KINSHIP, LINEAGE, AND AN EVOLUTIONARY PERSPECTIVE ON COOPERATIVE HUNTING GROUPS IN INDONESIA

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Work was conducted among traditional, subsistence whale hunters in Lamalera, Indonesia, in order to test if strict biological kinship or lineage membership is more important for explaining the organization of cooperative hunting parties ranging in size from 8 to 14 men. Crew identifications were collected for all 853 hunts that occurred between May 3 and August 5, 1999. Lineage identity and genetic relatedness were determined for a sample of 189 hunters. Results of matrix regression show that genetic kinship explains little of the hunters’ affiliations independent of lineage identity. Crew members are much more closely related to each other than expected by chance, but this is due to the correlation between lineage membership and genetic kinship. Lineage members are much more likely to affiliate in crews, but kin with $r < 0.5$ are just as likely not to affiliate. The results are discussed vis-à-vis the evolution of cooperation and group identity.

KEY WORDS: Affiliation; Cooperation; Culture; Hunting; Indonesia; Lineage theory

People frequently form cooperative groups in order to realize the benefits of collective action. Although humans are not the only species that forms social groups, we are unique in the degree to which we regularly rely on the help of conspecifics to satisfy basic needs such as subsistence, defense, and offspring care (Hill 2002). In simple foraging groups, people help one an-
other care for children (Ivey 2000), acquire difficult-to-obtain resources (Al-vard and Nolin 2002), share food (Kaplan and Hill 1985), and fight other groups (Chagnon 1979). In complex industrial society such instances are even easier to come by. Examples include unions, political parties, nation states, business firms, college fraternities, sports teams, and universities.

Inclusive fitness theory and its key mechanism of kin selection (Hamilton 1964a, 1964b; Maynard Smith 1964) offer sound evolutionary explanations for why cooperation among relatives should be common. Kin selection is the process by which traits are favored because of their beneficial effects on the survival of relatives (Grafen 1984). Because kin share genes as a result of common descent, behaviors that increase the reproductive success of relatives can also increase the future representation of ego’s genes. Thus, kin selection theory predicts that, all else being equal, individuals will be more likely to favor kin than non-kin, and close kin than more distant kin. Nepotism will evolve if the recipient of the favor is sufficiently related, the benefit is sufficiently great, or the cost sufficiently low. Biological kinship has been shown to be an important social organizing principle across a wide variety of taxa (Dugatkin 1997), and especially so in the social insects (Bourke 1997).

Within fields of study that take an evolutionary approach to human behavior, the role of biological kinship in explaining cooperative behavior within preindustrial societies is now taken for granted to some extent (Alexander 1987; Chagnon 1979, 1980; Hamilton 1975; see review by Voland 1998:363), although as I shall show, the extent of its importance is ambiguous (Brown 1991; Jones 2000; Richerson and Boyd 1998). Kinship, broadly defined, has also long been argued by cultural anthropologists to be the primary organizing principle in tribal societies (Kuper 1982, 1996). In spite of what appears to a common ground, however, there has been little work over the past twenty years to integrate the two approaches. Indeed, kinship within the field has been “denaturalized” by many cultural anthropologists in the late twentieth century (Collier and Yanagisako 1987; Schneider 1984; for a review see Peletz 1995). A standard critique of kin selection theory as it is applied to humans points to the incongruity between genetically defined and culturally defined kin, to put it simply. This point was made most strongly by Sahlins (1976:58) when he stated, “Kinship is a unique characteristic of human societies, distinguishable precisely by its freedom from natural relationships.” The hyperbole of this statement seems obvious. But while it is impossible to maintain the position that cultural kinship has nothing to do with genetic kinship, it is equally difficult to deny that people commonly organize themselves in ways that do not correspond to coefficients of relatedness.

Sahlins (1976:26) also wrote, “local kinship networks . . . will comprise a determinate and biased proportion of any person’s genealogical uni-
verse." This is most apparent in systems of unilineal descent. Genetic kinship makes no distinctions between individuals equivalently related. People who follow norms of unilineal descent, however, define as kin only those persons who share common descent through either the male or female parent. In such systems, two people who are each equally related to Ego genetically may be defined differently according to kinship norms—one as an in-group member, the other as an out-group member. In Sahlins’s words, “even so the son of a man’s brother may be one of the clan of the ancestor’s descendants while the son of his sister is an outsider and perhaps an enemy” (1976:12). In a patrilineal system the coefficient of relatedness for Ego and both his mother’s brother’s son and his father’s brother’s son (both called cousins in English) is 0.125. While the latter shares Ego’s lineage identity, the former does not. Sahlins argues that the social relationships between Ego and these individuals differ even though the genetic relationship is equivalent (Figure 1).

A social system based on genetic kinship, all other things being equal, predicts a bilateral descent or kindred system (implied by Murdock 1949:57). Kindreds are ego-based and consist of the group of all near relatives. In contrast to a unilineal system, in a kindred system no distinction is made between relatedness reckoned through either parent’s lineage. Cross-cultural work reveals that 36% of the 857 societies in Murdock’s ethnographic atlas have bilateral descent systems. Unilineal systems are more common: 47% in Murdock’s sample practice patrilineal descent, 14% practice matrilineal descent, and 3% claim a double descent system (Murdock 1967).

Structural-functional anthropologists of the mid twentieth century offered a number of hypotheses to explain why groups might develop uni-

![Figure 1](image_url)
lineal descent, though of course they did so without knowledge of kin selection theory. The most compelling argument is that group members organized by unilineal kinship ties have the advantage of unambiguous group identity (Murdock 1949:60–61). This is because only full siblings share an identical network of kin since only sibs share parents. Other classes of relatives—like cousins, for example—share only a portion of their kin. While any two or more cousins share one set of grandparents, they each also share a second set of grandparents with a different set of cousins (unless their parents were cousins themselves, of course).

