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Kin Preference and Partner Choice: Patrilineal Descent and Biological Kinship in Lamaleran Cooperative Relationships

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Abstract

This paper presents a comparison of social kinship (patrilineage) and biological kinship (genetic relatedness) in predicting cooperative relationships in two different economic contexts in the fishing and whaling village of Lamalera, Indonesia. A previous analysis of boat crew affiliation data collected in the village in 1999 found that social kinship (patrilineage) was a better predictor of crew affiliation than was genetic kinship. A replication of this analysis using similar data collected in 2006 finds the same pattern: lineage is a better predictor than genetic kinship of crew affiliation, and the two together explain little additional variance over that explained by lineage alone. However, an analogous test on food-sharing relationships finds the opposite pattern: biological kinship is a better predictor of food-sharing relationships than is social kinship. The difference between these two cooperative contexts is interpreted in terms of kin preferences that shape partner choice, and the relative autonomy with which individuals can seek to satisfy those preferences. Drawing on stable matching theory, it is suggested that unilineal descent may serve as a stable compromise among multiple individuals' incongruent partner preferences, with patriliney favored over matriliney in the crew-formation context because it leads to higher mean degrees of relatedness among male cooperators. In the context of food-sharing, kin preferences can be pursued relatively autonomously, without the necessity of coordinating preferences with those of other households through the institution of lineage.

Keywords

Kin selection; Lineage; Partner choice; Stable matching theory; Cooperation

Hamilton's (1964) theory of inclusive fitness, or kin selection, proposes that altruistic behaviors—those that benefit another at an expense to the actor—may be favored by natural selection if the recipients of the altruistic act are likely to share the alleles for the prosocial behavior with the altruist because of common descent. The condition under which altruism can evolve by kin selection is referred to as “Hamilton's Rule,” commonly expressed as $rb > c$, where b is the fitness benefit to the recipient, c is the fitness cost to the altruist, and r is Wright's (1922) coefficient of relatedness between the altruist and the recipient, a measure of the probability that two individuals will share alleles for some trait because of descent from a common ancestor. Much depends on the ratio of benefits to costs, but under most circumstances kin selection predicts that individuals will favor closer kin over more distant kin, and distant kin over unrelated individuals.

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The ubiquity of unilineal descent systems in human societies may appear inconsistent with the predictions of kin selection. Bilateral kinship systems closely follow biological genealogies and would appear to be more consistent with individuals' inclusive fitness interests. In contrast, unilineal systems exclude half of one's biological kin—those related through either one's mother or one's father. One might legitimately ask, as have critics of biological approaches to kinship (e.g., Sahlins 1976; Schneider 1984), if human behaviors toward kin have been shaped by natural selection, why have so many societies opted for systems of descent that would appear contrary to their predicted interests?

In response to this problem, a number of adaptive hypotheses for the origin and persistence of unilineal descent systems have been proposed. These hypotheses fall into two categories: those that attempt to explain a specific mode of unilineal descent (either patriliney or matriliney), and those that attempt to explain unilineality more generally. The former have tended to focus on the biological mechanisms of inheritance and differences in variance in reproductive success of sons and daughters. The latter have tended to focus on the advantages of unilineality as an institution of economic and social organization.

Hartung (1976) proposed one of the earliest adaptive hypotheses for the origin of patriliney. He suggested that patriliney may be favored because wealth directed to sons can have a greater effect on fitness than wealth directed toward daughters, as a consequence of the higher variance in reproductive success among males compared with females. Greater reproductive skew among males than females also means that patrilineally related kin may be on average more related than matrilineally related kin: where polygyny exists, more individuals share fathers (as half-siblings) than share mothers (Chagnon 1979; Hughes 1988). (A further explanation [Hartung 1976, 1977] for patriliney—that men favor investment in their male descendants because of the additional relatedness to them granted by a shared Y-chromosome—has been largely disregarded.)

Early adaptive explanations for matriliney, on the other hand, hinged on paternity uncertainty. In societies where paternity confidence is particularly low (<0.268 ; Greene 1978), a man may be probabilistically more closely related to his sister's child than his own, favoring investment in his sister's children (Alexander 1974; Flinn 1981; Greene 1978). Such levels of paternity confidence appear implausibly low for human societies. In response to this criticism, Hartung (1981) calculated that after several generations and at more plausible levels of paternity confidence a man may be probabilistically more related to a matrilineal heir than a patrilineal heir because of the compounding effects of paternity uncertainty across generations. However, these benefits take several generations before they are realized, and others (e.g., Holden et al. 2003) have questioned whether such a long-term strategy could persist in the face of the short-term advantages of investing in direct descendants. Consequently, paternity confidence alone is now considered an insufficient explanation for matriliney.

When the focus is withdrawn from fathers' interests, then others' preferences for matriliney becomes evident. Grandmothers and grandfathers both are probabilistically more closely related to their daughters' children than to their sons' at any level of paternity confidence less than one (Flinn 1981; Hartung 1985; Holden et al. 2003). Though higher variance in male reproductive success may bias inheritance toward sons (Hartung 1976), this advantage must be weighed against the probability that one's son's purported children may not be his. Holden et al. (2003) have calculated that when the ratio of the fitness benefit of investing in daughters to the benefit of investing in sons exceeds the probability of paternity confidence, then daughter-biased investment may be favored, resulting in matriliney. Their model appears consistent with two correlates of matriliney: lower paternity confidence and modes of

subsistence, such as horticulture, that disfavor resource-holding polygyny (see also Mattison 2011).

General explanations for unilineal descent systems have focused on their economic and institutional benefits. Social anthropologists have long recognized unilineal descent as an institution for organizing large corporate groups (see Kuper 1982 for a review). Placing this observation in an adaptive framework, van den Berghe (1979) has pointed out the need to organize large, clearly defined groups with mutually exclusive memberships for purposes of collective action. Individuals' bilateral kin groups may overlap but are not perfectly congruent, except those of full siblings. Unilineal descent defines congruent kin sets for all individuals related by common descent through one sex (Murdock 1949). It also simplifies coordination by defining a set of individuals who share the same norms governing cooperation (Alvard 2003). These benefits of collective action may outweigh the costs of excluding half of one's kin. Using population genetics models, Jones (2000) suggests that the effective degree of relatedness among such closed groups of cooperating kin may be elevated.

