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Kinship and Cooperation

The Axe Fight Revisited

Michael Alvard

Abstract Chagnon's analysis of a well-known axe fight in the Yanomamö village of Mishimishiböwei-teri (Chagnon and Bugos 1979) is among the earliest empirical tests of kin selection theory for explaining cooperation in humans. Kin selection theory describes how cooperation can be organized around genetic kinship and is a fundamental tool for understanding cooperation within family groups. Previous analysis on groups of cooperative Lamaleran whale hunters suggests that the role of genetic kinship as a principle for organizing cooperative human groups could be less important in certain cases than previously thought (Alvard *Human Nature* 14:129–163, 2003b). Evidence that supports a strong role for genetic kinship—groups are found to be more related than expected by chance—may be spurious because of the correlation between social structure and genetic kinship. Reanalysis of Chagnon's data using matrix regression techniques, however, confirms that genetic kinship was the primary organizing principle in the axe fight; affinal relations were also important, whereas lineage identity explained nothing.

Keywords Behavioral ecology · Kin selection · Alliance · Kinship · Yanomamö · Lamalera · Network analysis

Kin selection theory provides a critical tool that evolutionary biologists use for understanding the nature of sociality. It shows that organisms can increase their inclusive fitness both directly via their own reproduction and indirectly by helping genetically related individuals (Hamilton 1964a, b). Hamilton's rule is well known. Altruism is favored when the actor's fitness benefit (b) from an action directed at

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another, discounted by the pair's genetic relatedness (r), is greater than the fitness cost to the actor ($rb > c$). Because kin share genes owing to common descent, behaviors that increase the reproductive success of relatives can also increase the future representation of ego's genes. While it is clear that costs and benefits mediate the effects of genetic relatedness, as r approaches zero, according to Hamilton's equation, the likelihood of altruism also drops to zero. Thus, kin selection theory predicts that, all other things being equal, individuals will be more likely to favor kin than nonkin, and close kin than more distant kin.

Kin selection has been successful at explaining apparent altruism in a wide variety of organisms and contexts, including eusociality in insects (Hamilton 1964b), helping at the nest (Baglione et al. 2003; Hatchwell and Sharp 2006), alarm calling (Sherman 1977), and mating partnerships (Krakauer 2005). Among organisms who live in small family groups, kin selection provides a particularly robust explanation for much of the cooperation and altruism observed among close family members (Silk 2002). Evolutionary anthropologists were quick to realize kin selection theory's potential to explain aspects of human social behavior (Chagnon and Irons 1979). Evidence suggests that the higher than expected fertility displayed by human females, given their body size and the highly dependant offspring they produce (Kaplan et al. 2000), is at least partially subsidized by close consanguineous kin, such as grandmothers (Hawkes 2003) and other offspring (Kramer 2005), in addition to affines like husbands (Marlowe 2003). Work on altruistic cooperation among humans finds that helpers are often much more closely genetically related than expected by chance (Crognier et al. 2002; Gibson and Mace 2005; Kramer 2005; Borgerhoff Mulder 2007; Sear and Mace 2008; Tymicki 2004). Having close kin who help can lead to greater fertility for women (Bereczkei 1998; Sear et al. 2003). People are less likely to kill kin than nonkin (Daly and Wilson 1988; Johnson and Johnson 1991, 1997). Kin selection has been invoked to explain adoption in Oceania (Silk 1980, 1990), and garden labor exchange among farmers (Berte 1988; Hames 1987).

One of the first analyses to use kin selection theory to examine the role of genetic kinship for organizing human social behavior was Napoleon Chagnon's analysis of a Yanomamö axe fight that he observed in the village of Mishimishiböwei-teri, Venezuela (Chagnon and Bugos 1979). This work is significant for a variety of reasons. It can be viewed as one of the first attempts to direct the anthropological interest in kinship and nepotism within a context of Darwinism (Voland 1998). The analysis was published in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective* (Chagnon and Irons 1979), which many consider to be a seminal work of anthropological behavioral ecology. The fight is also a very well known ethnographic example because of the large number of people who have seen the film of its events and who read Chagnon's work as undergraduates in anthropology courses (Asch and Chagnon 1975). As will be discussed below, combatants on each side of the conflict were found to be both more related to one another than expected by chance and more related to their own group than to the other faction, matching basic predictions of kin selection theory.

While it is clear that kin selection is an important force favoring certain kinds of cooperation among close kin, there is growing evidence that kin selection is limited in a variety of ways. One principal limitation is its ability to generate cooperation in sizable groups without conflicts of interest (Alvard 2003b; Lukas et al. 2005; Wilson and Hölldobler 2005). Subsequent theoretical developments have generated a number of hypothetical mechanisms to explain cooperation in groups larger than can be organized by genetic kinship. This theory and the results from Lamalera, reviewed below, show that the cooperative coalitions that form to hunt whales are produced through alternative organizing mechanisms not attributable to kin selection that also, incidentally, produce higher levels of relatedness.

Many tests of kin selection, however, including Chagnon and Bugos's (1979) classic examination of the Yanomamö axe fight, have involved simply demonstrating that cooperators are closely related or more closely related than one would expect by chance. In order to learn if alternative mechanisms were at play in the axe fight, the methodology that produced the Lamalera results was applied to the original Yanomamö dataset. The results are discussed in the context of new theory to try to understand human cooperation.

The Yanomamö and the Axe Fight

The Yanomamö described here are swidden horticulturalists living in the rainforests of southern Venezuela. The considerable variation in the nature of Yanomamö villages follows variation in geography and ecology (Chagnon 1992). The description below is limited to the Yanomamö living in the lowland regions of the upper Orinoco and Mavava drainages and is derived from the work of Chagnon; the ethnographic present is the late 1960s and early 1970s (Chagnon 1968, 1974, 1979a, b, 1992). Yanomamö villages are small compared to Lamalera, ranging from 50 or so up to 250 individuals. Socially, they are organized into unnamed exogamous patrilineages that form alliances via spouse exchange. Chagnon points out that mate exchanges between lineages bind the descent groups into affinal alliances and at the same time increase the average degree of genetic relatedness within groups. Solidarity begins to deteriorate as village populations grow beyond 250 or so, and village fissioning often occurs. Villages eventually splinter for reasons often related to mate competition (Chagnon 1979b).

A number of variables are predicted to be important for explaining the pattern of affiliation in the axe fight. Much of this is discussed in Chagnon and Bugos's 1979 chapter, so only the matters germane to this paper will be reviewed here. The subject of that chapter is one conflict that occurred in the Yanomamö village of Mishimishimaböwei-teri in 1971. Mishimishimaböwei-teri had fissioned at some point preceding the fight. Leading up to the fight, members of the splinter group return for an extended visit and tensions rise among the hosts. The conflict is triggered when a member of the visiting group named Mohesiwä demands plantains from a host women, Sinabimi; she denies him the plantains and he beats her. After she returns to the village in tears, Sinabimi's half-brother Uuwä challenges Mohesiwä in the center of the village. Factions form that back each side of the clash and the conflict escalates to clubs, machetes, and then axes. As Chagnon notes, such fights are common, and the combination of photographic documentation and extensive demographic data make a detailed analysis possible.

Original Yanomamö Results

The two factions, host and visitors, formed with 13 and 17 members, respectively. Chagnon and Bugos (1979) made two specific predictions to test kin selection theory. The first was that each faction member would be more closely related genetically to their respective main fighter than to the other group's primary fighter. Second, members of each group would be more related to each other than to the other group. Consistent with both of their predictions, the authors reported that each of the factions, as a group, was indeed more closely related to the principal fighter of their own faction than to their opponents' principal fighter. The members of each faction were also more closely related to one another on average than they were to the other faction. The two groups were related to each other to the degree of mean $r=0.0633$.[1] The members of the visitors' faction were related to one another to the degree of mean $r=0.2124$. The members of the hosts' faction were related to one another to the degree of mean $r=0.0883$. Although stated somewhat convolutedly, it is clear that Chagnon and Bugos (1979) felt that genetic relatedness mediated the interpersonal behavior in the fight and that the results provided support for kin selection theory. They temper the interpretation, however, by stating, "It is also clear the relatedness alone cannot account for all the bonds of attraction or tactics of recruitment in events [like the axe fight].

