

Author Manuscript

Hum Nat. Author manuscript; available in PMC 2011 October 1

Published in final edited form as:

Hum Nat. 2010 October 1; 21(3): 243–268. doi:10.1007/s12110-010-9091-3.

Food-Sharing Networks in Lamalera, Indonesia: Reciprocity, Kinship, and Distance

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Abstract

Exponential random graph modeling (ERGM) is used here to test hypotheses derived from human behavioral ecology about the adaptive nature of human food sharing. Respondents in all (n=317) households in the fishing and sea-hunting village of Lamalera, Indonesia were asked to name those households to whom they had more frequently given (and from whom they had more frequently received) food during the preceding sea-hunting season. The responses were used to construct a social network of between-household food-sharing relationships in the village. The results show that kinship, proximity, and reciprocal sharing all strongly increase the probability of giving food to a household. The effects of kinship and distance are relatively independent of each other, while reciprocity is more common among residentially and genealogically close households. The results show support for reciprocal altruism as a motivation for food sharing while kinship and distance appear to be important partner-choice criteria.

Keywords

food sharing; cooperation; reciprocity; kin selection; social network analysis; ERGM

Food sharing is an example of an apparently altruistic behavior: those who give food provide a benefit to others at a cost to themselves. Under most circumstances it should be difficult for natural selection to promote the evolution of such behaviors, as, all else being equal, those who undertake altruistic acts towards others will do worse than those who reap the rewards of others' altruism without paying its costs (Hamilton 1963). Yet apparently altruistic behaviors such as food sharing can evolve, and a number of adaptive mechanisms have been proposed to explain how natural selection might favor the evolution of such behaviors. By studying the adaptive significance of food sharing, we hope to learn something about the evolution of altruistic behaviors more generally (Kaplan and Hill 1985, Smith 1988, Winterhalder 1997, Gurven 2004a).

In reconstructing the behavioral evolution of our species, food sharing has often been viewed as part of a suite of interrelated adaptations including hunting, central-place foraging, the sexual division of labor, and the nuclear family (Washburn & Lancaster 1968; Isaac 1978; Parker and Gibson 1979; Lovejoy 1981; McGrew and Feistner 1992). According to this view, differences in reproductive constraints between the sexes led to a sexual division of labor, with males pursuing high-variance meat resources and females pursuing more predictably acquired vegetal resources. Variance in meat acquisition favored sharing of meat within the group, and nutrient complementarity of animal and plant foods favored exchange of food between males and females. This in turn led to the establishment of the

human pair-bond and the nuclear family, with female sexual fidelity coevolving with paternal investment in offspring.

A competing view questions elements of this model, especially men's roles as provisioners (Hawkes ¹⁹⁹¹, 1993a,b;Hawkes et al 2001a;Hawkes and Bliege Bird 2002). In this alternative view, male hunting evolved not as paternal investment, but through status competition and mating effort. Men competed with other men to provide public goods shared by the group as a whole, and better hunters were rewarded with mating opportunities, higher status, or other social deference. While the relative importance of paternal provisioning and the evolutionary motivations of men's hunting effort continue to be actively debated (Bliege Bird and Bird 2008;Bliege Bird et al. 2009; Gurven and Hill 2009,2010;Guven et al. 2009;Hawkes et al. 2010), what seems increasingly clear is that human reproduction is a cooperative enterprise (Mace and Sear 2005;Sear and Mace 2008), and that intergenerational transfers of food were important in shaping evolutionarily derived features of human life history (Kaplan and Robson 2002;Robson and Kaplan 2003,Lee 2003,2008).

Theories of Food Sharing

A number of theories have been proposed as adaptive explanations for human food sharing. The brief review here assumes some familiarity on the part of the reader. For a more comprehensive review, see Gurven (2004a).

Kin Selection

Kin selection or inclusive fitness theory (Hamilton 1964) suggests that altruistic behaviors such as food sharing can evolve if they benefit other individuals who are likely to carry the same prosocial alleles. The probability that two individuals will share an allele by common descent is labeled r, Wright's (1922) coefficient of genetic relatedness, and altruistic behavior can be favored by natural selection when rb>c, where b and c are the fitness benefit to the recipient and cost to the donor of aid, respectively (Hamilton 1964). Kin selection does not predict that aid should be doled out in proportion to r, but does predict that, all else being equal, closer kin should be favored over more distant kin (Altman 1979, Dawkins 1979, Grafen 1980).

Kin selection has a mixed record as a predictor of food sharing. In Gurven's (2004a) review of the ethnographic literature, societies range from those in which hunters relinquish control over their kills and receive portions no larger than those of others, to those in which hunters control the distribution to other households and have special shares reserved for themselves and their families. Among the Hiwi (Gurven et al. 2000b) nuclear families are the primary consumers and show a weak kinship bias in distributions to other families. Households that share in Ifaluk are more closely related than the population on average (Betzig and Turke 1986). Kinship is a strong predictor of between-household sharing in the Iñupiaq communities of Deering and Wales, Alaska (Madganz et al. 2002), the Dolgan/Nganasan village of Ust'-Avam, Siberia (Ziker and Schnegg 2005, Ziker 2007), and the Achuar/ Quichua community of Conambo, Ecuador (Patton 2005). Sharing among the Ache shows considerable kin-bias on the reservation (Gurven et al. 2001), but this appears to be due to preferential reciprocal exchange with kin, rather than need-based sharing directed towards kin (Allen-Arave et al. 2008). The Ache show no evidence of kin-biased sharing on forest treks (Kaplan and Hill 1985). Among the Hadza, large prey is not distributed by the hunter, but by other individuals (Hawkes et al 2001b), though more recent research suggests hunters' families still receive larger shares than other families (B. Wood, personal communication). On Mer, residentially distant kin were not favored over residentially close non-kin in distributions of turtle meat (Bliege-Bird and Bird 1997). The Mikea studied by

Tucker (2004) shared little food despite living in a small community of six closely related households. Among the Ye'kwana there is little evidence that kinship influences meal sharing outside the nuclear family, though kinship is an important predictor in other modes of cooperation (Hames and McCabe 2007).

Reciprocal Altruism

Reciprocal altruism (Trivers 1971) provides another avenue by which altruistic behavior may evolve. When there are frequent reversals of fortune it may pay over time for haves to share with have-nots if there is a reasonable expectation that the have-nots will reciprocate in the future when their fortunes are reversed. Because of diminishing marginal valuation, the portion given is valued less by the donor than the recipient. When the expected value of a future return transfer exceeds the donor's current valuation of the portion to be given, then reciprocal sharing can be favored. This situation is more likely to occur when resources are unpredictably and asynchronously acquired, and explains why ethnographically meat is more commonly shared than other foods. Sharing in such circumstances reduces dietary variance, or risk, for both parties and can reduce the hazard of falling below a minimum threshold (Winterhalder 1986, 1990; Smith 1988). Because of differences in marginal valuation, accounts between reciprocators do not need to be precisely balanced so long as each party does marginally better than it would have had it not shared (Hill and Kaplan 1993; Gurven 2004a, b) but sharing should at least be contingent on past and future transfers from one's partner. The key to testing the hypothesis is testing for contingent exchange, a statistical correlation between frequency or amounts given and received within dyads (Hill and Kaplan 1993). However, other mechanisms can produce apparent contingency, and it can be difficult to tease apart underlying causes (de Waal and Luttrell 1988).

