AMERICAN JOURNAL OF HUMAN BIOLOGY 00:00–00 (2014)

Original Research Article

Marrying Kin in Small-Scale Societies

ROBERT S. WALKER[1]* AND DREW H. BAILEY[2]
[1]*Department of Anthropology, University of Missouri, Columbia, MO*
[2]*Department of Psychology, Carnegie Mellon University, Pittsburgh, PA*

ABSTRACT: Objectives: Marriages among kin have the dual effect of both increasing average group relatedness as well as reducing the total number of kin by eliminating more genealogically and geographically distant individuals from kinship networks. Marriage decisions therefore face a tradeoff between density of kin, or formation of intensive kinship systems, and the diversity of kin, or extensive kinship systems. This article tests the hypothesis that extensive kinship systems best characterize hunter-gatherer societies, whereas more intensive forms of subsistence, like horticultural, agricultural, and pastoral economies, are more likely to have intensive kinship systems.

Methods: Here, we investigate the wide range of variation in prevalence of kin marriages across a sample of 46 small-scale societies, split evenly between hunter-gatherers and agropastoralists (including horticulturalists), using genealogies that range in depth from 4 to 16 generations. Regression methods examine how subsistence and polygyny relate to spousal relatedness and inbreeding across societies.

Results: On average, hunter-gatherers show limited numbers of kin marriages and low levels of inbreeding, whereas some agropastoralists are characterized by much higher levels of both, especially in societies where polygynous marriages are more common.

Conclusion: Intensive kinship systems emerge in some intensive economies. This pattern may have favored a kin-selected increase in more large-scale cooperation and inequality occurring relatively recently in human history after the advent of domesticated plants and animals. Am. J. Hum. Biol. 00:000–000, 2014.

Social norms affect patterns of variation in human reproduction. For example, marriage prescriptions for cross-cousins (Flinn and Low, 1986) and other close kin categories like uncle-niece (Hornborg, 1988) tend to increase group relatedness and the density of kin networks via inbreeding. Social norms for polygynous marriages also increase group relatedness through higher reproductive skew because fewer men reproduce (Betzig, 2012). Finally, endogamous marriages and lineal fissions increase relatedness (Fix, 2004; Neel, 1967). Group relatedness in turn governs how strongly kin or group selection (Forster et al., 2006; Hamilton, 1964) favors social behaviors that involve collective action problems like raiding neighbors or keeping the peace (Bowles and Gintis, 2011).

Intensive kinship systems (Bugos, 1985) are defined as those that emphasize the above relatedness-increasing social norms of kin marriages, polygyny, endogamy, and lineal fissions because these behaviors create strongly overlapping networks of kin that often co-reside in the same community. Intensive systems often include marriage alliances between lineages leading to cross-cousin marriages and converging networks of kin (Lévi-Strauss, 1949). Fitness peaks have been observed for cousin marriages as measured by more offspring and grand-offspring (e.g., Chagnon, 1980; Helgason et al., 2008), implying that the small cost of inheriting deleterious alleles is more than compensated by social benefits of marriage alliances (Bittles and Black, 2010), creating a "Goldilocks Zone" of optimal mates at intermediate levels of relatedness. Kin marriages also reduce the dilution of inheritable family wealth, and may help with kin-based resource defense of such wealth, which is more important for many agropastoral societies as opposed to hunter-gatherer societies (Borgerhoff Mulder et al., 2009).

Extensive kinship systems are defined as lacking most, if not all, of the above relatedness-increasing social norms (Yellen and Harpending, 1972). Marrying unrelated or distantly related individuals increases the total possible numbers of kin by inclusion of a wider cast of individuals to form a more diverse kinship network. For example, while a bilateral cross-cousin marriage has a spouse, mother's brother's offspring, and father's sister's offspring as one and the same person, a marriage in an extensive kinship system has these three as separate individuals leading to a larger, yet less related, number of kin and affines. Extensive kinship systems include more geographically-distant marriages in other communities (Fix, 1999; MacDonald and Hewlett, 1999) to form alliances with a large number of affines in a diffuse kinship network (Bugos, 1985). This type of kinship network may be more important in unpredictable environments and for nomadic populations given that it provides a plethora of residential options. Hunter-gatherers that exploit a diversity of unevenly distributed food resources may need to hedge their bets by having kin in different places in times of need (Yellen and Harpending, 1972). This article extends previous studies by using marriage records to quantify the number of marriages at different levels of spousal relatedness and relates them to subsistence patterns using genealogies from small-scale populations around the world (Fig. 1).