Lamalera Analysis and Results

Lamalera is located on the island of Lambata, in the province of Nusa Tenggara Timur, Indonesia. The people of Lamalera are complex marine foragers whose subsistence activities revolve around cooperative hunting for large marine mammals and ray, and the trade for carbohydrates. The primary prey are sperm whale, accounting for the bulk of the prey harvested by weight, and ray, which account for the largest number of prey harvested (Alvard and Nolin 2002). The village has a population of approximately 1,200 people who are divided into 21 major named patrilineal clans, the larger of which are further divided into named lineages called *lango béla*. The named lineages manage whaling vessels called *téna* that are crewed by groups of 8–14 men. Previous work has shown that returns from whaling are greater than alternative forms of meat acquisition and that the cooperation during the hunts is best modeled as a game of coordination rather than a prisoner's dilemma (Alvard and Nolin 2002). Hunters are assured of their shares of the catch via a complex and mutually agreed upon set of distribution norms (Alvard 2002). Individual hunters, particularly harpooners, reap significant reproductive benefits. Harpooners have significantly more offspring than other men, marry significantly earlier, and start reproducing at an earlier age (Alvard and Gillespie 2004). For additional ethnographic details see Barnes (1996). Lamalera provides an excellent opportunity to test hypotheses for explaining cooperative behavior in the context of

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[1] The coefficient of relatedness (r) is defined as the probability that two individuals share a copy of an allele through common descent (Wright 1922).

big game hunting—a context that many feel was integral to the evolution of a number of uniquely human traits (Kaplan et al. 2000).

The dataset at Lamalera is larger and more complex than the Yanomamö dataset. The Yanomamö sample consists of one event with two factions consisting of 13 and 17 individuals each. In Lamalera, the sample consists of all 853 hunts that occurred over the course of 80 hunt days (between May 3 and August 5, 1999). Crew identifications were collected for each hunt. For each pair of individuals within the community the coefficient of relatedness was calculated using pedigrees developed from kinship data and a computer program written by Jeff Long (now at the University of New Mexico, Albuquerque).

Initially, the same test used by Chagnon and Bugos (1979) was applied to the Lamalera data. The basic kin selection hypothesis predicts that hunters who affiliate into hunting crews should be more closely related to one another than expected by chance. Hunting crews were indeed found to be much more related among themselves than if they assorted randomly. Using data on a sample of 189 of the hunters and 853 hunts,[2] it was shown that the average coefficient of relatedness within crews was $r=0.0362$ ($N=853$ hunts). This level of relatedness is approximately six times greater than what would be expected if crews formed randomly ($r=0.00631$, $p<0.0001$).

The Lamalera analyses went beyond simply testing to see if cooperators were more closely related than expected. A form of network analysis was applied, and the resulting data describe aspects of the *relationship* between individuals rather than characteristics of individuals themselves (Wasserman and Faust 1994). Kinship data are intrinsically suitable to this approach. Radcliff-Brown anticipated this development, as quoted by Hughes (1988:57): “The kind of mathematics which will be required ultimately for a full development of the science of society will not be metrical but will be . . . the calculus of relations (Radcliffe-Brown 1957).”

In Lamalera, affiliation was analyzed as a similarity matrix constructed from all hunter dyads.[3] Each hunter is represented by both a row and a column; the degree of affiliation is represented in each cell by the number of times that each dyad hunted together on the same boat on the same day. These data were reduced using multidimensional scaling and K-means cluster analysis (Bishop et al. 1975) to produce 20 clusters or coalitions of men who regularly crewed together on the same téna. The average coefficient of relatedness within these clusters, averaged across all clusters ($r=0.044$), was statistically equivalent to the result obtained from the sample of individual hunts (ranging from 0.125 to 0.0123; $N=20$, $p=0.4124$).

One strength of the network method is that other types of data that describe the relationships between members of a group can be used in the same way and hypotheses can be readily tested. In the earlier Lamalera analysis, the affiliation matrix serves as the independent variable and two matrices serve as the dependent variables. A lineage affiliation matrix was created by scoring a 1 in the cell for dyads having a common lineage. If the pair does not share a lineage a 0 is scored. The

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[2] The 290-man sample was limited to 189 by including only regular hunters (above the ninetieth percentile in number of days hunted) whose patriline was known and whose pedigrees were complete at least as far back as grandparents.

[3] The original axe fight kinship data were presented in matrix format, although a network analysis was not applied (Chagnon and Bugos 1979: tables 8.1–8.3).

biological kinship matrix is scored with the coefficient of relatedness (r) for the pair in each cell. The relationship between the normalized similarity affiliation matrix and the model matrices was examined using a matrix permutation or QAP (Quadratic Assignment Procedure) test (Freeman et al. 1992; Hubert and Schultz 1976; Krackhardt 1987).[4] This test involves first computing a Pearson's correlation coefficient between the corresponding cells of the two matrices. The rows and columns of the observed matrix are then randomly permutated and the correlation is computed again. The permutation is repeated (in this case, 2,000 times) in order to compute the proportion of times that a random correlation is larger than or equal to the observed correlation. A low proportion (<0.05) suggests a relationship between the matrices that is unlikely to occur by chance. Similar permutations techniques are used to do multiple matrix regression (Kapsalis and Berman 1996a, b; Smouse and Long 1992; Smouse et al. 1986).

The primary results were that, while significant, biological kinship alone explains only 3.9% of the variance in the affiliation (Alvard 2003b). When lineage identity is added for the multiple regression analysis, both variables explain 10.7% of the variance. As indicated by the standard parameter estimate, lineage's effect on affiliation is nearly 2.5 times as strong as genetic kinship ($\beta=0.0631$ vs. $\beta=0.2925$). More importantly, when genetic kinship is dropped from the multivariate analysis, the amount of variance remains virtually unchanged ($R^2=10.3$) and the strength of the estimate increases ($R^2=0.3215$.)

These results reflect the correlation between lineage membership and genetic kinship. In a patrilineal system all potential male cooperators who are relatives at $r=0.50$ (brothers, sons, and fathers) are also fellow lineage members; this is not true for male kin with more distant degrees of relatedness (uncles, cousins, and nephews). In terms of genetic kinship, nuclear kin ($r=0.5$) are more likely to affiliate, but more distant kin ($r<0.5$) are just as likely not to affiliate.

Additional (unpublished) analyses done to examine the results reviewed above confirmed the standard prediction from kin selection theory—that crews and clusters were more closely related than expected by chance. These new analyses found that not all cluster members were more related on average among their own members than they were to members of *other clusters* ($N * [N-1] = 380$ comparisons). Members of six of the 20 clusters (30%) were more related on average to members of at least one other cluster then they were to members of their own cluster. In addition, genetic relatedness within the clusters was significantly less than what could have been obtained with different mixes of the same hunters. Using a computer algorithm that swapped hunters between boats with the goal of maximizing mean relatedness within clusters, the mean relatedness across all 20 crew clusters nearly tripled to $r=0.115$ (a significant threefold increase from the observed $r=0.044$; $t=-4.57$, df=19, $p=0.00021$).[5]

In contrast to the predictions of kin selection theory, Lamaleran whale hunters clearly assort according to lineage identity and not to genetic kinship in spite of the

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[4] The procedures were performed using UCINET software (Borgatti et al. 2002).

[5] There are constraints to how crews are formed in the real world. For example, each real crew requires a harpooner and a helmsman. The simulation illustrates how closely related a crew could become if there were no constraints. The analysis was done in collaboration with Dr. David Carlson, Texas A&M University.

fact that initial analysis indicated positive assortment by genetic kinship. The next step was to check for this possibility in one of the earliest studies to test for predicted patterns of nepotism, the axe fight. Although Chagnon's conclusions seemed sound when originally presented, the results of the analysis applied to the Lamalera data opened the possibility that more could be learned from the classic Yanomamö work. Specifically, the possibility exists that the original results favoring kin selection could be spurious and better explained by lineage structures.

Applying the New Methodology to the Yanomamö Data

The Yanomamö data for this reanalysis come from three sources. The analysis focuses on the 30 individuals identified as fight participants by Chagnon and Bugos (1979). Genetic kinship data were obtained from Chagnon (personal communication) in a form slightly modified from the data presented in Chagnon and Bugos (1979) and the datasets included on the compact disk (CD) provided by Biella et al. (1997). A spreadsheet computer file included with the CD named DYADIC2 contains the coefficients of relatedness between all but nine participants.[6] Data obtained directly from Chagnon includes the missing individuals. Some of the coefficients also differ slightly from those in the original paper. For example, person #0029 and person #0517 are reported to be related at $r=0.1718$ in Chagnon and Bugos (1979). In the dyadic file, the value is listed as $r=0.17969$. These differences represent changes made to the dataset in the years subsequent to the publication of the original article and the CD (Chagnon, personal communication). The spreadsheet named PARTICIP.XLS, also on the CD, identifies the lineage to which each participant belongs, and his or her faction in the conflict. Finally, participants' spouses are identified in Appendix B of Chagnon's *Studying the Yanomamö* (1974).