Like kin selection, support for reciprocal altruism as a motivation for food sharing is mixed. In some societies hunters relinquish control of their kills, making it effectively impossible to direct shares to those from whom they have received in the past. Such appears to be the case, for instance, with hunted turtle meat among the Meriam (Bleige Bird et al. 2002). Evidence of contingent exchange on Ache forest treks, where game is distributed widely, is limited to non-meat foods (Gurven et al. 2002) but is much stronger at the settlement (Gurven et al 2002, Gurven 2006, Allen-Arave et al. 2008). Where hunters retain control of their kills evidence of reciprocity is stronger (Yanamamo: Hames 2000; Hiwi: Gurven et al. 2000b, Gurven 2004b; Iñupiat: Magdanz et al. 2002; Achuar/Quichua: Patton 2005). Additionally, a number of studies have demonstrated contingent reciprocity in meal sharing (Mikea: Tucker 2004; Dolgan/Nganasan: Ziker and Schnegg 2005; Ye'kwana: Hames and McCabe 2007).

Other Hypotheses: Tolerated Scrounging and Costly Signaling

Two other hypotheses, tolerated scrounging and costly signaling, are not directly tested in the analysis presented here but deserve mention. In its basic form, tolerated scrounging (Blurton Jones 1984, 1987) proposes that food is relinquished when the cost of defending it from the demands of others exceeds its marginal value to the possessor. How broadly food is shared through tolerated scrounging depends on how differentiated are individuals' valuation of resources and their ability to contest food resources, with greater differentiation producing narrower distributions (Winterhalder 1996, Stevens and Stephens 2002). When producers have absolute control over the food resources they produce then tolerated scrounging is an unlikely explanation for food transfers.

Costly signaling (Spence 1973, Zahavi 1975, 1977) proposes that natural selection can favor apparently altruistic sharing (or, more generally, other costly traits) when the act of sharing communicates otherwise unobservable information about the donor, and receipt of that information in turn promotes others to behave in ways that benefit the donor and offset the

costs of sharing. Costly signaling is related to the "show-off" hypothesis (Hawkes 1991, 1993a; Hawkes and Bliege Bird 2002), and is central to the debate about the adaptive significance of men's hunting effort. Costly signaling has been invoked to explain food sharing in settings where difficult-to-acquire prey are broadly distributed (Smith and Bliege Bird 2000, Sosis 2000, Smith et al. 2003). In these settings, sharing may be an indication of the skill, strength, or diligence of the producer and therefore his or her value as an ally or mate (Sosis, 2000, Smith and Bliege Bird 2000, Bliege Bird et al. 2001, Gintis et al 2001). An alternative application of costly signaling theory suggests that generous sharing may serve to signal cooperative intent or group commitment, thus securing social support from others during times of crisis (Gurven et al. 2000a, Sugiyama and Chacon 2000, Sugiyama 2004).

Distance

Distance is not an adaptive explanation for food sharing by itself, but is included in the analysis presented here primarily as a control variable. An increased propensity to share with residentially closer households does not uniquely support any one adaptive hypothesis, but in general, transfers to closer neighbors may be favored for three reasons. First, the transaction costs in time and energy of transferring food from one household to another increase with distance. Second, it is easier to acquire information about the available resources and relative need of closer neighbors than those further away. Third, neighbors interact more frequently and may have a higher probability of future interaction.

A number of studies have found significant distance effects on food-sharing behavior (Betzig and Turke 1986; Gurven et al. 2000a, 2001, 2002, ²⁰⁰⁴; Ziker 2004; Patton 2005; Hames and McCabe 2007; Allen-Arave et al. 2008). However, because people can choose where they live, distance is often correlated with other factors. For example, among the reservation-living Northern Ache (Allen-Arave et al. 2008), distance is correlated with kinship because more closely related families choose to reside near each other. In Conambo, distance has no effect on sharing once wife's kinship and political alliance are controlled for, suggesting residence choices may be guided by these considerations (Patton 2005). Similarly, among the Ye'kwana the distance effect on meal sharing becomes non-significant in a regression with reciprocity (Hames and McCabe 2007). In other societies residential choices are more constrained. For example in Ust'-Avam, Siberia, where government-provided housing was assigned to families as it was constructed, kinship and distance have independent statistical effects (Ziker 2004, Ziker and Schnegg 2005).

Empirical Considerations

One difficulty in testing between adaptive hypotheses for food sharing is that in many cases their predictions overlap. Another is that the hypotheses themselves are not mutually exclusive: it is possible that more than one of these mechanisms may be acting simultaneously in a population and that each may explain some proportion of the total observed variation in food sharing. Because of this human behavioral ecologists have increasingly turned to multivariate statistical methods in an attempt to tease apart the relative contribution of each of these hypotheses in explaining food-sharing behavior. Among the methods that have been applied are multiple linear regression (Gurven et al. 2001, 2002; Patton 2005), path analysis (Gurven et al. 2000b, Gurven 2004a), quadratic assignment procedure (Ziker and Schnegg 2005), and multilevel regression modeling (Allen-Arave et al. 2008).

The analysis of food-sharing data is not as straightforward as one might expect. One complication is that evolutionary hypotheses make predictions about the motivations and behaviors of individuals, but in human societies, families or households are typically the

Another problem is that the common statistical assumption of independence of cases is violated in food-sharing data. Fundamentally, food-sharing data are social network data, where households (or families or hearths) form the nodes of the network and transfers of food between households form the ties. One household's decision to share with another may not be simply a function of the characteristics of the two households, but also whether the target household shares back, or even if the two households have other sharing partners in common. This creates statistical dependence within and between dyads of households. Statistical methods exist that can control for some violations of the independence assumption, but for many food-sharing hypotheses the dependency between dyads is the outcome of interest. For example, when testing for contingent reciprocal exchange or indirect reciprocity it is the *non*-independence of cases in which we are interested.

This paper presents a social network analysis of food sharing relationships between households in the fishing and whaling village of Lamalera, Indonesia. The method used to analyze these data is exponential random graph modeling, or ERGM (Holland and Leinhardt 1981, Wasserman and Pattison 1996, Robins et al. 2007), a statistical method that accommodates the structural dependencies of network data. In the analyses presented here, the focus is on the effects of three dyadic covariates: between-household relatedness, between-household distance, and the presence or absence of return sharing within a dyad. These variables are used to test the relative explanatory power of two common hypotheses for food sharing: kin selection (Hamilton 1964) and reciprocal altruism (Trivers 1971).¹ Two questions are addressed: First, what is the effect of each hypothesis on the *probability* of one household sharing with another, and second, how much of the observed *variation* in food-sharing relationships between households is explained by each of the two hypotheses?

