

Hunter-Gatherers and Human Evolution

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Although few hunter-gatherers or foragers exist today, they are well documented in the ethnographic record. Anthropologists have been eager to study them since they assumed foragers represented a lifestyle that existed everywhere before 10,000 years ago and characterized our ancestors into some ill-defined but remote past. In the past few decades, that assumption has been challenged on several grounds. Ethnographically described foragers may be a biased sample that only continued to exist because they occupied marginal habitats less coveted by agricultural people.³ In addition, many foragers have been greatly influenced by their association with more powerful agricultural societies.⁴ It has even been suggested that Holocene foragers represent a new niche that appeared only with the climatic changes and faunal depletion at the end of the last major glaciation.⁵ Despite these issues, the ethnographic record of foragers provides the only direct observations of human behavior in the absence of agriculture, and as such is invaluable for testing hypotheses about human behavioral evolution.⁶

Holocene foragers may indeed have filled a new niche in many places, but by analyzing how climate, flora, and fauna influence ethnographic foragers we can gain insights into how Pleistocene foragers should have differed from them. Contact with agriculturalists poses a greater challenge. When more powerful societies that practice horticulture, pastoralism, or intensive agriculture (all referred to here as agriculturalists) come in contact with foragers, they can rapidly alter forager subsistence and culture. The significance of such contact, however, varies considerably. Many Pygmies, such as the Mbuti, speak only the Bantu language of their farmer neighbors for

whom they do some labor in exchange for food. On the other hand, the Hadza have had contact with agropastoralists for a long time but maintain their language. Their interaction has been limited mainly to the trade of meat and honey for iron and tobacco, and has altered the Hadza surprisingly little over the past century.⁷ All we can do is perhaps give extra weight to those with less contact. We might also give extra weight to those in richer habitats, though the bias toward marginal habitats is not as great as usually assumed.

The greatest obstacle to using foragers as analogs of our ancient ancestors is that virtually all foragers in the ethnographic record have complex technology compared to premodern hominins. Human niches are defined to a large extent by technology, even among foragers. There are horse-mounted, bow-and-arrow hunters of bison, harpoon hunters of walrus who travel in kayaks, salmon weir-fishers, and spear, blowgun, and net hunters. Technology has allowed human foragers to occupy the full spectrum of terrestrial habitats, producing a wide range of cultural variation. Our ancestors must have varied considerably as well, so it seems pointless to reconstruct a single type of society. How-

ever, because we think the first modern humans arose from a particular population living in Africa 160,000 to 200,000 years ago,⁸ there would have been a limited range of variation in that particular population at that particular time. As modern humans spread to diverse habitats and developed diverse technologies, socio-cultural variation increased. Because the archeological record, with a few exceptions like Tasmania,⁹ reveals a trend toward increasing efficiency in technological evolution, we can assume that there was less efficiency (in extracting resources, for example) as we go further back in time. It is mainly the effects of increased productivity associated with technology that we need to subtract from ethnographic foragers when extrapolating to much earlier times.

Ironically, while foragers may be problematic analogs of humans in the past, they are certainly the most useful exemplars of humans in the present. To know which of our traits are derived and therefore require a separate explanation from traits we share with *Pan*, we must first characterize extant species. When we compare humans with other species with respect to traits like diet, group size, home range, mating system, or mortality rates, we need to measure these traits in foragers, not agricultural populations, if we are to understand the relevant selective forces that shaped modern humans. Here I provide an overview of foragers to put humans in primate perspective and to examine some basic relationships between social organization, and habitat, and technology so that their effects can be accounted for when modeling hominin behavioral evolution.

THE FORAGER SAMPLE

The sample I use here is, to my knowledge, the largest forager dataset that exists (Fig. 1). I borrow heavily

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Box 1. Glossary

Absolute latitude—absolute value of latitude; that is, distance from the equator whether north (designated with positive numbers) or south (designated with negative numbers).

Primary biomass—the amount of plant biomass (kg/m^2), using Binford's equation.¹

Effective temperature (ET)— $18W - 10C / (W - C) + 8$, where W = mean temperature of the warmest month and C = mean temperature of the coldest month.

Hunting, gathering, fishing—The percent of foods acquired by each foraging activity (in some cases these are actual weight or calorie measurements, but in most cases only estimates of the ethnographer).

Ethno-linguistic group—the set of people sometimes referred to as a tribe who share a language.

Ethno-linguistic population—the population of the ethno-linguistic group.

Ethno-linguistic area—the total area occupied by the ethno-linguistic group.

Population density—ethno-linguistic population/total area of ethno-linguistic group.

Local group population—the mean population of the residential band (the people who regularly reside in the same camp or settlement). When maximums and minimums for a society were cited, these were averaged.

Number of moves—the number of times per year camp location is moved.

Male/female contribution to diet—the percent of the diet acquired by females or males. (In some cases these are actual weight or calorie measurements, but in others the values are

calculated from the percent contributed by each sex in hunting, gathering, and fishing.

Polygyny rate—the percent of married men or married women that are in a polygynous marriage. This is not the same as the percent of all men and women; for example, 100% of married men could be polygynous even with an operational sex ratio of 1, since many other men can be bachelors.

Local group area (home range)—by dividing the ethno-linguistic population by the local group population we can derive the number of local groups. We can derive the minimum area used by a local group if we divide the total area of the ethno-linguistic group by the number of local groups. This is a minimum estimate because it assumes nonoverlapping areas, whereas local groups tend to move into areas that overlap with those of other local groups. Even though females may have shorter day ranges than males, the main factor determining area covered in a year is moving the camp to a different area, not forays out from camp.

Total fertility rate (TFR)—the mean number of children a woman bears over her reproductive career.

Infant mortality rate—the percent of children who die within the first year of life.

Juvenile mortality rate—the percent of children who die within the first 15 years of life.

Interbirth interval (IBI)—the mean number of months between births regardless of survivorship.

Weaning age—years of age when nursing completely ends.

Age at first reproduction—mean age when females first give birth.

from previous researchers, especially Lewis Binford's book *Frames of Reference*.¹ Many other data come from tables in *The Foraging Spectrum* by Robert Kelly.¹⁰ Both Kelly and Binford relied heavily on George Peter Murdock's *Ethnographic Atlas*,¹¹ and I have added more from the Atlas and the Standard Cross-Cultural Sample (SCCS) in their updated, electronic form on the World Cultures CD.² I have also taken data from many other original sources (see Appendix). There are 478 societies altogether, with almost all deriving less than 10% of their diet from domesticated foods. On several important variables (Box 1), I report descriptive statistics in Tables 1 and 2.

Comparative analyses face the problem of non-independent data (Galton's Problem) whether the units are species, cultures, or individuals.¹² When the phylogenetic relationships between species are known, they can be used to avoid Type 1 or Type 2

errors. Across human societies it is less clear whether genetic or linguistic relatedness would be preferable for constructing phylogenies because of genetic mixing and language replacement. The SCCS was assembled to avoid Galton's Problem,¹³ but consists of only 186 societies, of which about one-fifth are foragers. The results I present on kinship, marital residence, and the mating system are mostly from my previous analyses of the SCCS. Because here I am more concerned with the full range of variation and central tendencies, I use the complete forager sample even though there is no satisfactory phylogeny yet. Because I present some correlations, I have broken the sample into Old World versus New World. If relationships found in the whole sample also hold within each hemisphere, we can have more confidence that the relationship is real.

In general, evolutionary theory predicts that individual behavior will be

adaptive and track ecological conditions, subject to constraints. Populations should also track local conditions since groups are seen as collections of fitness-maximizing individuals. This assumption should usually hold despite the fact that individuals are so often in conflict with each other. Two individuals might compete for scarce foods but both go about acquiring them with the same "most efficient" foraging strategy in a given environment. Thus, to the extent that certain aspects of social organization follow from foraging strategies, which in turn track ecology and technology, we should be able to explain relationships between habitat variation and social organization.