Taking a different approach, Palmer and Steadman (1997) have proposed that human kinship systems serve as descendant-leaving strategies that maximize the inclusive fitness interests of ancestors. Invoking Trivers's (1974) theory of parent-offspring conflict, they begin by noting that parents have an interest in reducing conflict and promoting altruism among their offspring. Similarly, grandparents have an interest in promoting altruism among all their grandchildren, even though those grandchildren may prefer to favor their own siblings over their cousins. Over time, these ancestral preferences and parental admonitions expand to encompass larger groups of related descendants and become formalized cultural traditions.

Building on this work, Quinlan and Flinn (2005) suggest that unilineal descent systems serve ancestors' inclusive-fitness interests by focusing the inheritance of durable resources. Unilineal norms of inheritance may, for example, constrain an heir from sharing access to or the benefits from an inherited resource with his non-lineage kin. This ensures the benefits of those resources accrue to the ancestor's descendants and are not dispersed among non-descendants. In this way, Quinlan and Flinn argue, unilineal descent systems may benefit the inclusive fitness interests of the bequeathing ancestor even at the expense of the interests of the heir. The hypotheses proposed by Palmer and Steadman (1997) and Quinlan and Flinn (2005) are interesting, but it is unclear how exactly ancestors are able to enforce such inheritance norms, and why heirs might persist in observing them even against their own interests.

The key question addressed in this paper is to what degree lineage systems actually constrain individuals from pursuing their inclusive fitness interests. Under such systems are people genuinely hindered from directing aid to biological kin outside their lineage? A few studies have statistically compared social kinship (that is, kinship as culturally defined according to the system of descent) and biological kinship (that is, probabilistic genetic relatedness through common descent) as predictors of affiliative behavior. Chagnon and Bugos's (1979) study of the division of a group of men into two factions during an axe fight among the Yanomamö of Venezuela showed that genetic kinship rather than lineage membership appeared to predict faction membership. A recent reanalysis of these data (Alvard 2009) using network regression methods supports this finding. Hawkes (1983) compared the effects of social kinship categories with genealogical relatedness in predicting garden labor help in the bilateral Highland New Guinea community of Binumarien. Her results showed that social kin ties were better predictors of garden help than were genetic ties, though the two were themselves strongly correlated. Alvard (2003) compared shared

lineage membership and genetic relatedness as predictors of shared boat crew membership for a group of men in the patrilineal village of Lamalera, Indonesia (the population considered in the present study). His results showed a stronger effect for social kinship than for biological kinship, and when combined together, biological kinship predicted little additional variance beyond that predicted by social kinship alone. Collectively, these few results do not provide any clear pattern, but instead they suggest the degree to which behavior follows social rather than biological kinship can vary depending on the setting and society.

Where a propensity to cooperate with kin is found, it is not necessarily an indication that kin selection is the mechanism promoting the cooperative behavior. Other mechanisms, such as synergistic mutualism (Maynard Smith 1983) or reciprocal altruism (Trivers 1971), may maintain the cooperative behavior, and kin selection in these contexts may instead be acting to shape partner choice (Noë and Hammerstein 1994, 1995). Partner choice is an important aspect of cooperative interactions that has only recently begun to receive attention. For example, partner choice is central to models of competitive altruism (Barclay and Willer 2007; Chiang 2010; Roberts 1998). Given that cooperation is favored in a particular setting, the question of who cooperates with whom also has important adaptive consequences for behavior. If potential partners vary in characteristics that affect the payoffs to cooperation, then natural selection may select for preferences that lead to adaptive choices.

Two examples come from recent studies of food sharing. In their analysis of food sharing among the reservation Ache, Allen-Arave et al. (2008) found that genetic kin are preferred exchange partners. Inconsistent with the predictions of kin-selection, kin with greater “need” (defined by the difference in productivity between the two households) did not receive more food. Instead, households that exchanged more were more closely related. They suggest that an apparent preference for kin as reciprocal partners may not be motivated by kin selection per se, but instead may be because kin are more likely to have qualities that are valued in reciprocal partners, such as trust or familiarity resulting from a history of past interactions as well as a higher probability of future interaction. Nolin (2010) found a similar preference for kin as reciprocal partners in the Lamalera food-sharing network data presented here. While kinship alone explained a modest amount of variation in sharing relationships, it explained little additional variation beyond that explained by reciprocity, and as the degree of relatedness between households increased, so did the propensity to reciprocate. Reconsiderations of evidence of kin selection in nonhuman animals have similarly concluded that direct fitness benefits resulting from mutualism or reciprocal altruism may be more important than indirect fitness benefits in predicting some cooperative behaviors previously attributed to kin selection (Chapais 2001; Clutton-Brock 2002; Griffin and West 2002).

What studies like these suggest is that close attention must be paid when invoking kin selection as an explanation for cooperative behavior. Are indirect fitness benefits promoting the cooperative behavior in question, or is kin preference instead acting as a partner choice mechanism in a cooperative setting better explained by some other adaptive mechanism providing direct fitness benefits? This is not to say that inclusive fitness is unimportant in settings of partner choice—it may very well be that kin are preferred partners because of the additional inclusive fitness dividend realized from cooperating with closely related kin compared with others (Wrangham 1982) and that kin selection has driven the evolution of the preference. However, it does not necessarily follow that the cooperative behavior in question is favored by natural selection *solely* because of the inclusive fitness benefits realized (Griffin and West 2002).

The study presented here tests the relative degree to which people's partner choices are shaped by social and biological kinship in the context of two cooperative subsistence activities in the village of Lamalera, Indonesia. The first context is the formation of whale boat hunting crews. This portion of the analysis replicates, using data collected in 2006, Alvard's (2003) analysis of crew affiliation data collected in 1999. The second context is the network of between-household food-sharing relationships in the village in 2006. It is important to note that the analysis presented here is *not* a test of kin selection as a mechanism maintaining cooperation in these two economic settings. Previous research suggests that cooperative hunting in Lamalera is maintained through mutualism (Alvard and Nolin 2002) and food sharing is primarily maintained by reciprocity (Nolin 2010). Instead, the test is, which model of kinship—the biological or the social—provides the better model of people's partner preferences in these cooperative contexts?