Site Description

Location and Population

Lamalera is a fishing and whaling village located on the south shore of the island of Lembata in the province of Nusa Tenggara Timur, Indonesia. The study population in July 2006 consisted of 1227 individuals residing in 317 separate households, stretched along 1.7 km of steep and rocky coast on either side of the main beach². Administratively Lamalera is divided into two *desa* or villages, Lamalera A and B, which are further divided into *dusun* or wards and *RT* or neighborhoods. Education and employment opportunities outside the village are a main cause of emigration; however, with the exception of a few salaried administrative and teaching jobs in the village, the local population relies on subsistence maritime foraging.

Lamalerans are Lamaholot speakers and share many cultural similarities with the other Lamaholot-speaking peoples of the region. These include patrilineal descent, brideprice, and historically, asymmetric marriage alliance and a dualist cosmology. Today marriage is no

¹The effects of household-level covariates and tests of the costly signaling hypothesis are addressed elsewhere (Nolin, in preparation). ²These numbers exclude three priests and their housekeeper as well as 18 students from other villages housed at the junior high school. Also excluded are the two outlying agricultural *dusun* of Lamamanu and Krokowolor. These are incorporated under the administration of Lamalera A and B, respectively, but are not themselves part of Lamalera historically considered (Barnes 1996).

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longer strictly bound by the alliance system and like most Lamaholot villages Lamalera is now Roman Catholic (Barnes 1996). Patrilineal clans are subdivided into lineages, each associated with its own great house. Historically, postmarital residence was patrilocal, but today is neolocal, a change advocated by resident priests in the mid-Twentieth Century (Barnes 1996). However, a combination of steep and rocky terrain, the saturation of suitable building sites within the village, and usufruct land rights held in common by lineages all place constraints on where a newly married couple may reside. As a result, parents and their adult offspring often reside in separate areas of the village.

Subsistence

From May through September of each year, a season locally called *léfa*, Lamaleran men cooperatively hunt large marine prey. The primary prey species taken are sperm whale³ (*Physeter macrocephalus*) and three species of ray: manta ray (*Mantis birostris*), golden brown ray (*Mobula kuhlii*), and whiptail devil ray (*Mobula diabolus*). Prey are hunted in large traditional boats called *téna* crewed by around 11 men (range: 8 to 16). Each *téna* is owned by a corporation of members primarily from within a single lineage. Opportunistic whale hunts, called *baléo*, also occur when whales are spotted during the off-season. Otherwise, fishing outside of *léfa* consists mainly gillnet fishing for flying fish (*Exocoetus volitans*) from small, two-man boats called *sapã*. There is some *sapã* fishing during *léfa* as well. See Barnes (1996) for a more extensive description of Lamaleran subsistence.

Motor boats (locally called *jonson* after a brand of outboard motor) have become more common in recent years. Motor boats focus on smaller, swifter prey and are not used to hunt sperm whales for fear of losing the expensive outboard motor (Nolin 2008). They are typically crewed by fewer men (mean 8.5, range 2 to 14) than *téna*. Nearly all are owned by a corporation of members organized similarly to a *téna* corporation. In 2006 *téna* and *jonson* were used as part of a mixed foraging strategy, with *téna* being used when whales had been sighted or were expected in the area and *jonson* being used otherwise. The 14 serviceable *téna* (compared to 20 in 1999) accounted for 216 (29.8%) boat-days between May 15 and September 9, 2006. The 15 *jonson* (compared to 2 in 1999) accounted for 509 (70.2%) boat-days during the same period. Both types of boats exhibited high variance in hunting success: 41.3% of *jonson* hunts were successful while only 20.8% of *téna* hunts were successful.⁴

The steep and rocky terrain surrounding Lamalera inhibits cultivation, though many households keep chickens and pigs, and less frequently goats and dogs. To acquire vegetal foods, women from Lamalera trade with women from agricultural communities in the interior of the island. Fish and cetacean meat from Lamalera is traded for staple carbohydrates, mainly bananas (*Musa sp.*), manioc (*Manihot esculenta*), rice (*Oryza sativa*), and maize (*Zea mays*), as well as other fruits and vegetables (Barnes and Barnes 1989). Stocks of maize stored above cooking hearths may be kept for years, and provide the primary source of food during times of famine (Barnes 1996).

³Indonesia is not a signatory to the International Convention on the Regulation of Whaling (IWC 2007), though Lamalera would almost certainly qualify for a subsistence exemption if Indonesia were to sign. Sperm whales are categorized as "vulnerable", the lowest of the "threatened" categories on the IUCN Red List (Taylor et al. 2009). Recent estimates of the global sperm whale population place the number around 360,000 (Whitehead 2003). Lamaleran subsistence whale hunting poses no conservation risk to global sperm whale populations. Other cetacean species hunted in Lamalera are of even lower conservation concern on the IUCN Red List or are currently unclassified.

⁴Sperm whales were rarely seen and none were caught during the study period, though one particularly large specimen was caught just before the study began and cured whale meat was in circulation throughout the study period.

Primary Distributions

Share rights in prey, called *umã*, are allocated according to a complex system of norms based around the roles of share-right holders and the anatomy of the prey species (Alvard 2002). Share-right holders in *téna* come from three main groups: members of the boat-owning corporation, the crewmen who participated in the hunt, and the craftsmen who built the boat and maintain its gear. Shares in *jonson* are allocated similarly, but with special shares allocated to the owner of the outboard motor and the buyer of the fuel. Following Alvard (2002), I refer to this distribution of shares to share-right holders as the primary distribution.

Cooperative hunting and the primary distribution of prey were the focus of field research conducted in 1999. At the primary level of production, Lamaleran subsistence appears consistent with a form of cooperation called synergistic mutualism (Maynard Smith and Szathmary 1995): at least for *téna*, individuals cooperate because their individual per capita return rates are higher from cooperative hunting than from more solitary pursuits like small boat fishing (Alvard and Nolin 2002). This pattern contrasts with other maritime foraging populations where risky subsistence activities are pursued despite the availability of other, higher-return alternatives (Meriam: Bliege Bird and Bird 1997, Bliege Bird et al 2001; Ifaluk: Sosis 2000). Such cases appear more consistent with costly signaling, and in the case of the Meriam are associated with a distribution regime consistent with tolerated theft (Bliege Bird and Bird 1997). In contrast, in Lamalera producers hold property rights to shares of the catch (Alvard 2002) and hunting appears mutualistic (Alvard and Nolin 2002). This pattern appears inconsistent with a tolerated theft/costly signaling explanation for primary distributions, which partially motivates the focus on kin selection and reciprocal altruism taken here. Though signaling may still motivate some between-household sharing, the relationship between status and sharing will be addressed elsewhere (Nolin, in preparation).