To illustrate how ecology and technology shape social organization, consider the equestrian foragers. Several North American Indian tribes became specialists in hunting bison from horseback during the 1700s, after the Spaniards introduced the horse.¹⁴ In

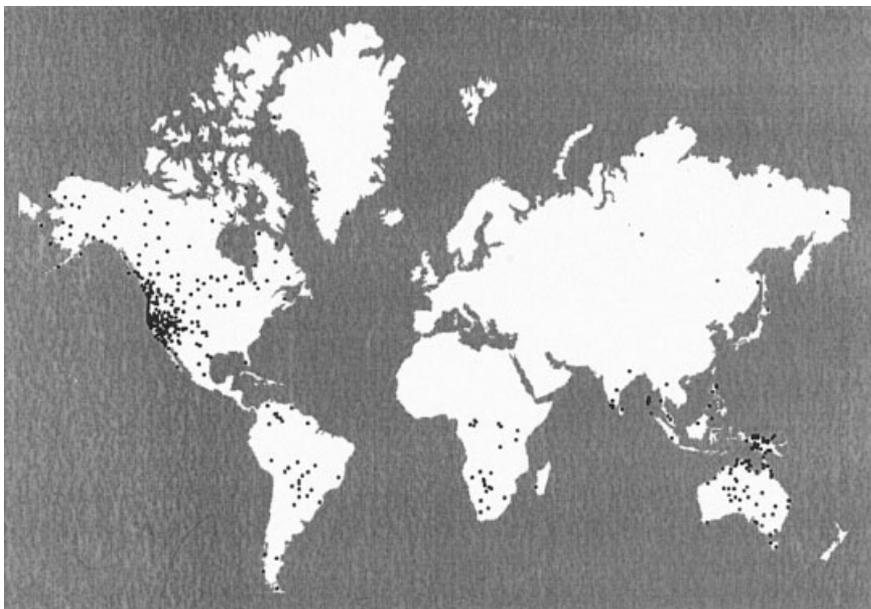


Figure 1. Geographic location of the total forager sample ($n = 478$).

the sample here, equestrian foragers have much larger home ranges and significantly larger local groups than do nonequestrian foragers. The horse increased hunting success rates and lowered travel costs, allowing the Plains Indians to specialize in hunting the high-yielding bison and follow them over vast distances in large groups.¹⁵ When reconstructing periods before horse domestication with data from ethnographic foragers, we can ignore the equestrian foragers. If we are interested in the period before 30,000 years ago, we might exclude the arctic foragers because it was only during the last 30,000 years that very cold areas were occupied by modern *sapiens*.¹⁶ Like the equestrian foragers, arctic foragers have larger home ranges than do others, but in their case it is due to the low density of foods, which requires covering large areas.

When we are interested in how human foragers respond to different environments, the full sample is most useful because it reveals how factors like very cold climates or horses alter traits like diet, group size, and home range. When we are interested in estimating parameters for modeling earlier periods, on the other hand, we need a more relevant sample. For this reason, I created a subsample by excluding those foragers who hunt from

horseback and those where effective temperature (ET) is $<13^{\circ}\text{C}$, which eliminates the arctic foragers (Table 1). I use the warm-climate, nonequestrian subsample for exploring traits during earlier periods, but results refer to the whole sample unless otherwise stated.

HABITAT VARIATION AND DIET

Primary biomass (kg/m^2) is a measure of the productivity of a habitat calculated from climate data.¹ The plant matter it measures provides food for animals and so limits their numbers (secondary biomass). It excludes animal biomass and includes inedible plant parts, so it is not an ideal measure of food abundance for humans. For example, rainforests contain less human food per kilogram of primary biomass than savannas do, but because there are so many more kg/m^2 of primary biomass in rainforests there is usually more total food energy present.¹⁰ Therefore, even though primary biomass is not ideal, it does provide a rough estimate of habitat quality, and since it has been calculated by Binford¹ for most of the foragers, I use his data. In the sample here, primary biomass peaks around latitude 15° North and approaches zero at the poles (Fig. 2). The northern

and southern hemispheres are not mirror images since there is more land mass in the northern hemisphere. Mainly as a consequence of temperature effects on primary biomass, as Lee,¹⁷ Kelly,¹⁰ and Binford¹ have previously reported, gathering falls off in colder temperatures at higher absolute latitudes, where there are fewer plants, whereas hunting and fishing increase (Fig. 3). Males, therefore, contribute more to the diet at higher absolute latitudes ($r = .480$, $P < .0005$, $n = 158$). Male contribution to diet is also higher where fishing is more important ($r = .510$, $P < .0005$, $n = 155$).

The “marginal habitat criticism” noted earlier assumes that areas ideal for agriculture would have been ideal for foraging and that areas bad for farming would have also been bad for foraging. This is not necessarily the case. Some areas unsuitable for planting can be quite good for foraging. The map of foragers (Fig. 1) shows that the main bias in the sample is a geographic one due to history. The absence of foragers in the circum-Mediterranean and most of Eurasia is not because that huge area has rich arable soil and other continents do not, but because complex state societies arose earlier there and had incorporated or replaced all the foragers before ethnographies were written. In addition, a large fraction of the foragers in marginal (low primary biomass) habitats are those in Central Australia, who were not pushed there by agriculturalists since there were no agriculturalists on the continent prior to about 1800. The habitats with the lowest primary biomass are those of the arctic foragers. When the cold-climate foragers are excluded, a comparison reveals that forager habitats are not less productive than those of agriculturalists (Box 2).¹⁸

Population density increases with primary biomass, as expected from basic ecological theory, but it levels off at a primary biomass of about $30 \text{ kg}/\text{m}^2$ (Fig. 4). The high-density foragers at primary biomass about $35 \text{ kg}/\text{m}^2$ are mostly the foragers of the northwest coast of North America. These complex foragers occupy habitats where salmon return to their freshwater spawning areas. Their

TABLE 1. Traits for the Total Sample and the Warm-Climate, Nonequestrian Subsample, by Hemisphere^a