Site Description

Lamalera is located on the island of Lembata, east of Flores and north of Timor, in Nusa Tenggara Timur province of southeast Indonesia. In July 2006, the study population consisted of 1,227 people residing in 317 households.¹ The village stretches along 1.7 km of steep and rocky coastline on either side of the beach that is the center of economic activity in the village. Lamalerans speak Lamaholot, a language ranging from east Flores through central Lembata, and share many cultural features with their Lamaholot-speaking neighbors. All residents except the very young or very aged also speak Indonesian, the national language. Like most of the region, Lamalera is Roman Catholic.

Lamalerans are maritime foragers who fish and hunt seasonally over the course of the year. Sperm whales, other toothed cetaceans, and three species of ray are hunted from traditional paddle-and-sail-powered boats called *téna*. The active hunting season, called *léfa*, runs from May through September of each year. Economic activity during the remainder of the year consists of fishing from small boats, primarily for flying fish using gill nets, though some small-boat fishing persists during *léfa* as well. In recent years, motor boats, called *jonson* after a common brand of outboard motor, have seen increasing use. These boats are not used to pursue whales, but instead are used to pursue smaller, swifter prey including ray, tuna, marlin, and porpoise. In 2006, *téna* and *jonson* were used side by side in a mixed foraging strategy: *téna* were used when whales had been sighted or were otherwise expected in the area, and *jonson* were otherwise used.

The steep and rocky terrain surrounding Lamalera discourages agriculture. Instead, vegetable foods are acquired through trade with agriculturalists from the interior of the island. Women from Lamalera exchange fish and whale meat for staples such as maize, bananas, manioc, and rice, as well as other fruits and vegetables, brought by women from other villages to a weekly market. Other sources of food include chickens, pigs, goats, and dogs kept by Lamalerans. Consumption of livestock is largely reserved for ceremonial occasions associated with marriages, deaths, and the building and repair of boats.

Kinship in Lamalera is patrilineal. Each clan or *suku* consists of one to five lineages, each associated with its own great house or *lango béla*. In 2006, 21 endogenous clans and 39 lineages were represented in the village. Lineages ranged from 4 to 69 members, and from 1 to 20 households. In addition, 55 exogenous clans were represented among outsiders who had married into the village and the few families of immigrant schoolteachers who had taken

¹This figure excludes the populations of the outlying agricultural hamlets of Lamamanu and Korkowolor, which the Indonesian government includes under the administration of Lamalera. Also excluded are 18 students from other villages residing in the junior high school dormitory, three resident priests, and their housekeeper.

up posts in Lamalera. Marriage in the village nominally follows a pattern of asymmetric marriage alliance among clans, though in practice the prescribed system is not always followed (Barnes 1996). Brideprice was traditionally paid in ivory but is now paid in cash (when paid at all). Postmarital residence is neolocal, reflecting a twentieth-century change from virilocal residence promoted by the church. A groom is expected to have built or secured a house for himself and his bride before marriage, though saturation of the preferred sites in this steep and rocky village means the new home may be some distance from either the bride's or groom's parents. Consequently, residential distance and (biological) kinship are only weakly correlated (Pearson's $r = -0.075$).

Cooperative Hunting and Crew Formation

Lineages are the primary means of coordinating economic activity in the village (Alvard 2003; Alvard and Nolin 2002). In the past, most lineage great houses were associated with the hunting boat, or *téna*, belonging to that lineage, though today many lineages do not have *téna* of their own. In 2006 there were 14 active *téna* operating in the village,² compared with 20 in 1999. *Téna* are "owned" by a corporation of individuals who hold share-rights or *umā* in any prey caught by virtue of underwriting the costs of construction and maintenance. Most corporate shareholders come from the lineage associated with that boat, though some shareholders, especially of minor types of corporate shares, may come from other clans or lineages. Several craftsmen, including the harpoon smith, the sail maker, and the master carpenter, are also entitled to shares of the catch, as are the harpooner and crewmen present on the boat on the day of a successful hunt. The specific portions assigned to individuals are governed by a complex system of norms based on the anatomy of the prey species. These norms, as well as estimates of typical share sizes, are described in greater detail by Alvard (2002).

Each *téna* is managed by a boat master or *téna alep*. Before the start of each hunting season, the *téna alep* will visit men in the village and try to secure commitments from them to crew on his boat during the coming *léfa*. Men generally join the crew of their own lineage but will sometimes join the crew of their mother's or wife's lineage (Alvard 2003). Although households holding corporate shares are by no means obligated to provide crew, they are likely to experience pressure from the *téna alep* and possibly others within their lineage if there are able-bodied men in the household. Households holding corporate shares may have an added incentive to provide crew because they will receive both their corporate share and a crew share from any prey caught; however, holding a corporate share in one boat and crewing on another can be an attractive strategy for reducing risk.

Jonson are comparatively new institutions, but most follow the *téna* model of organization. Each *jonson* is headed by a boat master or *jonson alep*, and a corporation of members hold share-rights in any prey caught. Commonly the boat master is the owner of the outboard motor, and the boat corporation members bear the costs of constructing and maintaining the boat itself. Like *téna*, *jonson* corporations are typically drawn from a single lineage, but in some cases they may also include a collection of close neighbors. There were 15 active *jonson* in 2006, compared with just two in 1999.

Although some effort is put into organizing committed crews before the start of the active hunting season, in practice crew formation is far more fluid (Alvard 2003). Men descend to the beach shortly after dawn each day and gather near the boat house of the boat they intend to join. *Téna* require a minimum crew of eight, including the harpooner, but in 2006 they had an average crew of 10.2 men. *Jonson* can be crewed by as few as four individuals but

²"Active" here is defined as having had at least one successful hunt during the hunting season in 2006.

have an average crew of 8.5 men. As crews are assembled, the boats are pushed out to sea. If a boat fails to assemble the minimum crew required (or has no harpooner), those men who have assembled will disperse and may join other crews for the day. Jonson appear less prone to this type of “coordinationfailure” (Alvard and Nolin 2002), but they may stay beached for extended periods if the motor breaks or if fuel runs out. The net effect is that while most boats tend to have a stable core group of crew members, there is also considerable overlap in crew participation between boats over the course of the active hunting season.

Food Sharing

Households have a number of options for dispensing with the shares they acquire from téna or jonson. Some portion will be consumed immediately. Part of the remainder may be preserved for weeks or even months by salting and drying it in the sun. Trade is one of the primary economic activities of women in Lamalera, and a portion of the catch may be traded at a weekly market (Barnes 1996; Barnes and Barnes 1989). A household can convert the fat and protein calories in meat and fish into carbohydrate calories by trading for maize, which can be stored for years.