In what sorts of contexts would the advantages of unambiguous group identity obtained via unilineal descent play out? The answers tend to revolve around corporate political solidarity where groups reap benefits from acting collectively in defense of either property or persons (Sahlins 1961). Numerous authors have stressed the advantages of unilineal descent in the context of conflict (Boehm 1992; Ember et al. 1974; Otterbein and Otterbein 1965; Sahlins 1961; Service 1962). Lower-order segments that organize by unilineal descent principles can more easily combine into higher-order segments when needed. Loyalties are not diffused like they are across kindreds. The advantage of such a system is exemplified by the Nuer and their territorial expansion at the expense of the Dinka (Evans-Pritchard 1940; Kelly 1985). Sahlins (1961) offers the Tiv expansion as another example. Other researchers argue that lineages are advantageous in a context where cooperatively held property is common (Goody 1962; Lowie 1920; Radcliffe-Brown 1935). Recent work on Chinese lineage systems, for example, show that lineages work to keep resources together and function to take advantage of economies of scale otherwise unattainable when inheritance disperses resources across bilateral kin (Cohen 1990; Freedman 1958).

While they differ in their foci, both sets of theories argue that unilineal descent systems are solutions to collective action problems. Van den Berghe (1979) evokes these earlier anthropologists when he tries to understand lineage systems from the perspective of kin selection theory. Like Sahlins, van den Berghe notes that at face value it is incongruous with kin selection theory that half of one’s kin be excluded from those considered culturally as kin. Rather than reject kin selection theory, as Sahlins (1976) did, van den Berghe offers a hypothesis that reconciles Sahlins’s critique with kin selection theory. Following Murdock (1949) and others, van den Berghe notes the problems of organizing kinsmen into collective action under a kindred system. If cooperative groupings were based solely on biological kinship, conflicts of interest would erupt between kin related to a degree less than \( r = 0.5 \). With which group of kin does one ally in a conflict? Who shares ownership of corporate property? With which set of cousins does one cooperate? Van den Berghe argues that lineage systems
solve this problem by normatively defining certain categories of biological relatives as kin and others as not kin. While disenfranchising half of one’s kindred may result in certain lost benefits, the hypothesis is that otherwise unattainable, within-lineage, collective-action benefits outweigh this cost.

Kin selection predicts that small cooperative groups focused around the nuclear family can easily form. Because relatedness drops off rapidly as the genealogical distance from the nuclear family increases (Brown 1991; Jones 2000; Richerson and Boyd 1999), it is more difficult to see how larger groups of closely related individuals can develop. While kin selection can easily explain the small-scale societies found among our non-human primate brethren, it is more difficult to explain the complexity found in even simple foraging societies.

Foraging societies are simple by comparison with modern societies, but even the simplest contemporary hunting and gathering peoples, like !Kung San and the peoples of Central Australia, link residential units of a few tens of people to create societies of a few hundred to a few thousand people. This multi-band “tribal” level of organization is absent in other apes (Rodseth et al. 1991; Boehm 1992). Especially in the simplest cases, tribes are held together by sentiments of common membership, expressed and reinforced by informal institutions of sharing, gift giving, ritual, and participation in dangerous collective exploits (Richerson and Boyd 1999:254).

This paper will explore these issues in the context of cooperative hunting. As I will argue in more detail below, groups involved in certain types of cooperation, technically referred to as coordination or mutualism, benefit greatly from social organization that produces unambiguous group membership. In the whaling community of Lamalera, sibships are not large enough to field a crew, much less produce enough members to form the corporate units required for maintaining whaling operations. Organization based on larger kindreds would provide ambiguous membership and the resulting problems discussed above. As a result, group identity based on unilineal descent is hypothesized to facilitate formation of sufficiently large corporate groups whose members have confidence in one another to follow norms of participation in resource acquisition, distribution, and defense.

Using affiliation data collected during hunts from the whaling community of Lamalera, I will test between strict kin selection and unilineal descent principles as hypothesized models organizing affiliation among hunters. Although the Lamalerans have norms of patrilineal descent, it is unclear whether affiliative behavior follows the norms or whether hunters affiliate by biological kinship regardless of the norms. Since lineage and biological kinship are correlated (see below), both hypotheses predict that affiliates will be more closely related than expected by chance. Following
the arguments outlined above, if lineage identity is more salient than biological kinship for men who organize themselves into hunting crews, lineage membership is predicted to explain a larger proportion of the variance in affiliation among crews after controlling for genealogical relationships. The strict kin selection argument predicts biological kinship per se will explain more of the variance in affiliation.

FIELD SITE

Data were collected between October 1998 and August 1999 at the village of Lamalera, which is located on the south side of the island of Lembata in the province of Nusa Tenggara Timur, Indonesia (Figure 2). The people of Lamalera are complex marine foragers. They are nonegalitarian, live at a relatively high population density for foragers, are not very mobile, and have specialized occupations, corporate descent groups, and food storage.

Subsistence at Lamalera revolves around cooperative hunting for large marine mammals and ray. The primary prey are sperm whale (*Physeter macrocephalus*) and ray (*Mantis birostris, Mobula kuhlii*, and *Mobula diabolus*). The Lamalerans produce little of their own carbohydrates; most are obtained in the form of maize, plantains, manioc, and rice at barter markets from villagers living in the interior of the island. Barnes (1996) provides a

![Figure 2. Field site location.](image-url)
detailed description of the study site. As of August 1999 there were 1,213 residents [328 adult males, 482 adult females, 403 individuals under the age of 18]. The Lamalerans reckon kinship normatively via patrilineal descent and practice asymmetric marriage alliance between descent groups (Barnes 1998). The village is divided into 21 major named patrilineal clans (suku), the larger of which are further divided into named lineages or segments called lango béla (great house). It is the segments that maintain whaling operations.

Eighteen of the segments maintain corporate whaling operations focused around traditional whaling vessels called téna. The eighteen sub-clans operated twenty active téna in 1999 (one sub-clan maintained three téna). Many clan segments do not operate their own whaling corporation. This is largely a function of segment size (Alvard 2002).