In the following analysis, faction affiliation is the dependent variable and represented by a matrix containing all dyads of the 30 participants in the fight—a 1 scores an allied relationship, a 0 scores an antagonistic one. In addition to genetic kinship and lineage identity, an independent variable indicating an affinal relationship between dyads was also examined. An affinal relationship was scored as 1 if one of the pair and the spouse of the other share a lineage. Although affinal ties were not examined for Lamalera, Chagnon emphasizes the importance of such ties in Yanomamö sociopolitics.

Table 1 presents the univariate regression results. Consistent with the original results, but in contrast to the results found in Lamalera, genetic relatedness is an important factor for explaining affiliative behavior in Mishimishiböwei-teri. Genetic kinship explains around 15% of the variance in faction affiliation, about four times the amount of variance in crew affiliation explained by kinship among the Lamalera whale hunters. Also in contrast to the Lamalera results, lineage membership explains very little of the variance in faction affiliation in the axe fight. Although significant ($p=0.01$), lineage membership alone explains only about 3% of the variance. Finally, affinal ties, on their own, have a significant effect ($p<0.000$) and explain 2% of the variance.

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[6] ID numbers 29, 67, 390, 517, 950, 1062, 1278, 1827, and 2505

Table 1 Univariate results of QAP regression

Independent variable	Standardized parameter estimate	p	R^2
Genetic kinship	0.3861	<0.000	0.149
Lineage	0.1723	0.010	0.030
Affinal	0.1437	<0.000	0.021

Table 2 presents the results of four multiple QAP regressions with different combinations of the three independent variables. Combining lineage ID and kinship finds that lineage no longer has a significant effect on faction (p=0.281; Table 2A). In addition, no more of the variance is explained than was the case for genetic kinship alone. This suggests that the small lineage effect observed in the univariate analysis was the result of covariance between lineage and genetic kinship. Lineage members are more closely related than expected by chance; the multiple regression controls for this, and as a result, lineage loses its power independent of kinship. The opposite result was found among the Lamalera whale hunters.

The regression with genetic kinship and the affinal relationship finds that both are significant and the amount of variance explained increases to nearly 18% (Table 2B). Having an affinal relationship significantly increases the probability that two participants are on the same side of the fight (p<0.000). The standardized coefficients indicate that genetic kinship has more than twice the effect as affinal relationships. In the absence of genetic kinship, lineage and affinal ties each have the same strength, as measured by the standardized parameter estimate, and both are significant, though the amount of variance explained by these two variables is less than half of those of analyses that include genetic kinship (Table 2C). Finally, an analysis with all three variables clearly shows that genetic kinship and affinal relationship each have independent effects, while lineage does not (Table 2D).

Table 2 Multivariate results of QAP regression

Independent variable	Standardized parameter estimate	p	R^2
A.			
Genetic kinship	0.3797	<0.000	0.148
Lineage	0.0154	0.281	
B.			
Genetic kinship	0.4001	<0.000	0.179
Affinal	0.1755	<0.000	
C.			
Lineage	0.2420	0.001	0.072
Affinal	0.2203	<0.000	
D.			
Genetic kinship	0.3674	<0.000	0.183
Lineage	0.0836	0.068	
Affinal	0.1993	<0.000	

The Axe Fight in Detail

These results can be better understood by examining in more detail how members of the lineages assorted during the fight (Fig. 1). Five lineages are represented in the fight: lineage 1222 with 15 participants, lineage 2967 with nine participants, lineage 2700 with 3, lineage 1443 with 2, and one lone member of lineage 2936. Importantly, lineage 1222 is split between the factions; seven members support the visitors and eight members support the home faction. Each half of 1222 is supported by two different, smaller lineages. All nine members of 2967, along with the one member of 2936, support the visiting half of 1222. The home faction's 1222 members are joined by the two 1443 and the three 2700 members.

The impact of genetic relatedness can be visualized in a multidimensional scaling (MDS) analysis that was applied to the matrix consisting of the coefficient of relatedness values for each pair in the entire sample. MDS is used to analyze similarities and dissimilarities between objects as distances in a Euclidean space (Borg and Groenen 2005; Kruskal and Wish 1978). Using the 30-person sample mentioned above, an MDS analysis specifying nine dimensions results in a stress value of 0.0391 after 12 iterations.[7]

Figure 2 presents a scatterplot of the first two dimensions. Dimension 1 clusters the participants into groupings that can be interpreted to match the factions. It correctly classifies all but five of the 30 participants (Fisher's exact, one tailed $p=0.0001$, Goodman and Kruskal's $\lambda=0.61$).[8] All 13 members of faction 2 (home) have positive score on dimension 1, 12 of the 17-member faction 1 (visitors) are assigned a negative score on dimension 1. The incorrectly assigned individuals will be discussed below.

The strength of kinship is apparent especially for faction 1 through two clusters of siblings (Fig. 3). According to Chagnon and Bugos, "It is also clear that the visitors are, as a group, much more highly related among themselves than are the members of the fighting group that opposed them, in the fight" (1979:226). The first cluster (cluster A, Fig. 3) consists of the older generation of lineage 2967 males—Daramasiwä (#336), Wadoshewä (#1929), and Yoroshianawä (#2194)—all full sibs, along with Hemoshabuma (#517), the lone member of lineage 2936, who is their strong nephew ($r=0.3125$).[9] Continuing along the negative end of the dimension 1 axis is another cluster (B) formed with full sibs—the brothers Mohesiwä (#1246), Törawä (#1837), Amomiawä (#67), and Morokaböwä (#1278), and their sister Naakahedami (#1312). This group forms the next generation of 2967 members, and all are Wadoshewä's offspring. Mohesiwä is the man who instigated the fracas by

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[7] Stress is the most common measure of goodness-of-fit for MDS analyses. A general rule of thumb is that a stress value larger than 0.15 is unacceptable (Kruskal and Wish 1978).

[8] Goodman and Kruskal's Lambda (λ) is a proportional reduction in error (PRE) statistic used to measure how knowledge of a participant's score on dimension 1 reduces the error in assigning him (or her) to his (or her) observed faction. The reduction in error is determined by comparing faction assignments made with knowledge of dimension 1 to assignments made randomly (Johnson 1988). A λ of 0.61 means that the error is reduced by nearly 61% over what is expected by chance.

[9] I use the term "strong" in this context to mean a relationship that has a degree of relatedness greater than is usually associated with the vernacular kin term. In this instance, a nephew, who would normally be related to an uncle by $r=0.25$, is actually more closely related because the pair is related in multiple ways (or "loops," to use Chagnon and Bugos's 1979 terminology).

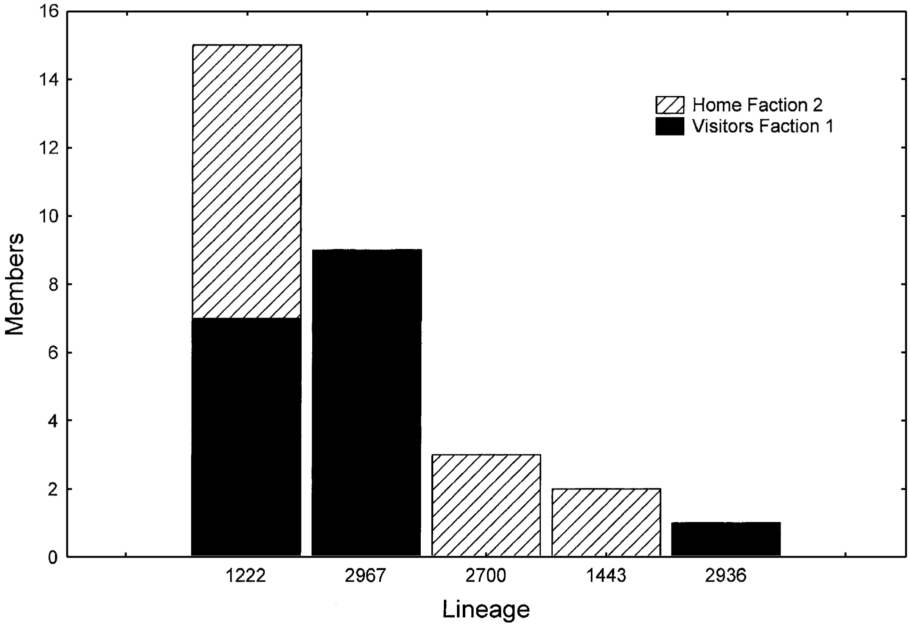

Fig 1 Lineages represented in the Yanomamö axe fight, and their members' distribution according to the two factions