As is common in settings where resource packages are large and asynchronously acquired, households in Lamalera commonly share some of their acquired food with other households. Such sharing helps alleviate harvest risk and reduces temporal variance in diet (Nolin 2008; Winterhalder 1986). Between-household gifts of food are called *běfānā*. The size of typical portions given varies with the prey species (Nolin 2008: Table 4.10) but is typically enough to provide one meal’s worth of meat or fish for the recipient household. Notably, vegetable foods are also shared, possibly because their acquisition covaries with the fishery harvest. In 2006, vegetable foods accounted for about a quarter of all transfers by frequency (Nolin 2008). Prepared foods are sometimes shared as well.

Unlike the primary distribution of prey among normatively recognized holders of share-rights, this secondary distribution of food between households is not governed by any formalized set of norms dictating, for instance, classes of individuals to whom one must give. The giving of *běfānā* is voluntary and discretionary, with both husbands and wives participating in sharing decisions. When other adults are resident in the household, they may also participate in these decisions. Relatives and neighbors are the most common donors and recipients (Nolin 2010). Repeated sharing occurs to and from a core set of households, with occasional “singleton” transfers to and from other households (Nolin 2008). Previous analyses have shown that the single greatest predictor of whether a household shares with another is reciprocal sharing from the potential recipient, while kinship and proximity appear primarily to shape preference among reciprocal partners (Nolin 2010).

Methods

Crew Participation

Field research was conducted from April through December of 2006. Each day during léfa from May 8 through September 9, 2006, local assistants observed the return of all large boats (téna and jonson).³ The names and roles of men participating in boat crews were recorded into notebooks as each boat returned. These books were collected and the data entered into the project database on a weekly basis, allowing the author to monitor the quality of the data collected as the project progressed. Over the course of the observation period there were 907 hunts over 88 hunt-days. A total of 6,870 man-days were recorded. All but 90 of these records could be positively matched to individuals listed in residents’

³Boats do not go out on Sundays or religious holidays. No data were collected on May 12 and 13.

genealogies (see below). There were 300 unique men identified among the remaining 6,780 records.

This sample of crew participation data was used to replicate a portion of Alvard's (2003) analysis. Following Alvard's procedure (2003:136-137), the sample was first reduced to the 271 men who were residents of Lamalera during the study period. This primarily excluded Lamaleran émigrés who participated in hunts during return visits to Lamalera. The sample was further reduced to the 255 men for whom genealogies including all four grandparents were available. This procedure primarily excluded individuals with one or more immigrant ancestors, but it was necessary to ensure higher precision in calculations of genetic relatedness (see below). The sample was again reduced to those 253 men for whom lineage was known. Finally, following Alvard (2003), a sample of "regular hunters" was drawn by retaining only those men who contributed six or more hunt-days.⁴ This final sample of 215 regular hunters contributed 6,049 or 88% of all observed man-days.

A 215×215 affiliation matrix was created from the final sample of 6,049 man-days contributed by the 215 regular hunters. Each cell in the affiliation matrix contains the number of days the pair of men of the corresponding row and column were listed together as crew on the same boat. However, not all men contributed the same number of man-days over the course of the hunting season. It is possible that some pairs of men appear to affiliate more frequently simply because they contributed more effort. Following the procedure used by Alvard (2003), the affiliation matrix was normalized by fitting homogenous margins of 100 man-days for all hunters using iterative proportional fitting or IPF (Bishop et al. 1975).⁵ The diagonal of the affiliation matrix is undefined, so structural zeroes were assigned along the diagonal; other zero-value cells in the affiliation matrix were assigned a small, positive value of 0.0001 before fitting (Freeman et al. 1992). The IPF procedure was performed in R 2.10.1 (R Development Core Team 2009) using the *loglin* function of the *stats* package. The resulting matrix provides a measure of affiliation for each of the 23,005 unique, unordered pairs formed by the 215 regular hunters, normalized for variation in participation among hunters. In the language of social network analysis, the resulting matrix describes a network of *undirected, valued* ties of shared crew affiliation. For simplicity, this matrix is referred to as the *crew affiliation matrix* in the discussion below.

Food Sharing

Following the end of léfa all 317 households were interviewed about their usual food-sharing habits over the preceding hunting season. These interviews treated the household as the unit of analysis, and any adult residents present in the household at the time of the interview were allowed to respond. A previous phase of the study (see Nolin 2008:141-144) suggested that repeated transfers to or from the same households accounted for most food sharing, with single transfers to or from other households accounting for the remainder. In pretesting, respondents were reluctant to rank other households according to the frequency with which they gave or received. Consequently, the question was reworded to elicit only those repeat donors and recipients who accounted for the greatest frequency of sharing. Respondents were asked to name those other households to whom they had "usually, more than once" given food during the preceding season, as well as those from whom they had "usually, more than once" received food over the same period. The order of these two

⁴Six days constitute a full work week in Lamalera, so this cutoff includes only those men who contributed at least one week's worth of labor to the fishery.

⁵Another method of normalizing the matrix is to express each pair's affiliation as the proportion of days that both men chose to go hunting that they also crewed on the same boat—that is, the number of times they crewed together over opportunities to do so. The resulting matrix is highly correlated ($r=0.895$) with the matrix derived using IPF. Results using this alternative matrix do not qualitatively differ from those obtained using the IPF matrix. I present the results using the IPF matrix here primarily to facilitate comparison with Alvard's (2003) results.

questions was alternated from interview to interview. No limit was placed on the number of nominations.

By asking households to report both giving and receiving relationships, this design censused all possible directed sharing relationships between households twice. To reduce Type II (false negative) errors resulting from faulty respondent recall, these two sets of responses were combined by taking the logical union of the sets of reported giving and receiving relationships (Nolin 2008). This produced a social network of binary, directed food-sharing relationships among households in the village. Additional details on these sharing data, how they were collected, and the rationale for the approach used in creating the network are provided elsewhere (Nolin 2010). The resulting network consists of 3,111 *directed, binary* sharing relationships out of the 100,172 possible ordered pairs among the 317 households in the village. This network is referred to as the *food-sharing matrix* in the discussion below.