Killing prey with a téna is a manifestly cooperative activity, impossible to accomplish alone (Alvard and Nolin 2002). Participants in each whaling operation are divided into three general categories: the crew, corporate members, and technicians. Téna are crewed by 8–14 men. Within crews are a number of specialized roles that are usually, though not exclusively, the prerogative of one man. These are the harpooner (lama fa), the harpooner’s helper (beréun alep), and the helmsmen (lama uri). The balance of the crew, which include two bailers (fai matã), man the oars. The technicians—the carpenter, sail maker, smith, and harpoon bamboo provider (often the harpooner)—are specialists and may or may not be clan members or crew. Finally, corporate members are lineage members who fill named corporate positions and are called upon to provide resources as needed; their contribution is most important when the boat is being rebuilt. Overseeing the operation is the téna alep (literally, boat owner) who acts as a nexus for the whaling operation to coordinate the three groups.

During the active whaling season, which lasts from May through September, boats go out daily except for Sundays, weather permitting. In 1999, 853 hunts were observed with 131 large game items harvested, providing approximately 40,103 kg of meat. In contrast to many hunters (Hawkes 2001), Lamalera hunters retain control of their prey after they return to the village. Meat distributions follow a complex set of norms with primary shares limited to crew, technicians, and corporate members of the boats that participate in the kill (see Alvard 2002).

Crew composition is flexible and varies through the season. Most boats, however, have a core set of crewmembers that go out together regularly, as I will show. The core members are usually from the corporate clan segment that owns the boat, but this is not always the case. Boat masters begin recruiting crews in the spring, especially in the relatively dead months of January and February when few people are at sea. Informants report a number of factors to explain why men crew certain téna. The most common response is that men who are kin and share lineage membership crew
boats together. Informants also report that men will sometimes crew on
the boats organized by their wife’s or mother’s lineage. This is especially
important for men who belong to lineages that do not have enough mem-
bers to field their own boat.

METHODS

On every foraging day the identity of all crewmembers for each téna was
recorded as the boats returned in the afternoon from the day’s hunt. Crew
counts were recorded each day as boats departed, facilitating completion
of the lists. Crew identifications were collected for all hunts that occurred
between May 3 and August 5, 1999. During the 853 téna hunts observed
over the course of the 80 hunt days, 290 men hunted for a total of 9,041
man-days.

Data on lineage memberships were obtained via interviews with
informants. Lineage membership is widely known and is easily elicited
from informants. Data were collected through interviews, and parentage
was determined for each individual. Biological kinship between pairs of
men is measured as the coefficient of relatedness \(r\), defined as the proba-
bility that two individuals share a copy of an allele through common
descent (Wright 1922). For pairs of individuals within the community, the
coefficient of relatedness was calculated using pedigrees developed from
the kinship data and a computer program written by Jeff Long (at the

A number of different samples are used in the analyses described below.
Most of the analyses focus on a sample of 189 of the 290 men who hunted.
The 189-man sample is created in the following way. Since the resolution
of \(r\) depends on the depth and completeness of the pedigree, the sample is
first limited to individuals whose pedigrees are complete at least as far
back as their grandparents. This ensures resolution to the level of \(r = 0.125\).
Second, the sample includes only men whose patriline is known. These
two filters produce a sample of 220 men. Finally, the sample includes only
regular hunters. This is done by excluding men who fell below the tenth
percentile in terms of the total number of days hunted. Men who hunted 6
days or more during the field season are included.

Affiliation is scored when two men crewed on the same boat on the same
day. Using the crew affiliation data, an affiliation matrix is created with each
hunter represented by both a row and a column. In each cell is placed the
number of times each pair of men participated on the same hunt on the
same day. The 189-man sample creates a matrix with 35,721 cells, although
only 17,766 are unique and non-reflexive pairs. During the field session,
men varied in the number of days they hunted; this number ranged from
71 to 6 days with a mean of 36 days \((N = 189)\). Because of this variance in
the propensity to go hunting, some pairs of men might appear to be more closely affiliated simply because they both hunted often. To solve this problem, the affiliation matrix is normalized using an iterative proportion fitting process. Following Bishop et al. (1975:97–101), homogenous margins are fit to the affiliation matrix. That is, for each dyad, the normalized number of affiliations is determined by assuming that all hunters hunted the same number of times (in this case, 100 times). To eliminate non-diagonal zeros, a small non-zero value (0.00001) is added before normalization, as suggested by Freeman et al. (1992). Finally, from the normalized matrix, a Pearson’s product-moment correlation similarity matrix is produced. In this matrix each cell contains the correlation score for each pair of men (row versus column) from the normalized matrix.

The model matrices are created as follows. The lineage affiliation matrix is 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 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 is examined using a matrix permutation test (QAP; Hubert and Schultz 1975; Krackhardt 1987). 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 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 (Smouse et al. 1986; Smouse and Long 1992; Kapsalis and Berman 1996).

In order to identify groups of men who affiliate, the similarity matrix was subjected to a multidimensional scaling analysis. Multidimensional scaling (MDS) is used to represent dissimilarities between objects as distances in a Euclidean space (Kruskal and Wish 1978). The results are plotted and used to visualize grouping patterns in the data. To associate emergent groups with boats, a $k$-means cluster analysis was applied to the three dimensions. This method is designed to minimize within-cluster variability while maximizing between-cluster variability and then assign individuals to each cluster (Bishop 1995).

RESULTS

Using the 189-man sample mentioned above, an MDS analysis specifying nine dimensions results in a stress value of 0.107 after 12 iterations. Visually, however, it is difficult to discern clusters of affiliating hunters among
the bi-variable scatter plots using pairs distributed across nine dimensions. An MDS analysis specifying three dimensions (stress value = 0.272), however, readily produced a plot where clusters could be visualized with the aid of the three-dimensional scatter plot display and rotation function of Data Desk 6.1 (©1999, Data Descriptions, Inc.) software. A visual examination of the three-dimensional plot shows 20 clusters corresponding to the 20 tèna. The MDS plot of the first two dimensions is presented in Figure 3.

