

Original Article

Means, variances, and ranges in reproductive success: comparative evidence

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Abstract

Data on reproductive success in traditional cultures suggest that for men, but not for women, range and variance rise as subsistence intensifies. For hunter–gatherers, ranges and variances tend to cluster in single digits: they reach 15 or 16, at the high end. For herder–gardeners, ranges and variances are more consistently in double digits: they get as high as 80 or 85. And for full-time agriculturalists in the first civilizations, ranges consistently ran to triple digits: emperors from Mesopotamia to Peru were the fathers of hundreds of children. In human societies, as in other animal societies, reproductive skew goes up with a more sedentary life.

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Days after his 25th birthday, in 1834, on the 5th of March, Charles Darwin caught sight of his old friend, Jemmy Button, in a harbor at Tierra del Fuego. The Beagle had dropped Jemmy off after a visit to England, plump, clean, and well dressed; but in a matter of months, he'd become a thin, haggard savage in a loincloth. “I never saw so complete and grievous a change,” Darwin wrote. Jemmy would have disagreed. He had no interest in going back across the Atlantic—the effect, his friend thought, of his finding pretty Yaghan woman, and having the chance to collect them. Half a century later, by the time he finished his book on *The Descent of Man*, Darwin had seen and read enough to know that it was a “very universal privilege” in Tierra del Fuego, as elsewhere, for some men to have more than one wife (Darwin, 1860/1962:228–229, 1871:2.323–354).

The vast majority of human societies have been polygynous societies. Most men have probably been monogamous, most of the time, but some men have always had sexual access to more than one woman (Flinn & Low, 1986; Murdock, 1949).

Polygyny has been measured in a variety of ways. They include: proportion of polygynously mated women (Hartung, 1982, 1983; Whiting, 1981), proportion of polygynously mated men (Murdock & Wilson, 1972; Murdock, 1967;

Whyte, 1978), proportion of polygynously mated men or women (Low, 1988), and maximum harem size (Betzig, 1982, 1986; see Low, 1988 for an overview). Most of those measures correlate well with one another—though the extent (number of men mated with more than one woman) and the intensity (number of women mated with one man) of polygyny may be expected to vary inversely. In any event, most of those measures were based on rough ethnographic estimates. Better evidence has become available over the last few years.

That evidence is brought together here. These data, the most complete we have, or are likely to have, on reproductive success in traditional cultures, suggest that ranges and variances are marginally higher for men than for women in hunting and gathering societies, and that ranges and variances for men, but not for women, go up in more sedentary groups (Table 1; Figs. 1–3).

For women, ranges and variances are low across all forms of subsistence. The most reproductively successful women in these samples gave birth to between 6 and 18 children, and estimates of female reproductive variance in these groups include a low of 3.57 (for the Aché of Paraguay) to a high of 12.69 (for the Bolivian Tsimane).

For men, both range and variance rise as subsistence intensifies (Table 1; Figs. 1–3). For foragers, male completed fertility reaches a high of 16 (for the Hadza of Tanzania), and reproductive variance reaches a high of 15.05 (for the Paraguayan Aché). For pastoralists and horticulturalists,

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Table 1
Means and variances in reproductive success for foragers, herders and gardeners, and farmers