As much as these normative institutions defining cooperative groups and property rights help to solve the coordination problems inherent in mutualistic hunting, they do little to reduce the high risk (variance) in hunting success. Most boats come home empty-handed on most days, and many days may elapse between one successful hunt and the next. Lamalerans have a number of mechanisms by which they can insulate themselves from risk. Much fish and cetacean meat can be cured by salting it and drying it in the sun. In the longer term, the protein and fat calories in meat can be converted into carbohydrate calories by trading meat for maize with agricultural groups from the interior of the island. A third way to mitigate risk is through food sharing.

Sharing

Once a household receives its share from a primary distribution, it is taken home where it is further divided into smaller portions. Some portions are hung on the household's drying rack for later consumption or trade. However, some are given away to other households as *běfãnã*, gifts of food from one household to another. Transferred portions of meat or fish vary in size depending on prey species (see Nolin 2009: Table 4.8), but typically provide the meat for a single meal for a household. For example, *běfãnã* from sperm whale consists of one portion of blubber weighing about 0.25 kg and one portion of flesh weighing about 0.15 kg. *Běfãnã* from manta ray typically consists of one portion of flesh weighing about 0.29 kg along with a slightly smaller portion of liver or cartilage. From most prey types, a household will typically give *běfãnã* to three or four other households (Nolin 2008: Table 4.10), or more from sperm whale. Vegetable foods are also shared, albeit with somewhat less frequency.⁵ This is likely because vegetable foods are also asynchronously acquired: one must first have fish to trade and so vegetable food acquisition covaries with fishery successs.

I refer to transfers of food between households as the secondary distribution. Unlike the primary distribution which is governed by a complex system of norms defining property rights, the secondary distribution is entirely discretionary. There are no explicit norms dictating to whom one must give or from what prey type, nor are there formalized reciprocal relationships as are found in some groups (Damas 1972, Weissner 2002). Instead, individuals are free to choose to whom they give *běfãnã*. Sharing decisions are not solely the right of the producer or shareholder: observations of secondary distributions suggest that both husband and wife, as well as other adults residing in the household are involved in sharing decisions.⁶

Methods

Sharing Interviews

Household sharing interviews with all 317 households in the village were conducted from September 12 through December 2, 2006, following the end of the active sea-hunting (*léfa*) season. Most (84%) of the interviews were conducted in the one month period from October 16 through November 16. Any one or more adults resident in the household and present at the time of the interview were allowed to respond. Respondents were asked to name those individuals to whom they had given (and, as a separate question, from whom they had received) *běfãnã* "usually, more than just once" during the preceding *léfa* hunting season. The order in which these questions were asked was alternated from interview to interview. Respondents expressed no reservations in answering these questions openly. Respondents were allowed to nominate as many donors or recipients as they wished, and responses were recorded into an ordinary notebook.⁷

Recall data is prone to memory error (Bernard et al. 1984). Two steps were taken to help mitigate this. First, by asking respondents to whom their household had given (or from whom it had received) "usually, more than just once" the goal was to identify those households that accounted for the most frequent and typical instances of a household's sharing.⁸ Research on informant recall suggests informants are able to recall repeated, long-term patterns of behavior more accurately than specific instances (Freeman et al. 1987). Second, bounding the questions in time over the preceding *léfa* was done to improve response accuracy by restricting recall to a bounded period (Loftus and Marburger 1983). While the resulting data lack the accuracy and resolution of direct behavioral observations, they have the advantage of providing a full census of the network of usual sharing relationships across the entire village. Because all households were asked to report on both giving and receiving relationships, all possible directed sharing relationships were censused twice. The implications of this are discussed below.

Genealogies and Between-Household Relatedness

Genealogies going back at least two generations (i.e. to the grandparental generation), and in many cases further, were collected during household interviews for all residents. These data were supplemented by similar genealogies collected in 1999 and by church parish records.

 $^{^{5}}$ Meat and fish account for 73% of foods transferred by frequency while vegetal foods account for 27%. In addition to direct transfers to other households food is shared in other ways, most commonly by contributing to or participating in communal meals associated with marriage and death rites or boat ceremonies. These modes of sharing occur less frequently and are not addressed here. See Nolin (2008).

^bFor example, both husband's and wife's kinship have independent and positive effects on sharing (Nolin 2008: Table 6.5).

⁷In pretesting, use of preprinted forms was found to bias the number of nominations towards the number of lines printed on the forms. ⁸The preferred method of capturing variation in sharing frequency was to ask respondents to rank the households they named in order of sharing frequency. However, in pretesting this method respondents were reluctant to provide rank-orderings. The common explanation offered was that "people give as they are able" and that how often one received from or gave to others depended primarily on the success of the fishery.

Coefficients of relatedness between all possible pairs of residents were then calculated from these genealogies using Descent, version 0.2.0.2 (Hagen 2005). The resulting coefficients distinguish relatedness at a minimum degree of r = 0.0625 (i.e. those sharing at least one grandparent), and for many dyads the resolution is higher yet.

From these values, several different pooled measures of between-household relatedness were calculated including the mean and maximum degrees of relatedness of all possible dyads formed using members of each household. Additionally, in an attempt to better capture the benefits of sharing on potential recipients (the *b* term in Hamilton's rule), a number of measures incorporating the reproductive value of recipients were constructed. Such measures were found to be *less* predictive than measures using the coefficient of relatedness alone, possibly because reproductive value fails to capture the economic productivity of post-reproductive individuals (Allen-Arave et al. 2008). The most predictive of all measures of between household relatedness, selected by AIC (Akaike 1974), was simply the maximum value of relatedness from either spouse of the donor household to any single member of the recipient household. This is the relatedness measure used here, and in the subsequent discussion, the terms kinship and relatedness refer to this value.

GPS Mapping and Between-Household Distances

Positions of households, paths, and other geographic features in the village were measured using a Garmin eTrex Legend handheld GPS receiver. All GPS positions were recorded in UTM meters, with a mean positional accuracy of ± 7.8 m (s.d. 1.1m), allowing distances between points to be calculated by applying the distance formula to the x-y-z coordinates of the two points. Distances between households located within the same geographically contiguous area of the village (where footpaths are dense) were calculated as straight-line distances. Distances between households in geographically distinct areas of the village were calculated along the paths connecting those areas. Although differences in elevation were included in calculations of between-point distances no attempt was made to account for the additional energetic effort of ascent or descent due to slope on path segments. Distances were denominated in kilometers and rounded to the nearest hundredth (i.e. 10m).

The Sharing Network

The responses from the household food-sharing interviews were used to construct a social network of between-household sharing within the village. The 317 households in Lamalera reported a total of 2412 out-directed (giving) ties, of which 2312 were identified as directed to other households within the village. A total of 2002 in-directed (receiving) ties were reported, of which 1982 were identified as originating from other households within the village.⁹ Ties to or from households outside the village were omitted and only ties among the 317 households in the study population were used to construct the network used here.¹⁰

There were 1183 directed ties confirmed by both members of the dyad, or 51% of reported giving ties and 60% of reported receiving ties. Low levels of agreement or "rate of reciprocation of response" are common in double-sampled network data (primarily due to poor recall, as discussed above) and the levels reported here are within the typical range found in other studies (Marsden 1990, adams and Moody 2007). Suppose some household A reports giving to household B, but B does not report receiving from A. Such discordant reports may occur because A has reported a sharing relationship that does not exist (a false positive), or B has failed to report one that does (a false negative). Discordant reports in the Lamalera sharing network data appear to be primarily due to false negatives rather than false

⁹These totals include 93 giving and 66 receiving ties mistakenly omitted from previous analyses (cf. Nolin 2008:153).