In order to quantify these apparent groups and assign hunters to one of the 20 clusters, a \( k \)-means cluster analysis is done first with the nine roots from the first MDS analysis. In all but three of the 189 cases, men assigned to the same cluster with the \( k \)-means analysis crewed most often on the same tèna. Men crewed on the boat assigned to the cluster between 63% and 99% of all their trips (Table 1). A \( k \)-means analysis using the roots from the MDS analysis specifying three dimensions produced exactly the same clusters as the analysis using nine dimensions. The polygons in Figure 3 indicate the clusters identified by both \( k \)-means analysis.

There are a number of ways to determine if affiliated men assort nonrandomly according to lineage membership. There are twenty clusters and 39 different lineages represented in the 189-man hunting sample, creating 780 possible associations. Using a simple chi-square test to determine

Figure 3. Scatterplot of the first two dimensions extracted from the MDS analysis.
whether the observed frequency of lineage members in clusters is nonran-
dom is inappropriate because the observed data include many associa-
tions with fewer than five occurrences. The fact that 680 associations did not occur at all provides a clue as to the non-random nature of the associ-
ations. As an alternative, I use Goodman and Kruskal’s Lambda ($\lambda$) as a
proportional reduction in error measure (PRE) to determine whether
knowledge of a hunter’s lineage reduces the error in assigning him to his
observed crew cluster. The reduction in error is determined by comparing
cluster assignments made with lineage knowledge to assignments made
randomly (Johnson 1988). This measure can also be interpreted as the
strength of association between the two categorical variables of lineage
identity and cluster (Reynolds 1977). The analysis shows that $\lambda = 0.597$ ($p < 0.000$). This means that the error is reduced by nearly 60% over what is
expected by chance and thus shows that the association between affiliation
and lineage identity is high. Table 2 shows the data. For 18 of the 20 clus-
ters, the lineage that organizes the ténä contributes the most crewmembers
to the associated cluster. In the two remaining clusters, the lineage that
organizes the ténä ties with one other lineage as the lineage that con-
tributes the most crewmembers to the associated cluster.
Table 2. Frequency of Lineages Represented in Crew Clusters

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* Denotes lineages that have been marked as significant due to their frequency in the crew clusters.
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The lineage that operates the têna is marked with an asterisk.
Since lineage membership in Lamalera is based on common agnatic descent, it is expected that fellow lineage members are more closely related than are people within the village as a whole. The data show that this is true for both clan and clan segments. I use as a null measure of $\bar{r}$ the average coefficient of relatedness for all dyads in the sample of 220 hunters for which pedigrees are known to the depth of grandparents. For all pairs of men in the 220-man sample, $\bar{r} = 0.00631$ (sd = 0.0448). Table 3 presents $\bar{r}$ within the 32 lineages represented in the 220-man sample. A $t$-test of indi-

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vidual means shows that relatedness within lineages is much greater than expected by chance ($\bar{r} = 0.1160$, $t = 7.266$, df = 40, $p < 0.0001$). Correlation of the lineage matrix and the biological kinship matrix produces a Pearson’s correlation coefficient of $r = 0.460$ ($p < 0.000; N = 189$).

As Table 3 shows, relatedness within lineages varies widely, and much of the variation is explained in terms of lineage size. Figure 4 shows a significant negative, logarithmic relationship between lineage size (total number lineage members) and within-lineage $\bar{r}$ for males in the 220-man sample. Large lineages become diffuse and members less related, though as I show elsewhere, it is easier for larger lineages to organize whaling operations because of the larger labor pool (Alvard 2002). This is consistent with the observation made earlier that relatedness declines as group size increases (Brown 1991).

If hunters assort non-randomly according to lineage membership, and lineage members are more closely related than expected by chance, then it is expected that affiliated men are also more closely related than expected by chance. Analysis shows that this is true for both the clusters extracted by the $k$-means procedure and actual téna crews. For the $k$-means clusters, $\bar{r} = 0.0440$ (sd = 0.03275; $N = 20$). This is significantly greater than the null ($t = 5.156$, df = 19, $p < 0.0001$). For téna crews, $\bar{r} = 0.0362$ (sd = .02678; $N = 853$). Again, this number is significantly greater than the null ($t = 4.995$,

*Figure 4.* Within-lineage relatedness as a function of lineage size. Large plot has a logarithmic scale; small plot is the same data plotted on a linear scale.
There is no significant difference in the relatedness of members of the \( k \)-means groups and the relatedness of téna crews \((t = -0.8287, \text{df} = 38, p = 0.4124)\). It is not surprising that crews and affiliates are more closely related than expected by chance. But the result still begs the question—do men affiliate with kin as predicted by kin selection, thus explaining the high degree of relatedness among hunting partners? Or, do hunters affiliate with fellow lineage members and the relatedness correlation is spurious and owing to the correlation between lineage membership and biological kinship? In the second case, hunters do not affiliate with others because the others are kin per se, but because they are fellow lineage members; the resulting higher degree of relatedness is incidental.

To test between these two possibilities, I use multiple matrix regression with the two independent variables of biological kinship and lineage membership; affiliation is the dependent variable. The results confirm that while biological kinship is still significant, lineage membership explains more of the variance in affiliation among the hunters. The matrix Pearson’s correlation for affiliation versus biological kinship is \( r = 0.198 \) \((p < 0.000; R^2 = 0.039)\). The Pearson’s correlation for lineage membership is \( r = 0.321 \) \((p < 0.000; R^2 = 0.103)\). The regression parameter estimate for lineage alone is about a third again as large as for kinship alone. For the multiple regression analysis, both variables explain 10.7% of the variance in affiliation. The contribution made by lineage membership is greater than that made by biological kinship, however (see the results of the regressions in Table 4). In this case, the partial regression coefficient for lineage is nearly four times as large as biological kinship. The addition of biological kinship does not substantially increase the strength of the model that includes only the lineage variable.