Region	Statistic	Primary Biomass (kg/m ²)	% Diet Gathering	% Diet Hunting	% Diet Fishing	% Male Contribution to Diet	Ethno-linguistic Pop.	Ethno-linguistic Area (km ²)	Pop. Density (Persons per km ²)	Local Group Pop.	Local Group Area (km ²)	Number of Moves per Year
Total Sample of Foragers												
Old W.	Mean	15.17	50.64*	25.1009	23.72	51.16	1393	24146	.23	32.10	592.35	8.87*
	N	105	114	114	114	35	160	105	105	91	82	105
	SD	16.17	23.00	13.95	25.86	18.78	2035	51889	.24	31.94	1079.78	9.15
	Min	.12	.00	.00	.00	25.00	4	45.50	.00	13.10	21.76	.00
	Max	59.27	90.30	65.00	90.00	100.00	11800	386880	1.23	250.00	5516.32	45.00
	Median	9.86	55.00	25.00	10.00	50.00	619	6880	.16	25.00	162.50	8.00
New W.	Mean	11.35	29.64	36.29*	33.52*	64.81*	1991*	43966*	.26	55.37*	2055.91*	7.00
	N	236	287	287	287	123	236	235	235	203	177	235
	SD	11.99	22.19	19.93	26.59	17.96	2594	89051	.40	51.08	3060.26	9.42
	Min	.02	.00	5.00	.00	20.00	23	270	.00	14.50	19.00	.00
	Max	46.25	80.00	90.00	95.00	100.00	14582	660000	3.09	275.00	21079.00	58.00
	Median	6.08	30.00	30.00	30.00	63.00	1163	12200	.09	35.00	708.00	4.00
Total	Mean	12.52	35.61	33.11	30.74	61.79	1749	37845	.25	48.17	1592.54	7.58
	N	341	401	401	401	158	396	340	340	294	259	340
	SD	13.51	24.27	19.09	26.72	18.96	2399	79900	.36	47.20	2687.00	9.36
	Min	.02	.00	.00	.00	20.00	4	46	.00	13.10	19.00	.00
	Max	59.27	90.30	90.00	95.00	100.00	14582	660000	3.09	275.00	21079.00	58.00
	Median	7.08	35.00	30.00	25.00	60.00	895	9050	.11	29.50	426.28	5.00
Warm-Climate, Nonequestrian Foragers												
Old W.	Mean	15.59	54.78*	24.23	20.78	46.83	991	18476	.24	30.52	473.13	8.86
	N	96	98	98	98	29	97	96	96	77	73	96
	SD	16.54	20.12	13.23	24.69	15.73	1526	34364	.24	31.30	838.55	9.40
	Min	.12	.00	.00	.00	25.00	35	46	.00	13.10	21.76	.00
	Max	59.27	90.30	55.00	90.00	80.00	11800	230000	1.23	250.00	4500.00	45.00
	Median	10.14	55.00	25.00	7.50	45.00	528	5500	.17	24.85	152.50	8.00
New W.	Mean	13.28	49.01	26.84	23.78	59.90*	1451	7185	.40*	47.53*	419.82	8.75
	N	79	81	81	81	32	78	78	78	53	52	78
	SD	14.04	14.19	13.31	19.97	13.98	1571	8968	.49	45.04	414.74	12.78
	Min	.02	10.00	5.00	.00	33.33	23	310	.01	14.50	46.72	.00
	Max	46.25	76.00	62.00	70.00	88.89	6500	40500	3.09	250.00	1830.00	58.00
	Median	5.65	50.00	25.00	20.00	57.50	875	3185	.23	32.00	278.76	5.50
Total	Mean	14.55	52.17+	25.41-	22.14-	53.68-	1196-	13414-	.31+	37.46-	450.96-	8.81
	N	175	179	179	179	61	175	174	174	130	125	174
	SD	15.46	17.87	13.29	22.66	16.12	1558	26758	.38	38.28	692.63	11.01
	Min	.02	.00	.00	.00	25.00	23	46	.00	13.10	21.76	.00
	Max	59.27	90.30	62.00	90.00	88.89	11800	230000	3.09	250.00	4500.00	58.00
	Median	9.86	55.00	25.00	15.00	52.50	565	3905	.18	25.58	174.90	7.00

^a Significantly higher mean values in one hemisphere are designated by (*). In the row for the warm-climate sample totals, (+) indicates a significantly higher, and (-) a significantly lower mean value for the warm-climate sample than the cold-climate sample.

rich supplies of fish, which these foragers preserve and consume year round, allow them to live in small territories in sedentary, socially stratified groups, often with frequent warfare and even slavery.¹⁹ It is not habitat richness per se that explains the special qualities of the complex foragers but the seasonally abundant anadromous fish, which promote storage and investment in time-consuming technologies, such as weirs and smoke houses, with delayed returns.²⁰ Complex foragers may not have been rare toward the end of the Pleistocene, but for modeling earlier periods we should exclude them, and most are

absent from the warm-climate sample.

GROUP SIZE, HOME RANGE, AND MOBILITY

Among foragers, there are typically three types of groups, the ethno-linguistic group (tribe), which may never assemble in one place; the residential or local group (camp or band); and the daily foraging party. Most foragers have several types of fission-fusion. First, every day the local group splits into smaller parties to forage (while some may remain in camp), then returns to camp to sleep. Foraging parties

may also fission or fuse. One camp (local group) may fuse with other camps and, two months later, fission off again. Individuals also move back and forth between camps. There is also residential mobility of a different sort when the whole local group moves the location of the camp to access new resource patches. The vast majority of foragers are quite mobile, especially in the warm-climate sample, where the median number of moves per year is 7 (Table 1).

Dunbar argues that the number of individuals one interacts with on a regular basis is limited by the ability to keep track of social interactions.²¹ On

TABLE 2. Demographic Traits for the Total Forager Sample^a

Region	Statistic	% Infant Mortality	% Juvenile Mortality	Total Fertility Rate	Female Age at 1 st Reproduction (Years)	Age at Weaning (Years)	Interbirth Interval (Years)	% Married Males Polygynous	% Married Females with Co-Wife	
Total Sample of Foragers										
Old World	Mean	24.83	41.36	4.96	18.34	3.20*	3.21	17.64	20.16	
	N	12	12	29	6	15	9	76	26	
	SD	9.89	11.79	1.50	1.66	.82	.82	18.87	28.11	
	Minimum	10.30	20.00	.81	15.90	2.00	1.75	.00	.00	
	Maximum	46.00	56.40	7.00	19.96	4.50	4.35	70.00	90.00	
New World	Mean	21.50	45.50	5.30	18.63	3.00	3.40	8.50	5.95	
	Mean	18.15	47.83	5.97	19.17	2.32	3.39	12.09	22.68	
	N	4	7	18	3	25	7	136	25	
	SD	5.22	9.62	1.84	1.53	.68	.66	10.18	19.21	
	Minimum	11.60	35.00	2.80	17.50	1.00	3.00	.00	2.00	
Total	Maximum	24.00	61.00	8.50	20.50	4.00	4.83	57.00	60.00	
	Median	18.50	45.00	6.20	19.50	2.50	3.08	10.00	18.00	
	Mean	23.16	43.74	5.35	18.61	2.65	3.29	14.08	21.40	
	N	16	19	47	9	40	16	212	51	
	SD	9.28	11.23	1.69	1.57	.84	.74	14.14	23.95	
	Minimum	10.30	20.00	.81	15.90	1.00	1.75	.00	.00	
	Maximum	46.00	61.00	8.50	20.50	4.50	4.83	70.00	90.00	
	Median	20.60	45.00	5.50	19.25	2.50	3.24	10.00	10.00	
	Warm-Climature, Nonequestrian Foragers									
	Old World	Mean	24.35	40.48	4.87	18.15	3.13	3.08	19.07	21.56
N		11	11	23	5	12	7	68	22	
SD		10.23	11.95	1.54	1.79	.71	.81	19.22	29.47	
Minimum		10.30	20.00	.81	15.90	2.00	1.75	.00	.00	
Maximum		46.00	56.40	7.00	19.96	4.50	4.00	70.00	90.00	
New World	Median	21.00	45.00	5.25	18.00	3.00	3.40	11.00	6.50	
	Mean	11.60000	48.33	6.38	19.50	2.40	3.04	10.22	29.89	
	N	1	3	5	1	6	2	45	9	
	SD	.	13.01	2.29	.	.81	.06	8.91	20.01	
	Minimum	11.60	35.00	2.80	19.50	1.25	3.00	.00	4.00	
Total	Maximum	11.60	61.00	8.50	19.50	3.50	3.08	33.00	55.00	
	Median	11.60000	49.00	6.80	19.50	2.29	3.04	5.00	37.00	
	Mean	23.2917	42.16	5.14	18.38	2.88	3.07	15.55	23.98	
	N	12	14	28	6	18	9	113	31	
	SD	10.42832	12.13	1.75	1.69	.80	.70	16.46	27.01	
	Minimum	10.30	20.00	.81	15.90	1.25	1.75	.00	.00	
	Maximum	46.00	61.00	8.50	19.96	4.50	4.00	70.00	90.00	
	Median	20.60000	45.50	5.50	18.75	3.00	3.08	8.00	10.00	

^a Significantly higher mean values in one hemisphere are designated by (*).

the basis of a correlation between group size and the size of the neocortex relative to the rest of the brain across anthropoid primates, he argues the group size of humans over some evolutionarily significant period must have been about 150.²¹ This is certainly at odds with the size of the most salient group among foragers, the local group, which has a median population of 30 (Table 1). Could local groups have been closer to 150 if foragers occupied richer habitats in the past? The data do not sup-

port this, since there is no correlation between local group size and primary biomass. In richer habitats, where concentrated foods can support larger groups, we see a higher population density since the area occupied by the local group shrinks to minimize travel energy expenditure, but there is no increase in local group size. Across the full range of primary biomass, local groups show a conspicuous tendency toward a population of 30 (Fig. 5).

