Reproductive Interests and Forager Mobility

Douglas H. MacDonald; Barry S. Hewlett

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Guided by life-history theory, we examine the contexts in which reproductive interests (e.g., attracting and keeping a spouse) shape forager mobility. Using quantitative intercultural and intracultural mating distance data, we report significant correlations between mating distance and population density not only among foragers but also among farmers. Further, in all of the cultures for which we could find data males on average traveled considerably farther than females in a lifetime, and among Aka foragers of Central Africa age and sex significantly impacted distances traveled. We propose a descriptive model of forager mobility that supplements existing subsistence-focused models by incorporating reproductive interests at all levels.

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The present paper was submitted 2 IX 98 and accepted 4 IX 98; the final version reached the Editor's office 24 IX 98.

Most anthropological studies of hunter-gatherer mobility emphasize the impact of the distribution of natural resources on the frequency and distance of camp movement. This focus is driven, in part, by the nature of hunter-gatherer archaeology (e.g., Binford 1980, 1983; Flannery 1986; Kelly 1983); mobility related to subsistence and residence movement is clearly visible in the archaeological record (e.g., in nonlocal lithic raw materials at bison kill sites [Wilmsen 1974:114]), whereas mobility related to reproductive concerns has no clear archaeological signature. Ethnographers also stress subsistence and residential travel in their research by recording group camp movements rather than the travel of individual foragers. This lack of attention to how reproductive interests influence hunter-gatherer mobility is exemplified in Kelly's (1995) recent state-of-the-art survey of hunter-gatherer lifeways, which takes an explicitly evolutionary ecological approach and devotes entire chapters to mobility and reproduction but does not discuss how the two may be related. Existing studies of forager mobility are valuable, and it is not our intent to dismiss subsistence concerns in favor of reproductive ones. Our study supplements the subsistence mobility data with quantitative data on how reproductive interests influence forager mobility.

Models of Hunter-Gatherer Mobility

We are not the first to point out the importance of reproductive interests for understanding forager mobility. Wobst (1974:166–67), Jochim (1976), Hassan (1981:150), Gaulin and Hoffman (1988:132), and Mandryk (1993:45) have hypothesized, modeled, or at least mentioned the importance of the search for marriage partners for establishing territories or identifying regional bands. However, they depend on anecdotal evidence and/or simulation models rather than quantitative field data to evaluate their hypotheses. While few data exist on the distances foragers travel seeking mates, most territorial models at least mention how mating might influence mobility.

Figure 1 summarizes three frequently cited forager territoriality/mobility models. Binford (1983:34–42) discusses Nunamiut mobility as having four levels: (*a*) foraging radius, (*b*) annual range, (*c*) extended range, and (*d*) lifetime range (fig. 1, *a*). The foraging radius includes the area used during daily subsistence, while the annual range is the region used during a year for logistic (subsistence) and residential purposes. Beyond that, the extended range is a no-man's-land that is used as a resource supply by new groups or by groups extending their annual ranges. Finally, the lifetime range is the region "over which they can expect to live during their lifetime" (p. 39). In this model the prime mover is resource distribution, but reproductive interests play a role, especially in movement into the lifetime range. As Binford explains, the boy, usually accompanied by an older relative, travels in order to learn the country in which he will spend his adulthood; however, he also
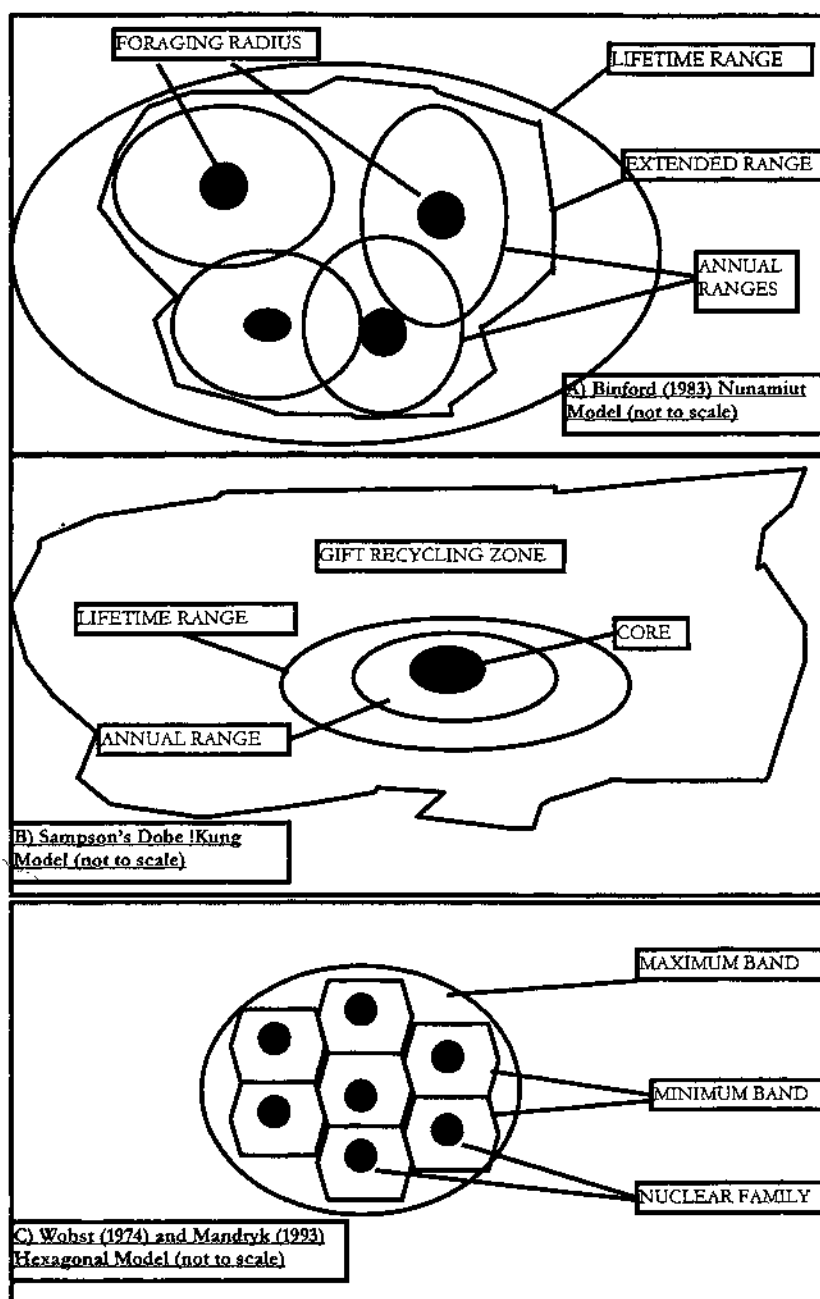
FIG. 1. *Three models of forager mobility.*

visits the camps of unwed girls, and those girls view him as being in their "courting country" (p. 39).

Sampson's (1988) concentric-zone model of !Kung San territoriality (fig. 1, *b*) identifies four major zones of movement used by individuals: (*a*) core range (daily subsistence), (*b*) annual range (annual subsistence territory), (*c*) lifetime range (greatest distance traveled in a lifetime), and (*d*) gift recycling zone (beyond individual travel realm but infiltrated by down-the-line trading). Here as in Binford's model, movement between zones is regulated by responses to resource availability. The potential role of reproductive interests is not discussed for any of the ranges.

Paleolithic settlement and mating systems have been the focus of discussion regarding minimum and maximum hunter-gatherer band sizes (Wobst 1974, Mandryk 1993). In these models, reproductive interests play a vital role in establishing the size and geographic packing of local and regional populations. Wobst (1974:173) proposes that Paleolithic hunter-gatherers utilized "three cultural units of predictable and consistent membership" (fig. 1, *c*): (*a*) the maximum band (175–475 peo-

ple), (b) the minimum band (25 people), and (c) the nuclear family. Within these cultural units, 25 and 175–475 are sometimes referred to as "magic" numbers (Wobst 1974:170; Lee and DeVore 1968:245–48). The minimum band size is large enough to support reliable cultural transmission between generations and to perform "the daily activities required for the group's survival ... through mutual food sharing and cooperation" (Wobst 1974:172). Thus it is regulated by subsistence concerns. In addition, however, it is large enough to survive fluctuations in life histories of individuals—implying the importance of reproductive interests. The maximum band size is a function of the number of individuals needed for an effective mating pool (Wobst 1974:166–67) and the geographic packing of such bands within a given region.

Mandryk (1993) takes Wobst's hypotheses one step farther. In her model, resource availability controls population density (Birdsell 1953), which in turn controls range size (pp. 46–47). Thus, the extent of mobility for both reproductive and subsistence concerns is a by-product of environmental productivity; the more "submarginal" the environment, the larger the ranges of individuals within populations. But access to subsistence resources as opposed to reproductive resources is the driving force (pp. 41–42). While Wobst's and Mandryk's models provide insight into the nature of hunter-gatherer territoriality as it relates to the reproductive viability of a given population, they do not test their models with quantitative field data.

Overall, the forager-mobility literature tends to focus on subsistence concerns and decisions. When reproductive interests are mentioned as playing a role, there is no explicit quantitative evaluation of that role. Reproductive interests are hypothesized to influence long-distance mobility only, and group/camp movement is emphasized. While these studies are extremely valuable, there is a need for systematic research on how reproductive interests influence forager travel.

Life-history theory prompted us to evaluate field data on forager mobility in alternative ways. One commonly employed life-history model (Hirshfield and Tinkle 1975) identifies two conceptually distinct categories of effort—somatic and reproductive—that are critical to individuals' biological success (see fig. 2). Somatic effort refers to ensuring one's physical survival—securing shelter and protection from predators and conspecifics, obtaining food, staying healthy, and so forth. Reproductive effort has to do with getting copies of one's self into subsequent generations. It is divided into three broad categories—mating effort (attracting, keeping, and guarding a spouse), parental effort (rearing children), and nepotistic effort (helping relatives besides one's own children). This paper focuses on the first of these. Life-history theory has experienced dramatic growth and elaboration in anthropology in the past few years (Hill and Hurtado 1996). The following basic components are important for this study: (1) a focus on the individual, (2) concern with reproductive as well as somatic effort,

and (3) the idea of trade-offs between costs and benefits for different activities.

Methods

Biological anthropologists and geneticists interested in microevolutionary processes use various terms—among them "matrimonial distance" (Yasuda 1975:85), "individual migration" (Wijsman and Cavalli-Sforza 1984:280), "parental distance" (Harpending 1976:161), "marriage distance" (Basu 1973:376; Boyce, Kuchemann, and Harrison 1967:335; Fix 1974:327), and "mating range or distance" (Cavalli-Sforza and Hewlett 1982:257)—to refer to the average distance between birthplaces for the couples interviewed in a given group. We adopt the term "mating distance" and use cross-cultural data on it to examine differences in mobility for reproductive purposes. We acknowledge that mating distance is only a proxy measure; individuals, especially foragers, travel extensively and by marrying age are unlikely to be living in the precise locations of their birth. Future research may provide more precise measures.

In order to accumulate comparative cross-cultural data on mating distance, we conducted a literature search and contacted ethnographers of foragers to request use of unpublished mating-distance data. The literature search yielded quantitative data on four hunter-gatherer groups, including the Aka (Cavalli-Sforza and Hewlett 1982:267), the !Kung (Harpending 1976:161), the Kiunga (Serjeantson 1975:403), and the G//ana (Cashdan 1984:459).