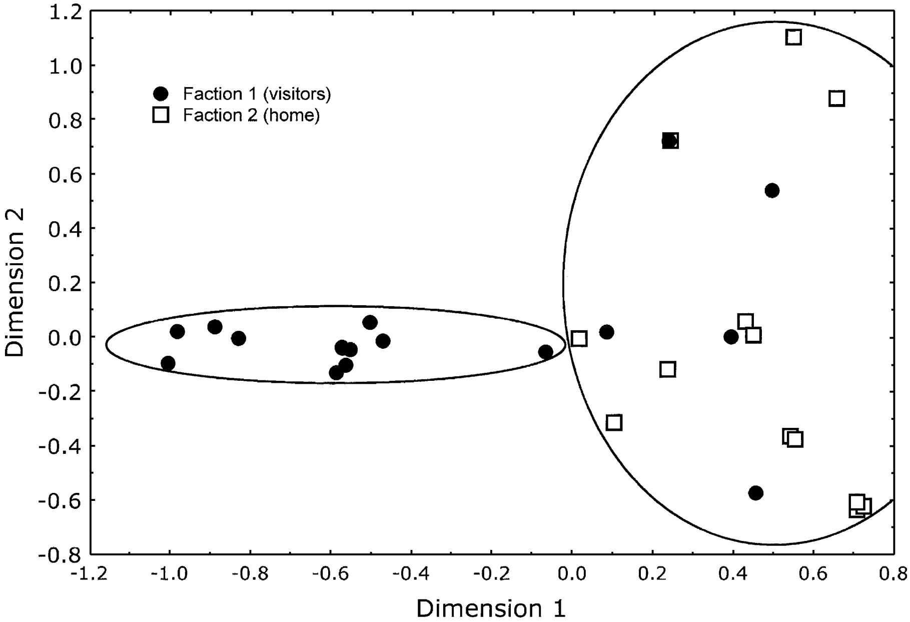

Fig. 2 Scatterplot of MDS dimensions 1 and 2 indicating the two factions

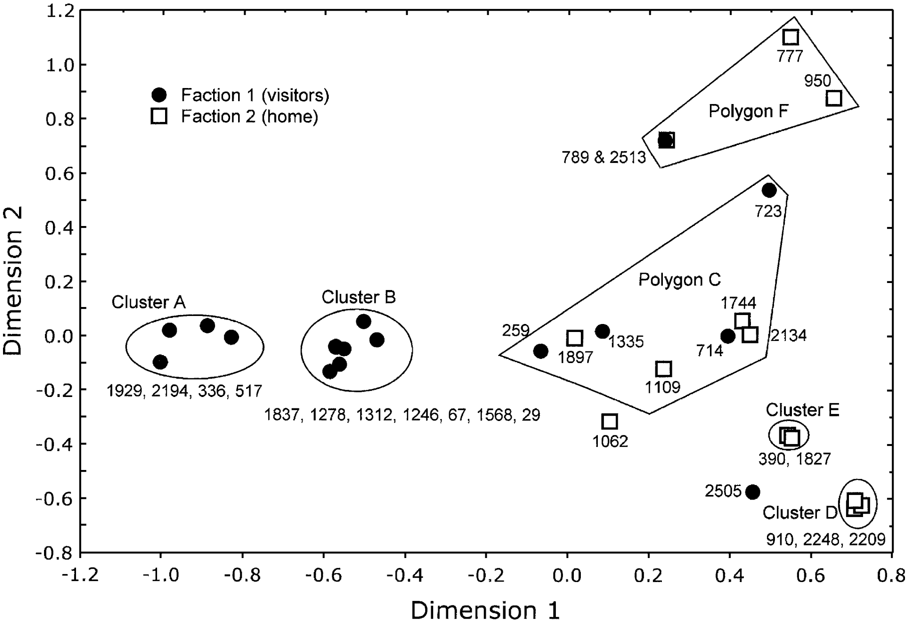

Fig. 3 Scatterplot of MDS dimensions 1 and 2 indicating the location of individuals

accosting Sinabimi, and Törawä is his younger brother, staunch supporter, and the youth whom Keböwä strikes with the axe near the end of the fight. They are joined in the cluster by Ruamowa (#1568, lineage 1222), their strong cousin (r=0.25) who also is Tourawa's brother-in-law, and Ahsökawä (#29, lineage 1222), who is Ruwamowä's strong half brother (r=0.32) and who also shares the associated relationships to the other lineage 2967 males.

As we move along the axis toward the positive end of dimension 1, we come to the bulk of lineage 1222 members. Among the fight participants, the core of lineage 1222 is formed by a group of sibs and half sibs who were all fathered by the same deceased man (#1650). This sib group is split between the two factions, and most are presented in polygon C: Borowama (#259), Uuwä (#1897), Nanokawä (#1335), Husiheami (#714), Sinabimi (#1744), and Iyaböwä (#723). Borowama is the mother of the 2967 sibs (cluster B) who form the majority lineage of faction 1 (the visitors). She is also Sinabimi's half sister. Sinabimi, as mentioned, is the woman who was accosted by Mohesiwä at the start of the fight. Borowama is at the center of the entire network and located on dimension 1 halfway between her set of offspring and her sibs. She sides with her husband Wadoshewä (#1929), their son Mohesiwä, and the rest of her offspring, rather than with her sister Sinabimi and the rest of her sibs and lineage mates. In fact, it is clear from Chagnon and Bugos (1979) and the film that Mohesiwä's mother (Borowama) and his sister (Naakahedami) are early and energetic verbal antagonists in the conflict. Borowama's half brother Uuwä, on the other hand, famously defends his half sister Sinabimi by challenging Mohesiwä at the initial stage of the conflict, whereas Borowama's full brother, Nanokawä, does not and instead follows his sister Borowama). This is perhaps because he is tied to lineage 2967 through a sibling marriage exchange: Nanokawä's sister's husband

(Wadoshewä) is Nanokawä's wife's (#2217) brother. Recall that Wadoshewä is Mohesiwä's father. Husiheami (#714; Borowama's co-wife to Wadoshewä as well as her half sister) and Iyaböwä (male, #723) also ally with the visitors against their half sister, Sinabimi. Finally, Maiyahariwä (#1109) is a more distant cousin: his grandfather and the grandfather of the 1222 sibs of polygon C are brothers.

The negative end of dimension 2 is anchored by the sib group (cluster D) that forms the base of lineage 2700: Yoinakuwä (#2248), husband of Sinabimi, and Keböwä (#910) his brother (these are the two men who escalate the fight to axes and machetes in defense of Sinabimi), and Yaukuima, their sister (#2209). They are cross cousins to the lineage 1222 sib group that forms polygon C, and in fact, all have spouses from lineage 1222), and are key allies with the faction 2 (home) half of lineage 1222. Note that Yaukuima (#2209) does not side with her husband Nanokawa, but with her brothers. Cluster E, Tomömamowä (#1827) and Hääma (#390), young and unmarried males, are a full sib pair who are parallel cousins to the sib group that forms polygon C; along with another parallel cousin, Kumishiwä (1062), they are also from lineage 1222 and allied with faction 2. As noted by Chagnon and Bugos (1979:231), this alliance appears to be related via the affinal links to the lineage 2700 sib group (cluster D) mentioned above. Kumishiwä's sister (#1614) is married to Yoinakuwä. The sister (#657) of Tomömamowä (#1827) and Hääma (#390) is married to Yoinakuwä's brother Keböwä.

Finally, Hererewä (#2505, lineage 2967) seems out of place and is an example of alliance via affinal tie. His mother (#457) is half sib with the lineage 2700 sib cluster (D): Keböwä (#910), Yaukuima (#2209), and Yoinakuwä (#2248; Sinabimi's husband). Hererewä allies himself against his uncles and their wives (and against his genetics) and sides with his more distantly genetically related lineage mates in lineage 2967. This may have to do with the fact that his wife (#1178) is Nanokawä's daughter, providing the affinal tie to faction 1's side of lineage 1222.

The positive end of dimension 2 is anchored by a father (Ishiweiwä, #777) and son (Kodedeari, #950) pair from lineage 1443—the other allies with the home faction of 1222. Kodedeari is Kaaböwä's (#789) maternal uncle. Next, Kaaböwä and his half sister Huuhuumi (#2513) have nearly identical kin networks; both belong to lineage 1222 and are located in the same location on the plot, but they are drawn to different factions. Huuhuumo is married to Mohesiwä, instigator of the incident that precipitated the fight and leader of faction 1. She sides with her husband rather than her brother.

It is clear from the MDS analysis that the strength of genetic kinship indicated from the matrix permutation test comes from the support that nuclear family members provided one another during the fight. Clusters of male siblings dominate each faction. Of course, siblings share lineage identity, and if it were not for the fact that the members of lineage 1222 split their allegiances, the relative strength of genetic kinship versus lineage identity as indicated by the statistical analysis above might not have been as clear. Based on that analysis, it might be tempting to say that, in the case of the axe fight, kinship trumped lineage loyalty, especially for members of lineage 1222. While it is true that lineage 1222 splintered, it did not do so in a way that suggests people were acting as would be predicted by Hamilton's rule. In fact, as mentioned above, the five participants misidentified by dimension 1 of the MDS analysis are more closely related to their kin in faction 2, but they nonetheless side with faction 1. Looking more closely at these individuals can tell us something about the nature of alliance formation in the axe fight case.