METHODS

Genealogies ($n = 46$) and marriage records ($n = 13{,}536$) are from the online database KinSources (http://

Contract grant sponsor: National Geographic Society Research and Exploration grant; Contract grant number: 9165-12.

*Correspondence to: Robert S. Walker. E-mail: walkerro@missouri.edu

Received 2 December 2013; Revision received 28 January 2014; Accepted 28 January 2014

DOI: 10.1002/ajhb.22527

Published online 00 Month 2014 in Wiley Online Library (wileyonlinelibrary.com).

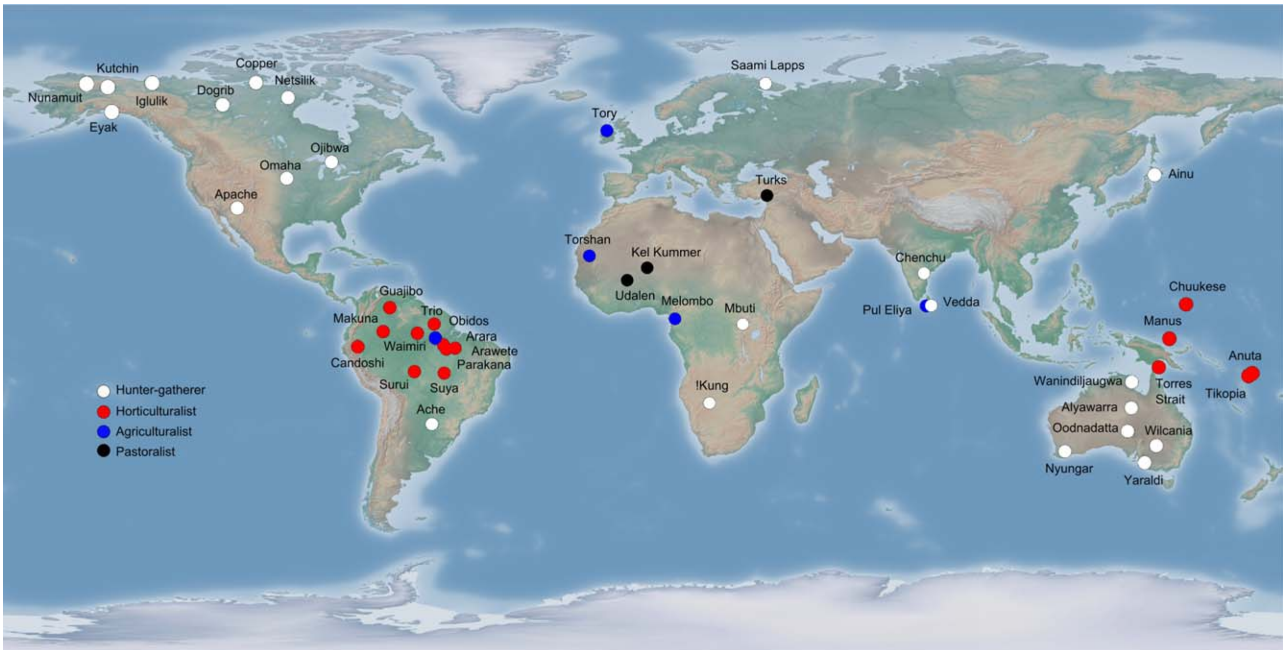

Fig. 1. Map of societies used in this study with designations for various subsistence categories.

kinsources.net) with the addition of Ache hunter-gatherers from Paraguay (Hill and Hurtado, 1996; Hill et al., 2011) and Suya horticulturalists from Brazil (Seeger, 1981; Walker et al., 2013). The sample of small-scale societies (Table 1) is lumped into either hunter-gatherers ($n = 23$) or horticulturalists, agriculturalists, and pastoralists ($n = 23$, referred to collectively as "agropastoralists"). Primarily pastoral populations, like the Tuareg (Kel Kummer and Udalen) and Turkish nomads, were included into the agropastoral category along with other farming societies with both intensive agricultural systems (e.g., plow use or irrigation systems) or less intensive economies such as slash-and-burn horticulturalists. Genealogies range in depth from 4 to 16 generations. Calculating spousal relatedness has the problem that different studies have varying degrees of quality in available genealogical information so the depth of the genealogy in number of generations is added to regression models as a quality control variable. Studies with fewer than 4 generations were excluded.