¹⁰Characteristics of out-of-network ties are presented in Nolin 2008, Tables 5.1 and 5.2.

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positives: a simple deterministic model of reporting error (not presented) indicates that the false positive rate cannot exceed even 1% and still produce a pattern of reported ties consistent with the observed data. On the other hand, the false negative rate could be as high as 45% and still produce a pattern of reported ties consistent with the observed data. In other words, respondents were honest but forgetful.

Taking the union of the two sets of responses (both reported giving and reported receiving) minimizes the number of false negatives in the data at the expense of maximizing false positives. Continuing the example above, this method assumes that A correctly reported giving to B, and that B failed to recall the relationship. Because the false negative rate vastly exceeds the false positive rate in this data set, then using the union of all responses will capture more actual ties within dyads, and have fewer overall errors, than using either the set of reported giving ties or reported receiving ties alone.

The analyses presented here thus use a network constructed from the union of the sets of reported giving and reported receiving ties. The resulting network consists of 3111 ties among the 317 households in the village. Ties in this network have the following properties: first, they are *directed*, having a household of origin and a household of destination, reflecting the direction of the reported sharing relationship; and second, they are *binary*, that is a directed sharing relationship is either present or absent. Ties do not reflect frequency or amounts transferred (beyond the stipulation that reported ties reflect "more than one" transfer) and so are best characterized as sharing *relationships*. The mean number of giving relationships per household (outdegree in network terminology) is 9.81 (s.d. 8.26, range 0 - 59); the mean number of receiving relationships (indegree) is 9.81 (s.d.4.48, range 0 - 31).¹¹ Of the 3111 directed ties in the network, 2088 or 67.1% of ties are reciprocated.

The Lamalera sharing network is plotted in Figure 1. The upper panel displays the sharing network geographically. The lower panel displays a Gower plot of the same data, in which households having a similar configuration of ties to other households are plotted more closely together. In both plots, the lighter shapes represent households in Lamalera A and the darker shapes those in Lamalera B. The different shapes represent different wards within each half of the village. Lines between households represent reported sharing relationships. Darker lines represent ties in both directions (reciprocal sharing) between the two households; lighter lines represent unidirectional ties (unreciprocated sharing). For clarity of presentation, arrows indicating the direction of ties are not displayed.

The plotted network in Figure 1 graphically displays the dependent variable of analyses, the pattern of sharing relationships among households in Lamalera. The goal is to assess how well distance, kinship, and reciprocity explain the observed pattern of ties between households. More specifically, the analyses address two questions: (1) What is the effect of each covariate on the probability of sharing between two households? and, (2) What proportion of the total variation in sharing relationships is best explained by each covariate?

Exponential Random Graph Modeling

Exponential Random Graph Modeling, or ERGM, is a statistical method for modeling the generative processes that produce social networks (Holland and Leinhardt 1981, Wasserman and Pattison 1996, Robins et al. 2007). In ERGM, the log-odds of a tie from one node to another in a graph (i.e. network) are modeled using a general exponential form analogous to logistic regression (Goodreau et al. 2008, Hunter et al. 2008). Ties can be modeled as a function of node and edge covariates. Additionally, ERGM differs from other methods of

¹¹Since every giving relationship is also a receiving relationship, mean outdegree and indegree must by definition be equal. Both are calculated as total ties divided by total households, or 3111/317 = 9.81.

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network regression principally in its ability to model structural elements of the network as covariates as well. This is done using Markov-chain Monte Carlo methods to estimate the probability distribution of the structural feature of interest from a sample of networks having the same number of nodes as the observed network. With the resulting information, log-odds coefficients can be estimated using maximum likelihood methods (Wasserman and Pattison 1996).The chief disadvantage of ERGM is that dependent-variable networks can consist only of binary ties.¹²

ERGM coefficients are interpreted in the same manner as logistic regression coefficients. Each coefficient represents the change in the log-odds of a tie due to a unit change in the corresponding covariate, all else being equal (Robins et al. 2007, Goodreau et al. 2008). The resulting log-odds coefficients are scaled to the underlying units of measurement of each covariate, making direct comparison of coefficients across covariates difficult. Additionally, log-odds are not themselves intuitive units to think about. As in logistic regression, converting log-odds to probabilities or odds ratios makes them easier to interpret and compare.

Results

The analyses presented here were performed using the statnet¹³ (Handcock et al. 2003, 2008) suite of packages for the statistical programming language R (R Development Core Team 2007). The dependent variable in these analyses is the network of directed sharing relationships among the n = 317 households in Lamalera, as plotted in Figure 1. The independent variables consist of the $n \times n$ matrices of between-household relatedness and distance, and *mutuality*, a structural property of a directed binary network indicating the presence or absence of reciprocal ties within a dyad.¹⁴ The sharing network was modeled as a function of each of these covariates individually, in pairwise combinations, and with all three covariates together. Models containing the mutuality term required MCMC estimation, as described above.

Table 1 presents the resulting model coefficients for the ERGM models. The first column provides a label indicating the terms included in the model. The subsequent columns contain the estimated coefficients (in bold) and standard errors of the estimates (in parentheses) for the covariates included in each model. Coefficients are expressed in log-odds. All of the reported coefficients were significant at p < 0.0001. Because the coefficients are sensitive to the underlying units of measurement it is not possible to compare the magnitude of the coefficients across columns. However, coefficients for the same covariate can be compared within a column to explore the effects of adding or removing other covariates from the models.

Edges (Intercept)

The edges term in an exponential random graph model is simply an intercept term controlling for the density of the network. In the current network the density (the number of observed ties divided by the number of possible ties) is 3111 / 100172 = 0.0311. To illustrate the interpretation of the term, taking the expit $(e^{x\beta} / (1 + e^{x\beta}))$ of the edges coefficient from the model containing only the edges term (Table 1, Model E) returns a

¹²Networks composed of valued ties can be binarized for use with ERGM, but this entails a loss of statistical information.
¹³A special volume on statnet of the Journal of Statistical Software (Volume 24, 2008) provides an excellent introduction for the interested user.

¹⁴*Mutuality*, indicating reciprocity in binary directed networks (Wasserman and Faust 1994), should not be confused with *mutualism*, a mode of cooperation itself plagued by a confusing proliferation of definitions (Brown 1983, Maynard Smith 1983, Conner 1986, Maynard Smith and Szathmary 1995). The similarity of the two terms in this context is unfortunate.

probability of a tie equal to the density of the network: $e^{-3.440} / (1 + e^{-3.440}) = 0.0311$. As in logistic regression, when additional terms are added to the model, the "edges" or intercept term reflects the baseline log-odds of a tie when the values of the other covariates are set to zero.