Two of these individuals are women; this is significant because only six women were involved in the conflict. In both cases it appears that the woman sides with her husband rather than her male siblings. Husiheami (#714, lineage 1222) sides with her husband Wadoshewä (#1929), his brothers, and Borowama, her co-wife and half sister. Huuhuumi (#2513, 1222), as mentioned above, sides with her husband Mohesiwä rather than her brother. The men who are incorrectly assigned clearly follow their affinal alliances. Nanokawä (#1335) follows his full sister Borowama, perhaps because he is tied to lineage 2967, the majority lineage in faction 1, through the sibling marriage exchange mentioned above. Hererewä's (#2505, lineage 2967) wife (#1178, lineage 1222) is Nanokawä's daughter; providing the affinal tie to faction 1's side of lineage 1222. Finally, Iyaböwä (#723) allies against his half sister Sinabimi and with the visitors. According to the dataset provided by Chagnon, he is married to a 42-year-old man (#256, lineage 1443), but this is obviously an error. In Chagnon's book (1974), his spouse is indicated as #2489, an 11-year-old female from the same lineage as he. This makes sense because the girl's father is Ruwamowä (#1568), and Iyaböwä is likely allying with his father-in-law.

It appears that marriage alliance and not genetic kinship played a role in the fracture of lineage 1222 and the overall structure of the two factions. Lineage 1222 is tightly linked via marriage to both lineage 2967 and lineage 2700, and many individuals appear to ally with their respective affinal lineages. Some women sided with their husbands and children, and some men sided with their wives' families. Of the 30 participants, 25 are married to a total of 36 spouses (a number of men have multiple spouses; lineage ID for 2 spouses is unknown). Of faction 1's 19 marriages, 13 are part of the 1222–2967 marriage alliance. In faction 2, 8 of the 15 marriages are part of the 1222–2700 marriage alliance (Table 3). Affinal links clearly weaken the lineage ties. The importance of affinal alliances for the Yanomamö is stressed by Chagnon (1975) in his analysis of village fissioning, which often involves lineages splitting as people side with affinal kin and their matrimonial concerns.

Table 3 Cross-tabulation of marriages between lineages for the two factions of the axe fight. The shaded cells indicate the number of marriages between members of lineage 1222 and members of lineages 2700 and 2967

Faction 1: Lineage marriage relationships

Ego's lineage	Spouse's Lineage				
	1222	1443	2700	2936	2967
1222	2	1	1	0	6
2936	0	0	0	0	1
2967	7	0	0	1	0

Faction 2: Lineage marriage relationships

Ego's lineage	Spouse's Lineage							
	81	200	1222	1380	1443	2700	2936	2967
1222	1	1	0	0	1	3	1	1
1443	1	0	0	1	0	0	0	0
2700	0	0	5	0	0	0	0	0

Discussion

> It is also clear the relatedness alone cannot account for all the bonds of attraction or tactics of recruitment in events such as the one analyzed here and that affinity or alliance likewise operates to build coalitions (Chagnon and Bugos 1979:237).

The initial analysis of genetic relationships at Lamalera indicated that hunting coalitions were significantly more related than expected by chance—an important prediction of Hamiltonian kin selection theory but one that was misleading in the Lamalera case. More comprehensive Lamalera analysis, reviewed above, indicate that lineage identity rather than genetic kinship was the major factor organizing cooperative hunting groups at that site. The conclusion that the Hamiltonian account was potentially specious at Lamalera provided part of the motivation for reexamining the Yanomamö axe fight using the new matrix methods. The reanalysis of the Yanomamö axe fight data supports Chagnon and Bugos's (1979) original conclusion that genetic kinship, rather than lineage, was the primary factor determining who helped whom; siblings, especially, tended to side with one another.

Further motivation for this reanalysis was provided by the mounting theoretical and empirical work that is reassessing kin selection's role in explaining altruism in general. In the 1960s and 1970s, kin selection and reciprocity were offered as alternative mechanisms to group selection to explain apparently altruistic behaviors. More recently, a number of researchers using new data and theory are concluding that kin selection appears to be more limited than initially thought as a satisfactory universal explanation of cooperation (Chapais 2001; Clutton-Brock 2002; Griffin and West 2002), especially for the large-scale cooperation seen among humans (Henrich 2004). Although genetic kinship can be important for the evolution of cooperation, it is clearly not essential, and in some cases can be a hindrance. Wilson (2005) points out that kin selection can be as much a dissolutive force as a binding one, at least in the social evolution of insects, and that the close genetic relatedness shared by members of the eusocial insects is as likely a consequence as a cause of group living (Wilson and Wilson 2007; Wilson 2005, 2008; Wilson and Hölldobler 2005).

Griffin and West (2002) note that the direct benefits of cooperation—those obtained by the individual himself rather than indirectly through the help provided to kin—have been underappreciated in previous work. Although limited dispersal can result in groups whose members are closely related to one another, in many cases individuals behave cooperatively because it is in their own direct self-interest, and benefits obtained indirectly through kin are secondary for the development of cooperative behavior. This conclusion is supported by recent research on food sharing by the Aché hunter-gathers now living on a reservation in Paraguay. Allen-Arave et al. (2008) show that Aché households transfer food in a manner more consistent with the direct fitness gains from expected reciprocity than the indirect fitness benefits from nepotistic investment. Although Aché share with kin, they do not share with the kin who could benefit the most. Rather, they share with kin who are more likely to pay them back—observations that match the hypothesis of reciprocity more closely than that of kin selection. Hames and McCabe (2007) come to similar conclusions with meal sharing among the Ye'kwana of Venezuela. Although there are cases that support the kin selection hypothesis (e.g., Ziker and Schnegg 2005), a recent review of food sharing among foragers and hunter horticulturalists by Gurven (2004) concludes that reciprocal altruism has more robust support than does kin selection.

These results suggest an important point. Appreciating the nature of the adaptive problem is critical for understanding the mechanisms that produce cooperative solutions (Hames and McCabe 2007). Diverse solutions like food sharing, coalitionary support, or large-group collective action are produced via different evolutionary mechanisms because the adaptive problems are often strikingly different. A similar point is raised by Alvard and Nolin (2002) when they argue that reciprocity, and the prisoner's dilemma game that is often used to model it, may not be the best paradigm for understanding certain cases of cooperation because reciprocity does not conform to the payoff structure of many socioecological conditions (see also Gurven and Winking 2008; Borgerhoff Mulder 2007; Winterhalder 1997). In some conditions it may be compelling to evoke kin selection. For example, a post hoc interpretation of this paper's results is that there are good inclusive fitness reasons for individuals to ally with close kin in the axe fight (e.g., avoiding death or serious injury of a kinsman). These same reasons are not apparent in the Lamalera case, where close kin are not numerous enough to form crews and less-related kin have diffuse interests.

These observations point to a key difference between the Lamalera and Yanomamö cases: group size. Lamaleran crews range between 8 and 14 and are very similar in size to the axe fight factions, but the population from which the hunting coalitions were culled is much larger. The village of Lamalera is an order of magnitude larger than Mishimishiböwei-teri in population, and hundreds participate in the village whale hunt, compared with the 30 Yanomamö participants in the axe fight. The axe fight involved a relatively small group of people. Recent theoretical developments (e.g., Lukas et al. 2005) suggest that the factions may have been at the large end of the range of group size that can be organized around genetic principles. For at least two reasons it is difficult for kin selection principles to produce the larger, cooperative, tribal groups commonly seen in humans (see detailed discussion in Alvard 2003b). First, in the absence of extreme reproductive skew, where a few members of a group reproduce much more than others—such as is the case in the social insects (Keller and Reeve 1994)—and high levels of endogamy, it is difficult to form large groups of closely related individuals. In most populations, as groups become larger the average degree of relatedness within the groups drops rapidly (Aviles et al. 2004; Campbell 1983; Lukas et al. 2005; Richerson and Boyd 1999).

Keller and Reeve (1994) were working with naked mole rats, whose reproductive skew and level of endogamy are similar to those of the eusocial insects (Reeve et al. 1990). Relative to other human populations, the Yanomamö could be characterized as having moderate levels of skew owing to polygyny and high levels of endogamy owing to bilateral cross-cousin marriage. This creates a context in which larger groups of closely related kin would be able to form, although there still are constraints to how large groups of close kin can grow.