Relatedness and Lineage

Genealogies on all household residents were collected as part of household interviews. In many cases, these interviews consisted of asking respondents to verify genealogies previously collected by Alvard's team in 1999, which had been further extended using parish baptismal registers. Informants were asked to provide genealogies as far back as their grandparents' generation.⁶ Where possible these genealogies were verified and extended using data from local parish registers. Wright's (1922) coefficient of relatedness was calculated from these genealogies for each pair of residents using Descent, version 0.2.0.2 (Hagen 2005).⁷ For genealogies complete to the grandparents' generation, the minimum detectable degree of relatedness is $r \geq 0.0625$ (one shared grandparent or closer); for many pairs of individuals in this dataset a higher-resolution calculation was possible. Respondents were also asked to provide the clan and lineage of all household residents. A few lineages are now so small that they no longer maintain a great house of their own and instead have merged with other lineages. For the purposes of this analysis, lineage was defined by the great house an individual attended for lineage functions rather than by the name of his or her historical lineage.

Several matrices were constructed from the genealogical and lineage data. For the analysis of crew affiliation, a 215×215 matrix indicating the degree of relatedness between regular hunters was constructed. Each cell of this matrix was populated with the estimated coefficient of relatedness between the pair of men defined by the corresponding row and column. This matrix is referred to as the *hunter relatedness* matrix in discussions below. The mean degree of relatedness among all 23,005 unique (unordered) hunter pairs was low, $r = 0.0071$. Closely related kin were sparse in this pool of hunters: only 1,718 dyads, or 7.5%, had any detectible (given the completeness of the genealogical data) degree of relatedness; 2.1% (475 dyads) were related by $r \geq 0.125$, 1.1% (251 dyads) were related by $r \geq 0.25$, and 0.6% (137 dyads) were related by $r \geq 0.5$.

Similarly, a 215×215 matrix indicating shared lineage between pairs of men was constructed. The cell values of this matrix were coded as 1 if the two men were from the same lineage, and as 0 otherwise. This matrix is referred to as the *hunter shared lineage*

⁶The majority (1,049 of 1,227) of residents' genealogies are complete at least as far as their grandparents' generation. Of the remaining 178 residents, all but 18 are incomplete because they themselves, or one or both of their parents, immigrated from outside the village (in which case additional ancestors were not recorded beyond the immigrating generation) or because they were born to an unmarried woman and so their father and paternal grandparents are unknown. The remaining 18 cases of incomplete genealogies are those of elderly individuals whose children were only able to provide the names of their parents' parents.

⁷These calculations assumed all children to be the biological offspring of their putative father.

matrix. Of the 23,005 unique (unordered) pairs of hunters, 745, or 3.2%, were of the same lineage.

Similar matrices were generated for the analysis of the 317×317 household-by-household food-sharing network. However, unlike the crew affiliation network, which consists of dyads of hunters, the sharing network consists of dyads of households. This complicates calculating a measure of between household relatedness. Ethnographic observations of the distribution of *bĕfānā* suggest that both husbands and wives take part in sharing decisions. For this reason, between-household relatedness was calculated relative to both the husband and wife of the donor household. First, the maximum degree of relatedness to any single individual in the recipient (column) household was calculated separately for the husband and wife of the donor (row) household. Then the husband's and wife's values were compared and the greater of the two values was used to populate the cells of the matrix.⁸ For simplicity, this matrix is referred to as the *household relatedness matrix*.

As with the hunter relatedness matrix, average between-household relatedness is relatively low and kin are sparse in this network. The mean degree of between-household relatedness is $r=0.016$. Of the 100,172 directed household dyads (ordered household pairs), 12,595 or 12.6% have any detectible degree of relatedness. Only 4.1% (4,125) of directed dyads are as closely related as first cousins ($r\geq 0.125$); only 2.1% (2,070 directed dyads) are as closely related as $r\geq 0.25$, and only 0.9% (917 directed dyads) are as closely related as $r\geq 0.5$.

Because descent in Lamalera is reckoned patrilineally, it might seem intuitive to assign each household to the lineage of the husband of that household. However, such an assignment overlooks the fact that patrilineages have both male and female members. Each household may be associated with two lineages: that of the husband and that of the wife. In Lamalera, where women contribute to household sharing decisions, it is especially important to consider the lineage of women in their roles as both donors and recipients. If shared lineage motivates between-household sharing, then both women and men may have an interest in directing shares to households of their co-lineage members, regardless of the recipient's gender.

As was done in constructing the household relatedness matrix, both husbands' and wives' interests were taken into account in constructing the household-by-household matrix of shared lineage. Each household was first assigned to the two lineages associated with that household. Household dyads were then scored as sharing a lineage if either of the lineages associated with the donor (row) household matched either of the two lineages associated with the recipient (column) household. Any match between households was coded as a cell value of 1; otherwise the cell value was coded as 0.⁹ This matrix is referred to as the *household shared lineage matrix*. Of the 50,082 unique (unordered) household pairs, 5,101 or 10.2% shared a lineage.

Analyses

To compare the effects of lineage and relatedness on crew formation, the crew affiliation matrix was regressed on the matrices of hunter shared lineage and hunter relatedness, separately and together. Because the dependent variable (the crew affiliation matrix) contains valued ties (i.e., the matrix cell values are continuous), ordinary least-square (OLS) regression was employed. Each element of the crew affiliation matrix was regressed against

⁸Several different methods of calculating between-household relatedness were tried. The metric described here produced a better fit (by AIC selection) to the sharing data than other methods, including taking the maximum degree of relatedness between any pair of individuals (drawn one each from the two households), or the average across all such pairs.

⁹Husbands' relatedness and lineage are more predictive of food sharing than are wives', though both are significant. This difference is not central to the argument presented here but is consistent with the ethnographic observation that both men and women have a voice in sharing decisions.

the corresponding element in the hunter relatedness matrix and the hunter shared lineage matrix. Network data such as these violate the OLS assumption of independence of cases. To control for non-independence of cases, a quadratic assignment procedure (QAP; Krackhardt 1987, 1988) permutation test was performed on each model. For each test, 2,000 permutations were calculated using Dekker et al.'s (2003, 2007) semi-partialling plus permutation method, as implemented in the *sna* (Butts 2008, 2009) package for R 2.10.1 (R Core Development Team 2009).

To compare the effects of shared lineage and relatedness on between-household food-sharing relationships, the food-sharing matrix was regressed on the matrices of household relatedness and household shared lineage, separately and together. Because the dependent variable is binary, matrix logistic regression was employed. Again, QAP permutation tests were employed to control for non-independence of cases, as described above.