	Male				Female				
	Range	Mean	Var	N	Range	Mean	Var	N	
Hunters and gatherers									
Aché (Paraguay)	0–13 ^a	6.40	15.05	48	0–12	7.84	3.57	25	Hill & Hurtado 1996
Aka (CAR)	0–14 ^b	6.34	8.64	29	2–11	6.23	5.20	34	Hewlett 1988
Hadza (Tanzania)	0–16 ^c	4.55	14.31	95	0–12	4.58	7.70	93	Marlowe, 2010
!Kung (Botswana)	0–12 ^d	5.14	8.60	32	1–9	4.69	4.87	62	Howell, 2000
Meriam (Australia)	0–12 ^e	3.63	11.69	19	0–11	2.06	6.43	49	Smith, Bliege Bird & Bird, 2003; Eric Smith, personal communication
Pastoralists and horticulturalists									
Kipsigis (Kenya)	0–80 ^f	12.42	85.58	107	0–12	6.6	5.9	260	Borgerhoff Mulder, 1988; Brown et al., 2009; Gillian Brown, personal communication
Pimbwe (Tanzania)	0–12 ^g	5.99	9.00	138	0–12	6.14	7.27	154	Borgerhoff Mulder, 2009
Tsimane (Bolivia)	0–22 ^h	9.06	19.93	62	0–15	8.91	12.69	112	Von Rueden, Gurven, & Kaplan, 2011; Mike Gurven, personal communication
Xavante (Brazil)	0–23 ⁱ	3.6	12.1	62	0–8	3.6	3.9	44	Salzano, Neel, & Maybury-Lewis, 1967
Yanomamö (Venezuela)	0–43 ^j	5.59	39.64	140	0–14	3.67	8.02	181	Chagnon, 1974, 1979b
Yomut (Iran)	0–30 ^k	5.12	8.07	267	0–18	3.87	7.09	216	Irons, 1979, 2000, personal communication
Intensive agriculturalists									
Mesopotamians	118+ S								Justin
Egyptians	49+ S								Fisher, 2001
Hindus	101 S								Dipavamsa, Mahavamsa
Aztecs	57 D+60 S								Alva Ixtlilxóchitl
Inca	300–400 D+S								Garcilaso de la Vega; Betanzos
Chinese	65 D+S								Song Shi, in Ebrey, 2002

CAR=Central African Republic; D=reported daughters; S=reported sons.

^a Number of live births for men and women aged 50–70.

^b Number of live births for men and women over age 41.

^c Number of children born to men and women aged 18 or over.

^d Number of children born to men 50 or over and women 45 or over. Note that three men who “had no reproductively successful marriages” were excluded from calculations of Mean, Var, and N.

^e Number of children born to men and women aged 50 or over. Note that for all adults 15 or over, the values are: for men, Mean=1.74, Var=5.79, N=114; and for women, Mean=1.56, Var=4.84, N=163.

^f Number of children surviving to age 21 born to men circumcised before 1938 or women married by the same year. Data were collected in 1983. These figures include all living or dead cohorts from Borgerhoff Mulder 1988, so they differ from values excluding “Living Maina” men as computed in Brown et al. 2009. Thanks to Gillian Brown (personal communication) for clarification.

^g Number of children surviving to age 5 for men and women over age 45. Note that sex differences are somewhat higher for number of children born: for men, Var=16.16, N=138; for women, Var=11.34, N=154.

^h Number of children born to men over 50 and women over 40.

ⁱ Number of surviving offspring for living individuals age 40 or over “plus recently deceased individuals for whom information was supplied by a surviving spouse.”

^j Total number of children born to deceased men and women in a Shamatari population. Note that for living Shamatari, the values are: for men, Mean=3.53, Var=12.40, N=137; and for women, Mean=3.24, Var=5.19, N=182.

^k Number of children born to men and women aged 45 and over.

men’s completed fertility reaches highs of 43 (for the Yanomamö of Venezuela) and 80 (for the Kenyan Kipsigis), and reproductive variance reaches a high of 39.64 (for the Yanomamö) or 85.58 (for the Kipsigis). And in the ancient civilizations that subsisted on full-time agriculture—from Mesopotamia to Peru—emperors fathered hundreds of children.

In short, for *Homo sapiens*, as for other species, until the last few centuries at least, reproductive skew seems to have gone up with a more settled life.

1. Hunters and gatherers

Foragers are notoriously egalitarian, and notoriously mobile. Conflict is common, and men often fight over

women. But when hunter-gatherers can’t all “hang up their quivers” and live together, it’s easy to vote with their feet and live apart (Lee, 1979:395; Lee & DeVore, 1968).

Most forager groups have low reproductive variance, at least partly as a result. For most of the hunter-gatherers included here, both ranges and variances tend to hover in, or around, single digits. At the high end, in the forests of Paraguay, Aché men report an average of 6.4 live births, with a variance of 15.05; and at the low end, in the Kalahari, !Kung men report fathering 5.14 children on average, with a variance of just 8.6. Ranges are similarly small. The most reproductively successful foragers in these samples fathered 12 (!Kung, Meriam), 13 (Aché), 14 (Aka), or 16 (Hadza) children (Table 1; Figs. 1–3).