A number of other factors may play a role in the relatively small amount of variance in affiliation explained by lineage identity. First, many of the hunters do not belong to lineages that have téna. For the 189-man sample, 49 (26%) of the 189 men belong to lineages that do not organize a téna. The

| Table 4. Matrix Regression Analyses with the Two Independent Variables of Kinship and Lineage Membership, and Affiliation as the Dependant Variable |
|-----------------|-----------------|-----------------|-----------------|
| **Independent Variable** | **Standardized Parameter** | **Estimate** | **\( p \)** | **\( R^2 \)** |
| A. Kinship | | 0.1976 | \(<0.000\) | 0.039 |
| B. Lineage membership | | 0.3215 | \(<0.000\) | 0.103 |
| C. Lineage membership | | 0.2925 | \(<0.000\) | 0.107 |
| | | Kinship | 0.0631 | \(<0.000\) |
Kinship, Lineage, and Cooperative Hunting Groups in Indonesia

balance of hunters belongs to lineages that have téna; 92 or 66% of these men went out most often on the téna organized by their lineage. Second, not all the téna went out every day—men often went out on other boats if their primary was not available. The number of days that particular boats went hunting ranged between 17 and 69 of the possible 80 observed hunting days. Some téna were able to hunt nearly every day—others had more difficulty. Accordingly, the number of boats that went out per day varied over the course of the season between 2 and 20 (mode = 9, $\bar{x} = 10.7$ boats, $N = 80$ days; Alvard and Nolin 2002). In addition, while the data were normalized as to hunting frequency, not all hunters hunted on the same days.

Third, some lineages are smaller than others and their hunters had to associate with more non-lineage members to participate in crews of sufficient size. Finally, informants also report that men sometimes go out on the boats owned by their wives’ or mothers’ lineages. Each of these factors presents its own analytic issues that will be addressed in future analyses.

The result presented in Table 4 obtains because pairs of men related to same degree (excluding siblings and father/son pairs) are just as likely to belong to different lineages and not affiliate as they are to share a lineage and affiliate during hunts. To demonstrate this, Figure 5 shows the number of dyads within clusters that share three categories of biological kinship, $r = 0.5, 0.25,$ and $0.125$. The data are from the 189-man sample but are further limited to men whose lineage actually organizes téna ($N = 140$ men). Affiliative clusters have more dyads related at $r = 0.50$ than they do dyads related at $r = 0.25$ or $0.125$. This is expected because groups of kin related at $r = 0.50$ all belong to the same lineage. Figure 5 also shows the number of dyads related at these levels formed between cluster members and non-cluster members. Kin related at $r = 0.125$ are much more likely to be found outside the affiliate cluster. Kin related at $r = 0.25$ and $r = 0.50$ are equally likely to be found inside as outside the cluster.

**DISCUSSION**

The preceding analyses show that hunters at Lamalera affiliate during cooperative hunts more strongly according to lineage membership than according to genetic kinship. While crew members are more closely related to one another than expected by chance, the analyses show that this is due to the correlation between lineage and biological kinship. Hunters are just as likely not to affiliate with non-nuclear kin because half of such kin are non-lineage members.

This paper’s results support the hypothesis of the cultural anthropologists discussed above, who have argued that the development of lineage systems facilitates collective action. It also supports the contention of van
den Berghe (1979), who argues that kin selection alone cannot structure cooperation in groups larger than the nuclear family because of the ambiguous group membership it provides. While the results do not refute kin selection theory, they do raise issues concerning the importance of kin selection for explaining certain cooperative behavior in humans, and the possibility of alternative mechanisms for the development of collective action.

A reassessment of the role of kinship in human societies is warranted given the ongoing reexamination of kin selection as an explanatory paradigm for cooperation among non-human animals. “The view that kin selection provides a satisfactory general explanation of specialized cooperative societies now appears less compelling than it did 20 years ago” (Clutton-Brock 2002:69). Kin selection provides a less persuasive argument for a number of reasons. First, better genetic data show that cooperative groups are often not more closely related than noncooperative groups. For example, recent empirical work on chimpanzees shows biological kinship plays a secondary role in structuring affiliative behavior among males (Goldberg and Wrangham 1997; Mitani et al. 2000). Cooperative territory and pride defense by male lions is not organized according to biological kinship (Grinnell et al. 1995). Studies using DNA analysis to determine the relationships within coalitions of male bottlenose dolphins cooperating to maintain mating access conclude that “The majority of male pairs within alliances were randomly related, although high relatedness values were found between males of different alliances in the resident population. These findings indicate that mechanisms other than kin selec-

Figure 5. Number of dyads with indicated degree of relatedness.
tion may be foremost in the development and maintenance of cooperation between male bottlenose dolphins” (Møller and Beheregaray 2001:1941).

Griffin and West (2002) argue that another reason kin selection is less compelling for explaining cooperative behavior is an increased awareness that direct fitness benefits to the “altruist” have been underestimated in previous work. Direct fitness benefits are those obtained by the individual himself, rather than indirectly through the help provided to kin (Maynard Smith 1964). A variety of other mechanisms can lead to cooperation independent of, or in addition to, biological kinship (Hirshleifer 1999; Mesterton-Gibbons and Dugatkin 1992). Griffin and West (2002) argue that in many cases apparently altruistic behavior has direct fitness benefits that may be the main factors influencing the degree of cooperation. They argue that although limited dispersal often results in groups made up of close kin, kin selection is not required to produce many of the cooperative groups found among birds and mammals. They conclude that in many cases, individuals behave cooperatively because it is in their own direct self-interest, while benefits obtained indirectly through kin are secondary for the development of the cooperative behavior (see also Chapais et al. 2001). The data from Lamalera are consistent with this argument.

For example, the well-known behavior referred to as “helping at the nest,” whereby individuals defer their own reproduction to help others rear offspring, has usually been explained via kin selection (Emlen 1982). Griffin and West (2002) cite recent work showing that helping occurs in some species that do not live in family groups, such as fairy wrens (Dunn et al. 1995). In other species, such as meerkats, the degree of helping done by subordinates is more a function of their own reproductive status than of kinship with the young they help (Clutton Brock et al. 2001). A number of hypotheses have been advanced to explain how direct benefits accrue to individuals in these cases. One explanation, referred to as “group augmentation,” can arise in the absence of kin selection if the mutualistic benefits of collective action are significant (Clutton-Brock 2002; Kokko et al. 2001). In this case, simply being part of a larger group provides individuals with sufficient direct benefits independent of any indirect benefits obtained via kin selection. (See Smith 1985 and Sosis 2000 for a discussion of this idea in regard to human foraging groups.) This last idea is important for the Lamalera case. The hunting data are consistent with the hypothesis that the benefits of collective action for individuals outweigh the costs of limiting association to a small set of kin.