Results

Crew Affiliation

The results of the regressions of the crew affiliation matrix on the hunter shared lineage and hunter relatedness matrices are presented in Table 1. The table presents standardized regression coefficients primarily to aid in comparison of effects across the two independent variables, but also because the dependent variable (the crew affiliation matrix fit using IPF) is not itself expressed in interpretable units. This also simplifies comparisons with previously published data (Alvard 2003: Table 4). The standardized coefficients express the effect on normalized frequency of crew affiliation, in units of standard deviation, of a one-standard-deviation change in the independent variable.

Model A shows that the degree of genetic relatedness between two hunters has a positive effect on the frequency with which they affiliate in boat crews. All coefficients are significant. A one-standard-deviation change in relatedness results in a 0.16 standard deviation change in frequency of affiliation. Hunter relatedness explains about 2.5% of variation in crew affiliation. The effect for shared lineage (Model B) is stronger than that for relatedness, and it explains more than twice as much variance (5.3%). However, when both hunter relatedness and hunter shared lineage are included in the same model, the effect of relatedness drops significantly while the effect of shared lineage remains relatively strong. More importantly, the inclusion of relatedness in a model with shared lineage explains little additional variation beyond that explained by shared lineage alone (5.6% vs. 5.3%).

Food Sharing

The results of the regressions of the food-sharing matrix on the household relatedness and household shared lineage matrices are presented in Table 2. Several methods have been proposed for standardizing logistic regression coefficients (Menard 2004). The method used here is Menard's (1995, 2004: Eq. 5) fully standardized logistic regression coefficient. It is interpreted as the effect (measured in units of standard deviation) on the log-odds of the dependent variable of a one-standard-deviation change in the independent variable. Similarly, several different pseudo- R^2 values have been suggested (Hagel and Mitchell 1992; Nagelkerke 1991). The R^2 statistic used here is a widely used statistic proposed by McFadden (1974) and is interpreted as the proportional reduction in error in predicting the dependent variable contributed by the terms in the model compared with a model with no predictors.

As with crew affiliation, both between-household relatedness (Model A) and household shared lineage membership (Model B) have statistically significant independent effects. However, in the case of between-household food sharing, it is relatedness rather than shared

lineage that has the greater effect, as reflected both in the larger standardized regression coefficient (0.40 vs. 0.20) and the larger pseudo- R^2 value (0.16 vs. 0.09). More strikingly, when both relatedness and shared lineage are included in the same regression (Model C), the combined model is only slightly more predictive than the model (A) including relatedness alone (pseudo- R^2 0.18 vs. 0.16). Household shared lineage membership and household relatedness are correlated with each other (matrix Pearson's $r=0.345$), and in models A and B each term captures part of the variance explained by the other (excluded) term. In the full model this is reflected in a shift in the standardized coefficients.

Discussion

The pattern of crew affiliation observed in the 2006 crew participation data matches the pattern found by Alvard (2003: Table 4) in his analysis of boat crew affiliation in 1999. His results also showed that shared lineage membership independently explained more variance than did genetic relatedness ($R^2=0.103$ vs. 0.039, respectively). Similarly, he found that combining shared lineage membership and genetic relatedness in the same model explained little additional variance beyond that explained by shared lineage membership alone ($R^2=0.107$ vs. 0.103, respectively).¹⁰

The food-sharing data show the opposite pattern of that seen for crew affiliation. While shared lineage and genetic relatedness both have independent effects, the combination of the two explains little additional variation beyond that explained by genetic relatedness alone ($R^2=0.178$ versus 0.159, respectively). This is readily seen in Fig. 1, which presents the R^2 (or pseudo- R^2) values for regressions reported in Tables 1 and 2. Alvard's (2003: Table 4) results for crew affiliation during the 1999 hunting season are presented for comparison. In the case of crew affiliation, both the 1999 hunting season and the 2006 hunting season data show a similar pattern: shared lineage explains more variance than does genetic relatedness, and the two together explain little more than does lineage alone. For food-sharing relationships, this pattern is reversed: genetic relatedness is the better predictor, and lineage explains little additional deviance than relatedness alone. What explains this difference?

Recall that in neither case does kin selection appear to be the adaptive mechanism promoting the cooperative behavior itself. In the first case, cooperative hunting appears best explained as synergistic mutualism (Maynard Smith 1983): men hunt cooperatively because their individual per capita return rates are higher than those from other alternatives—notably, small-boat fishing (Alvard and Nolin 2002). In the second case, reciprocal altruism (Trivers 1971) appears to explain most between-household food sharing: individuals disproportionately share with those who reciprocate, and this factor alone explains nearly half the variance in between-household sharing relationships (Nolin 2010). The question begged by the data presented here is therefore why lineage would be a better predictor of partner choice in one setting (crew formation) and biological kinship a better predictor in the other (food sharing).

Alvard's (2003), explanation for the better predictive power of lineage in the context of crew formation is that unilineal descent helps define discrete, bounded groups of cooperators which in turn facilitates the formation of whaling boat crews. If individuals were to try to form crews based on the basis of biological kinship, this would produce many overlapping bilateral kindreds but no clear groups (see also Alvard 2011). At the cost of excluding half

¹⁰During the 1999 season there were twenty active téna but only two jonson. Alvard's (2003) crew affiliation analysis focused only on the twenty téna crews. In 2006, there were 15 active jonson and 14 active téna. Crew participation data for both types of boats were pooled in the present analysis. Thus, the 1999 data reflect only téna crew participation whereas the 2006 data reflect both téna and jonson crew participation. Differences between téna and jonson crews may account for the lower variance explained in 2006 compared with 1999.

their genetic kin they are better able to coordinate with others to form crews to realize the benefits of mutualistic cooperation. Groups defined by shared lineage are also likely to share the same set of norms governing how cooperative hunting is to be organized and how the spoils are to be divided.

Food sharing, in contrast, does not necessitate the same degree of coordination as does hunting crew formation. In this respect, the key distinction between food sharing and crew formation is the degree of autonomy that individuals have in making their decisions. Recall that food sharing in Lamalera is voluntary and discretionary, with no formally articulated norms obliging individuals to share with particular other individuals. A household's sharing decisions can be made relatively independently of the choices made by other households. If reciprocal partnerships are valued, then a household's sharing decisions may be contingent on the choices of another household. Although a household may have many of these relationships, each such relationship is only dyadically contingent on the choices of the partner households. Instead, most of the coordination of preferences in food-sharing decisions may be within the household, between husband and wife. In the absence of the need to coordinate sharing decisions outside the household above the level of the dyad, individuals are better able to pursue kin preferences based on genetic relatedness.