Calculation of coefficients of relatedness for marital pairs (spousal relatedness) and coefficients of inbreeding (probability that both alleles at one locus are from the same ancestor, Wiggans et al., 1995; Wright, 1922), were calculated from genealogies in Ed Hagen's Descent software (http://itb.biologie.hu-berlin.de/~hagen/Descent). The following 4 categories were used to categorize the relatedness between spouses: [0,0.03125), [0.03125,0.0625), [0.0625,0.125), and [0.125,1). These are cutoffs of 1/32, 1/16, and 1/8 levels of relatedness. The latter represents relatedness greater than or equal to first cousins or greater than quadruple second cousins.

Linear regressions were run in SPSS (version 22) at the societal level with various outcome measures of spousal relatedness and inbreeding. A mixed model analyzed spousal relatedness at the level of marital pairs nested within societies. Relevant predictors variables are polygyny (calculated as the mean number of wives per married man), subsistence type (hunter-gatherer or agropastoral), and the interaction between the two variables. Polygyny was rescaled in the regressions by substracting one so that the interpretation of the main effect of subsistence type is the difference in the outcome variable between agropastoralists and hunter-gatherers under monogamy (when mean number of wives is 1).

RESULTS

Spousal relatedness

The proportion of marriages that involve kin of different levels of relatedness varies widely across societies. On one extreme are 879 Omaha marriages (Barnes, 1984; Dorsey, 1884) without a single case of related individuals marrying one another. On the other extreme are the Kel Kummer Tuareg (Chaventre, 1983) where 602 of the 1,139 marriages, or 53%, involve coefficients of relatedness that are greater than or equal to 0.125 (first cousin relatedness or higher).

The proportion of marriages for different ranges of relatedness varies widely but predictably with different categories of subsistence (Fig. 2). Hunter-gatherers have low spousal relatedness with an average spousal relatedness of only 0.004 across 23 societies (range 0–0.023). Some agropastoralists have much higher average levels of relatedness between spouses, averaging 0.029 across 23 societies (range 0–0.179), or over 7 times the average for hunter-gatherers (Fig. 3).

Inbreeding

Coefficients of inbreeding correlate strongly with mean spousal relatedness across societies ($r = 0.98$, $n = 46$, $P < 0.00001$). Coefficients of inbreeding range from 0 to

TABLE 1. Societies in this study with subsistence type, number of generations, number of marriages, mean number of wives per married man (polygyny), mean coefficient of inbreeding, and mean relatedness between spouses. Table is sorted by ascending inbreeding

Society	Subsistence	Generations	*N* marriages	Polygyny	Inbreeding	Spousal relatedness
Ainu	Hunter-gatherer	5	104	1.06	0	0.008
Eyak	Hunter-gatherer	4	94	1.18	0	0
Kutchin	Hunter-gatherer	4	29	1.07	0	0
Mbuti	Hunter-gatherer	5	243	1.05	0	0
Nunamuit	Hunter-gatherer	4	33	1.10	0	0
Omaha	Hunter-gatherer	7	879	1.33	0	0
Oodnadatta	Hunter-gatherer	4	69	1.21	0	0
Wilcania	Hunter-gatherer	4	152	1.04	0	0.001
Suya	Horticultural	5	57	1.12	0	0
Melombo	Agricultural	6	248	1.36	0	0
Yaraldi	Hunter-gatherer	6	298	1.18	0.00001	0.000
Manus	Horticultural	7	751	1.11	0.00007	0.000
Apache	Hunter-gatherer	5	129	1.03	0.00017	0.001
Nyungar	Hunter-gatherer	5	338	1.08	0.00021	0.002
Guahibo	Horticultural	5	97	1.03	0.00023	0.004
Saami Lapps	Hunter-gatherer	4	99	1.02	0.00032	0.001
Tikopia	Horticultural	14	96	1.10	0.00033	0.016
Tory	Agricultural	5	147	1.04	0.00037	0.004
Obidos	Agricultural	9	1397	1.22	0.00040	0.002
Wanindiljaugwa	Hunter-gatherer	4	209	2.03	0.00051	0.002
Netsilik	Hunter-gatherer	4	172	1.08	0.00062	0.003
Dogrib	Hunter-gatherer	4	106	1.06	0.00093	0.006
Iglulik	Hunter-gatherer	4	209	1.18	0.00097	0.010
Torres Strait	Horticultural	6	345	1.37	0.00101	0.007
Copper	Hunter-gatherer	4	101	1.06	0.00115	0.002
Chenchu	Hunter-gatherer	5	235	1.15	0.00129	0.006
Candoshi	Horticultural	6	449	1.22	0.00133	0.002
Waimiri-Atroari	Horticultural	4	103	1.39	0.00134	0.010
Trio	Horticultural	5	385	1.27	0.00146	0.003
!Kung	Hunter-gatherer	4	123	1.23	0.00265	0.005
Ojibwa	Hunter-gatherer	9	157	1.19	0.00317	0.007
Pul Eliya	Agricultural	7	60	1.15	0.00319	0.019
Chuukese	Horticultural	11	802	1.20	0.00391	0.009
Ache	Hunter-gatherer	8	134	1.04	0.00404	0.007
Alyawarra	Hunter-gatherer	6	114	1.34	0.00466	0.012
Anuta	Horticultural	15	206	1.13	0.00583	0.013
Vedda	Hunter-gatherer	5	20	1.18	0.00651	0.024
Makuna	Horticultural	6	109	1.25	0.00710	0.018
Udalen Tuareg	Pastoral	9	328	1.36	0.00833	0.026
Arawete	Horticultural	6	210	1.40	0.01032	0.026
Parakana	Horticultural	7	192	1.76	0.01138	0.060
Turks	Pastoral	8	862	1.14	0.01776	0.034
Surui	Horticultural	7	358	1.63	0.01942	0.059
Torshan	Agricultural	16	1094	1.30	0.01953	0.035
Kel Kummer Tuareg	Pastoral	14	1145	1.41	0.06708	0.132
Arara	Horticultural	5	48	1.78	0.07664	0.179