Qualitative data were located for the Nez Perce (Anastasio 1972:151), the Umatilla (Anastasio 1972:151), and the Anbarra (Australian coastal Aborigines) (White et al. 1990:177). For the Nez Perce and the Umatilla, Anastasio (1972:151) provides qualitative estimations for the frequency of marriages ("many," "some," and "few") between individuals of differing cultures. In order to compare these data with our quantitative data, we arbitrarily established a value for number of marriages for each of these relative terms (10 for "many", 5 for "some," and 1 for "few") and calculated the numbers of marriages across cultures on the basis of Anastasio's frequency estimates. We then calculated the distances between the edges of each culture's known territory. In order to account for the high frequency of intracultural marriages, we factored in 50 marriages with distances of 10 km. The mean mating distance was calculated by summing the distance between territories of the spouses in each couple and then dividing by the total number of marriages. The Anbarra mating distance is a relative value based on a statement that over 90% of mating distances were under 15 kilometers (White et al. 1990:177). Given this data manipulation, we do not include these groups in our statistical analyses. Future archival research may shed light on the accuracy of these qualitative mating-distance estimations.
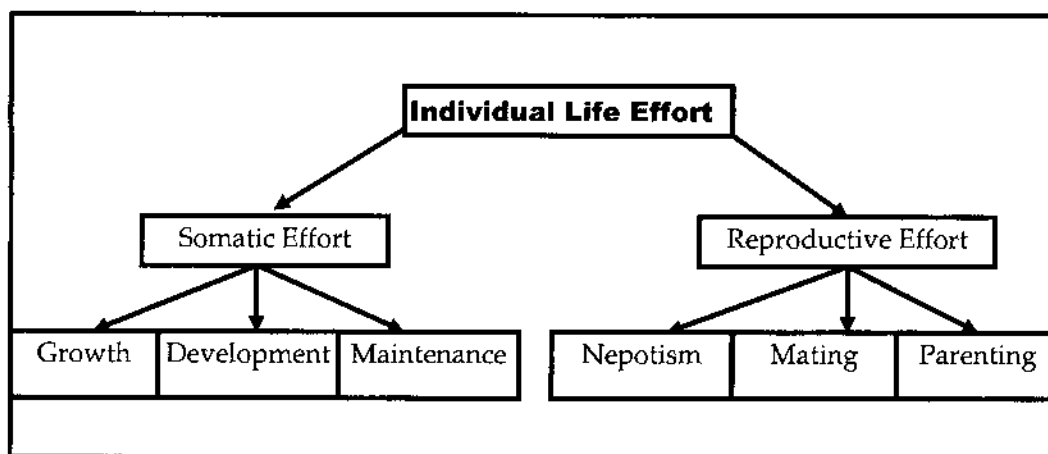
FIG. 2. *Components of life-history theory.*

The search for data from contemporary ethnographers generated one other excellent forager case study, that of Thomas and Janet Headland on the Agta. In order to determine if forager mobility is distinct from the mobiltiy of other socioeconomic groups, mating distances for six semisedentary horticultural groups and one agro-pastoralist group (Monique Borgerhoff Mulder, personal communication, 1997) were located and included in the sample.

In order to examine intracultural variability in mobility, we utilized detailed data from four groups: Aka (data collected by Hewlett), Agta (Thomas and Janet Headland, personal communication, 1997), !Kung (Harpending 1976), and Yanomamo (Biella, Chagnon, and Seaman 1997).

The Aka mobility data consisted of mating distances on 55 couples and exploration ranges for 109 individuals. Members of a sample of 41 Aka males, representing 20% of the adult Aka males living near Bagandou in the Lobaye region of the Central African Republic, were asked if they had been to each of 43 places. In addition, 68 Aka, representing 42% of the adult and adolescent Aka forager population in Ndele in the Haute Sangha region of the Central African Republic (about 200 km west of Bagandou), were asked if they had been to each of 70 places. Each respondent was also asked the frequency of visits to each place and the reasons for those visits. For each individual we calculated a mean exploration range based on the distances traveled to the various locations.

The Agta data consisted of mating distances for 806 couples calculated from the Headlands' unpublished data.

For the !Kung we used Harpending's (1976:161) data on mating distance for 358 !Kung couples in northwestern Botswana. These respondents included foragers, pastoralists, farmers, and laborers, but Harpending (pp. 154–55) states that of a census of 1,200 !Kung individuals approximately 900 subsisted entirely or mostly on hunted and gathered foods. For this reason, we identify the !Kung in this sample as hunter-gatherers.

In the case of the Yanomamo, Chagnon's (Biella, Chagnon, and Seaman 1997) 1971 census of 267 individuals provided raw data with which to calculate mating distance. We identified mother's and father's birthplaces for 46 couples and then used maps from Chagnon's CD-ROM and his Yanomamo ethnography (1992) to calculate mating distances for those couples.

Results

INTERCULTURAL VARIATION IN MATING DISTANCE

How far do individuals in small-scale societies travel to locate spouses? Table 1 and figure 3 summarize the mating distance data and suggest that foragers travel significantly farther for mates than horticulturalists ($t = 2.63$; $p = 0.03$; d.f. = 6). Classic work on the territory of the forager regional band (Wobst 1974:173) or dialectal tribe (Yengoyan 1968:185) suggests that population density influences the travel distance required to find a suitable number of potential marriage partners and this in turn influences the territorial limits of the band or tribe—the lower the population density, the farther one has to travel and the larger the regional band or tribe (Mandryk 1993:46–47). Jochim (1976) and Hewlett, van de Koppel, and Cavalli-Sforza (1982:425) hypothesize a relationship between mating distance and population density. Hewlett et al. found that Aka living in areas of lower population density traveled farther to find mates. This hypothesis is tested for several forager and horticultural societies in figure 4. When mating distance is correlated with the log of population density (persons/km²), the regression shows a very strong, significant ($p < .05$) relationship for all groups: $r = 0.87$ for the 5 forager societies, $r = 0.91$ for the 6 horticultural societies, and $r = 0.92$ for all 11 groups. As population

TABLE I
References for Intercultural Mean Mating Distance Data among Hunter-Gatherers, Horticulturalists, and Pastoralists

Group	Location	Reference
Hunter-gatherers		
Aka	Central African Republic	Cavalli-Sforza and Hewlett (1982:267)
!Kung	Kalahari, southern Africa	Harpending (1976:161)
Kiunga	New Guinea	Serjeantson (1975:400–413)
Agta	Casiguran region, Philippines	T. Headland, personal communication, 1997
G//ana	Kalahari, southern Africa	Cashdan (1984:459)
Anbarra[a]	Coastal Australia	White et al. (1990:177)
Umatilla[a]	Columbia Plateau, North America	Anastasio (1972:151)
Nez Perce[a]	Columbia Plateau, North America	Anastasio (1972:151)
Horticulturalists		
Santals	Bihar, India	Basu (1973:368)
Yanomamo	Venezuela	Biella, Chagnon, and Seaman (1997)
Sara	Chad	Crognier (1977:167)
Madang	Coastal Papua New Guinea	Serjeantson (1975:403)
Gainj/Kalam	Highland New Guinea	Wood, Smouse, and Long (1985:755)[b]
Semai	Satak region, Malaysia	Fix (1974:330)
Agro-pastoralists		
Kipsigis	East Africa	M. Borgerhoff Mulder, personal communication, 1997

[a] Qualitative data—not included in statistical analyses.
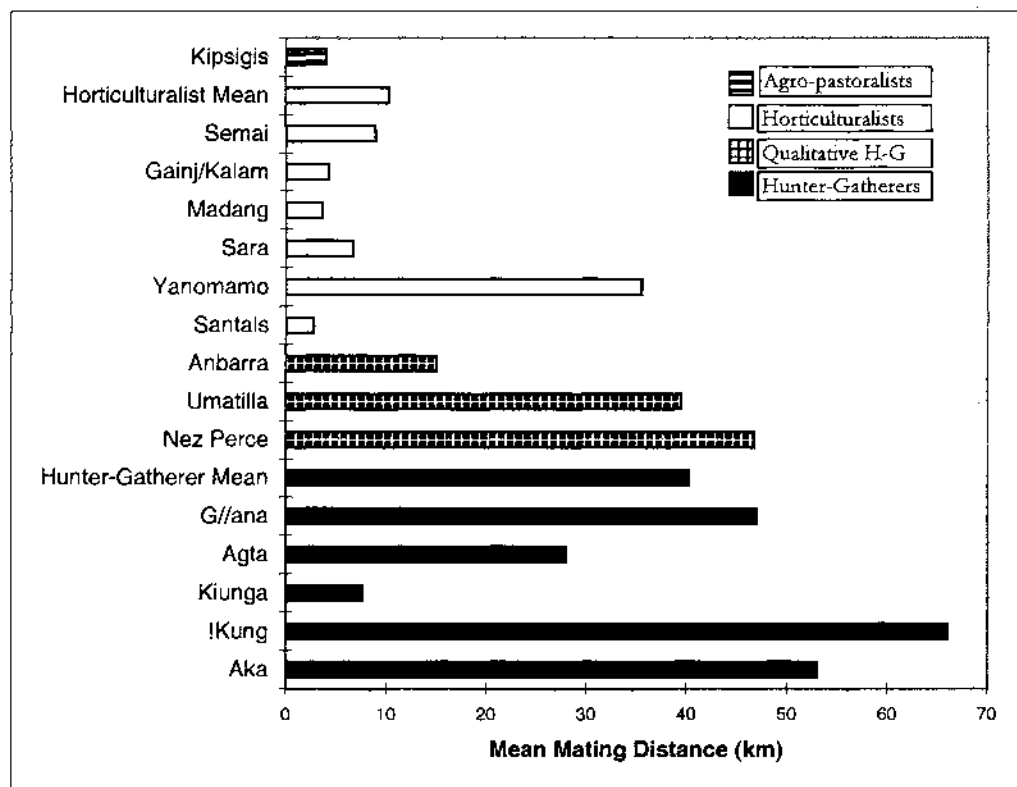[b] Mother-child distance.

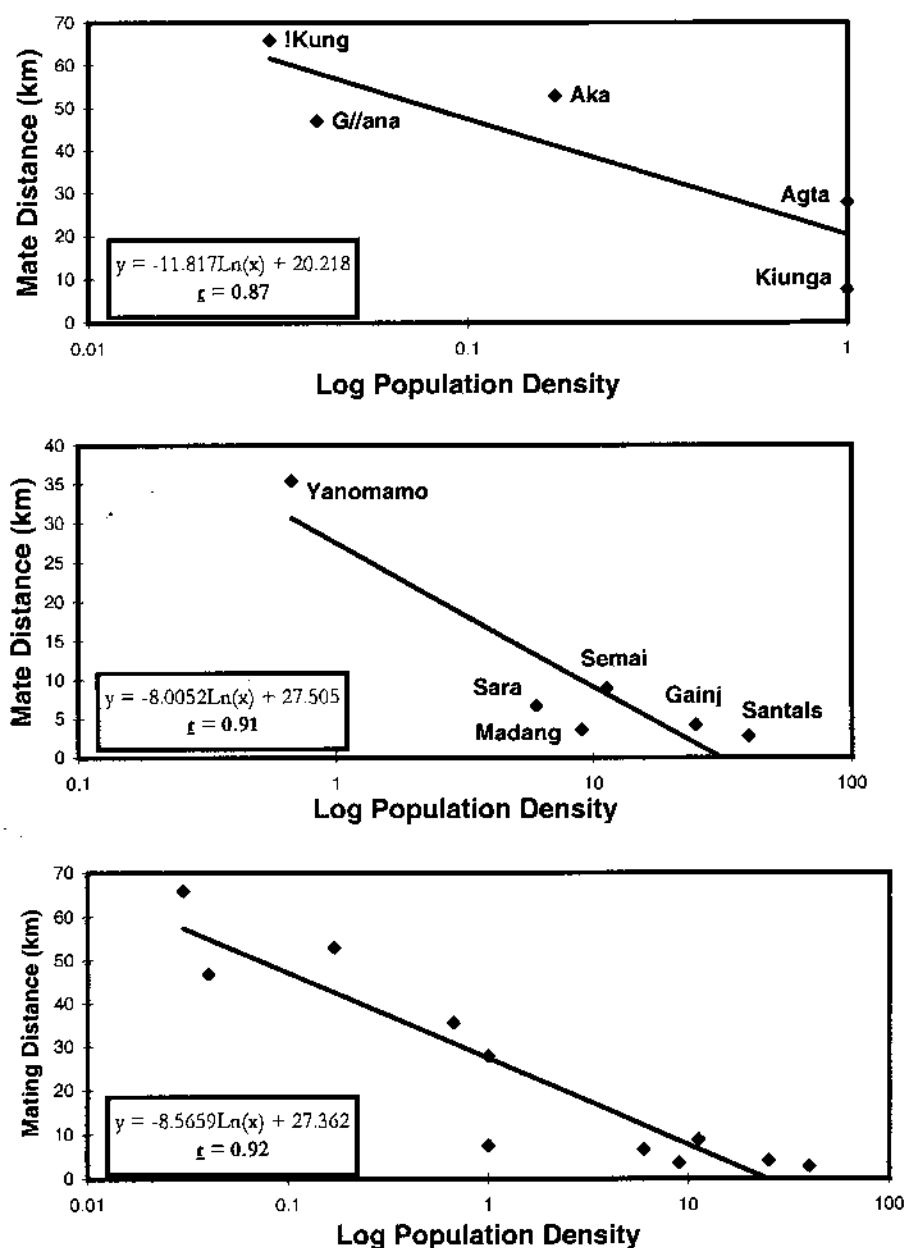FIG. 3. *Mean mating distances (km) in small-scale societies.*