In Lamalera, for example, there is a significant negative relationship between mean relatedness within a lineage and lineage size, even though large lineages are better able to organize whaling operations. Within the village of Mishimishiböwei-teri, the same relationship exists. The five lineages represented in the fight exhibit a negative relationship between the number of participants and their average relatedness ($R^2=0.61$ $p=0.07$). In particular, lineage 1222, the lineage with the largest number of members in the fight, has a low mean relatedness, though the two opposite sides of the conflict are significantly more related among themselves. In a sample of nine villages, Chagnon (1975: Fig. 3) found a negative relationship between village size and the average r within villages. As village size increases, average relatedness falls.

One factor examined with the Yanomamö data but not the Lamalera data was the impact of affinal relationships on faction formation.[10] Chagnon stressed the role of affinal relationships in Yanomamö life, especially in terms of mate acquisition. Exceptional male reproductive success is fundamentally the result of some males' ability to acquire multiple wives, which in turn depends on their, and their lineages', ability to form coalitions with males from other lineages (Chagnon 1980). Ideally, men from two localized lineages reciprocally exchange women with each other. To the extent that this occurs over time, the two lineages become closely linked in a variety of social and political ways, and conflict is reduced. Owing to the nature of Yanomamö marriage, these other males are likely to be kin as well. One outcome of this marriage system is the situation in which affinal kin in one's own village may be more closely related than many of one's own lineage members, and this condition places lineage at odds with genetic kinship once more. This was apparent in the axe fight.

Allegiance to one's lineage may exist only to the extent that association with fellow lineage members provides benefits. A key benefit of group fissioning is that it reduces competition for mates between more distantly related lineage members within the same village (Chagnon 1979b, 1980). Once a pattern of reciprocal exchange between lineage segments is established, close local affinal and nuclear family ties can trump more general lineage affiliations. This is apparent at the village level, just as in the axe fight, where genetic relatedness trumps lineage loyalties in many fission events; villages do not split along lineage lines, and the degree of relatedness is higher after fissioning within the new villages than before (Chagnon 1975, 1981). Pierre van den Berghe's lucid interpretation of Chagnon's Yanomamö work succinctly points out that "at least for the Yanomamö, unilineal descent is thus clearly not the paramount principle of social organization" (Van den Berghe 1979:148).

In addition, when groups become large, conflicts of interest develop that genetic kinship cannot resolve (Van den Berghe 1979). This can be seen when groups try to organize beyond the nuclear family. In an exogamous context, ego is equally related to his maternal and paternal cousins ($r=0.125$), but the two cousins are not related to each other at all (Alvard 2003b). This was one of the points stressed in the original Lamalera paper (Alvard 2003b); as group size increases it becomes difficult for

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[10] Affinal marriage alliance has not attracted the attention of human behavioral ecologists interested in cooperative relationships (other than Chagnon).

people to organize around a large, unambiguous contingent of close genetic kin. This conclusion was emphasized by a number of earlier students of unlineality (e.g., Ember et al. 1974; Sahlins 1961; Van den Berghe 1979).

An interpretation consistent with the data is that, among the Yanomamö, kin selection forces enhance close family allegiances at the expense of more inclusive organization principles, such as lineality, and this favors smaller Hamiltonian groups. Affinal ties and mating considerations also work to weaken lineage loyalties. In contrast, it appears that the Lamalerans have institutions (see Ostrom 1990; Paciotti and Borgerhoff Mulder 2004) in place that allow the formation of groups larger than could be produced via mechanisms based around genetic kinship. One could speculate that these mechanisms are related to the more robust lineage system developed, in part, to solve the organizational requirements of whaling operations. Although patrilineal descent principles are at play in Yanomamö society, it is clear that they are not as important for the Yanomamö as they are for other groups (Chagnon 1979a). The lineages are not named, for example, as they are in Lamalera and other societies. The primary function of Yanomamö lineages is to regulate marriage via the exchange of spouses in order to establish alliances with other descent groups (see also Van den Berghe 1979:455).[11] Paradoxically, this benefit seems to weaken lineages as cohesive institutions in the long run.

Among the Yanomamö, lineages find it increasingly difficult to maintain cohesion as villages become larger; this fact motivated Chagnon's work with village fissioning (Chagnon 1975, 1979b). The axe fight is a good case study. Lineage 1222 is Mishimishiböwei-teri's largest, but it is also the lineage that split in the fission that occurred subsequent to the fight, and in the axe fight itself.

Membership in a large group has many advantages, however, and although forces are at work to drive lineages apart, other forces work to keep them together. Chagnon points out that group size is a key to survival among the Yanomamö, and groups that are unable to maintain sufficient size fission into smaller units and are vulnerable to the predation of larger groups. The structure provided by a lineage system may be selected, in part, because it allows larger groups. Large lineages are the most important politically, and village headmen regularly come from the largest lineages within a village. Patrilineal descent in combination with polygyny, which is widespread among the Yanomamö Chagnon studied, allows the formation of larger groups than would be possible with matrilineal descent (Chagnon 1979a:388) owing to the greater reproductive success for males made possible by polygynous matings. Chagnon's argument describing the military advantages of large lineages to explain the cultural evolution of patrilineality versus matrilineality reads as a model for group selection (see Henrich 2004; Sahlins 1961). He goes on to show that not only are men from larger lineages more likely to be polygynous, but that women from larger lineages are able to produce larger numbers of children. Clearly, advantages accrue to people who can maintain large, cohesive groups, but the Yanomamö lack the ability to the extent found in other societies, such as the Lamalera whale hunters.

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[11] Lamalera lineages function in additional ways; lineages organize whaling operations as corporations. Decent groups in Lamalera are classically corporate in the sense that they exist as institutions in perpetuity, or at least beyond the life of any particular individual, and they hold property, such as the whaling boats.

These results suggest an interesting way of looking at how genetic kinship plays a role at various levels of cooperation. Part of the result at Lamalera may be explained by the size of the cooperative groups involved. Groups differ in their optimal size for a variety of reasons, and different principles of organization may work better at different scales (Richerson and Boyd 1999). A cross-cultural study of 15 small-scale societies found that while the economic lives of Amazonian horticulturalists like the Machiguenga and the Tsimane involve small groups that are almost entirely economically independent at the family level, Lamalera ranked as requiring the largest nonkin cooperative groups (Henrich et al. 2005). In other words, subsistence in Lamalera requires larger groups, and optimal sizes that are difficult to achieve with high degrees of average relatedness. It is likely that relatively larger groups are *required* for a subsistence strategy like that found at Lamalera to be competitive, but they cannot be formed using genetic kinship as a mechanism of organization. For the reasons discussed above, genetic kinship cannot resolve conflicting loyalties with sufficient certainty. Not all strategies require such large groups, however (Kelly 1995). Most ethnographically described hunters, like the Yanomamö, live in smaller groups whose membership can be supplied more easily by close kin. Although the Lamalera result suggests that kinship may not be the primary organizing factor for the groups of hunters at that site, surely in many situations it would be. This may explain why the Yanomamö have a harder time maintaining lineage cohesion; there is no compelling reason for them to do so, unlike at Lamalera.

It is becoming increasingly apparent that kin selection (and reciprocity) is not up to the task of producing cooperative solutions that require large groups as part of the answer (Boyd and Richerson 1988). There are alternatives, however. Clutton-Brock and colleagues refer to one process as “group augmentation,” where the mutualistic benefits of collective action arise though activities that can be done only, or more efficiently, as part of a larger group. Maynard Smith and Szathmary (1995) refer to this sort of cooperation as “synergistic mutualism.” Benefits can accrue to individuals in the absence of kin selection even when most group members are in fact kin (Clutton-Brock 2002; Kokko et al. 2001). In this case, simply being part of a larger group provides sufficient direct benefits independent of any indirect benefits obtained via kin selection.

The process of group augmentation may be analogous to a coordination game (in the parlance of game theory) or mutualism, where the individual benefits from coordinating activities are significant, but only if the activities are done as a group (Cooper 1999; Schelling 1960; Sugden 1986). This sort of mutualistic cooperation or coordination is at play among the Lamalera whale hunters (Alvard and Nolin 2002). Hunting in Lamalera can be described as a classic weak-link coordination game (Van Huyck et al. 1990), where a minimum number of men are required to crew a whaling boat successfully (Alvard and Nolin 2002). A close genetic relationship between the hunters is not needed for the cooperation to develop and in fact can be a hindrance as shown above. Nor are the defection problems often associated with reciprocity an issue because in a coordination problem individuals are always better off cooperating, even though it is not always easy to achieve.[12]

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[12] In the prisoner’s dilemma, in contrast, defectors always have a higher expected payoff than cooperators (Taylor and Nowak 2007).