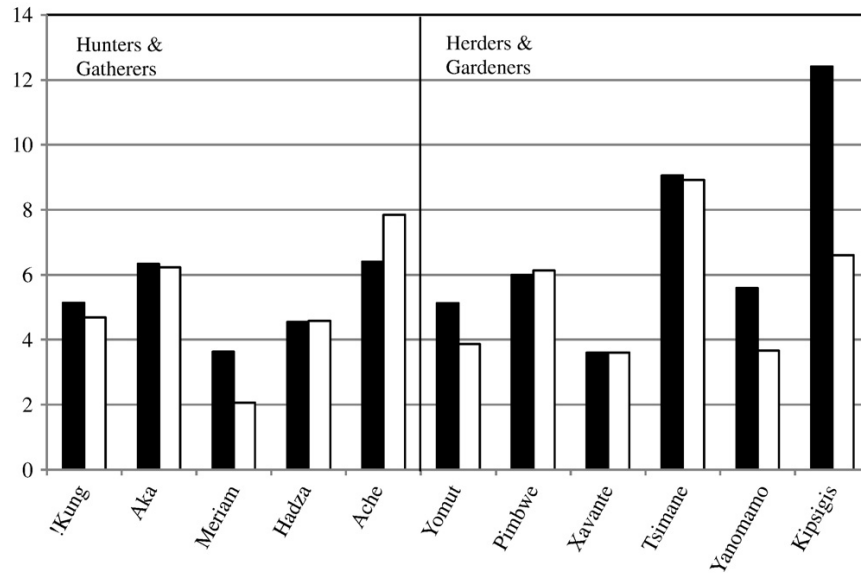


Fig. 1. Mean reproductive success for men and women in hunter-gatherer and herder-gardener populations. White bars for women, black bars for men.

The figures are similar for forager women. At the low end, Aché women report an average of 7.84 live births, with a variance of just 3.57; and at the high end, Hadza women report 4.58 children on average, with a variance of 7.7. Again, all of the ranges are small. The most reproductively successful forager mothers in this sample produced 9 (!Kung), 11 (Aka, Meriam), or 12 (Aché, Hadza) children (Table 1; Figs. 1–3).

In every one of these forager cultures, the most reproductively successful father had more children than the most reproductively successful mother. And reproductive variances for women were always lower. The highest variance reported for women (7.7 for the Hadza) is lower than the lowest variance reported for men (8.6 for the !Kung). But overall, the sex differences for hunter-gatherers are consistently small (compare Smith, 2004).

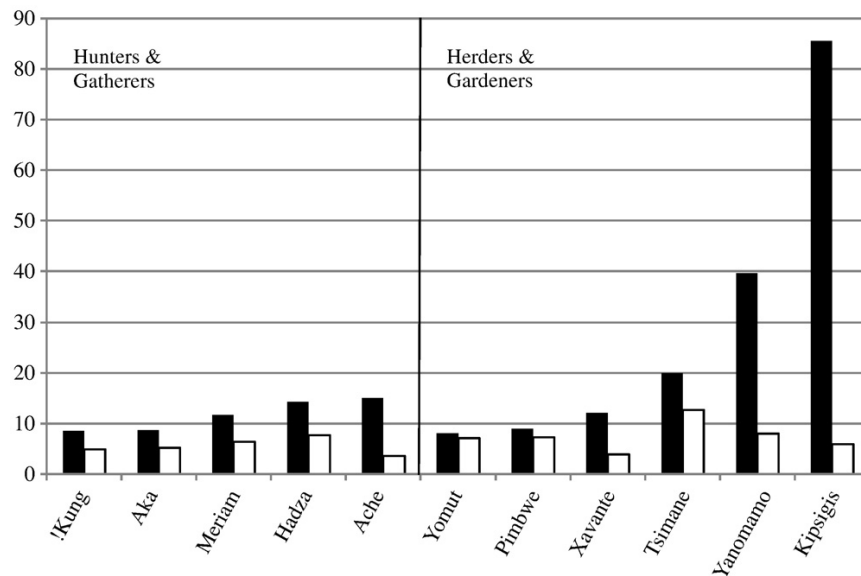


Fig. 2. Variance in reproductive success for men and women in hunter-gatherer and herder-gardener populations. White bars for women, black bars for men.