FIG. 4. *Mating distance (km) and the log of population density (n/km²) in hunter-gatherers* (top), *horticulturalists* (center), *and both together* (bottom).

density[2] decreases at a logarithmic rate, distance traveled to find a mate[3] significantly increases.

2. All population density data are from sources cited in table 1. Harpending (1976:154) counted roughly 2,500 !Kung living in northwestern Botswana, which he estimated to be an area of approximately 144,000 km² The resulting density of about .02/km² appeared low compared with data from other !Kung groups in the region (Kelly 1995:226), and therefore we increased it to .03/km² The regression in figure 4 remains strong and significant even when a density of 0.10 is used.

3. In two of the three cases in which we have raw data, the median mating distance is not significantly different from the mean (Aka mean = 55.8, median = 66; Yanomamo mean = 32.4, median = 28). This suggests that the value is an accurate measure of the central tendency and is not exaggerated by very high or low mating

These data are helpful for understanding the higher inbreeding rates of horticulturalists in comparison with foragers (Yellen and Harpending 1972:248). This higher rate is likely associated with decreased mobility, the reduced role of kinship networks, and increased reliance on local storage to minimize the risks of food deficit. Cashdan (1984:458–60) provides a provocative discussion of the transition of the G//ana of southern Africa

distances. For the Agta (mean = 27.9, median = 13.7), however, the median is considerably lower than the mean. This is because many individuals married within their own villages and mating distance was zero in those cases. Future research will examine the significance of these differences in central-tendency values.
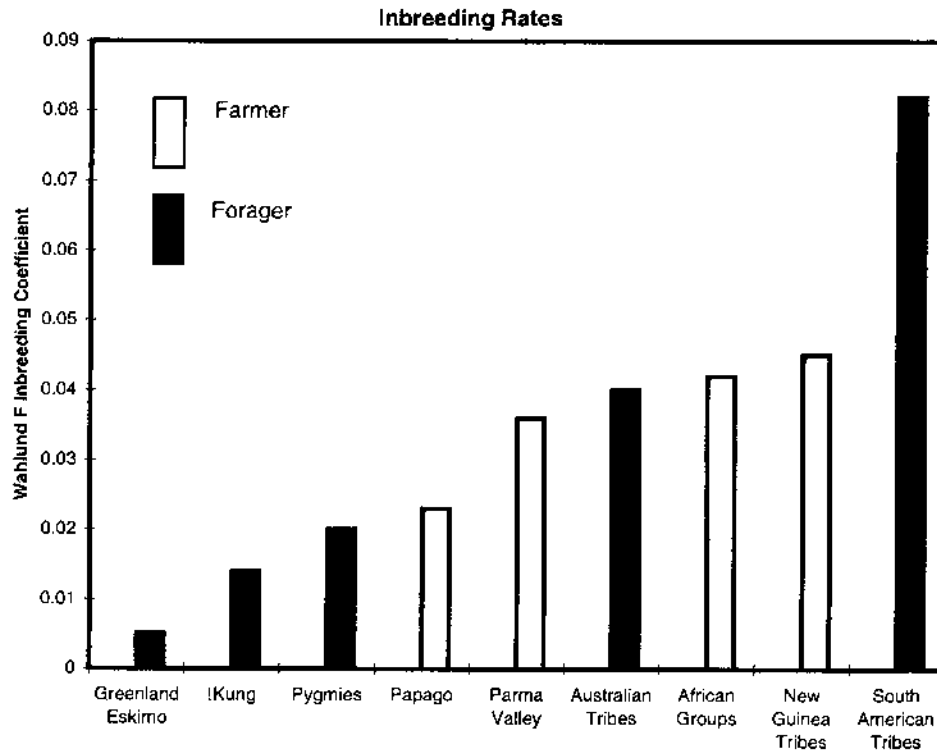
Inbreeding Rates

FIG. 5. *Inbreeding rates among hunter-gatherers and farmers (data from Yellen and Harpending 1972:248).*

from a mobile, hunter-gatherer to a sedentary, farmer lifestyle. She shows that the reliance of sedentary G//ana on storage alleviated their previous need as hunter-gatherers to be highly mobile and maintain large kin networks. With this transition, as would be expected, she found reduced mating distances. This decrease has also been observed among Aka who farm (Cavalli-Sforza and Hewlett 1982:260). With a decrease in the scope and frequency of kin networks among higher-density sedentary groups, individuals travel shorter distances for spouses, and the likelihood of marrying a relative increases.

In support of this hypothesis, Yellen and Harpending (1972:248) reveal that higher-density nucleated groups have higher rates of inbreeding than mobile hunter-gatherers. They use the Wahlund *F* inbreeding coefficient to compare settled agricultural peoples with hunter-gatherers. Figure 5 summarizes the inbreeding coefficient data and demonstrates the differences in rates of inbreeding between farmers and foragers. As Yellen and Harpending (1972:248) state, "While these [values] are not strictly comparable, because of variation in sample size and local group size, the lower values do seem to be associated with hunter-gatherers."

These data further support the hypothesis that population density[4] is a significant factor in determining dis-

4. Birdsell (1953) and others (see Kelly 1995:226 for a discussion) have shown that rainfall and food abundance (e.g., carrying capacity) are significant factors in regulating regional population densities. Thus, while population density significantly affects distance traveled to find a mate, other environmental factors control density.

tance traveled to find a mate. With high population densities, individual travel to find a mate is significantly reduced and inbreeding is more likely to occur. Thus, both our horticulturalist data and Yellen and Harpending's (1972) agriculturalist data support the hypothesis observed among foragers that population density significantly affects degree of mobility, inbreeding, and mating distance. As Yellen and Harpending (p. 249) state, "All these genetic parameters [of foragers] contrast markedly with those of agriculturalists, who are more endogamous, more inbred, and who marry within a smaller radius."

INTRACULTURAL VARIATION IN MATING DISTANCE

While the intercultural mating distance data demonstrate the importance of reproductive interests for understanding forager (as well as farmer) mobility and territory, the data are group means and do not tell us about variation among individuals (e.g., male-female, young-old, rich-poor) within groups. Figure 6 demonstrates the enormous variability in mating distance found within each of four groups—Agta, Aka, Yanomamo, and !Kung. Many individuals find mates nearby, especially within 0–40 km of their birthplaces. This distance is certainly within the usual area of most subsistence activity. Nevertheless, some persons have to travel more than twice as far as the average individual. In order to understand and explain such within-group variability, we tested three hypotheses generated in large part from neoevolutionary theory.
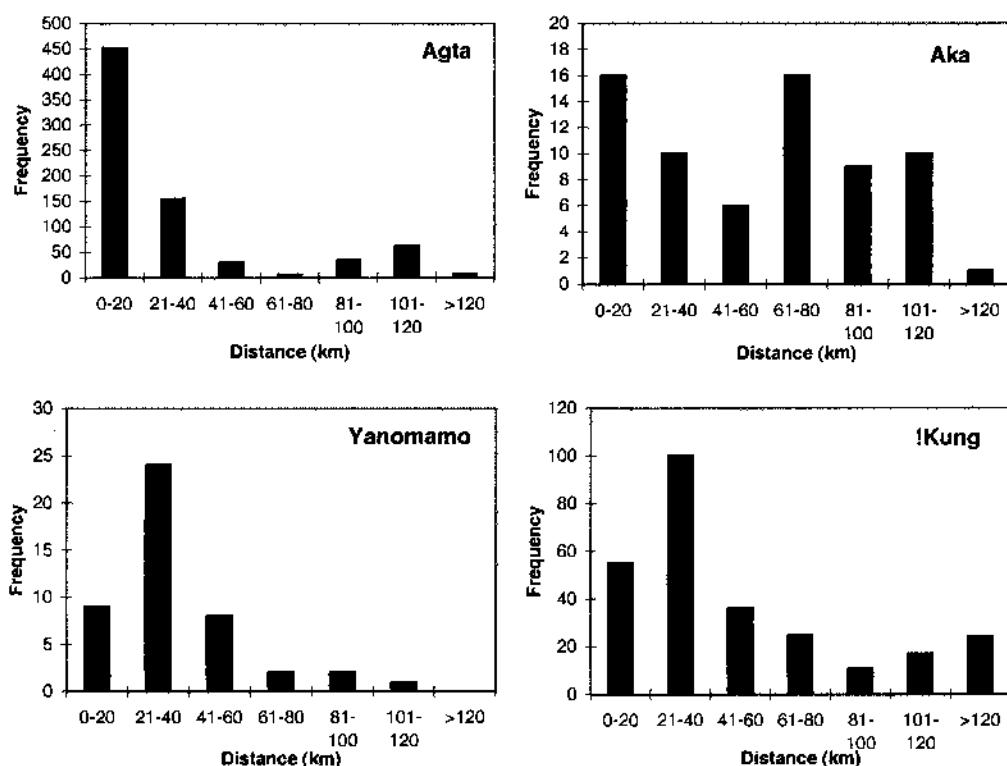
FIG. 6. *Intracultural variation in mating distance among Agta, Aka, Yanomamo, and !Kung.*

Sexual selection and parental investment theory (Trivers 1972) suggests that women are the limiting resource among humans, since they do most of the investing in offspring (Gaulin and Hoffman 1988:131–32). Consequently, there is competition among men for the resource, and women are predicted to do the mate choosing. Men are also predicted to undertake the riskier tasks (hunting large game, climbing trees, etc.) because they have more to gain reproductively if they are successful. The farther one travels from the local subsistence area, the greater the risk and uncertainty (less knowledge about environment and others). Thus, evolutionary theory suggests that, in general, competing males should travel farther and more frequently than choosing females.