Hadza camps are at their smallest

during the rainy season and their largest at the end of the dry season. This is because there are only so many permanent waterholes, which limits the number of possible camp locations. When rain removes this constraint, the default is to disperse into smaller groups in which the Hadza say there is less bickering. This suggests a possible explanation for the remarkable consistency in local group population across forager habitats. Free-rider problems probably set an upper limit

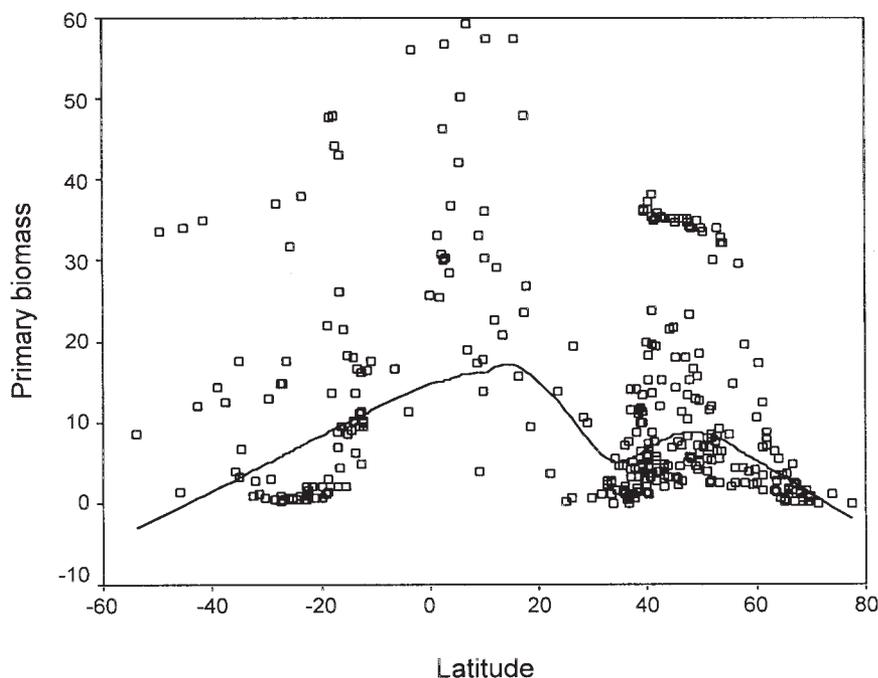


Figure 2. Primary biomass of forager habitats by latitude ($n = 341$). Fit line is Lowess smoothed.

on optimal, or equilibrium group size.¹⁵ Beyond 30, conflicts between families may cause fissioning, and it is only when there are external constraints, like the prevalent warfare of some equestrian and complex foragers, that there are larger local groups.

Home range is the area an individual occupies over a whole year. Because few home range data exist, I calculated a minimum estimate of home range, which I call local group area (see Box 1). The more hunting contributes to the diet, the larger is the local group area and the more frequently camps move (Fig. 6), especially when we exclude the sedentary foragers. Only 25% of the foragers in the sample are sedentary, and most of these are the complex foragers of the Pacific Northwest. There is less mobility where fishing, rather than hunting or gathering, accounts for more of the diet (Fig. 6). Thus, our ancestors may have been quite mobile before fishing was important. Home ranges are smaller in the warm-climate sample, where hunting contributes less to the diet, so they may have been somewhat smaller in the distant past if hunting was less important. Among warm-climate foragers, local group area (home

range) decreases as primary biomass increases, since resources are more concentrated. However, once primary biomass reaches about 10 kg/m^2 , local group area does not continue to de-

crease (Fig. 7). This implies that most warm-climate Late Pleistocene foragers, even in rich habitats, probably had very large home ranges of about 175 km^2 (Table 1). This is larger than the city limits of Washington D.C., too large an area to defend as an exclusive territory,²² given the population density (median = $.18 \text{ km}^2$). However, residents might have repulsed outsiders upon encounter as do some foragers and some carnivores with large home ranges (Table 3).²³⁻²⁵

As primary biomass increases, the total area of the ethno-linguistic group shrinks but the population remains fairly stable (median = 875 cold; 565 warm). Presumably, there are only so many people who can remain tied together in terms of language, as Birdsell argued with his magic number of 500.²⁶ Foragers tend to have friendly, co-equal relations with other local groups but not with other ethno-linguistic groups, at least when those others are agriculturalists. But what was it like before there were any agriculturalists? Australians are instructive since at the time of European contact all were foragers. While there were ethno-linguistic boundaries, they were not very sharp. There was some

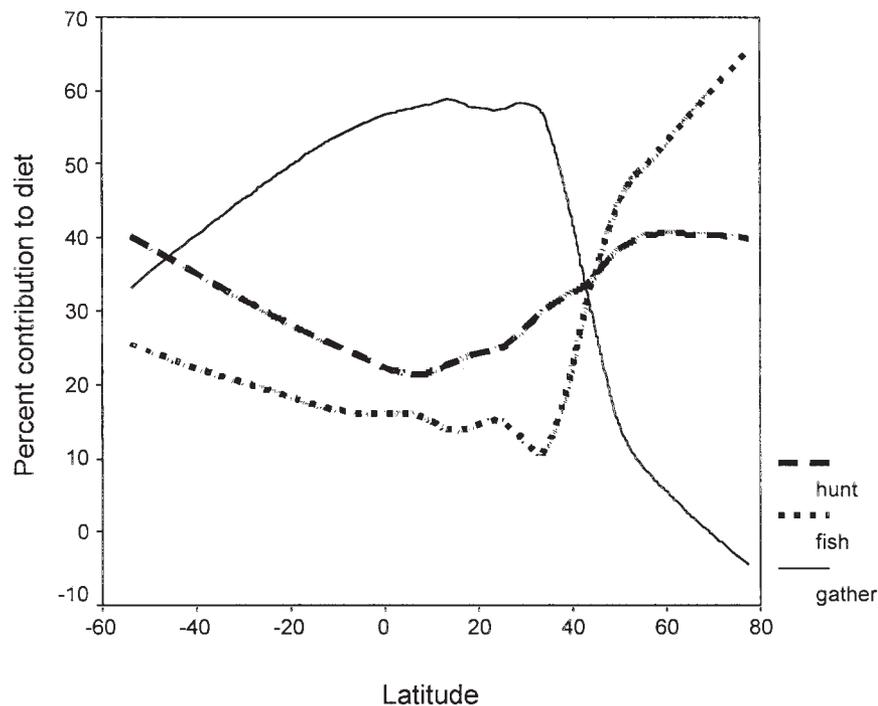


Figure 3. Contribution to diet from gathering, hunting, and fishing by latitude ($n = 398$). The southern hemisphere is plotted with negative latitudes. Fit lines are Lowess smoothed.

Box 2. Habitat Productivity

To test if forager habitats are marginal we can compare them to the habitats of agriculturalists using the Standard Cross-Cultural Sample (SCCS), which includes 186 societies chosen to maximize geographic and linguistic independence.² Because primary biomass estimates are available only for the foragers, however, we need an-

other measure of habitat quality. Net primary productivity (NPP) measures yearly plant growth and can be calculated from satellite data (see Appendix). Using NPP, we find that indeed there is a lower habitat quality among the 36 foragers than the 150 agriculturalists. However, when we exclude those so-

cieties in colder climates where ET is less than 13°C (the cold-climate foragers), there is no difference in NPP ($t = .183, P = .856, n = 139$: 17 foragers, 122 agriculturalists, equal variances). Warm-climate forager habitats are not less productive than those of agricultural societies in this sample.

intermarriage between adjacent groups,^{27,28} but there was also some warfare.²⁹ Along with the evolution of language came both the means to tie together several local groups and the basis for dividing one cluster of local groups from others. Since the ethno-linguistic group is largely defined by language, there is no analog of ethnicity in other mammals, and the continuous movement of individuals back and forth between local groups within the ethno-linguistic group is probably unique to humans.