0.076 for the Arara, Carib-speaking horticulturalists in Brazil. The second highest inbreeding coefficient of 0.067 is the Kel Kummer Tuareg with prescribed cousin and mostly endogamous marriages (Nicolaisen, 1963). Only horticulturalists, agriculturalists, and pastoralists show coefficients that are >0.025 with all the hunter-gatherer societies less than this value. The hunter-gatherer sample has a variance of inbreeding coefficients that is 3 orders of magnitude lower than for more intensive subsistence regimes. In other words, while some agropastoralists have high levels of inbreeding, none of the hunter-gatherers do.

Regression analyses

We regressed each of the spousal relatedness measures and inbreeding on polygyny, subsistence type, and their interaction, which combined explain approximately half the variance in our outcome variables (Table 2). Results for spousal relatedness are nearly identical for regressions at the societal level and at the level of marital pair. In all 7 regression models, the polygyny-by-subsistence interaction effect was statistically significant, but the main effect of polygyny was not. In all of these models, results indicated higher levels of spousal relatedness and inbreeding among agropastoralists as polygyny increased, and no effect of polygyny on either spousal relatedness or inbreeding among hunter-gatherers. The consistent pattern is shown in Figure 4 for the smallest spousal relatedness category. The effects were modest for the two intermediate spousal relatedness outcomes ([0.03125,0.0625), [0.0625,0.125)) because these outcomes were the least informative of high versus low levels of spousal relatedness. These effects indicate that generally higher levels of spousal relatedness and inbreeding values among some agropastoralists were closely related to their higher levels of polygyny.

We checked for differences in spousal relatedness with first, second, and third wives but found no relationship between spousal relatedness and wife order. In other words, primary and secondary wives (and so on where applicable) have similar levels of relatedness with their husband.

DISCUSSION

We show that hunter-gatherers generally have limited numbers of kin marriages and low levels of inbreeding, or extensive kinship systems, further corroborating previous results and predictions (Fix, 1999; MacDonald and Hewlett, 1999; Yellen and Harpending, 1972, Bugos, 1985). In contrast, some agropastoralists, especially those with more polygynous marriages, have more kin marriages and inbreeding that form intensive kinship systems. Some agropastoralists live in more related communities, at least in part because of a number of social norms that affect reproduction and coresidence patterns. These include kin marriages, marriage alliances, endogamy, polygyny, and lineal fissions. Hunter-gatherers generally lack or have a lower prevalence of these relatedness-increasing social behaviors. Fission-fusion dynamics lead to considerable gene flow in hunter-gatherers and exogamous marriages disrupt the coresidence of consanguineal kin (Hill et al., 2011). This is at least part of the reason why polygyny does not vary with inbreeding across hunter-gatherers.