Distance

Distance has a significant effect on the probability of a sharing relationship between two households (Table 1, Model ED). Increasing the distance between two households by 1 km decreases the log-odds of a sharing tie between them by -6.233. More intuitively, odds ratios (OR) can be calculated to compare cases. For example, the odds of a food-giving relationship to a household 100m away is twelve times the odds for a household 500m away (OR = $e^{(-6.233*0.1 - -6.233*0.5)} = 12.1$).

Kinship

A unit increase in between-household relatedness results in a 9.612 increase in the log-odds of a tie (Table 1, Model EK). However, since *r* ordinarily ranges from 0 to 0.5, a "unit increase" in relatedness makes little sense. For comparison, the odds of sharing with a sibling are 37 times the odds of sharing with a first cousin (OR = $e^{(9.612*0.5 - 9.612*0.125)} =$ 36.8), and 122 times the odds of sharing with an unrelated individual (OR = $e^{(9.612*0.5 - 9.612*0)} = 122.2$)

Mutuality

The mutuality coefficient represents the increase in the log-odds of a sharing tie from household A to household B, given the presence of a reciprocal tie from B to A. Mutuality (Table 1, Model EM) is a significant and strong predictor of the log-odds of a sharing relationship between two households. The odds of a tie from A to B are an impressive 192 times greater when there is a return sharing relationship from B to A than when a return sharing relationship is absent (OR = $e^{(5.258*1-5.258*0)} = 192.1$).

Pairwise Models

Models EDK, EDM, EKM in Table 1 present the resulting coefficients from models including each pair of covariates. When both kinship and distance are entered into the model together (Model EKD) there is little change in the magnitude of the coefficients (kinship: 9.612 vs. 9.604; distance: -6.233 vs. -5.808), suggesting their effects are relatively independent of each other.¹⁵ However, introducing mutuality into a model with either distance or kinship results in a modest reduction in the size of the mutuality coefficient (5.258 vs. 4.571 or 4.838) but substantial changes in the distance (-6.233 vs. -4.061) and kinship (9.612 vs. 5.712) log-odds coefficients. This suggests a correlation between mutuality and both distance and kinship. Specifically, it suggests mutual ties are more common between geographically and genealogically closer households.

Full Model

Figure 2 plots the estimated probability of a food-giving relationship to another household calculated for varying values of distance, kinship, and the presence or absence of mutuality using the coefficients estimated by the full model (Table 1, Model EDKM). Distance between households increases from 0 km to 1 km in 100m intervals along the *x*-axis. The probability of a sharing tie between two households is reported on the *y*-axis. The three solid lines in the upper portion of the figure represent cases where mutuality is present (i.e. the

 $^{^{15}}$ The matrix Pearson correlation between kinship and distance is -0.075.

probability of a tie from A to B, given the presence of a reciprocal tie directed from B to A). The three dashed lines at the bottom represent cases where mutuality is absent. The pairs of lines marked with squares, circles, and triangles represent levels of kinship of r = 0.5, r = 0.25, and r = 0, respectively.

This figure provides a visually intuitive means of comparing the effects of different covariates in the full model. For example, the estimated probability of having a food-giving relationship to an unrelated household located 500m away when that household reciprocates the sharing relationship (the solid line marked with triangles, at 0.5 km) is about 0.24. This is 44 times greater than the estimated probability of sharing with an unrelated household at the same distance when mutuality is absent (the dashed line marked with triangles, at 0.5 km).

Figure 2 demonstrates how the probability of sharing declines with distance. By comparing across curves, the effect of distance on the probability of sharing can be compared for different combinations of relatedness and mutuality. For example, the estimated probability of sharing with a reciprocating nephew living 700m (solid line marked with circles, distance 0.7 km) is about the same as that for a reciprocating stranger living 300m away (solid line marked with triangles, distance 0.3 km).

Kinship clearly has a strong effect on the probability of sharing. Increasing the degree of relatedness to the recipient household substantially increases the probability of a sharing relationship. For example, when mutuality is absent, the probability of sharing with a residentially adjacent non-relative is about p = 0.04 compared to about p = 0.16 when r = 0.25, and p = 0.47 when r = 0.5. When mutuality is present, the probability of sharing with an adjacent non-relative is about p = 0.70 compared to about p = 0.92 when r = 0.25, and p = 0.98 when r = 0.5.

The presence of mutuality has an even more pronounced effect on the probability of a sharing relationship than kinship. For comparison, an increase in relatedness from 0 to 0.5 has the effect of increasing the probability of sharing with an adjacent neighbor when mutuality is absent from 0.04 to 0.47 whereas introducing mutuality into the relationship while keeping the households unrelated increases the probability from 0.04 to 0.70.

Comparison of Models and Deviance Explained

The discussion up to this point has focused on the first question: What are the effects of individual covariates on the probability of sharing between households? Let us now turn to the second question: How much of the total variation in the distribution of ties among households in the network can be explained by each covariate?

Table 2 presents goodness-of-fit statistics for the ERGM models presented in Table 1. The first column provides the model labels. The second column gives the AIC values for each model. Note that this is simply the residual deviance (column 5) plus twice the number of model parameters (which can be inferred from the model labels in column 1). A lower AIC value indicates better model fit. The general pattern among AIC scores shows that inclusion of mutuality into the model greatly improves model fit while inclusion of kinship and/or distance has a more modest effect. The full model shows the best fit to the observed data. All pairwise comparisons of nested models show significant differences between models (log-liklihood ratio tests; results not presented).

In models in which coefficients are estimated using maximum likelihood estimation, the deviance can be interpreted in the same way as the sums of squares in an ANOVA (DeMaris 1992). The total deviance in the null model is 138,868, analogous to the total sum of squares

(TSS) in an ANOVA. The third column of the table gives the total deviance explained (analogous to the estimated sum of squares or ESS), and the fifth column gives the model residual deviance (analogous to the residual sum of squares or RSS).

These values can be used to calculate the total deviance explained by each model (DeMaris 1992, Pampel 2000). The fourth column expresses the deviance explained by the model as a proportion of the total (null) deviance, a pseudo- R^2 statistic (Hagle and Mitchell 1992). However, note that the first model with just the intercept or "edges" term alone explains 80% of the total deviance (Model E, column 4). This represents the proportion of total deviance explained simply knowing the density of the network (or, equivalently, the random probability of a tie) differs from 0.5, and is uninformative with regard to the hypotheses considered here. To compare the predictive strength of each covariate, it is more informative to treat the residual deviance from this intercept model as a baseline and calculate the proportion of the residual deviance from this model explained by each subsequent model. These proportions are given in the last column of the table and are interpreted as the percentage of residual deviance explained by each model, *controlling for the density of the network*.