Cooperative behavior cannot be predicted using Hamilton’s equation with a focus solely on the coefficient of relatedness unless the costs and benefits of cooperating with kin are held constant (Dawkins 1979; Smith 1979; Grafen 1985). In many cases, however, costs and benefits of alternative social behaviors vary independently of biological kinship relationships. An important question is how much of the variance in cooperative behavior is
explained by genetic kinship between partners and how much is due to the costs and benefits of cooperation independent of the coefficient of relatedness between the partners. One way to interpret the previous discussion is that in some cases cooperation can be predicted primarily in terms of costs and benefits to the participants with little or no reference to genetic kinship. In the anthropological case, Hawkes (1983) anticipated some of these arguments when she addressed Sahlin's critique of kin selection and noted the role of socially determined identities for qualifying predictions of kin selection in humans. More recently, Turke (1996:854) notes that a number of studies make clear that genetic relationships do matter in human social organization, while admitting that the evidence "does not deny the existence and importance of classificatory kinship systems or the existence and importance of friendships and alliances outside the sphere of genetic relationships. There is more to human sociality than nepotism based on degrees of genetic relationship."

“What more there is” may be found among emerging solutions to cooperative dilemmas focused around positive assortment (Bowles and Gintis 2000; Boyd and Richerson 1993; Dawkins 1989; Dugatkin and Wilson 2000; Pepper and Smuts 2002; Wilson 1977). Positive assortment occurs when a population is structured in such a way that individuals tend to form groups with others with whom they share traits. Such assortative interaction can facilitate cooperation because individuals who cooperate without discrimination are vulnerable to noncooperators who take advantage of the cooperator’s willingness to act collectively. Genetic kinship can provide this association because kin are more likely to be of the same type. Cooperative, kin-selected behaviors evolve because they are preferentially directed at like-types (Hamilton 1975). For example, the tit-for-tat solution to the prisoner’s dilemma will spread among a population of cheaters only if tit-for-taters can somehow preferentially identify and play with other tit-for-taters (Axelrod and Hamilton 1981). One way for this to happen within a population of defectors is if pairs of relatives, who are more likely to share the tendency to play tit-for-tat, cooperate via kin selection (Axelrod 1984).

Recent theory suggests that individuals use a variety of mechanisms, in addition to biological kinship, to identify fellow cooperators. These mechanisms involve honest signals linked to discriminating cooperative behavior that allow fellow cooperators to identify one another. The classic example is the “green beard” solution discussed by Dawkins (1989). Imagine that the trait of having a green beard is associated with the trait of cooperating with other green beards. This hirsute signal allows cooperators to assort by type, direct cooperative behavior at fellow cooperators, and avoid costs of free riding (e.g., Keller and Ross 1998). Similar models have been developed within anthropology and elsewhere to explain the rise of
group markers, such as dress, speech patterns, and ornamentation, which allow individuals to identify like-types and assort positively (Boyd and Richerson 1987; Nettle and Dunbar 1997; Riolo et al. 2001; van den Berghe 1981; Wiessner 1983). The key problem with the green beard solutions offered by these models is that the systems are vulnerable to individuals who mimic the signal (i.e., grow a green beard) but are not forthcoming with the cooperative behavior (Dawkins 1989). These “cheaters” do better because they receive the benefits but do not pay the cost. This is especially likely if the signal is relatively cheap to imitate and the benefits of cheating are sufficient.

This problem is not as ruinous to the positive assortment hypothesis as it may appear. In game theory, most collective action is modeled as a prisoner’s dilemma. The key feature of the prisoner’s dilemma, of course, is that the cooperative strategy is never a player’s best response to an opponent in spite of the fact that mutual cooperation is better than mutual defection (Colman 1995). Cooperation in such a context is true altruism, and cheating has benefits. When cooperation is structured this way, the green beard solution is vulnerable to cheaters.

As alluded to above, however, there is an increased understanding that much behavior viewed broadly as cooperation might be better understood as mutualism or coordination rather than a prisoner’s dilemma (Alvard and Nolin 2002; Clements and Stephens 1995; Dugatkin 1997; Hirshleifer 1999; McElreath et al. 2003). This is important because “green beard” solutions to collective action problems are more feasible if payoffs are structured as coordination rather than a prisoner’s dilemma because there is no benefit for individuals to cheat (McElreath et al. 2003).

Coordination games are characterized by common interest among players (Binmore 1994; Cooper 1999). In social situations structured as coordination, benefits accrue to individuals through collective action, and individuals are better off cooperating than they are defecting. While gains exist for collective action in a prisoner’s dilemma, individuals are nonetheless always better off defecting. Mutualism, as discussed above and understood by most evolutionary anthropologists (Hawkes 1992:275), is structurally a coordination game. Coordination problems are among the most basic of social problems. The classic example is the pure coordination involved in choosing the side of the street on which to drive. There is no benefit to cheating in such a game. Driving on the right or on the left is equally good, as long as everyone drives on the same side. In spite of the apparent simplicity, however, considerable evidence shows that cooperative solutions to such coordination problems are not as easy to obtain as one might intuitively think, and results of coordination failure in experimental contexts have been widely reported, especially in larger groups (Batillo et al. 2001; van Huyck et al. 1990; see review in Ochs 1995).
Thomas Schelling in *The Strategy of Conflict* (1960) noted that people readily solve coordination problems in certain contexts. Schelling’s classic example is the relative ease with which people can solve the following coordination problem: two friends must meet in New York City, but for some reason have separated and cannot communicate. There are many places to meet, all of which are equally satisfactory—as long as both friends choose the same location. The idea of cheating is not applicable here, since both friends have a preference to cooperate. In informal experiments conducted by Schelling, more than 50% of students from New Haven, Connecticut, chose Grand Central Station as the place to meet. When asked to name a time, almost all chose noon. Formal experiments provided similar results in a number of different contexts (Mehta et al. 1994). These results are extraordinary, given that there are a near infinite number of possible meeting locations.