Such a prediction is supported by evolutionary psychological studies of male versus female spatial abilities not only among humans (Dabbs et al. 1998, Gaulin and Hoffman 1988, Moffat, Hampson, and Hatzipantelis 1998) but also among nonhuman primates and mammals. Such research suggests that the larger ranges of males compared with females across various mammal species "may have a common evolutionary basis" (Moffat et al. 1998:74). Gaulin and Hoffman (1988) suggest that, as among other mammals, male humans strive to defend large territories as a reproductive strategy for maximizing access to the largest number of females. Another hypothesis is that enhanced male spatial abilities evolved because "males predominantly hunted and females predominantly foraged" (Silverman and Eals 1992:534) during the ancestral period. A solution to this adaptive problem may combine the two explanations. In other words, it is likely that enhanced male spatial ability was adaptive for both somatic and reproductive success.

Some anthropologists may consider it unnecessary to evaluate male versus female mobility among foragers because men usually hunt and women usually gather and therefore men will, on average, have greater mobility than women. While this is generally true, as Gaulin and Hoffman (1988) point out, foragers do not travel, especially long distances, for subsistence reasons alone. They may travel to locate mates, to visit friends and family, to seek a great healer, to flee accusations of sorcery, or simply to explore a territory. Table 2 summarizes quantitative and qualitative data on male versus female mobility in both forager and farmer groups, and, as evolutionary theory predicts, males consistently travel farther than females. But, again, foragers travel for many reasons, and the link to reproductive interests is not clear.

The Aka are the only group for which we have data on both mating distances and exploration ranges (mean distance traveled by an individual in a lifetime) on the same individuals (17 men and 22 women). Figure 7 examines the relationship between Aka male and female exploration range and mating distance and demonstrates a significant ($r = 0.51$; $p < 0.05$; d.f. $= 16$) relationship between exploration and mating ranges for men but not for women ($r = 0.10$; $p = 0.62$, d.f. $= 21$).

TABLE 2
Sex and Mobility

Group	Male Travel (mean km)	Female Travel (mean km)	Male-to-Female Travel Ratio	Male Greater?	Reference
Aka	58.3	32.4	1.8:1	Yes	Hewlett, van de Koppel, and Cavalli-Sforza (1982:423)
Alyawara	50	20	2.5:1	Yes	O'Connell and Hawkes (1984)
Efe	–	–	–	Yes	Bailey (1991) and personal communication, 1997
G//ana	–	–	–	Yes	Cashdan (1984:457)
Inuit	–	–	–	Yes	N. Graburn, personal communication, 1997
Nukak	–	–	–	Yes	Politis (1996)
Nunamiut	–	–	–	Yes	Binford (1983)
Yanomamo	–	–	–	Yes	R. Hames, personal communication, 1997
Kipsigis	89.7	21.7	4.2:1	Yes	Gaulin and Hoffman (1988:144)
Falachig	–	–	3.5:1	Yes	Gaulin and Hoffman (1988:144)
Trinidad	–	–	2.1:1	Yes	Flinn (1988:194)
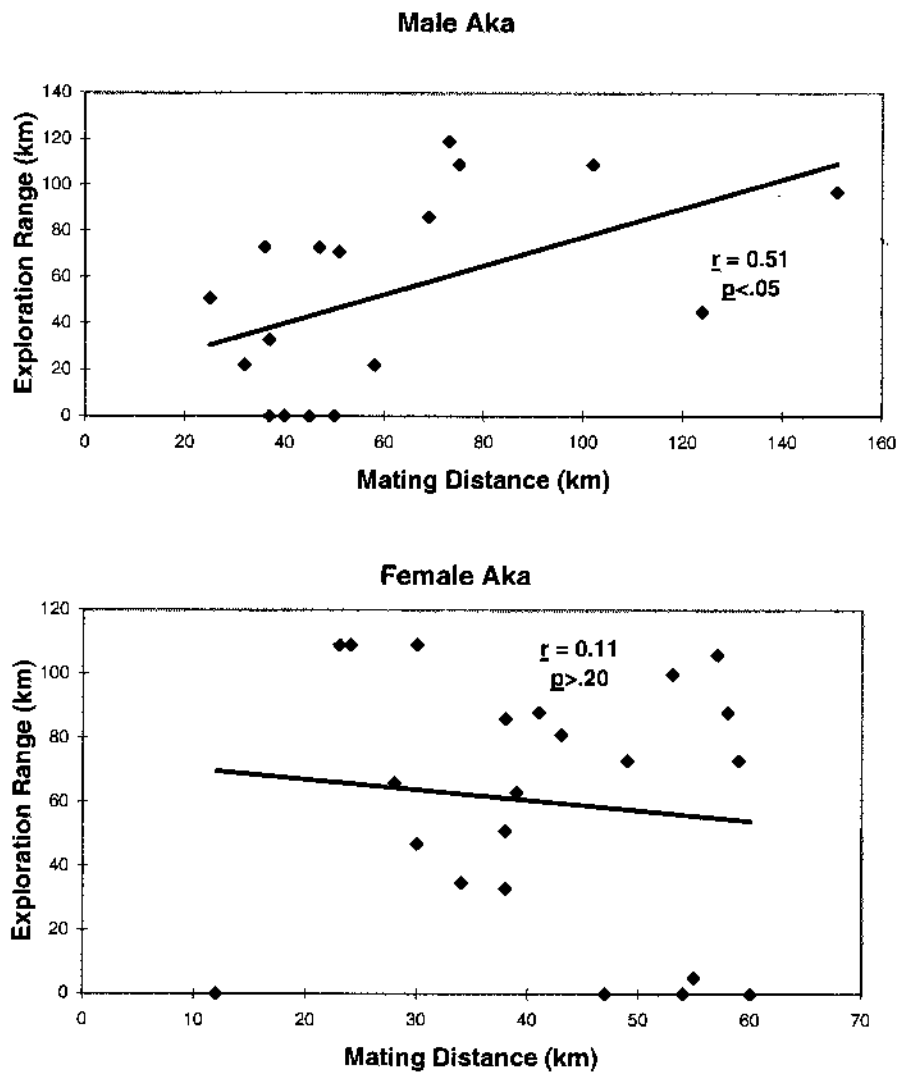
Male Aka

Female Aka

FIG. 7. *Exploration range and mating distance for male and female Aka foragers.*
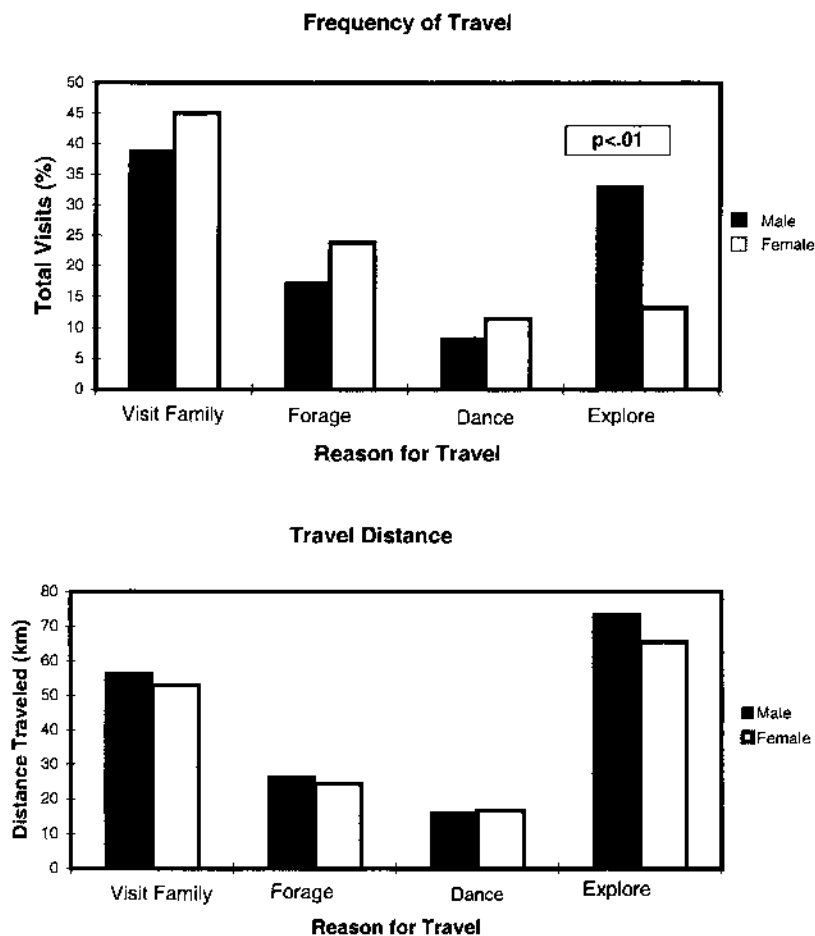
Frequency of Travel

Travel Distance

FIG. 8. *Sex differences among Aka foragers in frequency of travel and travel distance.*

These data suggest that the exploration range of men is, in part, a function of their search for mates (Cavalli-Sforza and Hewlett 1982:268; Hewlett, van de Koppel, and Cavalli-Sforza 1986). Thus Aka men are more likely than Aka women to travel and explore an area and locate a mate during these travels.

Figure 8 summarizes Aka men's and women's reasons for travel and the mean distances for that travel. There are no statistical differences between men and women in the distance they travel for given reasons, but there is a significant difference ($p < 0.01$) in the *frequency* with which Aka men and women travel long distances for exploration of potential resources (travel to conservation project, lumber mill, coffee plantation). Aka who make these especially long-distance trips do it only a few times in their lifetimes—most have negative experiences on them (lack of food, prejudice against "pygmies," etc.).

Figure 9 examines both sex and age variables in relation to Aka exploration ranges and indicates that males travel farther than females at each age point but especially during young adulthood, when the differences are significant. This is obviously an important time in the search for mates. The sample sizes for adolescents and

the aged are admittedly very small and may contribute to the absence of significant differences.

"Wealth" among foragers is based upon kin resources rather than material resources in that the frequency and scope of all kinds of sharing are influenced by the number of one's close relatives. Thus, wealthy individuals are better able to survive times of scarcity because of the increased variety of available resources provided by family members living in various communities, both locally and regionally (Hawkes 1992:291). Among the Aka, men with no or few brothers had the largest mating distances (Hewlett 1988:271). Because the Aka sample was very small, we tested the hypothesis that mating distance was inversely related to wealth (as measured by number of siblings) with a subsample of Agta provided by the Headlands. For the 13 men in their sample with the largest mating distances and the 19 men with the smallest mating distances the prediction that the individuals who traveled farthest to find a spouse would have significantly fewer siblings than those who traveled the least was not supported ($t = 2.09$; $p = 0.10$; d.f. = 19). The mean number of siblings for those who traveled farthest was 4.23 while the mean for those who traveled least was 2.89. Headland (1987:
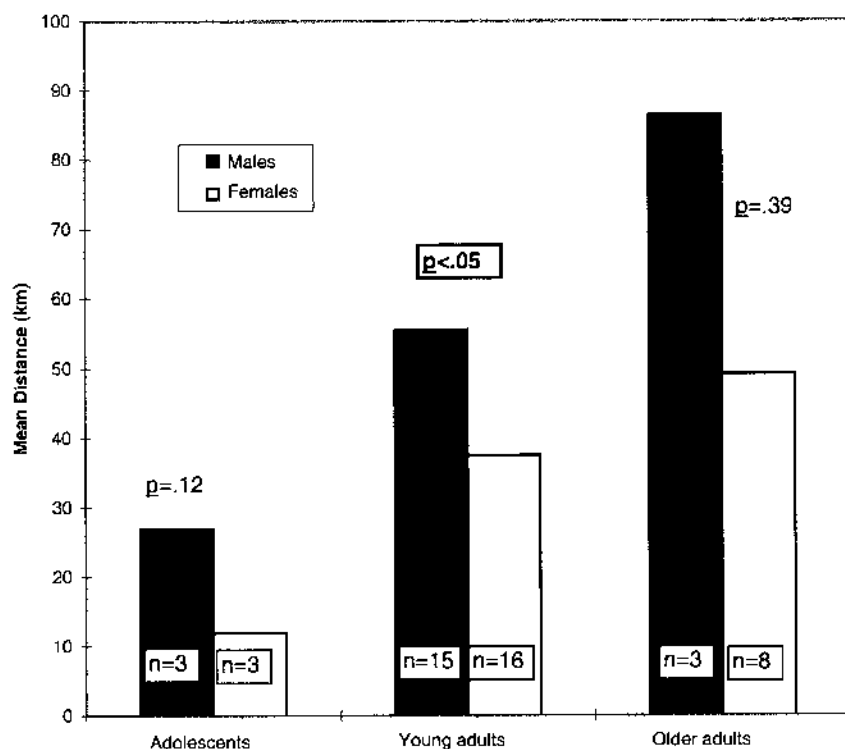
FIG. 9. *Differences in mean distance traveled by age and sex among Aka foragers.*

267–68] explains that because the Agta forbid marriage between families already allied through marriage, a young man with many married brothers will have to travel to distant villages to find a mate, as his older brothers will have married women from families in neighboring ones. The differences between Aka and Agta may be due in part to different subsistence systems. The Aka are cooperative net hunters, while Agta foragers often rely on set trap lines. While Aka depend upon brothers to hunt cooperatively, it may be beneficial for Agta to disperse their kin resources in order to minimize risk. In any case, the Agta marriage rule supports our general proposition that reproductive interests play a role in shaping Agta mobility.