KINSHIP, MARITAL RESIDENCE, AND DISPERSAL

In most mammals, members of at least one sex leave their natal group at maturity, perhaps to avoid inbreeding.³⁰ Among human foragers, couples often live with either the husband's family (virilocal) or the wife's family (uxorilocal). Virilocal residence is sometimes assumed to be analogous to male philopatry since males stay with their kin while females disperse.³¹ This analogy is more appropriate for sedentary agricultur-

alists than for foragers who frequently move in and out of camps; still, marital residence does capture something about potential nepotistic aid. There has long been a debate about the most common pattern of marital residence among foragers.^{32,33} The dominant view over the past few decades has been that foragers, like agricultural societies, are mostly virilocal.^{31,34,35} An analysis of foragers that takes account of residence in the early and later years of marriage does not support this.³⁶ Most foragers are multilocal; the couple resides in camps with the wife's kin at times, the husband's kin at other times, occasionally with both, and sometimes with neither.

Bilateral descent, tracing kin through both mother and father, is more prevalent among foragers (75%) than agriculturalists (25%), who are most often patrilineal.³⁶ One advantage of patrilineal descent is that it is easier to assemble a large group of reliable allies in times of warfare or disputes, since people know which patrilineal clan they belong to and where their loyalties lie. This is probably one reason that patrilineal descent dominates among agriculturalists.³⁷ However, an advantage of bilateral descent is that it maximizes the number of kin ties across camps, which facilitates visiting, finding mates, and moving to access seasonal resources.³² Because bilateral descent, which facilitates multilocal residence, is possible only if one knows one's father as well as mother, multilocal residence likely evolved after pair bonding.

Language makes kin terms possible, makes it easier to keep track of all of one's kin, and makes it easier to invent

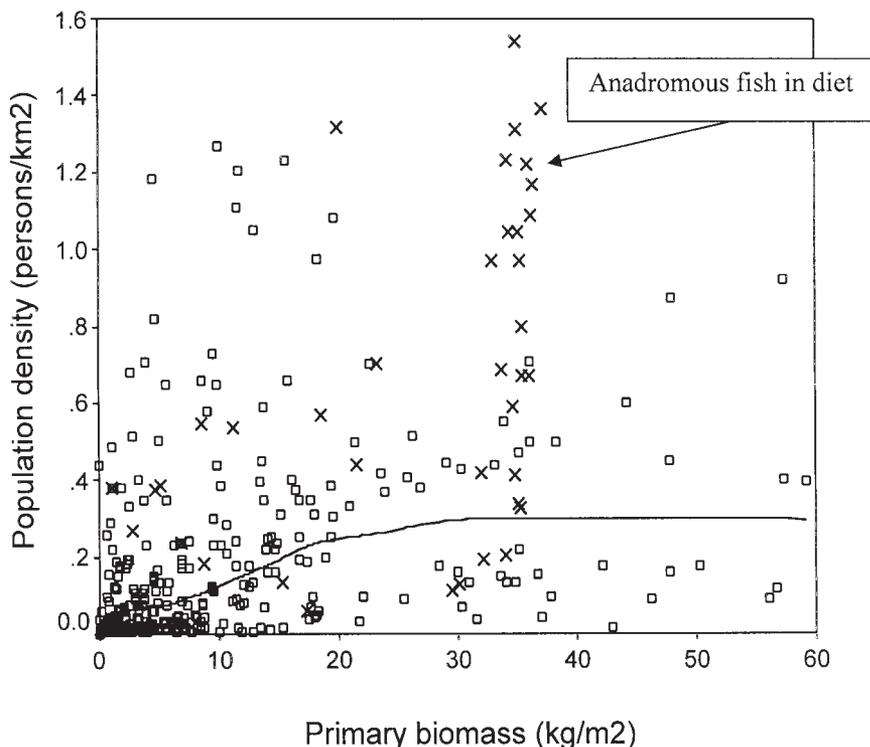


Figure 4. Population density (people/km²) by primary biomass of habitat ($n = 340$). Xs indicate subsistence at least partly based on anadromous fish. Fit line is Lowess smoothed ($r = .378, P < .005, n = 340$).

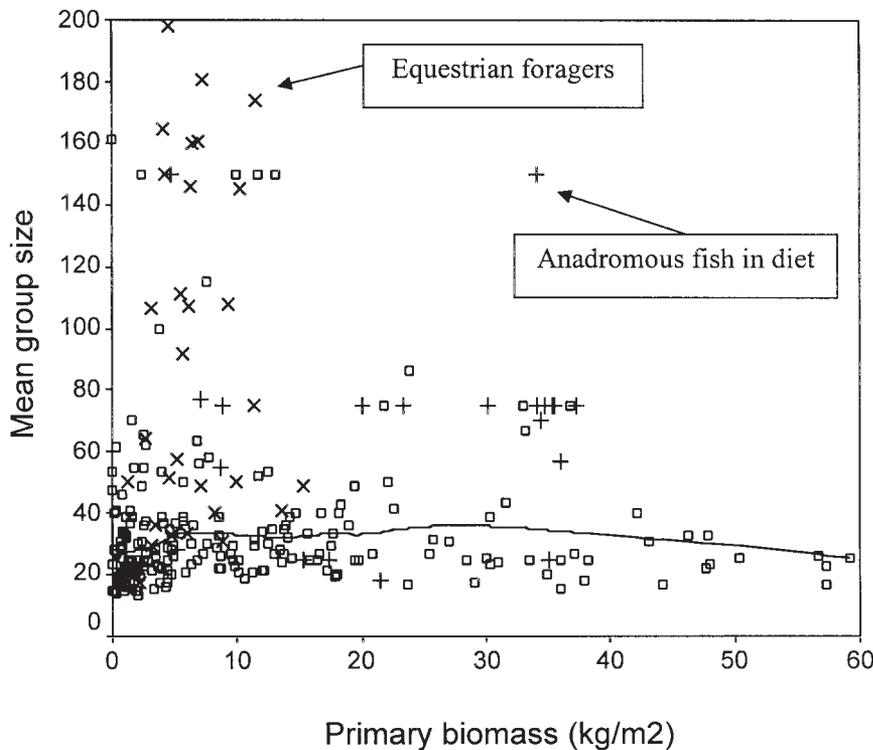


Figure 5. Local group population by primary biomass of the habitat ($n = 260$). Xs indicate equestrian foragers; +s indicate subsistence at least partly based on anadromous fish. Fit line is Lowess smoothed ($r = .000$, $P = .997$, $n = 260$).

possible that early hominin males did more hunting than females as well. The specialization in hunting or scavenging by males in contrast to gathering by females may have begun much later, but perhaps as early as 2.5 mya.³⁹ The common view that males only hunt and females only gather is false, however. For example, Australian females do considerable hunting of small animals,⁴⁰ while males in many foraging societies collect honey and gather fruit.⁴¹ Among some net foragers, such as the Aka, men and women hunt together.⁴² Still, the sexual division of foraging labor among humans stands in real contrast to the behavior of our ape cousins and other mammals (Table 3).

We know little about the actual mating system of foragers since there are no DNA paternity exclusion data. What I describe is only the observable "social" mating system, which probably under-represents actual polyandrous mating. There is considerable variation, ranging from the Andaman Islands, where polygyny is said not to exist at all,⁴³ to Australia, where 70%

fictive kin, so it facilitates movement between groups. It is difficult to say what dispersal was like before language, but if we exclude the predominantly virilocal agriculturalists, it is worth noting that we come to a different conclusion about the most likely ancestral state. Since both sexes disperse some in gibbons, orangutans, and gorillas, as well as in human foragers, the most parsimonious scenario has strict male philopatry among chimpanzees evolving only after the *Pan-Homo* split and before chimpanzees and bonobos separate. The same is true for exaggerated sexual swellings and large testes (Table 3). Among the extant hominoids, only the two species of *Pan* live in promiscuous, multi-male, multi-female groups with extremely male-biased philopatry.