How do the players decide where to meet each other? Schelling speculated that people are often able to coordinate around what he called focal points. He argued that it is the salience or prominence of focal points that draws people to them, and that what is prominent depends on the time and place and who the players are (Schelling 1960:58). Sugden (1986:49) agrees that people use *shared notions* of prominence to solve coordination problems. The ideas of shared notions and focal points have much in common with norms. Norms are regularities of behavior maintained through shared ideas of right and wrong (see McAdams 1997 for a review). Norms have increasingly been viewed as a way in which coordination is more easily achieved (Ellickson 1991; Lewis 1969; McElreath et al. 2003; Ostrom 1990; Posner and Rasmusen 1999).

Ellickson (1991) argues that norms function to reduce transaction costs for achieving cooperative outcomes. Transaction costs accrue when people establish and maintain property rights, broadly construed. Such activities might include inspection, rule enforcement, policing, and measurement (Allen 1991). Without norms of road travel, for example, drivers would need to slow their rate of travel when approaching oncoming traffic to determine which side of the road they should choose to avoid a collision. Norms enable such inspection transaction costs to be avoided. Because coordination problems are common, there are great advantages for individuals to associate with others who are more likely to share norms. Interacting with others who do not share norms or conventions of behavior increases the difficulty of solving otherwise simple coordination problems as a result of high transaction costs. The problems that ensue when one interacts frequently with others who do not share norms are well known to field anthropologists.

This brings us back to the issue of positive assortment. One solution to coordination problems is for individuals to preferentially assort with oth-
ers who hold ideas similar to their own. How can individuals predict what others think and will do? How do participants in a collective action know that fellows share beliefs concerning behavior critical for coordination? There are a number of options. One could attempt to learn on one’s own the beliefs of all potential cooperative partners. This could, however, prove difficult, time consuming, and error prone. In the Lamalera case, there were 290 hunters in 1999 plus more individuals participating either as craftsmen or corporate members. The numerous prey species also differ in ways that might affect distribution patterns.

When defectors are not a threat, as is the case in coordination games, the green beard solution becomes more tenable. McElreath et al. (2003) formalized a model to show how marked groups can arise when social interactions are structured as coordination games. They show that under plausible conditions, selection can favor an association between markers and normative behavior because it pays for individuals to signal honestly when collective actions are structured as coordination games. In a related argument, Gil-White (2001) notes that people reify ethnic groups despite the fact that ethnic essences do not exist. He hypothesizes that selection favored this cognitive process because stereotyping people in terms of ethnic groups facilitates inductive generalizations about their nonobvious properties. Following Barth (1969), he argues that these generalizations help predict many strongly correlated yet hidden properties of others—such as commitments to certain interactional norms. This, in turn, helps people to predict behavior, assort positively, and solve common coordination problems like those mentioned earlier. Atran (2001:537) agrees that “People cognitively privilege essentialized groups as providing the most dependable or trustworthy context for forming and inferring beliefs about themselves and others and for taking life-enhancing collective action based upon those beliefs (mating, war, economic cooperation).”

Social psychologists have long understood it is not difficult to get people to assume collective identities. The ease with which people associate themselves and others with groups implies strong selective advantages during our evolutionary history. The classic work of Henri Tajfel shows that it is very easy to induce members of even “minimal groups” to readily assume a shared identity. Members of these so-called minimal groups have no face-to-face interaction and no history of interaction. In experimental situations, simply classifying people according to arbitrary markers like eye color creates the groups. Group members show a strong tendency to discriminate and favor group members at the expense of others (Tajfel 1981; Tajfel and Fraser 1978; see Diehl 1990 for a review). Most of the work has tended to focus on the prejudice directed at out-group members (for example, Peters 1987), although the role of group identity for enabling within-group collective action is significant (for example,
Kelly and Kelly 1994; Kerr and Kaufman-Gilliland 1994). Recent experimental work shows how group identity and intragroup competition can significantly increase the likelihood of efficient outcomes in coordination games (Bornstein et al. 2002).

Elsewhere, I have described the kinds of cooperative hunting found at Lamalera as coordination (Alvard and Nolin 2002). Groups of men who cooperatively hunt whales enjoy greater per capita return rates than do solitary fishers. The success of the subsistence strategy, however, rests on each participant’s shared understanding and expectations of both their own role in the collective action and the roles of the other participants. Put simply, cooperative hunting is mutually beneficial to participants only as long as hunters associate with others who can be expected to share ideas of what constitutes normative behavior.

For example, in Lamalera a whale is butchered and divided into 14 major shares that vary in size and quality. The shares are generally distributed to four types of recipients, the crew, corporate members, craftsmen, and two special clans (Alvard 2002). In Lamalera the crew (méng) receive the bulk of their shares from the torso of the whale, extending just posterior of the pectoral fins to roughly the end of the rib cage. The major corporate share (kefoko seba) is divided by 5 to 14 shareholders, depending on the boat. It consists of the torso of the whale from just posterior of the méng section extending back about 1.5 to 2 m. One could easily imagine, however, a number of equally satisfying alternative schemes for butchering and distributing the whale shares. There is no reason that the méng share could not be extracted from the location where the kefoko seba is extracted, and vice versa. A hunter should be indifferent to many of these alternatives because in many instances the amount and quality of meat and fat are independent of the anatomical part of the whale from which they originate. While a hunter should be indifferent to which particular norm is used, it is critical that all the hunters share the same norms for butchering and distribution. Men cooperating within a téna crew hunt with the assurance that their fellows will not lay claim to shares that they themselves believe they own. Without such assurance, it is easy to imagine that cooperative hunting may not be worth the effort. Imagine the transaction costs for resolving claims to téna harvests if norms of distribution did not exist for the whalers at Lamalera. Without shared norms of behavior, like the rules of meat distribution at Lamalera, it is likely that cooperative behavior would collapse in response to high transaction costs.