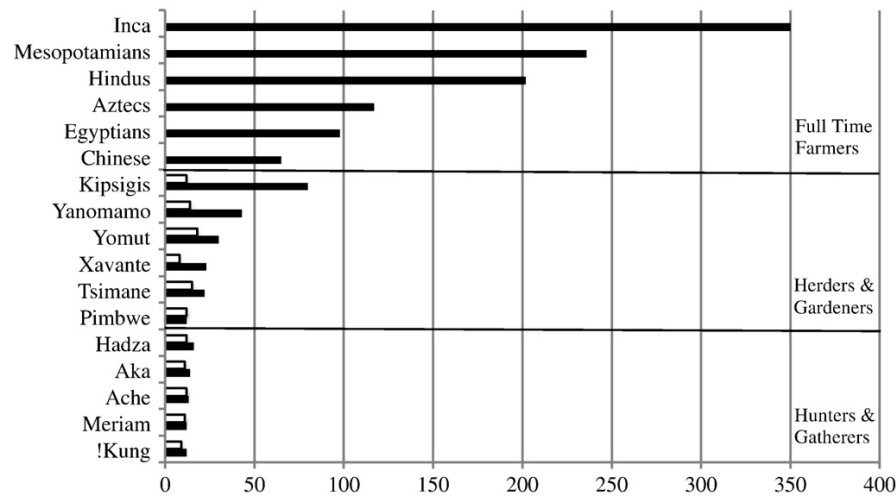


Fig. 3. Range in reproductive success for men and women in hunter-gatherer, herder-gardener, and full-time farmer populations. White bars for women, black bars for men.

2. Herders and gardeners

Semisedentary people are less mobile, and more reproductively variable, than foragers. Men tend to compete over women, and villages tend to fission. But some fission more often than others. Where villages do stay together, reproductive skew tends to rise (Chagnon & Bugos, 1979; Chagnon, 1974, 1979a).

Both ranges and variances in reproductive success are higher for herder-gardeners than for hunter-gatherers, and they tend to reach double digits for men. At the low end, Yomut herders and Pimbwe gardeners report reproductive variances less than 10: the values are 8.07 for the Yomut and 9.00 for the Pimbwe. But at the high end, reproductive variance for both Yanomamö gardeners and Kipsigis herders is over 20: the values are 39.64 for the Yanomamö and 85.58 for the agropastoral Kipsigis. Successful, semisedentary fathers in this sample all number their children in double digits, from 12 (Pimbwe) to 22 (Tsimane), to 23 (Xavante), to 30 (Yomut), to 43 (Yanomamö), to 80 (Kipsigis).

But ranges and variances for herder-gardener women remain in, or around, single digits. At the low end, Xavante women report a variance of just 3.9; at the high end, Tsimane women report a reproductive variance of 12.69. Ranges are also low: the most successful mothers in the semisedentary sample produced 8 (Xavante), 12 (Kipsigis, Pimbwe), 14 (Yanomamö), 15 (Tsimane), or 18 (Yomut) children.

So sexual selection is again in the predicted direction, and increases with sedentism. For the pastoralists and horticulturalists in this sample, reproductive variances for men are always greater than those for women; and in some cases (Yanomamö and Kipsigis), they're 5 to 15 times as high. Ranges are also greater. In some herder-gardener cultures, the most reproductively successful fathers (Yanomamö and Kipsigis) have three to seven times as many children as the

most reproductively successful mothers (compare Brown, Laland, & Bergerhoff Mulder, 2009).

3. Full-time farmers

As Robert Carneiro pointed out in a classic paper a generation ago, the world's first civilizations began on areas of circumscribed agricultural land—where the alluvium was set off by mountains or deserts, and “escape in every direction” was blocked. After the benefits of staying, and the costs of leaving, became high enough, people started to settle down in the early states (Carneiro, 1970:374–375, 1986).

And in every one of the six pristine civilizations—in Mesopotamia, Egypt, India, China, Mexico, and Peru—emperors collected hundreds of women and had hundreds of children (Table 1; Fig. 3; see Service, 1975 on the first six civilizations; see Betzig, 1986, 1993 on harems).