THE SEXUAL DIVISION OF FORAGING LABOR AND THE MATING SYSTEM

Among chimpanzees 71% to 90% of hunting is done by males,³⁸ so it is

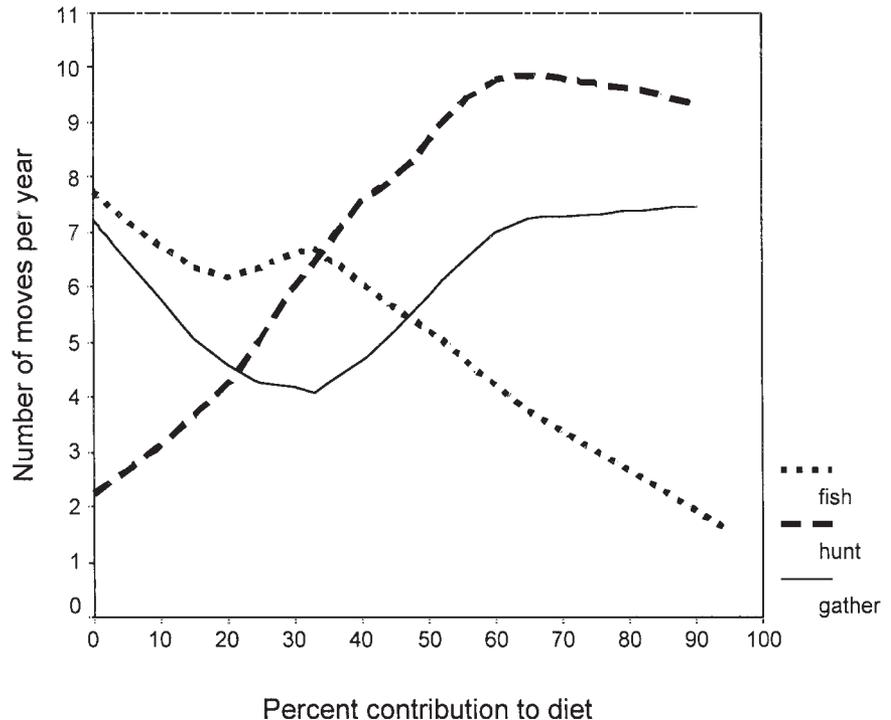


Figure 6. Number of residential moves per year by the percent contribution to the diet from hunting, gathering, and fishing ($n = 340$). Fit lines are Lowess smoothed. (Whole sample, number of moves by fishing: $r = -.302$, $P < .0005$, $n = 340$; hunting: $r = .259$, $P < .0005$, $n = 340$; gathering: $r = .122$, $P = .024$, $n = 340$). Fishing is also significant within Old and New World; hunting is only significant in the New World; gathering by itself is not significant within either hemisphere.

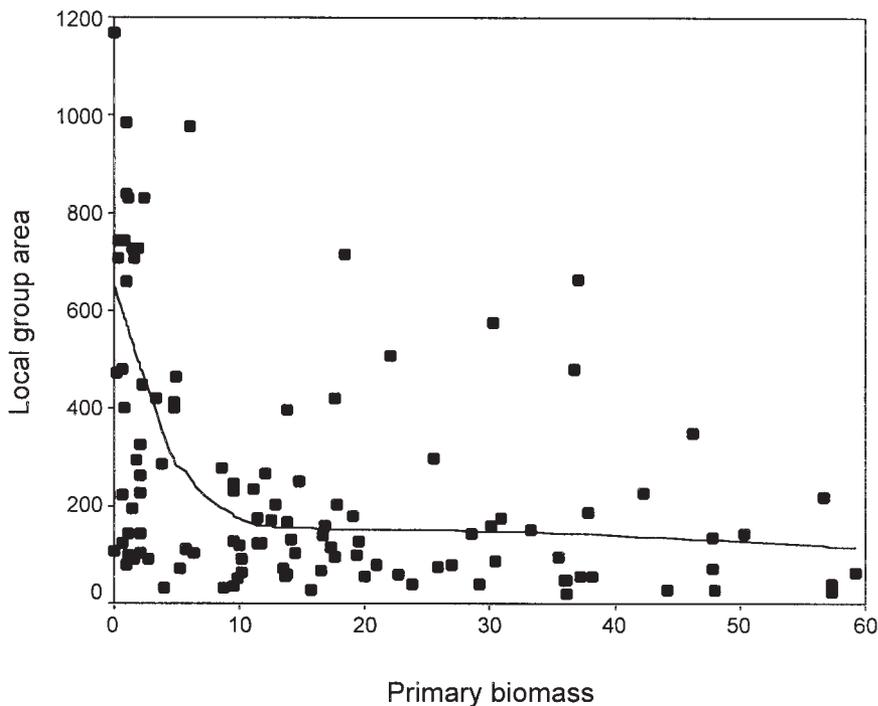


Figure 7. Local group area (home range) by primary biomass of the habitat for warm-climate, nonequestrian foragers ($n = 125$). Fit line is Lowess smoothed ($r = -.318$, $P < .0005$, $n = 125$).

of married men among the Tiwi can be polygynous⁴⁴ (Table 2). Polygyny in Australia is related to gerontocracy; old men have much higher status (and more wives) than young men do. The percentage of married women with a co-wife better captures the degree of reproductive skew, since a polygynous man may have 2 wives or 10, which will affect the number of bachelors. In the total forager sample this ranges from 0% to 90% (median = 10). In the SCCS, about 10% of foraging societies are monogamous, 60% slightly polygynous (<20% have co-wives), and 30% generally polygynous (>20% have co-wives), making foragers as polygynous as agriculturalists.⁴⁵ Even where there is considerable polygyny, however, most marriages are monogamous⁴⁵ and, except in Australia, two wives is often the maximum. In the SCCS, in societies where male contribution to diet is higher, there is less polygyny.⁴⁵ Hence, human foraging societies fit a pattern seen across mammalian species, where males are most likely to invest in offspring in socially monogamous species, while the vast majority of species in which

males invest little or nothing are polygynous.⁴⁶

Among most foragers, men's foods, especially larger game, are shared widely outside the household.^{10,47} This means that the best hunter's household may eat no better than the households of poor hunters, which forces us to ask what benefit a woman would gain from marrying a good hunter. Some have suggested that a man's hunting success signals something about his quality other than his provisioning value to his own household.^{47,48} While that may be true, I found that Hadza men who were not stepfathers brought more calories back to camp when their wives were nursing an infant and had decreased productivity.⁴¹ Hadza men, therefore, appear to compensate for their nursing wives' lower productivity, which suggests that pair bonds may be maintained by the benefits of a sexual division of labor within households.

Age at weaning ranges from 1 to 4.5 years (median = 2.5), which is considerably younger than the 4.8 years for chimpanzees and bonobos (Tables 2 and 3). Infant mortality ranges from

10% to 46% (median = 21) and juvenile mortality from 20% to 61% (median = 45), slightly lower than the rate for chimpanzees.⁴⁹ Total fertility rate ranges from 0.81–8.5 (median = 5.5). As I have reported elsewhere,⁵⁰ higher mean male contribution to diet across foraging societies predicts a younger age at weaning, a higher total fertility rate, and greater female reproductive success, but not a lower offspring mortality rate. Even when infant and juvenile mortality is high, where men contribute more to the diet a greater absolute number of offspring survive to the age of 15 years. This implies that women may use food from men mainly to speed up their rate of reproduction.

CENTRAL PLACES, FOOD SHARING, AND EGALITARIANISM

Central place foraging is typical of most human foragers, as it is among many birds and social carnivores (Table 3). Because there are species that return to central places without food (among them hamadryas, *Papio hamadryas*, and spider monkeys, *Ateles geoffroyi*), a better term for those who do take food back might be central-place provisioners.⁵¹ One reason for having a central place is to leave vulnerable or burdensome young in a safe place. Hadza mothers take their nursing infants with them when they go foraging but leave weanlings in camp because they are too young to keep up and too big to carry. Someone needs to stay in camp to look out for them and so food must be taken back. Perhaps this sets a lower limit on local group size among foragers; with less than 25 people and most adults out foraging, there might often be too few people available to baby-sit.