Discussion

LEVELS OF FORAGER MOBILITY

The Aka mobility study indicates three levels of mobility more or less resembling those outlined in figure 1 for the Nunamiut and the !Kung. Figure 10 depicts a parsimonious model incorporating reproductive and subsistence interests as a supplement to existing subsistence and group-based models.

The first level of the model is called *micromovement* and refers to individual and group mobility for subsistence rounds. Reproductive concerns are also important, as some individuals find mates on this level. This level corresponds to the foraging radius in Binford's model, the nuclear family and the minimum band in Wobst's model, and the core and the annual range in Sampson's model.

The second level of mobility is called *mesomovement* and refers to travel at intermediate distances to visit friends and relatives. Clans with long histories of reciprocal marriage exchange are often found on this level, and the mean mating distance of a population is likely to fall within this range. Long-term marriage links are the primary feature of this level of mobility, but in difficult times (e.g., shortage of resources and social conflicts) families may undertake mesomovements and remain away for long periods. This level is also likely to include the mean number of people one gets to know and learn from during one's lifetime. It is a close approximation to the annual range in Binford's and Sampson's models and the maximum band in Wobst's model.

The final level is called *macromovement* and refers to mobility to explore exotic sites for potential or especially scarce resources (reproductive or somatic). There are more risks involved with this exploratory travel, and therefore not everyone participates, but the benefits are potentially great. Males with few kin resources or individuals with unusual backgrounds (e.g., problems with sorcery) are likely to travel these long distances. Individuals may explicitly look for mates or find them along the way. We suggest that men will be more likely than women to make these long trips and that they will likely be infrequent unless the new potential resources
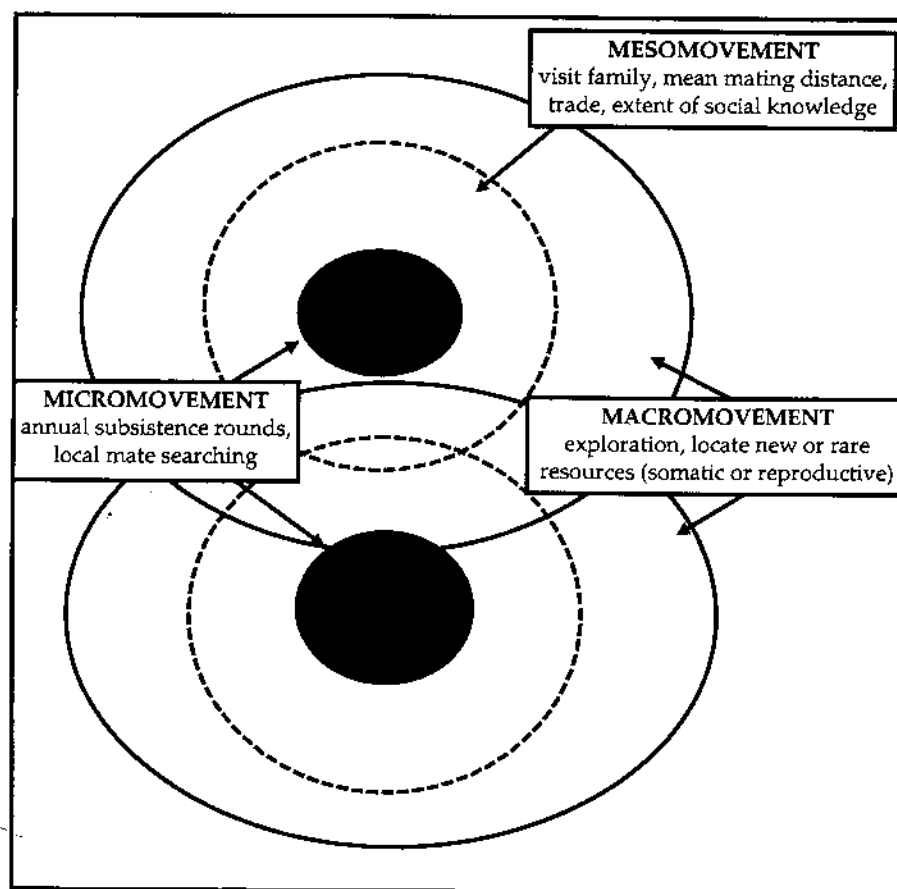
FIG. 10. *Models of forager mobility. Overlapping areas indicate hypothetical contacts between two forager-mobility realms.*

are considered better than existing ones. This level is similar to the extended and lifetime ranges in Binford's model and the lifetime range in Sampson's model.

An individual's mobility realm is likely to overlap that of individuals from other regions and cultures, and here there may be trade, mating, and information exchange (as well as aggression). Such territorial overlaps, if frequently encountered, often lead to the establishment of interregional and cross-cultural movements of goods (e.g., trade networks). For example, Sampson (1988) states that !Kung often possess trade items which derive from regions beyond normal travel realms (e.g., the gift recycling zone in figure 1, b). Such trade networks operate as integral parts of established mobility realms.

PRIME MOVERS

Life-history theory suggests trade-offs between somatic and reproductive efforts. Data on hunter-gatherers such as those we provide here suggest that mobility occurs for multiple reasons. It is therefore often difficult if not impossible to identify "prime movers." For instance, research by Hawkes (1991) and Hill and Hurtado (1996: 318) suggests that the acquisition of game by men has

more to do with mating effort than with the provisioning of family members. These data are consistent with our proposition that micromovement may be motivated by reproductive as well as subsistence concerns. Aka mesomovement occurs to visit family, but it is not always clear whether it is primarily to search for or maintain mates or to develop subsistence risk-minimization strategies. At the macromovement level, men in particular explore for all types of resources.

While we have presented data indicating the importance of reproductive interests at all levels of mobility, we are not suggesting that reproductive interests replace somatic interests or constitute prime movers. There are often multiple reasons for travel; thus, while there may be an emic prime mover or inspiration for travel (such as desire to find a mate, move camp, hunt, or gather), there can be other motives. Thus, we urge analysts of prehistoric and contemporary forager mobility to consider the entire gamut of concerns, from somatic to reproductive. We especially encourage the continued collection of all types of forager mobility data. Specifically, there is a need for more quantitative studies of within-group differences in mobility and of the way in which reproductive interests shape female mobility.

This study has important implications for the assessment of mobility of foragers in prehistoric contexts. The mating-distance data suggest that the large territories of foragers seen in the regional distribution of stone and other raw materials may in part represent mating ranges. Thus, archaeologists need to begin to identify signatures of mobility for reproductive concerns. This task is a daunting one, especially in light of the fragmentary nature of the archaeological record and the fact that not all types of travel leave artifactual signatures. However, there may be creative means by which archaeologists can at least suggest nonsomatic purposes of travel.

The sacred-stone scenario of Gould and Saggers (1985: 122) may provide one means by which to identify long-distance travel for reproductive, religious, or other purely social reasons. The authors suggest that the Aborigines of Australia's Central Desert directly procured high-quality stones from exotic locations of symbolic importance. By curating such stones, individuals maintained links with the exotic locale, which had symbolic value for religious, social, or even reproductive purposes. MacDonald (1998) has suggested that the excavation of artifacts made from nonlocal stones at sites where local stone is high-quality and abundant may point to nontechnological motives (e.g., symbolic remembrance of special locations or events) for tool curation. Folsom foragers of the northern Plains of North America transported small quantities of exotic stone long distances into the Knife River flint quarries of western North Dakota, a region in which high-quality stone was ubiquitous. Because there was no *obvious* technological reason to curate such stone, MacDonald suggests that individuals kept it as a memento of travel and that this may have helped them attract mates. Determining the exact motive (e.g., religious, reproductive, social) for mobility is, however, likely beyond the capabilities of prehistorians.

MAGIC NUMBERS AND LIMITATIONS

The strong relationship between mating distance and population density is consistent with previous propositions (Birdsell 1953, Lee and DeVore 1968, Wobst 1974, Yengoyan 1968) that there are magic numbers in terms of what it takes to maintain a population. The regression lines in figure 4 indicate that most people locate spouses in a population of 600 individuals. This is remarkably close to the frequently cited magic number 500 for what Wobst calls a maximum band. Our proposed model suggests that this average number occurs at the mesomovement level, but it is important to emphasize that this is a mean—that many people find spouses within a smaller range and some people have to travel and meet substantially more than 600 individuals to attract a spouse.

This study has several limitations. First, whereas life-history theory identifies at least three components to reproductive efforts—mating, parenting, and nepotistic—we have focused on the first. It is obvious that

forager mobility is also influenced by what parents want to do for their children and other family members, but ethnographic data do not exist to evaluate these other components.

Second, we recognize that cultural categories such as kinship terminologies and marriage rules can influence reproductive decisions and how far one has to travel to find a mate, but we do not have sufficient data to evaluate to what degree such factors influence forager mobility. Chagnon (1992), the only one to have evaluated this in a horticultural community, suggests that Yanomamo are always breaking the kinship rules in order to marry persons of their own choosing. The strong relationship between population density and mating distance among such diverse societies as we describe here[5] suggests that the impact of kinship terminologies and marriage rules may be minimal. Many cultural anthropologists would argue otherwise, and it is certainly worthy of further study. While kinship and descent rules may not have a great impact on reproductive mobility, "cultural" (nonsomatic or reproductive) factors (e.g., death in camp, sorcery accusations) can and do impact individuals' or groups' mobility.

Third, contemporary ethnographic data on foragers and horticulturalists have built-in biases. Most of the remaining "traditional" or "small-scale" peoples live in tropical forests, and all traditional peoples are influenced by the global economic system. Consequently, the factors we identify apply primarily to tropical forest peoples, and we are not in a position to evaluate how much of contemporary forager mobility is influenced by global forces. Finally, because very few data exist on this topic, the analysis is obviously limited by small numbers.

Conclusion

This study has examined intercultural and intracultural variability in forager mobility. First, we have presented quantitative data showing a significant correlation between mating distance and population density not only among foragers but also among farmers.