It is interesting to speculate that different organizing mechanisms may play more or less important roles depending on the context. To reap the benefits of cooperation, individuals have to make decisions about whom they should affiliate with based on expectations of others' behaviors. The organizing mechanisms help answer the question, "Whom can I trust?" (Alcorta and Sosis 2005; Barclay 2004; Henrich 2006; Nesse 2001; Tomasello et al. 2005). Each of the key mechanisms thought to play an important role in the evolution of cooperation shares the principle of positive assortment; the mechanisms produce a context in which cooperators can identify and interact with each other and avoid defectors, freeloaders, or others with different loyalties and norms of conduct (Fletcher and Doebeli 2006; Taylor and Nowak 2007; Wilson and Dugatkin 1997). For problems that require small groups, genetic kinship is sufficient. For more complex coordination problems that require larger groups, socially constructed and culturally transmitted identities based on *notions* of kinship—lineages and clans, for example—allow the formation of larger affiliations (Alvard 2003a; Jones 2000, 2003; Quinlan and Flinn 2005). Systems of unilineal descent provide great advantages when tribal groups are in conflict with other groups that are more simply organized. The classic examples are the segmental systems of East Africa, where lower-order segments organized by unilineal descent easily combine into higher-order segments when needed. The Nuer and their territorial expansion at the expense of the Dinka is a good example (Evans-Pritchard 1940; Kelly 1985). In larger armies, men form kin-like bonds with men who are otherwise strangers. It is clear that the bonds that men *may* form during warfare *can* be independent of genetic kinship, especially when examined from a local point of view—during actual battles, for example.

Historically, there is some evidence that segmentary lineage systems are replaced, in turn, with even more inclusive organizing principles. Two examples come to mind, but there are surely more. In 508 BC the ancient, clan-based requirement of Athenian citizenship (phratries) was replaced with one based on locality (demes; Lambert 1993). A similar process occurred early in the formation of the Mongol empire, when Genghis Khan dissolved his followers' steppe tribal identities and replaced them with a Mongol imperial identity (Weatherford 2004). In both these cases, societies that had moved beyond Hamiltonian-based social organization to form classic lineage-based systems evolved further to adopt social structures that allowed even larger, more inclusive groups. Understanding these higher-order mechanisms, and in what sort of contexts they are favored, is a major challenge for evolutionary anthropologists.

References

Alcorta, C. S., & Sosis, R. (2005). Ritual, emotion, and sacred symbols: The evolution of religion as an adaptive complex. *Human Nature, 16*, 323–359.

Allen-Arave, W., Gurven, M., & Hill, K. (2008). Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an Ache reservation. *Evolution and Human Behavior, 29*, 305–318.

Alvard, M. (2002). Carcass ownership and meat distribution by big-game cooperative hunters. *Research in Economic Anthropology, 21*, 99–132.

Alvard, M. (2003a). The adaptive nature of culture. *Evolutionary Anthropology, 12*, 136–149.

Alvard, M. (2003b). Kinship, lineage, and an evolutionary perspective on cooperative hunting groups in Indonesia. *Human Nature, 14*, 129–163.

Alvard, M., & Gillespie, A. (2004). Good Lamalera whale hunters accrue reproductive benefits. *Research in Economic Anthropology, 23*, 225–247.

Alvard, M., & Nolin, D. (2002). Rousseau's whale hunt? Coordination among big-game hunters. *Current Anthropology, 43*, 533–559.

Asch, T., & Chagnon, N. (1975). "The Ax fight" (film). Watertown: Documentary Educational Resources.

Aviles, L., Fletcher, J. A., & Cutter, A. D. (2004). The kin composition of social groups: Trading group size for degree of altruism. *American Naturalist, 164*, 132–144.

Baglione, V., Canestrari, D., Marcos, J. M., & Ekman, J. (2003). Kin selection in cooperative alliances of carrion crows. *Science, 300*, 1947–1949.

Barclay, P. (2004). Trustworthiness and competitive altruism can also solve the "Tragedy of the Commons." *Evolution and Human Behavior, 25*, 209–220.

Barnes, R. H. (1996). *Sea hunters of Indonesia: Fishers and weavers of Lamalera*. New York: Clarendon.

Bereczkei, T. (1998). Kinship network, direct childcare, and fertility among Hungarians and Gypsies. *Evolution and Human Behavior, 19*, 283–298.

Berte, N. (1988). K'ekchi' horticultural labor exchange: Productive and reproductive. In L. Betzig, M. Borgerhoff Mulder & P. Turke (Eds.), *Human reproductive behaviour: A Darwinian perspective* (pp. 83–96). New York: Cambridge University Press.

Biella, P., Chagnon, N., & Seaman, G. (1997). *Yanomamo interactive: The ax fight (CD/ROM)*. Ft. Worth: Harcourt Brace.

Bishop, Y. M. M., Fienberg, S. E., & Holland, P. W. (1975). *Discrete multivariate analysis: Theory and practice*. Cambridge: MIT.

Borg, I., & Groenen, P. (2005). *Modern multidimensional scaling: Theory and applications* (2nd ed.). New York: Springer.

Borgatti, S., Everett, M., & Freeman, L. (2002). *UCINET for Windows: Software for social network analysis.* Lexington, KY: Analytic Technologies. (Available at http://www.analytictech.com/).

Borgerhoff Mulder, M. (2007). Hamilton's rule and kin competition: The Kipsigis case. *Evolution and Human Behavior, 28*, 299–312.

Boyd, R., & Richerson, P. J. (1988). The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology, 132*, 337–356.

Campbell, D. (1983). The two distinct routes beyond kin selection to ultrasociality: Implications for the humanities and social sciences. In D. Bridgeman (Ed.), *Nature of prosocial development: Theories and strategies* (pp. 71–81). New York: Academic.

Chagnon, N. (1968). Yanomamo social organization and warfare. In M. Fried, M. Harris & R. Murphy (Eds.), *War: The anthropology of armed conflict and aggression* (pp. 109–159). New York: Natural History.

Chagnon, N. (1974). *Studying the Yanomamö*. New York: Holt.

Chagnon, N. (1975). Geneaology, solidarity, and relatedness: Limits to local group size and patterns of fissioning in an expanding population. *Yearbook of Physical Anthropology, 19*, 95–110.

Chagnon, N. (1979a). Is reproductive success equal in egalitarian societies? In N. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 374–401). North Scituate: Duxbury.

Chagnon, N. (1979b). Mate competition, favoring close kin and fissioning among the Yanomamo Indians. In N. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 86–132). North Scituate: Duxbury.

Chagnon, N. (1980). Kin selection theory, kinship, marriage and fitness among the Yanomamö Indians. In R. Alexander & D. Tinkle (Eds.), *Sociobiology: Beyond nature/nurture?* (pp. 545–571). New York: Westview.

Chagnon, N. (1981). Terminological kinship, genealogical relatedness and village fissioning among the Yanomamö Indians. In R. Alexander & D. Tinkle (Eds.), *Natural selection and social behavior* (pp. 490–508). New York: Chiron.

Chagnon, N. (1992). *Yanomamö* (4th ed.). Fort Worth: Harcourt Brace Jovanovich.

Chagnon, N., & Bugos, P. (1979). Kin selection and conflict: An analysis of a Yanomamö ax fight. In N. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 213–238). North Scituate: Duxbury.

Chagnon, N., & Irons, W. (eds). (1979). *Evolutionary biology and human social behavior: An anthropological perspective*. North Scituate: Duxbury.

Chapais, B. (2001). Primate nepotism: What is the explanatory value of kin selection? *International Journal of Primatology, 22*, 203–229.

Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science, 296*, 69–72.

Cooper, R. (1999). *Coordination games: Complementarities and macroeconomics*. New York: Cambridge University Press.

Crognier, E., Villena, M., & Vargas, E. (2002). Helping patterns and reproductive success in Aymara communities. *American Journal of Human Biology, 14*, 372–379.

Daly, M., & Wilson, M. (1988). *Homicide*. New York: Aldine de Gruyter.

Ember, C. R., Ember, M., & Pasternak, B. (1974). On the development of unilineal descent. *Journal of Anthropological Research, 30*, 69–94.

Evans-Pritchard, E. (1940). *The Nuer: A description of the modes of livelihood and political institutions of a Neolithic people*. Oxford: Clarendon.

Fletcher, J. A., & Doebeli, M. (2006). How altruism evolves: Assortment and synergy. *Journal of Evolutionary Biology, 19*, 1389–1393.

Freeman, L. C., Freeman, S. C., & Romney, A. K. (1992). The implications of social structure for dominance hierarchies in red deer, *Cervus elaphus* L. *Animal Behaviour, 44*, 239–245.

Gibson, M. A., & Mace, R. (2005). Helpful grandmothers in rural Ethiopia: A study of the effect of kin on child survival and growth. *Evolution and Human Behavior, 26*, 469–482.