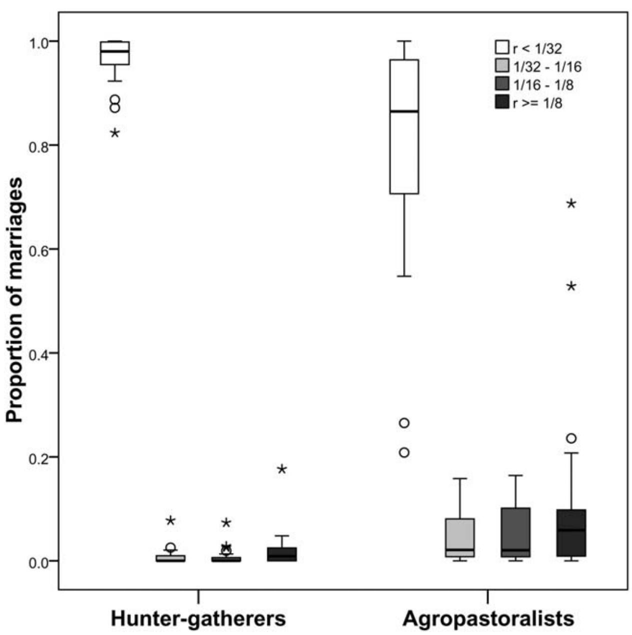

Fig. 2. Boxplots of the proportion of marriages for different ranges of relatedness as a function of subsistence. Hunter-gatherers generally have low spousal relatedness, while some agropastoralists (including horticulturalists) have higher levels of relatedness between spouses.

We note that some horticultural (e.g, Suya) and agricultural (e.g., Melombo) societies have limited spousal relatedness and inbreeding with marriage profiles that look similar to those of hunter-gatherers. Therefore, instead of generalizing all agropastoralists as having intensive kinship, a better measure is a continuous scale of kinship intensity indexed by mean spousal relatedness (Fig. 3) and coefficients of inbreeding that covary with polygyny (Fig. 4, Table 2) and increase group relatedness. Among agropastoralists, polygyny may be a proxy for reproductive and political inequality as well as complexity in social organization and accompanying marriage norms. If so, then complexity, leadership, spousal and group relatedness and a number of other cultural traits may all be interrelated (Table 3).

Cooperation forms around consanguineal relatedness (Bowles and Gintis, 2011; Forster et al., 2006; Hamilton, 1964). Humans are unusual in that we have large social groupings with embedded families formed around relatively stable pair-bonds (Alexander, 1979; Chapais, 2008; Rodseth et al., 1991). Hunter-gatherers have fluid fission/fusion social dynamics that break up the coresidence of sibling sets and lead to rather low levels of group

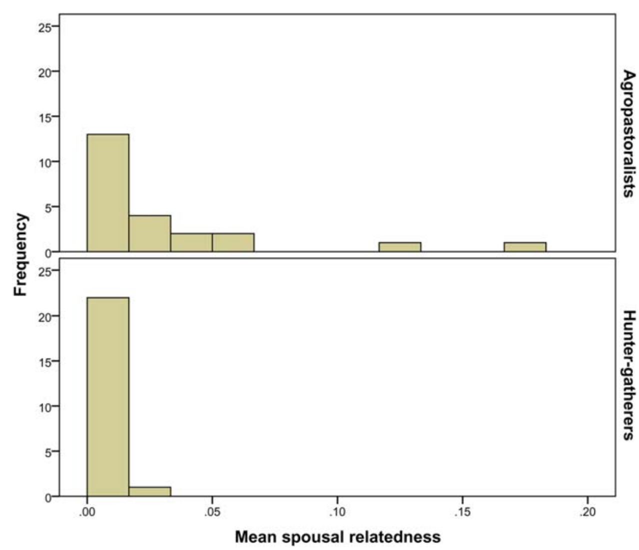

Fig. 3. Frequency distributions of mean spousal relatedness for agropastoralists (including horticulturalists) (top) and hunter-gatherers (bottom).