In the Ancient Near East, where civilization began, the emperor Shulgi, the law giver and ziggurat builder, left behind the names of at least 54 *dumu lugal* (or princes, or “sons of the king”) and *dumu-SAL lugal* (or princesses, or “daughters of the king”)—“because I am a strong man, rejoicing in my loins,” as he bragged in stone (Sollberger, 1954–56 and Gelb, 1979; Shulgi, *King of the Road*). Upriver on the Tigris, Ashurbanipal, the Assyrian emperor, left records of Harem Governesses and Weavers: he listed 13 governesses, 145 weavers, 52 maids, and 260 miscellaneous women, in his clay tablet library at Nineveh (Fales & Postgate, 1992, tablets 21–26). Down on the Euphrates, at Babylon, Nebuchadnezzar II, who sent an army into Jerusalem, kept a House of the Palace Women; and Belshazzar brought out gold and silver vessels from Jerusalem's temple “so that his wives and concubines might drink from them” (Wadi-Brisa Inscription; Daniel

5:2–3). The Persians were well known for their harems: Artaxerxes II is supposed to have fathered 115 bastard *sons*, besides 3 legitimate ones (Justin, *Epitome*, 10.1). And in the first histories, put together by Hebrew scribes, Solomon collected 1000 women, and his boy Rehoboam fathered 88 children (1 Kings 11:3, 2 Chronicles 11:21; see Betzig, 2005, 2009a for reviews).

In Egypt, civilization rose up at around the same time, and there were more polygynous men. In the Old Kingdom, when the pyramid builder Sneferu went out for a row on his private lake, he took along 20 women “with the shapeliest bodies, breasts and braids, who have not yet given birth,” and dressed them in fishnets (Papyrus Westcar). In the Middle Kingdom, Amenemhat I was done in after a conspiracy in his harem: “Has discord been fostered within the palace?” his biographer asked (Teaching of Amenemhet I). And in the New Kingdom, where the tomb of Ramesses II held chambers for dozens of sons, the names of 49 “king’s sons” and “bodily king’s sons” were written in stone. Another 50 Ramesside inscriptions are associated with unnamed *sons*, and there should have been roughly as many daughters (Fisher, 2001; Weeks, 2006).

There were more harems in Asia. In India, Ashoka, the “Sorrowless” Mauryan emperor, won his throne after a massive fratricide: “Having killed his hundred brothers, alone continuing his race, Ashoka was anointed king” (Mahavamsa, 5.18; Dipavamsa, 6.22). Then he reassured subjects, in rock edicts, that he’d look after their welfare, “whether I am eating or in the closed female apartments, in the inner chamber, in the royal rancho, on horseback or in pleasure orchards” (Rock Edicts, 6). The better part of a millennium later, Vatsayana’s (1964) *Kamasutra* advised compassionate Gupta emperors to drink milk boiled with the testicles of rams or goats, so they might “enjoy many women” in a night. Compassionate women were advised to learn architecture, mineralogy, cockfighting, and gymnastics, as an emperor may have “thousands of other wives” competing for his attention (Kamasutra, 1.3, 5.6, 7.1).

But the greatest of all emperors probably lived in the greatest of all empires. Chinese dynastic histories offer short lists of imperial children—65 are mentioned for the Northern Song emperor, Huizong (Ebrey, 2002). But most of these emperors kept enormous harems, and some must have fathered over a hundred children. When the man who unified China, the First August Emperor of Qin, connected his 270 palaces together, he filled them with more than 10,000 women, “beautiful women and bells and drums that he’d taken from the feudal rulers,” said China’s first historian, Sima Qian (Sima Qian, Shi Ji, 6). That number would grow by an order of magnitude. Yangdi, the Sui Dynasty emperor who built the Grand Canal and rebuilt the Great Wall, was credited by an official historian with 100,000 women in his palace at Yangzhou, alone, and when the Yuan dynasty founder, Kublai Khan, put up a capital at Beijing, he left a summer palace at Xanadu behind, with room in the excavations for another 100,000 (Wei, 2008). Marco Polo,

the Venetian who lived for 17 years at Kublai’s court, thought this emperor was particularly fond of Tartars. “Every year, 100 of the most beautiful maidens of this tribe are sent to the Great Khan,” he wrote, with half a dozen introduced to the emperor every three nights; “and so, throughout the year, there are reliefs of maidens by 6 and 6” (Marco Polo, Book, 2.8). Genetic evidence backs that up. A Y chromosome linkage represented in 8% of sampled Asian men is arguably borne by descendants of Kublai and his Mongolian grandfather, Genghis Khan (Zerjal et al., 2003; compare Xue et al., 2005).