Griffin, A. S., & West, S. A. (2002). Kin selection: Fact and fiction. *Trends in Ecology and Evolution, 17*, 15–21.

Gurven, M. (2004). To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences, 27*, 543–560.

Gurven, M., & Winking, J. (2008). Collective action in action: Prosocial behavior in and out of the laboratory. *American Anthropologist, 110*, 179–190.

Hames, R. (1987). Garden labor exchange among the Ye'kwana. *Ethology and Sociobiolology, 8*, 259–284.

Hames, R., & McCabe, C. (2007). Meal sharing among the Ye'kwana. *Human Nature, 18*, 1–21.

Hamilton, W. D. (1964a). Genetical evolution of social behaviour, I. *Journal of Theoretical Biology, 7*, 1–16.

Hamilton, W. D. (1964b). Genetical evolution of social behaviour, 2. *Journal of Theoretical Biology, 7*, 17–52.

Hatchwell, B. J., & Sharp, S. P. (2006). Kin selection, constraints, and the evolution of cooperative breeding in long-tailed tits. *Advances in the Study of Behavior, 36*, 355–395.

Hawkes, K. (2003). Grandmothers and the evolution of human longevity. *American Journal of Human Biology, 15*, 380–400.

Henrich, J. (2004). Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior and Organization, 53*, 3–35.

Henrich, J. (2006). Cooperation, punishment, and the evolution of human institutions. *Science, 312*, 60–61.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., et al. (2005). "Economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences, 28*, 795–855.

Hubert, L., & Schultz, J. (1976). Quadratic assignment as a general data-analysis strategy. *British Journal of Mathematical and Statistical Psychology, 29*, 190–241.

Hughes, A. L. (1988). *Evolution and human kinship*. New York: Oxford University Press.

Johnson, A. (1988). Relationships between nominal-scale variables. In A. Johnson (Ed.), *Statistics* (pp. 146–149). San Diego: Harcourt Brace Jovanovich.

Johnson, S. B., & Johnson, R. C. (1991). Support and conflict of kinsmen in Norse earldoms, Icelandic families, and the English royalty. *Ethology and Sociobiology, 12*, 211–220.

Johnson, R. C., & Johnson, S. B. (1997). Kinship and the quest for wealth and power as influences on conflict in the Punjab, 1839–1845. *Evolution and Human Behavior, 18*, 341–348.

Jones, D. (2000). Group nepotism and human kinship. *Current Anthropology, 41*, 779–809.

Jones, D. (2003). The generative psychology of kinship, Part 1: Cognitive universals and evolutionary psychology. *Evolution and Human Behavior, 24*, 303–319.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology, 9*, 156–185.

Kapsalis, E., & Berman, C. M. (1996a). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*), 1: Criteria for kinship. *Behaviour, 133*, 1209–1234.

Kapsalis, E., & Berman, C. M. (1996b). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*), 2: Testing predictions for three hypothesized organizing principles. *Behaviour, 133*, 1235–1263.

Keller, L., & Reeve, H. K. (1994). Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution, 9*, 98–102.

Kelly, R. C. (1985). *The Nuer conquest: The structure and development of an expansionist system*. Ann Arbor: University of Michigan Press.

Kelly, R. L. (1995). *The foraging spectrum: Diversity in hunter-gatherer lifeways*. Washington: Smithsonian Institution.

Kokko, H., Johnstone, R. A., & Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London, B: Biological Sciences, 268*, 187–196.

Krackhardt, D. (1987). QAP partialling as a test of spuriousness. *Social Networks, 9*, 171–186.

Krakauer, A. H. (2005). Kin selection and cooperative courtship in wild turkeys. *Nature, 434*, 69–72.

Kramer, K. L. (2005). Children's help and the pace of reproduction: Cooperative breeding in humans. *Evolutionary Anthropology, 14*, 224–237.

Kruskal, J., & Wish, M. (1978). *Multidimensional scaling*. Beverly Hills: Sage.

Lambert, S. D. (1993). *The phratries of Attica*. Ann Arbor: University of Michigan Press.

Lukas, D., Reynolds, V., Boesch, C., & Vigilant, L. (2005). To what extent does living in a group mean living with kin? *Molecular Ecology, 14*, 2181–2196.

Marlowe, F. W. (2003). A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior, 24*, 217–229.

Maynard Smith, J., & Szathmary, E. (1995). *The major transitions in evolution*. New York: Oxford University Press.

Nesse, R. M. (2001). *Evolution and the capacity for commitment*. New York: Russell Sage Foundation.

Ostrom, E. (1990). *Governing the commons: The evolution of institutions for collective action*. New York: Cambridge University Press.

Paciotti, B., & Borgerhoff Mulder, M. (2004). Sungusungu: The role of preexisting and evolving social institutions among Tanzanian vigilante organizations. *Human Organization, 63*, 112–124.

Quinlan, R. J., & Flinn, M. V. (2005). Kinship, sex, and fitness in a Caribbean community. *Human Nature, 16*, 32–57.

Radcliffe-Brown, A. R. (1957). *A natural science of society*. Glencoe: Free.

Reeve, H. K., Westneat, D. F., Noon, W. A., Sherman, P. W., & Aquadro, C. F. (1990). DNA fingerprinting reveals high-levels of inbreeding in colonies of the eusocial naked mole-rat. *Proceedings of the National Academy of Sciences (USA), 87*, 2496–2500.

Richerson, P. J., & Boyd, R. (1999). Complex societies: The evolutionary origins of a crude superorganism. *Human Nature, 10*, 253–289.

Sahlins, M. D. (1961). The segmentary lineage: An organization of predatory expansion. *American Anthropologist, 63*, 322–345.

Schelling, T. (1960). *The strategy of conflict*. Cambridge: Harvard University Press.

Sear, R., & Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior, 29*, 1–18.

Sear, R., Mace, R., & McGregor, I. A. (2003). The effects of kin on female fertility in rural Gambia. *Evolution and Human Behavior, 24*, 25–42.

Sherman, P. (1977). Nepotism and the evolution of alarm calls. *Science, 197*, 1246–1253.

Silk, J. B. (1980). Adaption and kinship in Oceania. *American Anthropologist, 82*, 799–820.

Silk, J. B. (1990). Human adoption in evolutionary perspective. *Human Nature, 1*, 25–52.

Silk, J. B. (2002). Kin selection in primate groups. *International Journal of Primatology, 23*, 849–875.

Smouse, P. E., & Long, J. C. (1992). Matrix correlation analysis in anthropology and genetics. *Yearbook of Physical Anthropology, 35*, 187–213.

Smouse, P. E., Long, J. C., & Sokal, R. R. (1986). Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology, 35*, 627–632.

Sugden, R. (1986). *The economics of rights, co-operation, and welfare*. Oxford: Blackwell.

Taylor, C., & Nowak, M. A. (2007). Transforming the dilemma. *Evolution, 61*, 2281–2292.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences, 28*, 675–691.

Tymicki, K. (2004). Kin influence on female reproductive behavior: The evidence from reconstitution of the Bejsce Parish registers, 18th to 20th centuries, Poland. *American Journal of Human Biology, 16*, 508–522.

Van den Berghe, P. L. (1979). *Human family systems: An evolutionary view*. New York: Elsevier.

Van Huyck, J. B., Battalio, R. C., & Beil, R. O. (1990). Tacit coordination games, strategic uncertainty, and coordination failure. *American Economic Review, 80*, 234–248.

Voland, E. (1998). Evolutionary ecology of human reproduction. *Annual Review of Anthropology, 27*, 347–374.

Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications*. New York: Cambridge University Press.

Weatherford, J. M. (2004). *Genghis Khan and the making of the modern world* (1st ed.). New York: Crown.

Wilson, E. O. (2005). Kin selection as the key to altruism: Its rise and fall. *Social Research, 72*, 159–166.

Wilson, E. O. (2008). One giant leap: How insects achieved altruism and colonial life. *Bioscience, 58*, 17–25.

Wilson, D. S., & Dugatkin, L. A. (1997). Group selection and assortative interactions. *American Naturalist, 149*, 336–351.

Wilson, E. O., & Hölldobler, B. (2005). Eusociality: Origin and consequences. *Proceedings of the National Academy of Sciences (USA), 102*, 13367–13371.

Wilson, D. S., & Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology, 82*, 327–348.

Winterhalder, B. (1997). Gifts given, gifts taken: The behavioral ecology of nonmarket, intragroup exchange. *Journal of Archaeological Research, 5*, 121–168.

Wright, S. (1922). Coefficients of inbreeding and relationship. *American Naturalist, 56*, 330–338.

Ziker, J., & Schnegg, M. (2005). Food sharing at meals: Kinship, reciprocity, and clustering in the Taimyr Autonomous Okrug, northern Russia. *Human Nature, 16*, 178–210.

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