TABLE 2. Regression models of different measures of spousal relatedness and inbreeding as functions of subsistence (agropastoral vs. hunter-gatherer), polygyny, and the interaction between the two while adjusting for generations (genealogical depth)

Dependent variable	Intercept	Agropastoral	Polygyny	Polygyny X Agropastoral	Generations	R^2
Mean spousal relatedness	−0.009	−0.029[a]	0.001	0.153[b]	0.003[a]	0.59
Proportion marriages $r < 1/32$	1.073[b]	0.140[a]	−0.002	−0.829[b]	−0.022[b]	0.71
Proportion marriages r $1/32 - 1/16$	−0.023[a]	−0.010	−0.011	0.097[a]	0.007[a]	0.49
Proportion marriages r $1/16 - 1/8$	−0.030[a]	−0.030	0.011	0.162[b]	0.007[a]	0.67
Proportion marriages $r > 1/8$	−0.019	−0.104[a]	0.003	0.570[b]	0.008	0.53
Inbreeding	−0.006	−0.012[a]	0.001	0.060[b]	0.001[a]	0.48
Spousal relatedness	−0.010	−0.029[a]	0.001	0.151[b]	0.003[a]	

All models are at the societal level except the last model, spousal relatedness, which is at the level of marital pairs nested within societies.
[a]Refers to $P < 0.05$.
[b]Refers to $P < 0.001$.

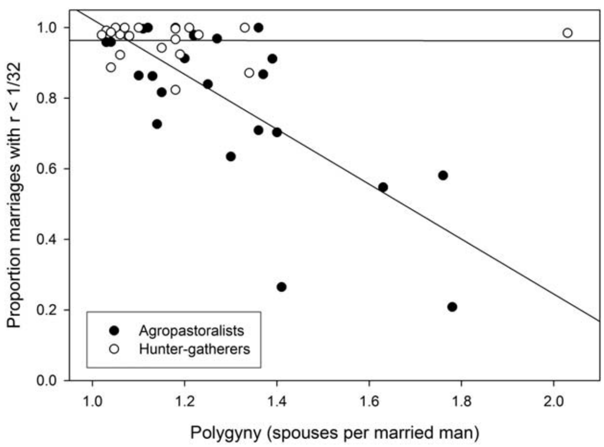

Fig. 4. Relationship between the proportion of marriages with low spousal relatedness ($r < 1/32$), including the most common situation of no relatedness ($r = 0$), and our measure of polygyny. The strongest effect is an interaction between agropastoral subsistence (including horticulturalists) and polygyny such that agropastoralists with higher levels of polygyny also have more related spouses.

TABLE 3. Generalization of expected cultural differences between extensive and intensive human kinship systems

Cultural trait	Extensive kinship	Intensive kinship
Kin marriages	Few	Many
Inbreeding	Low	High
Marriage distance	Often far	Often close
Marriages	Exogamous	Endogamous
Marriage alliances	Diffuse	Reciprocal
Regulation of reproduction	Weak	Strong
Affines	Unrelated, More	Related, Fewer
Fissions	Familial	Lineal
Group size	Smaller	Larger
Polygyny	Mostly low	High
Kinship network	Diverse	Dense
Group relatedness	Low	High
Economy	Hunter-gatherer	Agropastoral
Political inequality	Low	High
Heritable wealth	N/A	Important
Resource defense (Warfare)	Low	High

relatedness (Hill et al., 2011). Therefore, some have discounted genetic relatedness as a primary driver for human cooperation, especially in wider social spheres. However, agropastoral systems with the potential for dense networks of kin may have allowed kin selection to favor an increase in large-scale cooperation (e.g., tribal warfare, peace-making, cooperative labor, political inequality, etc.) that have increased in importance relatively recently in human history after the advent of domesticated crops and animals.

Social norms concerning marriage decisions differ drastically across societies, perhaps most notably between nomadic hunter-gatherers and intensive agropastoral economies. These norms strongly alter patterns of reproduction and kinship. Hopefully, future research will pursue the downstream behavioral effects of individuals living in communities of intensive versus extensive kinship regimes, perhaps offering a kin-selection explanation for the emergence of large-scale cooperation, complexity, and inequality.

ACKNOWLEDGMENTS

This article benefited from help and advice from Woodrow Denham, Ray Hames, and Kim Hill.