In fact, one might wonder why lineage has any positive effect on food sharing at all. Food sharing reduces risk and temporal variance in resources when covariance in harvest success is low (Winterhalder 1986). The crew formation analysis suggests that lineage members are more likely to be on the same boat together, meaning that lineage members are likely to receive shares from the same boats. Lineage members are also likely to have corporate shares in the same boats (Alvard 2002). This generally suggests high harvest covariance among lineage members and should reduce their attractiveness as sharing partners. If, as previously suggested (Nolin 2010), reciprocity is the main motivation for food sharing in Lamalera, one might ask why households would share food with households of lineage members at all. We might, in fact, predict a negative relationship between lineage co-membership and sharing. The answer is that while lineage members do have high covariance (and refrain from sharing) on days when they go out on the same boat, on days when a man cannot go out, it is frequently his fellow crew members (who are also frequently lineage members) that support him with donations of food.

Economists who study partner-choosing behavior such as this refer to it as *matching*. In matching models a set of agents self-assort into groups (typically pairs) based on ordinal preferences over the set of potential partners. The goal of much of this research is to determine under what conditions a stable matching exists and can be identified (see, for example, Chung 2000; Irving 1985; Tan 1991). Stability in this sense means that no pair (or coalition) of actors currently not matched with each other would both prefer to be matched with each other rather than with their current partners. The most robust result from this research is that in two-sided, one-to-one matching models (such as a marriage market) there is always at least one stable matching (Gale and Shapely 1962).¹¹ Stable matchings may exist in other settings, but this is not guaranteed (Roth and Sotomayor 1990).

Although most of the work in matching theory has focused on two-sided matching (Roth and Sotomayor 1990), one important model called the Stable Roommate Problem deals with matching when all actors are drawn from a single set. In these models pairs are formed based on actors' preferences regarding other members of the group. With as few as four actors it is possible to specify sets of preferences that result in no stable matchings (Gale and Shapely 1962). In simulations in which preferences are randomly assigned, the probability

¹¹See Bergstrom and Real (2000) for an evolutionary application of two-sided matching theory to mate choice.

of a stable matching decreases with increasing population size (Irving 1985). However, when actors can be arranged along a single dimension such that those who are closer more strongly prefer to be matched (a property called “single-peaked preference”), then there is a unique stable matching (Bartholdi and Trick 1986).

From a matching standpoint, food-sharing relationships pose little problem: reciprocal partners presumably select each other based on mutual preferences, but more importantly, “matching” with one individual does not automatically preclude matching with another. Crew formation, on the other hand, resembles a Stable Roommate Problem, but with crews of eight or more rather than pairs. Imagine that each individual hunter has ordered preferences regarding all other hunters with whom he might form a crew. If genetic kinship influences these preferences, then the fact that no two individuals (besides full siblings) have the same set of biological kin means that no two individuals are likely to have perfectly congruent preferences. Two individuals may wish to crew together but may be in complete disagreement about other preferred partners.

If natural selection has favored the evolution of a kin preference in cooperative partner choice contexts, then it may be that unilineal cooperative groups represent a relatively stable n -person matching, given individuals’ differing kin preferences. Although Bartholdi and Trick’s (1986) stability condition has only been demonstrated for pairs, it may be that restricting individuals’ preferences to unilineal kin produces the one-dimensional single-peaked preferences that appear to facilitate stable matchings. Unilineal kinship assures that at least some of every group member’s partner preferences are satisfied, and that every member has some positive (however small it may be) relatedness to every other member. Furthermore such a coalition or matching may be stable in the game theoretical sense that no other group of similar size could be formed from the same population that satisfies its members’ preferences as well as or better than the coalition defined by unilineal descent.

The functionalist explanation for unilineal descent suggests it serves to define large, discretely bounded and mutually exclusive groups (van den Berghe 1979) who share a set of norms that facilitates coordination (Alvard 2003). However, unilineal descent is not the only possible mechanism by which large groups of people can be organized. Humans can, and do, also organize themselves into large, mutually exclusive groups on the basis of other criteria, such as geographic boundaries, age-sets, initiation rites, or other markers that distinguish group members from non-members. One reason lineage systems may be so common is that they retain a higher average degree of relatedness among group members (van den Berghe 1979), better satisfying individuals’ preferences to assort with kin.

Why, then, choose patriline over matriline (or vice versa)? At face value, the two systems ought to be equally effective at organizing large, distinct groups of highly related individuals. Figure 2 suggests why either patriline or matriline might be favored. The two identical pedigrees are shaded according to patrilineal (upper panel) or matrilineal (lower panel) descent. In either case, the sex through which descent is reckoned has a higher mean within-lineage relatedness to co-lineage members *of the same sex* than does the other sex. For example, in the pedigrees presented in Fig. 2, the patrilineally related men in the upper panel have a mean degree of relatedness of $r=0.35$, while the women in the same patriline have a mean degree of relatedness of $r=0.275$. Under matriline (the lower panel) these figures are reversed. The sex from which cooperative groups are formed will have higher within-group relatedness when descent is reckoned through that sex. In economic terms, the form of lineal descent corresponding to the cooperatively organized sex will better satisfy their kin preferences, and may result in more stable matchings when groups are formed. Thus, when local ecology favors cooperation among males, then patriline may be the

preferred mode of unilineal descent; where cooperation among women is favored, matriliney may be preferred.

These examples are speculative, and without further empirical support, as well as more formal modeling, this matching theory explanation for unilineal descent systems may remain less convincing than other explanations. However, it is also not mutually exclusive of other, previously proposed hypotheses that use parental investment, reproductive skew, inheritance, and paternity uncertainty to explain patriliney and matriliney. Several mechanisms might be operating simultaneously to favor one mode of descent over another. In this context, the ability of unilineal descent systems to satisfy some of all members' preferences to affiliate with kin may be a contributing factor to the stability and ubiquity of these forms of descent.

