841
provide more opportunities for cooperation and advantage in 842
competitive interactions with other groups. Because Ache 843
provisioning of the "needy" may be a cooperative behavior 844
backed by third party punishment (Hill and Gurven 2004), 845
we must consider the possibility that this cultural convention 846
has evolved through cultural group selection (see Bowles 847
2006; Boyd, Gintis, Bowles, & Richerson, 2003; and 848
Henrich 2004). 849

850 5.4. Implications for previous kin selection studies

851 Among the Ache at Arroyo Bandera, relatedness is a 852
statistically significant predictor of food transfers only until 853
we control for the interaction of relatedness with dyadic 854
contingency. Early empirical tests of kin selection theory 855
commonly measured only relatedness and neglected to 856
investigate the ratio of benefit of aid for the recipient to the 857
cost of providing aid for the actor (Kurland, 1980). 858
Researchers commonly attributed cooperation among kin 859
to the process of kin selection without considering processes 860
such as reciprocal altruism that may occur among kin. The 861
conclusions from such studies warrant reconsideration.

862 If nepotism in social interactions sometimes results from 863
factors such as proximity, familiarity, trust, or higher 864
expectations of cooperation, then indirect fitness benefits 865
may play a smaller role in shaping cooperation among kin 866
than evolutionary researchers have previously assumed. In an 867
early introductory sociobiology text, Barash (1982, p. 74) 868
proclaims, "... inclusive fitness provides a coherent theory for 869
the biology of nepotism among living things." The empirical 870
body of evidence to back this up, however, is heavily biased 871
by studies in which juveniles obtain adult provisioning. 872
Evidence presented in this paper suggests that nepotistic aid 873
to adults (in humans at least) may sometimes represent 874
investment in direct fitness benefits. Even if nepotism in 875
social interactions involves additive inclusive fitness payoffs 876
on top of larger direct fitness payoffs from cooperation then 877
claims that genetic ties provide the "social glue" for these 878
partnerships may overstate the role of kin selection.

879 Understanding the contexts in which the gains from 880
nepotistic aid come primarily from reciprocal benefits and 881
those in which they come primarily in indirect fitness 882
impacts requires consideration of the adaptive problem that 883
each specific instance of aid solves (Hames 2004). On the 884
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.

Acknowledgments

We thank the residents of Arroyo Bandera for graciously sharing their community with us and for allowing us to collect these data. Allen-Arave extends much gratitude to Martin Daly, Daniel Fessler, Raymond Hames, Jeremy Koster, Eric Alden Smith, Margo Wilson, and an anonymous reviewer for their thoughtful comments, and to Edward Bedrick for enlightening analysis discussions. Allen-Arave accepts responsibility for any errors that remain. The National Science Foundation (grant #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.

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