LITERATURE CITED

Alexander RD. 1979. Darwinism and human affairs. Seattle: University of Washington Press.
Barnes RH. 1984. Two Crows denies it: A history of controversy in Omaha sociology. Lincoln: University of Nebraska Press.
Betzig L. 2012. Means, variances, and ranges in reproductive success: comparative evidence. Evol Human Behavior 33:309–317.
Bittles AH, Black ML. 2010. Consanguineous marriage and human evolution. Annu Rev Anthropol 39:193–207.
Borgerhoff Mulder M, Bowles S, Hertz T, Bell A, Beise J, Clark G, Fazzio I, Gurven M, Hill KR, Hooper P, Irons W, Kaplan H, Leonetti DL, Marlowe F, Naidu S, Nolin D, Piraino P, Quinlan RJ, Sear S, Shenk M, Smith EA, Wiessner P. 2009. The intergenerational transmission of wealth and the dynamics of inequality in pre-modern societies. Science 326:682–688.
Bowles S, Gintis H. 2011. A cooperative species: human reciprocity and its evolution. Princeton, NJ: Princeton University Press.
Bugos PE. 1985. An evolutionary ecological analysis of the social organization of the Ayoreo of the Northern Gran Chaco. Phd Dissertation, Evanston, Ill, Northwestern University.
Chagnon NA. 1980. Kin selection theory, kinship, marriage, and fitness among the Yanomamo Indians. In: Barlow G, Silverberg J, editors. Sociobiology: Beyond nature/nurture? Boulder, CO: Westview Press. p. 545–571.
Chapais B. 2008. Primeval kinship: how pair bonding gave birth to human society. Cambridge, MA: Harvard University Press.
Chaventré A. 1983. Evolution anthropo-biologique d'une population touarègue. Les Kel Kummer et leurs apparentés. Paris PUF, INED.
Dorsey JO. 1884. Omaha sociology. Third annual report of the Bureau of Ethnology to the secretary of the Smithsonian, 1881–1882: 205−307.
Fix AG. 1999. Migration and colonization in human microevolution. Cambridge: Cambridge University Press.
Fix AG. 2004. Kin-structured migration: causes and consequences. Am J Hum Biol 16:387−394.
Flinn MV, Low BS. 1986. Resource distribution, social competition, and mating patterns in human societies. In: Rubenstein D, Wrangham R, editors. Ecological aspects of social evolution. Princeton NJ: Princeton University Press. p. 217–243.
Forster KR, Wenseleers T, Ratnieks FLW. 2006. Kin selection is the key to altruism. Trends Ecol Evolution 21:57–60.
Hamilton WD. 1964. The genetical evolution of social behaviour I & II. J. Theor Biol 7:1–52.
Helgason A, Pálsson S, Guobjartsson D, et al. 2008. An association between the kinship and fertility of human couples. Science 319:813–815.
Hill KR, Hurtado AM. 1996. Ache life history: the ecology and demography of a foraging people. New York: Aldine de Gruyter.
Hill KR, Walker RS, Bozicevic M, Eder J, Headland T, Hewlett B, Hurtado AM, Marlowe F, Wiessner P, Wood B. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. Science 331:1286–1289.
Hornborg, A. 1988. Dualism and Hierarchy in Lowland South America. Trajectories of Indigenous Social Organization. Acta Universitatis Upsaliensis, Uppsala Studies in Cultural Anthropology. p 9.
Lévi-Strauss C. 1949. Les Structures Élémentaires de la Parenté. Paris: Presses Universitaires de France.
MacDonald DH, Hewlett BS. 1999. Reproductive Interests and Forager Mobility. Curr Anthropol 40:501–524.
Neel JV. 1967. The genetic structure of primitive human populations. J Hum Genet 12:1–16.
Nicolaisen J. 1963. Ecology and culture of the pastoral Tuareg. Copenhagen: National Museum of Copenhagen.
Rodseth L, Wrangham RW, Harrigan AM, Smuts BB. 1991. The human community as a primate society. Curr Anthropol 32:221–254.
Seeger A. 1981. Nature and Society in Central Brazil. Cambridge: Harvard University Press.
Walker RS, Beckerman S, Flinn MV, Gurven M, von Rueden CR, Kramer KL, Greaves RD, Córdoba L, Villar D, Hagen EH, Koster JM, Sugiyama L, Hunter TE, Hill KR. 2013. Living with kin in lowland horticultural societies. Curr Anthropol 54:96–103.
Wiggans GR, Van Raden PM, Zuurbier J. 1995. Calculation and use of inbreeding coefficients for genetic evaluation of United States dairy cattle. J Dairy Sci 78:1584–1590.
Wright S. 1922. Coefficients of inbreeding and relationship. Am Nat 56: 330–338.
Yellen J, Harpending H. 1972. Hunter-gatherer populations and archaeological inference. World Archaeol 4:244–253.