Summary

In Lamalera, kin preference appears to manifest itself differently in different economic settings. When households make food-sharing decisions, they are free to do so relatively autonomously from the decisions of other households; consequently, genetic relatedness is a better predictor than lineage in this setting. When men make decisions about which boat crews to join, their choices are contingent on those made by others, and shared lineage membership is a better predictor than genetic relatedness in this setting. The key difference between the two is the degree to which individuals are free to pursue their kin preferences autonomously versus the degree to which they must coordinate those preferences with others. Unilineal descent offers a normative solution to the problem of coordinating multiple individuals' conflicting kin preferences by defining discrete groups of cooperating individuals, and this solution may be stable in the sense that it satisfies at least some of the preferences of all its members. Given that unilineal descent of some form is favored in the setting of cooperative hunting in Lamalera, patrilineal descent may be favored over matrilineal descent because it increases the mean degree of within-group relatedness for men.

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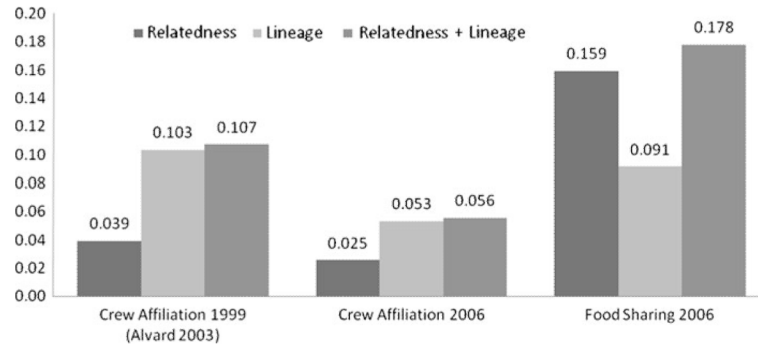


Fig. 1.

Variation in hunters' crew affiliations and between-household food-sharing relationships explained by genetic relatedness, shared lineage, or both. Crew affiliation data from 1999 are from Alvard (2003: Table 4). Numbers on the y-axis and above the bars provide the R^2 or pseudo- R^2 values. Note that in the case of crew affiliation, genetic relatedness adds little explanatory power beyond that provided by lineage, while in the case of food sharing, lineage adds little explanatory power beyond that provided by genetic relatedness

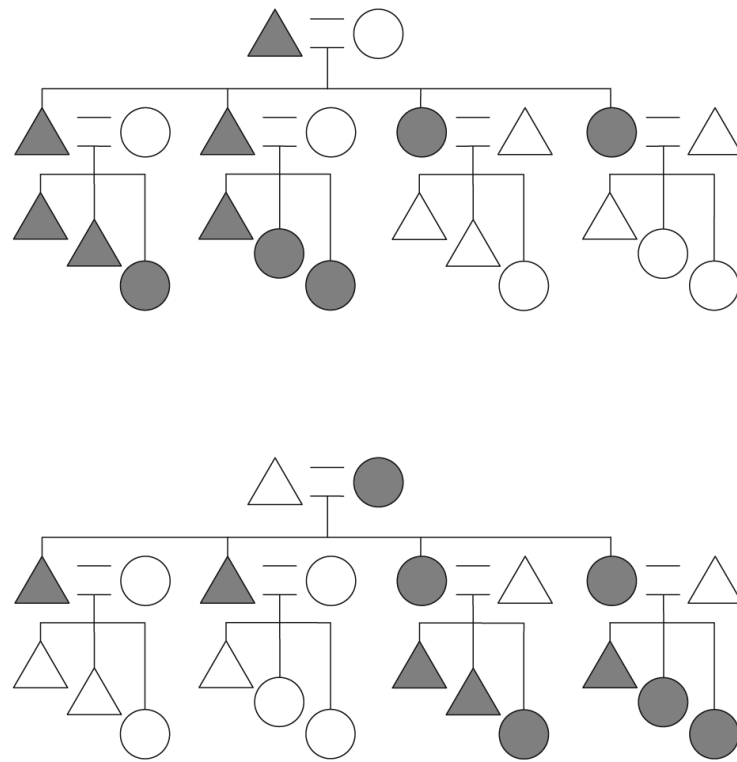


Fig. 2. Two pedigrees shaded according to lineage membership. Upper panel: patrilineal lineage membership. Lower panel: matrilineal lineage membership. The sex through which descent is reckoned has higher mean within-lineage relatedness. Mean relatedness of patrilineally related men: $r=0.35$; mean relatedness of patrilineally related women $r=0.275$. Mean relatedness of matrilineally related men: $r=0.275$; mean relatedness of matrilineally related women: $r=0.35$

Table 1

Ordinary least-squares matrix regression of fitted crew affiliation matrix on relatedness and shared lineage

| Model | Independent Variable | Standardized Coefficient \pm S.E. | p^a | R^2^b |
|-------|----------------------|-------------------------------------|---------|---------|
| A | Relatedness | 0.1595 \pm 0.0065 | <0.0001 | 0.0254 |
| B | Shared Lineage | 0.2301 \pm 0.0064 | <0.0001 | 0.0529 |
| C | Relatedness | 0.0602 \pm 0.0074 | <0.0001 | 0.0556 |
| | Shared Lineage | 0.2003 \pm 0.0074 | <0.0001 | |

^aQAP permutation tests using Dekker's (Dekker et al. 2003) semi-partialling plus permutation method with 2,000 iterations

^bModel significance: Model A: $F(1,23003)=1,286, p<0.0001$; Model B: $F(1,23003)=600.8, p<0.0001$; Model C: $F(2,23002)=678.2, p<0.0001$

Table 2

Logistic matrix regression of food-sharing network on between-household relatedness and household shared lineage

| Model | Independent Variable | Standardized Coefficient \pm S.E. ^a | <i>p</i> ^b | <i>R</i> ^{2c} |
|-------|----------------------|--|-----------------------|------------------------|
| A | Relatedness | 0.3995 \pm 0.0059 | <0.0001 | 0.1593 |
| B | Shared Lineage | 0.2020 \pm 0.0037 | <0.0001 | 0.0913 |
| C | Relatedness | 0.2711 \pm 0.0058 | <0.0001 | 0.1777 |
| | Shared Lineage | 0.2247 \pm 0.0092 | <0.0001 | |

^aMenard's (1995) fully standardized logistic regression coefficient

^bQAP permutation tests using Dekker's (Dekker et al. 2003) semi-partialling plus permutation method with 2,000 iterations

^cMcFadden's (1974) pseudo-*R*² for logistic regression: the proportion of residual deviance (RD) in an intercept-only (null) model explained by the full model, calculated as (RD_{null} - RD_{full})/RD_{null}