Is there any evidence of variation in meat distribution norms between lineages? As might be predicted, there is little variation between boats with respect to the division of a whale among cooperating boats. When multiple boats kill a whale, the carcass must first be divided between the participating corporations before it is distributed within each corporation. The tacit rule is that the whale will be divided into the 14 whole shares and
that those whole shares will be divided evenly between the participating corporations first (Alvard 2002).

Within each corporation, there is variation with respect to how different species are distributed. This is especially the case for corporate shares that vary considerably depending on species. For a whale, there are six corporate whole share types. Some are small, with many shareholders; others are larger, with few shareholders. Corporations vary in regards to the number of shareholders for the various corporate shares and the identity of those shareholders. For example, the corporation share called kefoko seba, mentioned above, is divided among 5 to 14 people, depending on the boat. For some boats, the jaw or mina share is given to one or two people who have specific rights to it; for five of the boats it is divided among the kefoko seba shareholders. With respect to the division of ray, there are differences as well. For example, all crewmembers receive a futu share, which consists of one or more fillets of red meat from the wings. This is common across all boats. All boats also have a share called topo meki, a very large steak cut from the left wing. It rotates at the discretion of the butcher among all crewmembers but the harpooner. For some boats, the crewman receiving the topo meki does not receive any further futu from the ray (as if he had received a harpooner’s share), but for most boats the crewman receiving the topo meki also receives a complete regular crew share.

How do the hunters at Lamalera know that their fellows share the same norms of behavior without expending considerable transaction costs learning for themselves? This paper has shown that hunters tend to assort according to lineage membership. I believe that lineage membership acts as an unambiguous, easily observed marker (like a green beard) that allows individuals to identify others who have a higher probability of sharing norms. Preferring to affiliate with someone who shares lineage identity increases the probability that they also share ideas of what is normative; it decreases anonymity, and provides assurance that fellows play by the same rules (see Barth 1969).

In contrast, groups organized along strict genealogical lines are ego-specific; as a result, strict biological kinship provides an ambiguous signal. My cousin, for example, might easily view himself as a member of a competing kindred with alternative norms. Kinship (based solely on genealogical distance) is not a marker with sufficient resolution to organize collective action in groups larger than the nuclear family. Although the above discussion suggests that kin selection theory may not be the best way to explain large-group cooperative behavior in humans, it is a mistake to conclude, as do many cultural anthropologists, that inclusive fitness theory fails utterly to predict behavior. A predilection to assort according to kinship does provide an exaptation, especially among simple societies.

“...[W]hy do people settle on kinship as the convention so often? One possible answer: given that so much of the social system in small-scale
societies is based on kinship, it’s a very convenient pre-adaptation on which to hang your coalition structure” (Smith 2003). Kin selection predicts that, all other things being equal, individuals should prefer to cooperate with kin rather than non-kin—this is a powerful prediction and helps explain the widespread relationship found between biological kinship and social organization in humans. In many cases, however, cooperation is predicted to occur regardless of (even in spite of) the kin relations between agents. In these cases, kin selection theory has less to say.

At some point in our recent evolutionary history, humans evolved the ability to transmit information culturally, and subsequently we see a dramatic increase in evidence of cultural diversity in the archaeological record (Klein 1999; Mellars 1998). The transition in the Upper Paleolithic represents a watershed in the course of human evolution. I speculate that the adaptive advantages of being able to solve coordination problems may have been part of the selective forces that favored the development of the traits implicit in such cultural complexity (Alvard 2003). As I have shown, hunting provides a suite of such coordination problems.8 The idea that culture evolved in order to facilitate the planning and coordination involved in hunting is not new (e.g., Montagu 1976; Washburn and Lancaster 1968). The reasoning, however, has been by and large vague and untested. Cooperative hunting was probably more common in our evolutionary past than it is today. Hill (2002) notes that without projectile weaponry and poison, both of which are recent innovations, it is difficult to imagine how many of the large game species present in hominid archaeological assemblages could have been killed without cooperation. The data presented here suggest that cooperative hunting is exactly the sort of coordination problem whose solution is facilitated by the ability of actors to establish and communicate behavioral norms. The ability to identify via inductive generalizations others who share social norms and cooperative intent has immense adaptive value in terms of synergistic rewards—even if they come at a nepotistic cost.

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NOTES

1. To avoid confusion, I use the terms biological kinship and genetic kinship to refer to what is measured by the coefficients of relatedness.

2. Most of Sahlins’s criticisms of kin selection theory were not as cogent; for example he argued that kin selection theory could not apply to animals because they could not do the math to calculate degrees of relatedness. Dawkins replied famously in the second edition of The Selfish Gene (1989) that a snail shell is an exquisite logarithmic spiral, in spite of the fact that snails cannot read log tables.

3. The issue of whether people “do as they say” is not a trivial one (e.g., Cronk 1999).

4. 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).

5. This is lower than the previously published average coefficients of relatedness for whaling crews. Morgan (1979) reports \( r = 0.274 \) for nine crews among the Yupik whale hunters. Smith (1985) reports \( r = 0.013 \) to 0.185 for a variety of hunt types among Inuit foraging groups.

6. See Gintis, Smith, and Bowles (2001) for an alternative solution to the green beard problem obtained via costly signaling which works even if payoffs are structured as a prisoner’s dilemma rather than mutualism.

7. Technically, traffic laws are not norms because they are written and enforced by the state.

8. It should be stressed that coordination problems are common and are not limited to hunting behavior. Depending on the context, marriage could be construed a coordination problem where each member of the pair shares the common interest of producing offspring (Hadfield 1999). A recent example of how insufficient coordination can be costly is the Mars Climate Orbiter. Designed to orbit Mars and collect data on the Martian atmosphere, in September 1999 it crashed into the planet’s atmosphere during its approach to the planet and was destroyed. The cause was a lack of coordination in units of measure. A segment of navigation-related software used English units of measure (pounds) rather than the required metric units (newtons). As a result, an erroneous trajectory was computed (Mars Climate Orbiter Mishap Investigation Board 1999).

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