Second, we have compared male and female travel and found that, for all of the societies with appropriate data, males, on average, travel considerably farther than females in a lifetime. Data on the Aka indicated a relationship between mating distance and exploration range for males but not for females. Males also had greater exploration ranges at every age but especially during young adulthood, when competition for mates is greatest. Wealth was identified as a possible factor influencing forager mobility, but a test of the hypothesis with Agta data indicated no significant difference in wealth (number of siblings) between individuals who traveled farthest and least to find mates.

5. Agta and !Kung utilize Eskimo, Aka Hawaiian, and Yanomamo Iroquois kin terms. Aka and Yanomamo are patrilineal while !Kung and Agta are bilateral.

Finally, we have presented a parsimonious model of forager mobility that incorporates reproductive as well as subsistence concerns at all levels of mobility and thus supplements forager-mobility and territorial models which consider mating important only at the maximal or regional band level.

Comments

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MacDonald and Hewlett correctly argue that previous studies of forager mobility have focused primarily on subsistence constraints and ignored mating effort as an independent variable. The major contribution of their paper is demonstrating that some portion of forager mobility can be explained by mating effort. This is an important point. The difference in mobility by age and sex, for example, is consistent with what is predicted by sexual selection theory. The paper has a number of problems, however.

My guess is that, if pressed, most researchers would acknowledge that mating effort does affect mobility. A more interesting question is how much of the variability in forager mobility can be explained by considering mating behavior. If the subsistence pattern is adequately described for a particular group, mating factors are a good candidate to explain the residual unexplained variance for mobility. The residual, however, may be large or small, and it surely varies between populations. While MacDonald and Hewlett show that reproductive interests affect mobility, we do not get a sense of to what extent they are important.

If one wants to understand the importance of mate search for overall mobility, one way to start is to compare the frequency of mating mobility with that of all mobility. When MacDonald and Hewlett construct Aka exploration range, they present data on the stated reasons that Aka individuals travel and use these data to show that some exploration is related to mating. They do not, however, use them to try to learn what portion of total mobility might be related to mate search. Admittedly, the data set is not particularly well-suited to that purpose. Subjects were asked whether they had ever been to each of 70 places and if so why. The data set is biased toward places the observer could name and knew about. For example, is it possible that residential moves during foraging trips in the forest were undersampled because these moves were to places in the forest that did not have names? It is hard for a reader to know the answer to that question without knowing more about the 70 places. Consequently, the data on the Aka do not tell us what fraction of overall mobility reproductive interests can explain.

Another problem is that the measure of mating distance used here is not actually the distance individuals traveled to acquire their mates but the distance between birthplaces of married couples. I understand the difficulty of operationalizing variables with real data, and MacDonald and Hewlett do state a caveat. The mating distance value they devise should, however, be divided by two, since mating occurs between two individuals and each mate travels some fraction of the total distance.

The attempt to integrate their work into evolutionary theory is good, because there is much that evolutionary theory can contribute to an understanding of traits such as ranging behavior. Sexual selection is critical for understanding many behaviors that are otherwise inexplicable in terms of selection for survival (or somatic effort, in the authors' terms). MacDonald and Hewlett do not, however, put their research in a context that includes some of the classic work in the area of landscape use and mating behavior. For example, models created by Wrangham (1979) and Emlen and Oring (1977) both argue that females map themselves on the resource landscape because they are reproductively limited by resources. At the same time, since females are the limiting resource for males, males move according to female distribution. If humans follow a similar pattern, at least part of male mobility is patterned by female mobility, and female mobility is patterned by subsistence concerns. It is true that, for human females, males are an important source of resources. However, this analysis suggests that subsistence and resource distribution may still be the prime mover for mobility.

Since archeologists seem to be part of the intended audience of the paper, it is a good idea to discuss how they might include reproductive concerns in their analysis of prehistoric forager mobility. Theoretically this is important, but, as MacDonald and Hewlett point out, it is a challenge for archeologists to achieve such behavioral resolution. What might the site signature of a mating excursion look like? The brief discussion of the sacred stones is interesting in that it offers mating concerns as an explanation for behavior that might remain unexplained if only subsistence concerns were considered. Among marine hunters in Lamalera, Indonesia, for example, as late as this century males had to provide elephant tusks as bride-price (Barnes 1996). This proved quite a challenge, since there are no elephants on the island. The presence of such items in the archeological record is inexplicable outside the context of sexually selected behavior.

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This article presents new thoughts and data and tests hypotheses on an important but neglected subject, population structure in the socioeconomic systems of hunter-gatherers and horticulturists. Moreover, it does

so by a quantitative approach that is unfortunately rare in field anthropology but should become a rule whenever possible. Qualitative statements are useful for providing ideas and hypotheses but not for testing them. The article touches on a number of points of considerable interest and makes various statements, some of which are completely new.

There are two alternative approaches to measuring two relevant major parameters of population structure. One uses the "size of the isolate," *N*, and the frequency of exchange with neighbors, *m*. The other uses population density and average mating distance, which are a little easier to observe and measure with hunter-gatherers and shifting cultivators. The two approaches are found in two classical theoretical studies of "isolation by distance," by Malecot (1948) and by Wright (1946). For precision, mating distance is an approximation of the distance between the birthplaces of parents and children, and it is not without importance that there is usually a difference between the distance between the birthplaces of mother and children and that between those of father and children. For MacDonald and Hewlett's rather general level of analysis mating distance is adequate.

The results of the two approaches can be translated one into the other. In fact, MacDonald and Hewlett calculate from population density data the isolate size, *N*, ca. 600, and this is one important conclusion of their paper. They note that it is somewhat above the minimum calculated by Wobst to avoid excessive inbreeding and close to one of the two famous "magic numbers," 500 for the "tribe." The development of fully sedentary agriculture of course caused major increases in the sizes of tribes.

Another important finding is the strong inverse correlation between population density and mating distance. This is a very reasonable expectation, and it is reassuring that the correlation is so high. It is interesting that the range of observed mating distances is less than 100:1, much smaller than that of population densities, which is closer to 10,000:1 fig. 4, *bottom*). This apparent discrepancy is not at all surprising, because mating distance varies on the kilometer scale while density is calculated per square kilometer. In order to keep the isolate size constant, one would expect a linear relationship between the logarithm of mating distance and that of population density, with slope $1/2$. In fact, the correlation seems to remain almost unchanged by plotting the ordinate on a log scale, but the slope is somewhat less than $1/2$ (I could not calculate it exactly, because the original values are not given except in graphic form). As a consequence, the isolate size thus calculated is definitely smaller for hunter-gatherers than for horticulturalists. This would seem to contrast with Yellen and Harpending's statement, cited by the authors, that farmers have more inbreeding than hunter-gatherers. There are, however, other factors that can influence inbreeding; in my experience the shape of the distribution of individual mating distances is more skewed in the case of farmers. According to Colin Turnbull, Aka and other Pygmies often follow the rule that it is better to "marry far." This is certainly wise from a genetic point of view, but it is also wise from that of increasing resource availability, as a Pygmy husband acquires the right to also use his wife's hunting territory. In the smallest hunter-gatherer communities, such as those of the Inuit, who probably have the lowest population density of all, great care is taken to avoid cousin marriages (Sutter and Tabah 1956).

Another important factor that may increase inbreeding in early farmers in spite of their higher population density is the dimensionality of the geographic distribution of people. As the research of Wright and Malecot has shown, a one-dimensional distribution of the population greatly increases drift and inbreeding. Early farmers usually have to clear the land they plant and are highly dependent on roads, which are few and in the beginning scarcely reticulated. Hunter-gatherers in the same forest are much less dependent on roads, and their trails are probably more highly reticulated. Farmers do not like to walk in the forest, while Pygmies are and, presumably, European Mesolithics were completely at ease in it.

Finally, a very interesting point is raised by the observation that there is a reasonable correlation between the exploration range and mating distance for males but not for females. It would seem that increasing one's exploration range has a beneficial effect on inbreeding avoidance. It is not necessary, however, for both sexes to have a broad exploration range. What matters is that mating distance remains reasonably high, and the male tendency to explore farther from one's usual living places will favor this. But travel linked with the exploration effort is only part of the displacements over a lifetime. There is another source of movement which probably does not appear in the exploration range: the data collected by MacDonald and Hewlett do not show where the married couple will settle, but Aka Pygmies are mostly patrilineal and women are likely to join the husband's band at marriage. Thus women bear a major part of the displacement burden connected with marriage, and this is not included, strictly speaking, in the exploration range. One source of possible confusion is that it is not always specified whether mating distance is calculated between places of residence or places of birth.

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MacDonald and Hewlett correctly note that theoretical approaches to forager mobility have dealt with the issue from a narrow economic and ecological perspective. These approaches have ignored the potential social and reproductive functions of mobility or what simply can be called intervillage visiting. Therefore, MacDonald and Hewlett are to be congratulated for developing a

broad theoretical perspective that may encompass all dimensions of mobility. This piece was sufficiently stimulating that it has led me to analyze and write up previously collected field data on patterns of Yanomamö intervillage visiting (Hames n.d.) some of which I discuss here.

MacDonald and Hewlett begin by suggesting that we use a conventional life-historical approach of first dividing behaviors into somatic and reproductive efforts and then dividing reproductive effort into mating, parental, and nepotistic efforts and focusing on the first of these. However, there is a certain amount of vagueness in these categories. For example, in my research more than half of Yanomamo visits to neighboring villages are for *reahu* or *braiai* alliance-building ceremonies and for shamanic diagnoses and cures of illnesses. It is unclear how such visits map onto a life-history classification of effort. At the same time, these are Yanomamö descriptions of the purpose of visits and may mask reproductive strivings. For example, during intervillage ceremonials young men have the opportunity to dress in their best finery, dance before the entire village, and participate in dueling. Thus they may provide males with opportunities to show off (as in a lek) or engage in direct male-male demonstrations of prowess.

Contrary to what MacDonald and Hewlett claim, one may not automatically conclude that a negative correlation between mating distance and population density indicates higher inbreeding rates. This relationship presumably shows the cumulative number of potential mates encountered at particular distances at given population densities. This means that low-density foragers must travel farther than high-density horticulturalists to encounter an equal number of potential mates. If we assume random mating and that foragers and horticulturalists always want to sample 500 potential mates, foragers will have to travel farther than horticulturalists to encounter the same number of potential mates simply because they encounter few potential mates per unit travel. This is what they seem to suggest in their conclusion when they note that "the regression lines in figure 4 indicate that most people locate spouses in a population of 600 individuals." Higher inbreeding rates for horticulturalists could be implied in figure 4 if the relationship took the form of a negative *j*-curve and the upper slope indicated more potential mates encountered per unit distance than the lower slope. Perhaps the data they used to generate figure 4 show this, but it cannot be easily derived from the figures themselves.

The only way to show that inbreeding varies with subsistence emphasis is to do what Yellen and Harpending did (1972): measure actual rates of inbreeding among foragers and food producers. Although having a small pool of potential mates may increase the probability of inbreeding, marriage rules themselves may have an equally powerful effect. For example, the practice of sororal polygyny or sister exchange leading to bilateral cross-cousin marriage will increase rates of inbreeding. In the course of this discussion MacDonald and Hewlett suggest that foragers opt for unrelated or distantly re-

TABLE I
Reported Subsistence Ranges for Yanomamö Villages

Maximum Radius (km)	Area (km²)	Source
14	615	Hames (1980:48)
5–10	78–314	Good (1989:54–60)
10[a]	305	Smole (1976)
28–30	2,463–2,827	Colchester (1984:229)
15	707	Lizot (1978:132)

[a] Estimated from area exploited.

lated spouses to disperse kinship linkages over a wide geographic range while food producers may choose mates to concentrate kinship linkages over a much narrower geographic range. This is an interesting observation and merits further elaboration to elucidate the specific environmental factors that lead foragers and food producers to concentrate or disperse relatedness through marriage.