As Glynn Isaac⁵² long ago suggested and Nicholas Blurton Jones⁵³ later modeled, food sharing among foragers probably began with tolerated scrounging not so different from the meat sharing seen in chimpanzees, who sometimes hold out their hands in a begging gesture, often turn their backs to beggars, and sometimes grab meat away from others.⁵⁴ Resisting the demands of several other hungry adults could be especially dangerous in a species capable

TABLE 3. Warm-Climate Nonequestrian Foragers Compared with African Apes and Some Social Carnivores^a

Trait	Foragers <i>Homo sapiens</i>	Chimp <i>Pan troglodytes</i>	Bonobo <i>Pan paniscus</i>	Gorilla <i>Gorilla gorilla</i>	Wild Dog <i>Lycaon pictus</i>	Lion <i>Panthera leo</i>	Hyena <i>Crocuta crocuta</i>
Dietary niche	Omnivore	Frugivore/ Folivore	Frugivore/ Herbivore/ Folivore	Folivore/ Herbivore/ Frugivore	Carnivore	Carnivore	Carnivore
Dispersal	Bisexual multilocal ³⁶	Female ³⁰	Female ⁷³	Bisexual ³⁰	Female, ⁷⁴ bisexual ^{75,76}	Male, bisexual ⁷⁶	Male ⁷⁶
Group (local) population Min-max	26 13-250	40 15-120 community = 50 ⁷⁷	34 30-60 ⁷⁸	11, 6 mt, 9 lowland 2-20 ⁷⁹	10 20/60 ⁷⁹	13 ⁷⁹	55 3/80 ⁷⁹
Population density (Individuals per km ²)	.18 .00-3.09	.09-5 ⁷⁸	2-3 ⁷⁸	.5-10 ⁸⁰	<.05 ⁷⁹	.12-.38 ⁷⁹	1.77 ⁷⁹ Ngorongoro
Group composition	Multimale, Multifemale camps	Multimale, multifemale community, parties	Multimale, multifemale groups, parties	Unimale, multifemale groups	Multimale, multifemale packs	Multimale, multifemale prides	Multimale, multifemale clans
Mating system	Pair bond, Monogamy polygyny	Promiscuity	Promiscuity	Pair bond, Harem Polygyny	Monogamy, cooperative breeding	Promiscuous but estrus pairs	Promiscuous
Sexual Swellings	None	Exaggerated	Exaggerated	Slight	None	None	None
Division of foraging labor	Yes	No	No	No	Male provisions pregnant female ⁷⁵	No ⁷⁹	No ⁷⁹
Provisioning beyond weaning	Yes	A bit ⁵⁴	A bit	No	Yes	Yes	A bit
Food sharing among adults	Yes, lots	A bit ⁵⁴	A bit ⁸¹	No ⁷⁹	A lot ⁷⁹	Yes, grudgingly ⁷⁹	Yes, grudgingly ⁷⁹
Foraging pattern	Central place provisioning	Feed as you go	Feed as you go	Feed as you go	From den only when infants	From lair only when infants	From burrow or den only when infants
Grouping pattern	Fission-fusion, ♂s often alone	Fission-fusion, ♀s often alone	Fission-fusion, ♀s more social than chimp	Cohesive ♂ harem group, bachelors out	Fission-fusion, group hunt	Fission-fusion	Fission-fusion hunt alone, pairs
Day range (km) ♀/♂	9.5/14.1 n = 8/n = 6	3/5 ⁷⁷	2.4/2.4 ⁷⁷	1.1/1.1 (.5- 2.1) ⁸²	10 ⁷⁹	4.5/8 (1.9- 14.4) ⁸³	10 ⁷⁹
Home range Min-max (km ²)	175 (median) 22-4,500	12.5 5-50 ⁷⁹	45 30-60 ⁷⁸	24.4 8.2-40 ⁸²	1,700 1500-2,000 ⁷⁴	200 20-400 ⁷⁹	500 30-2,000 ⁷⁹

^a Numbers are means or medians, followed by ranges.

of forming temporary coalitions, as presumably our ancestors were. Such coalitions can create what Boehm⁵⁵ calls a reverse dominance hierarchy, resulting in egalitarianism. Food sharing would have lowered variation in daily food consumption,⁵⁶ which should have lowered mortality rates and altered life-history patterns.⁵⁷ Central-place provisioning increases food sharing, since taking food back to camp creates more opportunities for scrounging.⁵¹ Because central-place provisioning makes food sharing and egalitarianism more likely, if central places can be detected archaeologically, their earliest appearance might set an upper limit on the antiquity of egalitarianism.

A HIGHLY VARIABLE AND UNUSUAL PRIMATE SPECIES

Tables 1 and 2 show considerable variation. They also reveal many sig-

nificant differences between Old World and New World foragers. Less of the diet comes from gathering and more from hunting and fishing in the New World, and male contribution to diet is higher. Ethno-linguistic population and area are larger, as is the local group area (home range). There are fewer moves per year, and the age at weaning is younger.

There are also differences between the cold- and warm-climate samples. Many of the differences mirror those between New and Old World. This is partly due to the fact that there are so many northern foragers in the New World, with the mean absolute latitude being 44° and ET 13°C, compared to 15° absolute latitude and ET of 20°C for the Old World. The latitude difference between New and Old World is present even in the warm-climate sample (NW = 32°, 16°C; OW = 17°, 19°C). When latitude is

controlled, many of the differences between New World and Old World disappear, though fishing is still more important and total area of the ethno-linguistic group is still larger in the New World.

In comparative perspective, humans are so behaviorally diverse that societies are more like different species than different populations of one species, although there are some common features shared by most. In some of their widely shared features, human foragers resemble social carnivores more than they do our closest primate relatives. Like wild dogs, foragers have long day ranges, large home ranges, central places, provisioning, food sharing, and bisexual dispersal (Table 3). Many of these traits are probably due to technology that allows us to acquire large amounts of food that can be transported and is consequently more

TABLE 4. Technologies, With Earliest Dates Proposed (ya = years ago), Area Where Found, and Probable Effects the Innovation Had

Trait	Earliest Evidence	Where	Probable Effect
Iron	3500 ya ⁶⁰	South-West Asia	Time saving in arrow making, axes, more trade
Poison	11,000 ya, cited in ⁸⁴	Zambia	Fast killing of large game by lone hunter, more meat
Bow (see arrow points)	11,000 ya ⁶¹	Germany	Effective killing at a distance
Spears	17,000 ya ⁶²	France	Uni-male hunting, killing at a distance, more meat
Nets	22–29,000 ya ⁸⁵	Czech Republic	Bi-sexual hunting, effective fishing
Microoliths (arrow points), bows implied	65–70,000 ya ^{86–88}	Tanzania South Africa	Effective killing at a distance, uni-male hunting, more meat
Fishing harpoons	75,000 ⁸⁸ 80,000 ya ⁸⁹	Congo	Greater male contribution to diet, lower mobility
Shellfish	125,000 ya ⁹⁰	South Africa	Coastal niche
Spears	400,000 ya ⁶³	Germany	Hunting of larger game, before this mostly scavenging, more meat, and better defense
Fire	790,000 ⁹¹ 1.6 mya ⁹²	Israel Africa	Protection from predators, lower mortality, warmth, cooking
Acheulean handaxe, cleaver	1.7 mya ⁹³	East Africa	Butchering, more meat, or opening beehives to get more honey
Oldowan chopper, hammerstone, scraper	2.6 my ⁹⁴	East Africa	Food processing, scavenging, tool manufacture
Carrying devices	?	Africa	Infant carrying, leather, straw or wooden devices to carry food to a central place
Wooden digging stick?	?	Africa	Digging tubers, thus adaptation to more open habitat, larger home range
Pounding/throwing rocks, hitting and jabbing sticks?	6 my?	Africa	Protection from predators, food processing, preadaptation for more open habitat

likely to be transferred. This does not have to be meat; any food, such as honey, that is taken back to a central place in large quantities is more likely to provoke demand-sharing.⁵⁶ While technology has intensified greatly in just the past 100,000 years, if the hominin divergence from *Pan* entailed a shift to high-quality but difficult-to-acquire foods dispersed in a more open habitat with increased threat of predation, some increase in technology may have been selected for from the very beginning.^{9,58}

TECHNOLOGICAL CHANGE

The behavioral evolution of our ancestors must be reconstructed trait by trait, with the time period and area specified.^{34,59} For certain traits, the ethnographic foragers are relevant for only the past few thousand years; for other traits they may be informative about hominins millions of years ago. Table 4 shows some of the important

technologies and their probable effects. There is not space here to do justice to the complexity and ambiguity in the archeological record, so I have chosen to show both the oldest solid dates, as well as the oldest proposed dates, regardless of how controversial.