Distance and kinship both explain similar amounts of the density-controlled residual deviance, explaining 18.2% and 15.9% respectively. When both are included together (Model EDK) these effects are nearly additive: together they explain 30.9% of the density-controlled residual deviance. This suggests that the effects of distance and kinship are relatively independent of each other. Mutuality has a much stronger effect, explaining 44.9% (Model EM). Combining mutuality with distance or kinship produces only modest improvements in the model, explaining 48.6% (Model EDM) and 47.2% (Model EKM) of the density-controlled residual deviance. The predictive effects of distance or kinship are not additive with mutuality in the same way that they are with each other. This reflects a correlation between mutuality and both distance and kinship, as discussed above. All three covariates together (Model EDKM) explain 51.8% of the density-controlled residual deviance.

Discussion

Reciprocal Altruism

It is tempting to conclude that these results show strong evidence of reciprocity, however such a conclusion must be made cautiously. While an absence of mutuality in the network would conclusively rule out reciprocal altruism as a motivation for food-sharing in Lamalera, its presence could be consistent with other hypotheses (de Waal and Luttrell 1988). Any tendency towards positive assortment resulting from symmetrical preferences within a dyad (such as a propensity to share with kin or to scrounge shares from residentially close neighbors) could potentially produce patterns of mutual ties in a network.

Other arguments suggest that intentional reciprocity accounts for the mutuality effect observed here. In networks simulated from the observed data, using only the estimated propensity to share with residentially and genetically close households (and not mutuality) to generate simulated ties between households, mutuality by itself explains an average of 7.1% (s.d. 1.3%) of the density-controlled residual deviance in the simulated networks.¹⁶ However, when combined with distance and kinship, mutuality explains on average only 0.1% more than the amount explained by distance and kinship in the absence of a mutuality term. In other words, while distance and kinship can produce modest amounts of apparent

¹⁶One hundred networks were simulated using the coefficients from Table 2, Model EDK. ERGM models were then estimated on each of the simulated networks and their results averaged to produce the density-controlled residual deviance estimates reported.

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mutuality in a simulated network, once the generative effects of distance and kinship are accounted for the apparent mutuality effect disappears. Furthermore, in the observed Lamalera sharing network, mutuality individually explains *more* variation that either kinship or distance explains individually. Artifactual mutuality produced by symmetrical kinship or proximity preferences simply cannot explain the magnitude of the mutuality effect observed in the network. The most parsimonious explanation is that mutuality in the Lamalera sharing network reflects deliberate reciprocity among households.

Kin Selection

Kinship greatly increases the probability of a food-sharing relationship from one household to another, but explains only moderate amounts of variation in the sharing network as a whole. This may be because kin are relatively sparse in the village: only 4.1% of household dyads are related as closely as first cousins or better. Furthermore, when combined with mutuality, kinship explains very little (2.3%) additional variation beyond that explained by mutuality alone, reflecting a preference for mutual exchange with close kin. Other studies have reported a similar preference. Among the reservation Ache, individuals do not preferentially give to kin based on recipient "need" (as would be predicted by kin selection) but instead show a strong preference for reciprocal exchange with kin, and when an interaction term between kinship and contingent exchange is included, kinship loses its independent predictive power (Allen-Arave et al. 2008). Ziker and Schnegg (2005) similarly report a propensity towards reciprocal meal sharing among closer kin in Ust'-Avam, albeit with frequent asymmetric transfers to kin as well.

Is food sharing in Lamalera motivated in part by kin selection; that is, is sharing motivated by the inclusive fitness benefits of giving to kin in need, independently of the expectation of future reciprocation? Need has not been considered in the analysis presented here, largely because of the difficulty of constructing a long-term estimate of household need encompassing the entire active hunting season. While a recipient's need at the time of any given transfer may be greater than that of the donor, when averaged over the course of the four-month hunting season, the donor's and recipient's access to resources may appear similar. However, if kin were more tolerant of non-reciprocation by kin than non-kin, as predicted by inclusive fitness theory, then we might expect to find a greater proportion of unreciprocated ties among kin than non-kin. In fact, the opposite is true in the Lamalera sharing network: as the degree of relatedness between households increases, so does the proportion of mutual ties, increasing from 62.2% of ties between households related by r<0.125, to 79.6% of ties between households related by r=0.5.

Interpreting a similar pattern among the reservation Ache, Allen-Arave et al (2008) conclude that, while reciprocal altruism provides the "adaptive function" promoting food sharing, kin tend to have qualities valued in reciprocal exchange partners, resulting in the observed preference for reciprocal exchange among kin. A similar pattern seems to hold in Lamalera. An important distinction here is between the adaptive mechanism motivating the cooperative behavior and the adaptive mechanism of *partner choice*. As discussed in the biological markets literature, partner choice in cooperative contexts poses interesting adaptive problems of its own (Noë 2001). If potential cooperative partners vary in traits that affect their attractiveness as partners, then natural selection may produce adaptive preferences for better partners (Noë and Hammerstein 1994, 1995). Thus it may be that while reciprocal altruism provides the main adaptive mechanism promoting food sharing in Lamalera, kin selection is primarily important as a force shaping partner choice.

Distance

Distance is also a significant predictor of food-sharing relationships in Lamalera. As discussed earlier, while previous studies have found distance effects on food sharing, these are often confounded with other variables, notably kinship, because people may choose to reside near close relatives. In Lamalera, suitable residential sites are limited by the steep and rocky terrain, usufruct rights in land, and saturation of preferable sites. Though people might wish to live closer to their kin they are frequently not be able to do so. Thus, kinship and distance are relatively independent predictors of food sharing in Lamalera. The scale of the village may also be an important factor: in smaller communities there is less variation in between-household distances than that seen in Lamalera.

Like kinship, distance explains little (3.7%) additional variance in sharing relationships beyond that explained by mutuality, reflecting a tendency to engage in mutual exchange with residentially close neighbors. This suggests that residential distance, like kinship, may be an important partner-choice criterion. Close neighbors may be preferred sharing partners because the transaction costs of exchanges are low, because the resources and need of neighbors is easier to monitor, and because neighbors interact more frequently.

Conclusions

The data presented here suffer from a number of shortcomings. Foremost, they are based on informants' self-reports of past sharing behavior, and like all recall data are subject to significant memory error. As discussed, this source of error was partially mitigated by combining donors' and recipients' responses, but there are undoubtedly sharing relationships that *neither* party reported and which are consequently not represented in the network. Nonetheless, relying on informant recall was necessary in order to obtain a full census of the village-wide sharing network, representing a trade-off between accuracy and completeness.

A related problem is the dichotomization of the underlying continuous variable. This necessarily results in a loss of statistical information and a reduction in power of statistical tests. Informants were asked to report only those sharing relationships represented by more than one transfer during the study period. The exclusion of "singleton" transfers might inflate the observed level of reciprocity if such transfers are less frequently reciprocated. Similarly, higher resolution data on frequencies or amounts transferred might strengthen the statistical relationships observed here.