MacDonald and Hewlett observe that the Yanomamö, like the Agta, !Kung, and Aka, find mates within 0–40 km of their birthplaces. They go on to note that "this distance is certainly within the usual area of most subsistence activity," a conclusion based on Chagnon's data presented in Biella, Chagnon, and Seaman (1997). Data collected by other Yanomamö ethnographers (table 1) show that Yanomamö rarely travel more than 15 km for subsistence activities (the upper limit is for hunting expeditions lasting several days). In the population bloc of eight villages that I studied in 1975–76 (Hames 1983) nearly all marriages except village-endogamous ones occurred at distances greater than 15 km. Furthermore, the mean distance of visits for Yanomamö men and women is approximately 40 km, and approximately 45% of all visits were to villages more than 55 km away. This suggests that Yanomamö's mating range is two to three times greater than their subsistence range.

The Yanomamö data I have on travel distances and frequencies for men and women show patterns similar to the Aka one. Like the Aka, Yanomamö men and women visit other villages equally frequently and the frequency of visiting increases with age. In contrast to the Aka situation, there is no difference between men and women in distance traveled in intervillage visiting. This lack of difference is not in accord with my communicated impressions regarding Yanomamö travel as presented in MacDonald and Hewlett's table 2. There may be two reasons for this. First, my sample is small, consisting of 9 women and 10 men over the age of 12 years, and only one of the men was without a spouse. Second, my measures of visiting documented what a sample of men and women did over a ten-month period (from August 1975 through June 1976) and not over their lifetimes.

In conclusion, I believe that the authors have opened up a new and vital area of research, and it is my hope that researchers will begin to make intervillage visiting a serious concern.

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This is an important synthesis of the limited information available about mating distances in low-technology societies. There is an unfortunate gap between those of us who focus on food and those of us who focus on reproduction as prime movers in human affairs. MacDonald and Hewlett make this gap explicit in their discussion of models, and they suggest that population density is the critical variable driving mating distances, via the quest for mates.

The interesting findings are the correlation between mating distance and log population density and the apparent continuum between foragers and gardeners in this relationship. There seems to be nothing special about being a forager except lower population density.

It is not clear to me why there should be such a relationship. If the number of potential mates is crucial, then mating distance ought to be inversely proportional to the square of density. Can the authors falsify this with their data?

An important application of data about mating distance is to predict the speed of spread of genes. The pioneering paper by Weiss and Maruyama (1976) cast doubt on the feasibility of the multiregional model of modern human origins on the basis of rates of gene diffusion given what was known then about mating distances. Unfortunately, the statistic that these models use is not mating distance but mean squared mating distance, that is, the square of the mean added to the variance. Can the authors give us estimates of this statistic for the populations they describe?

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While human mobility, like other human behavior, performs multiple social and ecological functions, previous studies on hunter-gatherer mobility have mainly been analyzed in relation to land and resource use and other ecological aspects. In my own research on the Mbuti in Congo I found that young men in particular often traveled in search of mates, but these trips have never been analyzed in a systematic way. Therefore, this paper on reproductive interest in forager mobility makes an important contribution to the study of human mobility. The focus on individuals' movement also supplements previous studies focusing on the movement of entire camps or parts of them. Moreover, the finding of the basis for the "magic" number 500 for regional group size from the correlation (regression lines) between mating distance and population density is extremely interesting.

MacDonald and Hewlett analyze mobility mainly from data on the distance between mating partners. As factors influencing this distance they consider five variables, some of which are interrelated: subsistence mode (foraging vs. horticulture), population density, sex, age, and "wealth" (number of siblings). Most of their results seem natural and understandable; higher mobility occurs among foraging and less densely populated groups and, among males, in adolescents in particular. It is not clear, however, why they predict that "wealthier" men show less mobility.

Marriage as a human form of mating is not just a matter of encountering a mate. Through exchanges of gifts and services and performance of ceremonies at marriage and on the birth and death of their offspring it involves an enduring relationship between the husband, the wife, and their relatives. These social factors undoubtedly play a part in choosing a partner from a distance. The wife's side does not usually want her to marry too far away because of the difficulty in asking the husband's side for payment and service. While MacDonald and Hewlett have not analyzed marriage rules and postmarital residence patterns, I think the relationship between mobility and strict vs. loose rules of marriage and residence deserves further examination.

I have reported elsewhere (Ichikawa 1978) that 86% of the 125 Mbuti men sampled in the Ituri Forest found their spouses in a band within 10 km from their own, whereas some of them traveled 50 km or more away from home. This seems in accord with the results of MacDonald and Hewlett in that even among foragers many find their mates nearby (0–40 km), whereas some have to travel very far. In order to explain this intracultural difference, MacDonald and Hewlett postulate reproductive as well as somatic value arising from the "riskier task" of high mobility. However, they do not present any data on the positive relationship of higher mobility with reproductive success (in terms of number of wives and offspring) or description of the cultural values placed on this "riskier task."

MacDonald and Hewlett point out that hunter-gatherers usually find their marriage partners from more distant places than horticulturalists. While this may be true for "traditional" isolated foraging societies, the situation has long been changed by intercultural relationships between foragers and horticulturalists. In particular, horticulturalists seem to travel farther today because of access to means of transportation, even in remote areas. In fact, the Bantu-speaking horticulturalists in Ituri have spatially more extensive kinship networks than the Mbuti hunter-gatherers, who sometimes travel with those horticulturalists and find mates. Reproductive interest still plays a part in their mobility, but forager mobility may not be fully understood unless it is analyzed in conjunction with that of

the horticulturalists who maintain close relationships with them.

Although statistical data explain little in themselves, they may provide an avenue for enquiry into the process that has generated the statistical difference. We need to know more about reasons other than population density and "evolutionary basis" for higher mobility among foragers, males, and less "wealthy" men, and we also need descriptive as well as statistical data on the relationship between reproductive interest as expressed by mobility and reproductive success as represented by number of wives or offspring and on the cultural values on mobility which sustain this interest and success.

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19 I 99

This is an intriguing and readable contribution to studies of hunter-gatherer mobility and demography. Archaeologists who deal with patterns of exchange among nomadic foragers will find food for thought here. I have a few quibbles with the analysis. I am concerned that correlation and causality are conflated in the observation that the correlation between men's exploration and mating ranges is evidence that the former is a product of men's search for mates. The paragraph that follows this discussion does not provide overwhelmingly convincing evidence that men travel in order to find mates. There is no difference in the reasons for traveling, only in the frequency with which men make long trips—trips they apparently do not enjoy. I am left not knowing if Aka men travel to find mates or if they get mates from afar because they travel. If searching for mates was important, why would they not say so?

Also, I was not sure of the wealth measure: why use siblings? This would not work for American families. From Hewlett's previous work I know that the number of brothers works for the Aka as a wealth measure, but can the same standard be used for the Agta (and does it matter that brothers could not be used for the Agta but only siblings)?

I am not sure that archaeologists will find the model proposed here any more useful than others. When archaeologists talk about mobility, they are primarily talking about residential mobility over the course of a year, but MacDonald and Hewlett are primarily talking about logistical/individual mobility over the course of a lifetime. I do not see how their model incorporates subsistence interests as they say it does. Archaeologists have long treated the presence of "exotic" raw materials as a signal that some people "interacted" with others from far away and have always thought that mating was included in "interaction." I am not sure what is new for archaeologists here: we still do not know how to differentiate "sacred stones" from evidence of mate procurement, logistical transport of stone for tools, exchange, alliance formation (on some basis other than marriage), or migration.

I wish that two aspects of the paper had been left out. The mating-distance data for the Umatilla, Anbarra, and Nez Perce are a bit dubious—I am not sure why these particular "fudge factors" were chosen (why is "some" five times as much as "a few" but "many" only twice as much as "some"?). No matter, these figures are not used in the statistical analysis—but then why are they here? Second, I do not think that the research in evolutionary psychology supports their view. I cannot elaborate here, but none of the three major claims of evolutionary psychologists—that men's and women's different performances on memory/rotation tests show a difference in the way men and women reckon space, that this difference is universal, and that this difference is a product of natural selection—has been demonstrated. MacDonald and Hewlett's using them to substantiate their argument detracts from it.

I am carping. The bottom line is that this is a novel contribution that will enhance regional-scale analyses of prehistoric hunter-gatherer social organization.

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I appreciate this stimulating discussion of how mating shapes forager mobility, and I identify with the focus on nonsubsistence-related mobility. As MacDonald and Hewlett point out, too commonly archaeologists tend to relate all forager mobility to somatic effort. In their summary of previous models of hunter-gather mobility they acknowledge my interest in reproductive concerns yet characterize part of my argument as implying that access to subsistence resources—as opposed to reproductive interests—is the driving force behind mobility. I would like to clarify that although I do discuss environmental-productivity and resource-availability constraints on range size and thus population density and the extent of mobility, my specific interests lie in determining not the driving force behind the mobility but the ultimate costs of mobility. These costs are calculated by proxy as distances traveled pursuant to mate exchange and maintenance of the communication network that ensures future mate exchanges (and thus are in some ways similar to MacDonald and Hewlett's calculation of mean mating distance). While many variables are important to the continued existence of forager systems, I consider the social mobility costs related to the maintenance of mating networks most critical because of their relation to biological viability.

MacDonald and Hewlett present three main "observations." The first, in the domain of intercultural variation, relates to the widely held and intuitively obvious relationship between mating distance and population density—that as population density decreases mating

distance increases. While I have never doubted the validity of this relationship, it is gratifying to see it supported quantitatively by ethnographic field evidence. The second, in the domain of intracultural variation, offers limited evidence to support intuitive theoretical assumptions that in many societies males travel farther than females (I would like to see more data for this relationship.) The third is the claim to have incorporated reproductive concerns at all levels of mobility rather than only at the mating-network level. This point I am a little less sure of, as I also am of their having *explained* inter- and intracultural variation in forager mobility.

Regarding the claim of bringing mating issues into the local level they state that many (I calculate 20% in three of the four cases shown in fig. 6) individuals find mates nearby and especially within 0–40 km of their birthplaces—which corresponds to the level of their model they label "micromovement." MacDonald and Hewlett note that this distance is within the usual area of individual and group subsistence activity. I would note that it does not, however, necessarily follow that these mates are in fact found within the minimum band. The most common range size for hunter-gatherers is associated with a distance between the centers of minimum bands of ca. 20 km (Mandryk 1993). While marriages within 0–40 km may certainly include strictly local within-band linkages, they can also include mates from the next tier of surrounding minimum bands. At lower population densities even the second tier of surrounding groups might be accessible within 40 km. I find it interesting that for two of the four groups shown in figure 6 it is the 21–40 km distance that is the most frequent mating distance recorded—a distance that I would argue certainly equates with the next tier of bands at several different population densities—and therefore question the strength of the argument for local reproductive interests. I am certainly not arguing against the need to highlight reproductive interests. I am just not convinced that the mating-network framework as proposed by Wobst (1974) has really been improved upon by this suggestion. I think that MacDonald and Hewlett's data actually support Wobst's model and that the important mating relationships are at the meso, not micro, scale of their proposed model of forager mobility. I also think that there should be more overlap between mesomovement areas of the neighboring groups depicted in figure 10.

I applaud the challenge to identify archaeological signatures of reproductive mobility—a task that MacDonald and Hewlett demonstrate, with the inventive example of Folsom long-distance travel for mate exchange, is not quite impossible. Finally, they mention that it is difficult if not impossible to identify "prime movers" for mobility. Of course. What I believe they are arguing—and I would certainly agree with—is that we should stop attempting to disembed social and economic aspects of forager mobility. Let us resist the urge to identify prime movers or single-factor explanations

entirely and work instead to acknowledge and emphasize the complex links of causality.