Many foragers acquire iron through trade and use it to make arrowheads. Iron first appeared about 2000 to 1500 B.C. in Western Asia,⁶⁰ and by 600 B.C. had spread far and wide in the Old World, though not to Australia. Iron's superiority for durable, effective tools and weapons explains why it is so highly valued and spread so rapidly. Since most contemporary foragers use iron rather than stone or bone points, they probably spend less time on tool manufacture per tool than did Pleistocene foragers and so have more time to allocate to other activities. Other fairly recent hunting technologies include traps, snares, and nets (Table 4). As noted, net hunting can

influence the sexual division of labor because males and females more often hunt together.⁴² The possession of iron tools, cooking pots, factory-made water buckets, and cloth make contemporary foragers different from Pleistocene foragers, but do not make them so different as to be uninformative.

Because the quality of their arrow poison can vary, the Hadza often hit animals that do not die. Hunting large game without poison would have been more difficult. Poison use has received little attention archeologically and will not be easy to document. Hadza men with bows and poisoned arrows usually hunt alone because the challenge is getting close enough to prey to get a shot before being detected, and two people only increase the chance of detection. Bows may have caused a switch from group hunting to more individual hunting, or at least hunting in smaller groups. Even though game may have been more

plentiful in the Pleistocene, without nets or the bow and arrow, iron points and poison, it is difficult to see how earlier hominins could have matched the hunting success of contemporary foragers. The bow was such a technological leap forward that it could have led to an increase in meat consumption and population growth rates, eventually reducing game populations in certain areas and hastening the adoption of agriculture.

Foragers without the bow are the most useful analogs for humans living before 100,000 ya, and that leaves only the Australians and Tasmanians. However, even the Australians had the spear thrower (or atlatl), which greatly enhances efficiency. The oldest known spear thrower is not much older than the oldest known bow^{61,62} (Table 4). Wooden spears without stone points have been found in Germany associated with horse bones dating to 400,000 ya.⁶³ Without spear throwers a lone hunter would have great difficulty killing large game, especially if spears were used to thrust rather than throw, since that requires getting very close to game. If large-game hunting occurred, it probably required cooperative groups. Before effective projectiles, hunters may have run down and clubbed small game or extracted animals from burrows.⁶⁴ The slow speed of bipeds would not have prevented them from eating large game acquired by scavenging, however. Among the Hadza, even women armed with only their digging sticks occasionally scare off a leopard and take its kill.⁶⁵ Before effective hunting, males could have focused more on honey and plant foods, so their daily hauls of food did not have to be lower but must have been different. In this sample, male contribution to diet is significantly lower in Australia, where there was no bow, than in the rest of the warm-climate sample (38% versus 56%). However, primary biomass is also lower, so this could be related to habitat rather than technology.

As noted, male contribution to diet is higher where fishing is more important. Even in the warm-climate sample, male contribution to diet is significantly higher where fishing accounts for $\geq 20\%$ of the diet (58% versus 49%). Since several other traits, such

as lower mobility, are associated with fishing (Fig. 6), dating the origin of fishing is important (Table 4). In the ethnographic record, fishing is done with spears, bows, weirs, nets, baskets, and poison. Because many of these technologies probably did not appear prior to modern *H. sapiens*, we might use foragers who do little fishing as guides to earlier periods.

All foragers in the ethnographic record use fire, but dates for its first use are controversial.⁶⁶ Controlled use of fire would have had radical effects in a variety of ways. Fires are deliberately set by some foragers to burn underbrush and encourage new growth for game to eat.⁶⁷ Fire is used to harden digging sticks, curve bows, and straighten arrows. Smoke from torches is used to stun bees while collecting honey. Fires probably keep predators away from camps, which must have lowered mortality rates. Fire allowed occupation of colder habitats, and cooking probably increased the value of some foods, perhaps expanding the hominin diet.⁶⁸

Stone tools appear 2.6 mya, but it is implausible that these represent the earliest tool use. Since chimpanzees wield sticks and occasionally throw stones or use them as hammers,⁶⁹ tool use could have begun even before the *Homo-Pan* split. While some tool use may have existed throughout hominin evolution, there has been a rapid increase in technological sophistication in our species. Given the somewhat recent evolution of complex projectiles and nets, male foraging long ago had to be quite different, but female foraging did not; the behavior of modern females is, therefore, more instructive for earlier periods. Hadza females forage in groups of about 5 women, some infants and older children, collecting baobab fruit that falls to the ground, gathering berries, and digging up a variety of tubers with digging sticks, which they also use to defend themselves. Hadza women, and women in many other warm-climate foraging societies with simple technology, might be reasonable guides to hominin foraging patterns over a very long time. Females may have pioneered the earliest and still important technologies: digging sticks, rocks for pounding nuts and seeds, and

devices for carrying infants and foods (Table 4).

CONCLUSION

The forager data allow us to explore relationships between habitat and social organization and compare humans to other species. Such relationships, in conjunction with the fossil and archeological record, can help model the behavior of our ancestors at different times in the past. The main obstacle is not contact with agriculturalists or climate change or bias toward marginal habitats, but technology; all foragers in the ethnographic record possess complex technology compared to all

The bow was such a technological leap forward that it could have led to an increase in meat consumption and population growth rates, eventually reducing game populations in certain areas and hastening the adoption of agriculture.

hominins before modern *sapiens*. However, even Lower Paleolithic technology may have afforded some surplus production, which in some ways made hominins more like social carnivores than other apes. Contemporary foragers are not living fossils, but because they are pre-agricultural they are the most relevant analogs for at least Late Pleistocene humans. As long as we take into account the effects of technology, the behavioral ecology of contemporary foragers can provide important insights into human evolution.

APPENDIX

There are 478 societies in the sample used in this paper, though not all are necessarily equally distinct ethno-

linguistic groups. Societies are included if less than ten percent of their diet comes from domesticated foods, but I err on the side of inclusion to present the most comprehensive sample where good quantitative data exist. Thus, some may eat more than 10% of domesticated food through trade or periodic horticulture, or live at missions but go on lengthy treks during which data are collected, as do, for example, the Ache of Paraguay.

Many sources of data not cited in the text are cited in the appendices of my analyses of male dietary contribution⁵⁰ and mating systems.⁴⁵ Additional data come from various other sources such as Bofi,⁷⁰ and 56 societies on the island of New Guinea where very little is known beyond estimates of the percent of diet coming from foraging.⁷¹ For these and a few others, I filled in missing data on exact location, ethno-linguistic populations, and a few other variables using the *Ethnologue*.⁷²

Productivity Comparison

Using satellite-gathered data on temperature, leaf cover, and solar radiation, the MODIS algorithm calculates an estimate of annual net primary production (NPP) or the amount of new plant growth in grams/meter²/year as a proxy for habitat quality (equation in: Allen RG, Pereira LS, Raes D, Smith M. 1998. FAO Irrigation and Drainage Paper No. 56: Crop evapotranspiration guidelines for computing crop water requirements: www.fao.org. For MODIS data: http://www.nts.gumt.edu/). Foragers vs. agriculturalists: NPP = 572 vs. 788, $P < .0024$, using only those societies where $ET \geq 13^{\circ}C$, NPP = 848 vs. 869, $P = .856$.

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