The focus on the single currency of food is another problem. People reciprocate aid received in a number of forms besides food, including labor, social support, and other materials goods. Limiting the focus to the single currency of food likely underestimates the degree to which sharing is reciprocated. It may also miss important types of aid (such as allocare) that are primarily directed towards kin. Expanding studies of cooperation to include multiple currencies is an important direction for future research.

How representative are the sharing relationships reported here of long-term behavior? The active hunting season represents the most productive season of the year, and since most between-household food sharing occurs immediately following primary distributions, most between-household sharing likely occurs during this period. How sharing changes during the remainder of the year remains an unanswered and interesting question. It is also unclear how representative the 2006 hunting season was of other hunting seasons. Had one or more whales been caught, sharing patterns might have differed.

In Lamalera, kinship, proximity, and mutuality (reciprocity) all have a positive effect on the probability of a sharing relationship from one household to another. Mutuality has a greater

effect than either distance or kinship and explains more of the total variation. Kinship and distance interact strongly with mutuality, reflecting a tendency towards mutual exchange with closer kin. Controlling for network density, kinship, mutuality, and distance together explain about half of the variation observed in the Lamalera food sharing network. Reciprocal altruism is well supported as an explanation for Lamaleran food sharing, but kinship and distance explain little additional variation beyond that explained by mutuality. Kinship and distance instead appear to act as *partner choice* mechanisms, shaping adaptive preferences for reciprocal partners.

It has not been the purpose of the analysis presented here to address the ongoing debate about the adaptive significance of men's hunting effort. However, a few points on this topic deserve mention. At both the primary and secondary levels of distribution, producers have recognized property rights in food, suggesting that tolerated scrounging is a poor adaptive explanation for most food transfers in Lamalera. Furthermore, both husbands and wives participate in household sharing decisions, and are able to preferentially direct shares towards kin and those who reciprocate. This suggests a greater concern for household and kin provisioning than for men's status. While costly signaling may still explain some sharing in Lamalera (Nolin, in preparation), the findings presented here appear inconsistent with a signaling explanation for men's foraging effort.

One final question that might be asked about Lamalera is, why share at all? Other mechanisms for managing risk in food stocks exist in Lamalera. In the medium term (weeks or months) meat and fish can be cured and stored for later consumption. In the long term, fish and meat can be traded for maize, which can be stored for years. One reason might be a preference for fresh over cured meat. This might occur if the future value of cured meat were sufficiently discounted because of nutritional degradation due to spoilage, or the possibility of loss to vermin. It might also be that the macronutrients present in meat are more highly valued than the carbohydrate calories of vegetable foods.

However, food sharing is not just about risk reduction. For example, the Huaorani share meat even though it can be sold for cash (Franzen and Eaves 2007). Hiwi women sometimes exchange prepared roots foraged together on the same day (Gurven et al. 2000b). Gurven (2004a) reports other ethnographic examples of apparently symbolic sharing. Instead of reducing variance, some sharing may act as a signal of commitment to the exchange relationship (Roberts 1998, Gintis et al. 2001) or to the group (Gurven et al. 2000a). In Lamalera, with its economic dependence on cooperative subsistence, some food sharing may function as an affirmation of relationships of mutual aid that go far beyond the exchange of food.

Acknowledgments

Many thanks to the residents of Lamalera, Indonesia for their patience, help, and hospitality, especially to my hosts, Y.B. Blikololong and family. I thank Michael Alvard, Steven Goodreau, Darryl Holman, Donna Leonetti, and Eric Smith for comments on earlier drafts of this manuscript, and Wesley Allen-Arave, Michael Gurven, Hillard Kaplan, Jeremy Koster, Paul Leslie, and Mary Shenk for insightful discussions on this topic. Field research was conducted under the auspices of the Indonesian Institute of Sciences (LIPI), with the cooperation of research counterpart Dedi Adhuri. Field research was funded by a National Science Foundation Dissertation Improvement Award (BCS-0514559). Postdoctoral research supported by a *Eunice Kennedy Shriver* National Institute of Child Health and Human Development Population Training Award (5 T32 HD007168) t the Carolina Population Center, University of North Carolina, Chapel Hill.

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Figure 1. Plots of the Lamaleran Food-Sharing Network

Upper panel: Households plotted in geographic space. Lower panel: Gower plot (households with similar constellations of ties to other hosueholds are plotted closer together.) Light and dark colors represent households in Lamalera A and B, respectively. Different shapes represent different wards within each half of the village. Darker lines represent reciprocal sharing relationships between households; lighter lines represent uni-directional sharing, with arrows indicating direction removed for clarity. Positions of individual households in the upper panel have been altered slightly to preserve anonymity of responses.

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	0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1 Distance (km)

Figure 2.

Probability of a sharing relationship (y-axis) from one household to another by distance (x-axis), between-household relatedness (r), and presence (t) or absence (f) of mutuality (m).

Table 1

Exponential random graph model estimated log-odds coefficients.

		Coef	ficients ^a	
Model ^b	Edges	Distance	Kinship	Mutuality
Е	-3.440 (0.182)			
ED	-1.587 (0.029)	-6.233 (0.135)		
EK	-3.845 (0.022)		9.612 (0.143)	
EM	-4.543 (0.023)			5.258 (0.051)
EDK	-2.077 (0.033)	-5.808 (0.136)	9.604 (0.178)	
EDM	-3.117 (0.023)	-4.061 (0.108)		4.571 (0.014)
EKM	-4.635 (0.018)		5.712 (0.113)	4.838 (0.015)
EDKM	-3.200 (0.025)	-4.007 (0.110)	6.127 (0.056)	4.056 (0.016)

 a Upper values in bold are coefficient estimates; lower values in parentheses are standard errors. Models including the mutuality term include an additional MCMC s.e. of 0.002 or less on all coefficients. All coefficients significant at p < 0.0001.

 b Model terms: E = Edges (intercept), D = distance, K = kinship, M = mutuality. Models run in statnet (Handcock et al. 2003, 2008).

 C Models including the Mutuality term used the following MCMC settings: burnin= 20,000, interval=2500, MCMCsamplesize = 100,000, maxit=20, steplength=0.25.

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Model ^a	AIC	Deviance Explained	Deviance Explained ^b	Kesidual Deviance	% RDE ^c
ш	27,729	111,141	80.0%	27,727	
ED	22,690	116,182	83.7%	22,686	18.2%
EK	23,314	115,558	83.2%	23,310	15.9%
EM	15,294	123,577	89.0%	15,290	44.9%
EDK	19,152	119,721	86.2%	19,146	30.9%
EDM	14,254	124,620	89.7%	14,248	48.6%
EKM	14,632	124,242	89.5%	14,626	47.2%
EDKM	13,378	125,498	90.4%	13,370	51.8%

b Deviance explained by the model divided by the total (null) deviance (138,868).

^c Percent of Residual Deviance Explained: Percentage of residual deviance from model E explained by the model, i.e. (27,727 – Residual Deviance) / 27,727.