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In this interesting paper MacDonald and Hewlett seemingly confirm (with admittedly small samples) a long-suspected relationship between mating distance and population density, begin teasing apart differences in mobility between males and females, age-groups, etc., and, with refreshing modesty, extend existing models of mobility. There are, it seems to me, just a few matters warranting comment. One is the role of incest taboos and how who is off-limits mating-wise and who is not varies with increasing population density. MacDonald and Hewlett suggest that the likelihood of marrying a relative rises with increased sedentism—though why that should necessarily be so is unclear, especially as they also assume that population density is higher. They further imply—and MacDonald argues explicitly elsewhere (1998b:229)—that taboos against marrying within one's group "are likely relaxed" in more densely populated sedentary communities. There is evidence, however, that the reverse is true (Durham 1992), and doesn't that stand to reason, since greater population density would allow a wider range of mate selection, offering the possibility of exogamy and prohibition (as partners) of a broader range of kin?

I am also curious about the consequences of variance in the age/sex composition of a group: 25 might be a "magic number," but not if by bad decisions or worse luck a group finds itself loaded with individuals past reproductive age or dominantly of one sex or the other. Are there circumstances in which 25 is not large enough to survive fluctuations in life histories? and would that affect mobility decisions?

Finally, there is the matter of reproduction and mobility on "human-free" landscapes. The ethnographic cases are of people with neighbors. What of the situation—which occurred as colonizers entered New Worlds (the Americas, Australia, or remote Oceania)—of small, low-density populations on lands devoid of any other people? The nearest mates were either within the group (and obviously the size of the initial group has bearing here) or back where they came from, and returning may not have been a viable option. Assuming that the colonization process was not driven by demic expansion, how does a group move far away from other people and yet still maintain a "critical mass" of population and reproductive viability while living (initially) in relatively small numbers spread thinly over large areas?

Demographic demands would have been more or less severe depending on the local breeding population's size, growth rates, age and sex composition, and degree

of environmental uncertainty (and the inverse: knowledge of landscape resources), the environmental constraints on group size and population densities, and how rapidly it was moving from its homeland and/or other groups (Borgerhoff Mulder 1992)—and under some ecological circumstances groups may have been dispersing rapidly.

Our mobility models generally assume that a forager has relatively complete information about resource distribution and yields on the basis of which to decide how long to stay and when to leave a patch (Kaplan and Hill 1992, Kelly 1995). Yet this is clearly not the case for the first Americans or the first Australians (the first groups into remote Oceania are a somewhat different matter; they brought resources with them). Colonizers moving across increasingly unfamiliar landscapes had to identify and/or locate vital resources. The greatest effort in information acquisition should occur in patchy environments that vary temporally and in large scale—effectively the ecological situation in which new colonists found themselves (the scale would change over time, presumably, as groups accumulated knowledge of the environment and resources). There are reasons to think that on such an unknown landscape, selection would favor rapid and extensive exploration.

Colonization is thus, in a sense, a compromise between maximizing the amount of information acquired (which might involve maximizing dispersal rates and distances), sustaining energetic return rates, and maintaining vital reproductive links. Given MacDonald and Hewlett's arguments about population density and mating distance, this suggests several implications, among them the following (see also Meltzer 1998): (1) Colonizing groups must have maintained large and more "open" social networks across large areas (Lourandos 1997). (2) They may have regularly aggregated (to exchange mates, resources, and information), and this may have involved return migrations. The presence of exotic stone in sites will surely reveal something of this, though linking exotics to "showing off" is rather problematic (after all, many exotics—at least in North American Paleoindian sites with which I am familiar—are often heavily resharpened, badly worn, and discarded; evidently something besides just showing off is at work). (3) Some small groups of highly mobile foragers, with attenuated ties to distant home groups and without nearby populations with which to seek mates, may have gone extinct, the casualties of slower growth rates dropping them below a critical demographic threshold or perhaps stochastic environmental or climatic events. The latter raises the question of whether there are circumstances where density is so low and distances so high that maintaining links is impossible. If so, what are the reproductive options, and might there be implications at this far end of the mating-distance scale for the boundaries on incest taboos? And could this imply that there might be upper limits on colonization dispersal distances, as constrained by mating distance?

Reply

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We appreciate the commentators' insightful critiques, new data, and ideas for future research. It is especially gratifying that ethnographers (Alvard, Ichikawa, Hames), human geneticists (Cavalli-Sforza, Harpending), and archaeologists (Mandryk, Meltzer) all find something useful in the data or the theoretical framework. We are also delighted with the unpublished mobility data (Hames), the extended population-genetic analysis of our data (Cavalli-Sforza), and the excellent ethnographic examples of how reproductive interests influence mobility (Alvard, Ichikawa). We had hoped that the paper would stimulate more systematic research on forager mobility, but it appears that some ethnographers already have mobility data in hand.

We agree with Hames that the lines between life-history categories (fig. 2) are blurred and that it is often impossible to distinguish single somatic or reproductive motives of behavior, but his new data and previous research (Hames 1983) demonstrate the utility of a life-history approach. Alvard points to the importance of female mobility and emphasis on subsistence resources as influencing male mobility, but the Aka data on reasons for travel indicate no differences between men and women.

Most commentators consider the systematic evaluation of the relationship between population density and mating distance an important contribution, but many point out that the hypothesis itself had been advanced by others but simply never tested. Alvard is critical of the mating-distance value and suggests that it should be divided by two to reflect the fact that both males and females participate in mate seeking. This is similar to Harpending's suggestion that the mating distance ought to be inversely proportional to the square of density, which implies that men and women are traveling equal distances. While this is partially accurate, the Aka data indicate a relationship between mating and exploration for males but not for females, and most studies of foragers indicate that males travel farther than females (MacDonald 1999). We also wanted to retain previous researchers' definition of mating distance. As Cavalli-Sforza points out, distance between birthplaces is not the only or necessarily the best measure, but it is a reasonable one, in part because it is relatively easy to collect in the field.

Kelly is also legitimately critical of our inclusion of the Umatilla, Nez Perce, and Anbarra qualitative data. The values are speculative, but we decided to include them if only to generate ideas for more accurate qualitative measures. The fact that they fit rather well with our other data convinced us that they might be close approximations. Nevertheless, we want to repeat that

these data were not included in the statistical analysis. Our recent research has revealed one other mean mating-distance value for a group of hunter-gatherers: the Birhor of India (mean mating distance, 45.9 km; population density, .22/km²) (Williams 1974). This increases the sample of foragers to 6 and the total forager/farmer sample to 12. The regression correlation remains strong and significant for both the forager ($r^2 = .81$) and the total sample ($r^2 = .86$).

Several researchers (Cavalli-Sforza, Hames, Harpending, Ichikawa, and Meltzer) are critical of the logic underlying our inference that higher population density and sedentism inevitably lead to higher rates of inbreeding. Yellen and Harpending's (1972) data (fig. 5) demonstrate that farmers have higher rates of inbreeding than foragers, but why this is the case is unclear. Hames and Meltzer point out that low-density foragers will run into the same problems of inbreeding if individuals tend to encounter a similar number of individuals from which to select a spouse. Cavalli-Sforza suggests a cultural explanation for the lower inbreeding rates of foragers: that many foragers encourage individuals to "marry far." As we said in our paper, such far-flung kinship ties not only reduce inbreeding but also help reduce economic risk by increasing the regional distribution of reciprocal relationships. As we noted, Cashdan shows that these far-flung ties break down with sedentism as storage replaces kin ties as a risk minimization device.

Hames and Ichikawa suggest that other social factors, such as marriage rules and residence patterns, will impact mating distance. While our anthropological intuitions agree with these propositions, they need empirical study because our limited data suggest otherwise. Our results are consistent with Chagnon's (1992) study of Yanomamo marriage, in which he demonstrates that cross-cousin marriage rules are regularly modified/broken when an individual's reproductive fitness is jeopardized. The correlation between mating distance and population density is strong despite the clearly disparate marriage and residence rules of the cultures in this small sample.

We are pleased that most researchers see some value in the intracultural analysis of Aka and Agta mobility. The case studies enable us to begin to understand the factors that shape an individual's mobility. Alvard is critical of our failure to explain how much variation in travel can be accounted for by reproductive interests. This is difficult in part because of the problems with life-history categories previously mentioned, but it is also due to the fact that this was retrospective analysis—the reanalysis of existing data with evolutionary hypotheses. This is, of course, not the best science.

Ichikawa and Kelly find our measure of "wealth" (kinship resources) problematic. Kelly asks why kin ties, however accurate a measure of wealth for the Aka, should be useful for the Agta. This is a good question, and future studies need to assess the variability in "wealth" measures among various foraging groups. Perhaps a different measure of wealth for the Agta would

explain why individuals with more brothers travel farther for mates than individuals with fewer brothers. Ichikawa questions the evolutionary rationale behind the hypothesis that wealthier individuals should have lower mating distances. Parental investment and sexual-selection theory suggest that individuals with more "resources" will be more likely to attract nearby mates. While this logic explains some of the intracultural variance in Aka travel, it fails to account for it in the Agta case.

The final group of comments addresses the mobility model, particularly as it relates to archaeological contexts. Kelly and Mandryk do not see the model as more useful than existing ones. We, of course, disagree, considering our model more parsimonious and more inclusive, but it does need modification and clarification. First, we agree with Mandryk that is incorrect to suggest that the micromovement level is analogous to Wobst's minimal band (i.e., camp). As she points out, marriage often occurs with close-by neighboring minimal bands. Second, Hames and Mandryk feel that the "important" mating relationships are at the mesomovement rather than the micromovement level. We clearly state that the mean (and possibly the modal) mating distance is likely to be at the mesomovement level. In discussing mating at the micromovement level we simply wanted to point out that mating and reproductive interests are significant at all levels of mobility. As Hames states, "nearly all marriages except village-endogamous ones occurred at distances greater than 15 km." Our point was that reproductive interests do influence activity and mobility close to home—be it within 15 km or 30 km for different Yanomamo groups (see the variation in subsistence ranges in his table 1). Nowhere do we state, as Mandryk suggests, that most foragers find mates at the micromovement level or 0–40 km range. If we were to estimate the mean number of individuals a person would encounter at the various movement levels, it would be 100 at the micromovement level, 500 at the mesomovement level, and 1,000 at the macromovement level. The distances a person traveled to meet this number of individuals would vary by culture and population density.

Finally, Meltzer provides a provocative discussion of the role of our mating-distance/population-density data in understanding forager behavior in "human-free" landscapes. He asks whether our data might have implications for the upper limits on forager colonization in the latest Pleistocene. As MacDonald (1998, 1999) has shown elsewhere, mating distance would definitely constrain Paleo-Indian dispersal distances. In other words, the transient-explorer model of colonization (Beaton 1991) is unlikely, as it would inevitably lead to high levels of inbreeding and extinction of some groups. Such events are unknown to extant foragers. Beaton's estate-settlers model is much more likely, as Paleo-Indian territories slowly expanded over many generations. In this scenario there is no lack of information regarding new landscapes because there were really no new terri-

tories. Generation after generation lived in similar environments and did not move so rapidly that a lack of information jeopardized the fitness of individuals. While exploration beyond territorial boundaries surely occurred, it may have been tempered by oral histories that spoke of the dangers of the territory beyond.

Overall, the commentators have provided provocative and insightful critiques that have forced us to reevaluate the logic of our arguments and new data and rich ethnographic examples that support and extend our understanding of forager mobility. Finally, each commentator has suggested numerous lines of further research on forager decision making.

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