And as in the Old World, so in the New. In the Valley of Mexico, Nezahualcoyotl—poet, architect, engineer, and friend of the Aztec emperor Moctechuzoma I—had a zoo, gardens, music hall, ball court and 300 rooms in his palace, where his women, “reared in seclusion,” raised Nezahualcoyotl’s 57 daughters and 60 sons (Alva Ixtlilxóchitl, Nezahualcoyotl Acolmiztli, 4.2). Three generations later, Moctechuzoma II’s palaces amazed Hernán Cortés and the Europeans who came after him (Cortés, 1520). The Spanish were able to get so many Aztecs to help them fight because Moctechuzoma’s taxmen had “carried off their daughters and wives”—said Bernal Díaz, who fought with Cortés as a young man (Díaz, Discovery, 60). Moctechuzoma’s ancestors had always fathered many sons on many wives, “this being something that appertained to the dignity of a ruler”—said the Spanish viceroy, Antonio de Mendoza (Codex Mendoza, folio 2). Emperors collected raw cotton and textiles, maize, and other staples as tribute, “and provinces that lacked foodstuffs and clothing paid in maidens”—said the Dominican, Diego Durán (Durán, History, 25). And “since the lords and chiefs stole all the women for themselves, an ordinary Indian could scarcely find a woman when he wished to marry”—said the Franciscan Toribio de Benavente Motolinía (Motolinía, History, 2.7).

It was worse in Peru. Conscripted labor was *mit’a* (or “turn”), in the native Quechua, and accounts were kept in *kipu* knots, which recorded quantities of tens, hundreds, thousands, and tens of thousands of units of tribute produced. Emperors kept estates at Pisac, Ollantaytambo, Machu Picchu, Cuzco, and so on, and a third part of their *mit’a* revenue was spent on women. “A judge or commissioner named by the Inca was dispatched to each province, and his only responsibility was this matter of collecting girls,” - said Bernabé Cobo, the Jesuit historian of New Spain (Cobo, Discovery, 2.34). Houses of Virgins were set up all over the empire, and “all of them had many children,” - said the conquistador Pedro Cieza de León (Cieza de León, Discovery, 2.10-11). Garcilaso de la Vega, who was the son of an Inca noble and a Spanish lord, and Juan de Betanzos, who was Spanish but married an Inca noble, put together some numbers. In the generations before the conquest, the emperor Pachakuti had 300 or 400 children by various women, the emperor Thupa Yupanki had 300 children, the emperor Qhapaq Yupanki left over 250 sons and daughters, and the emperor Wayna Qhapaq left over 200

sons (Garcilaso de la Vega, *Royal Commentaries*, 4, 6.34, 7.26, 8.8, 9.15, 36; Betanzos, Narrative, 1.23). Guaman Poma de Ayala, who was the son of nobles, added that access to women was strictly prescribed by law. “Principal persons” got 50, *hunu kurakas* (heads of 10,000 households) got 30, *waranqa kurakas* (heads of 1000) got 15, *pachaka kurakas* (heads of 100) got 8, *chunka kamayuqs* (heads of 10) got 5, and the “poor Indian” took whatever was left (Poma de Ayala, First Chronicle, 134).

4. Discussion

Over our long prehistory as foragers, *H. sapiens* would have been mostly monogamous. As subsistence intensified and sedentism increased, reproductive variance would have gone up. Some men would have fathered children by larger numbers of women, but larger numbers of men would have done without. That conclusion is supported by the descriptive evidence in the ethnographic record. The quantitative evidence compiled here is supportive, too.

Ethnographers’ statements are more or less impressionistic, and demographers define their variables in different ways (see Table 1). Most of the data used here are completed fertility measures. Adults are 40 or older in all but one case: only the Hazda demographer included adults at or over the age of 18 years. And fertility is measured as numbers of live births in all but three cases: Xavante demographers included all “surviving” children, without specifying an age cutoff; Pimbwe demographers included children surviving to age 5; and the Kipsigis data include children surviving to age 21. Sampling adults at older ages should raise estimates of range and variance in reproductive success, and so should including children at younger ages. Range and variance for one hunter-gatherer group in this sample, the Hadza, will be underestimated. Range and variance estimates for the Xavante, Pimbwe, and Kipsigis, all herder-forager societies, should also be low.

No preliterate culture written about by ethnographers or demographers is pristine. For the societies in the cross-cultural record, and for the societies described here, subsistence practices are mixed. All of the people in this sample supplement their subsistence, to some extent, by producing or trading for agricultural goods. But most get the majority of their calories by hunting, gathering, herding, or gardening in traditional ways.

For some hunter-gatherers, resources are more predictable and abundant than for others. !Kung with access to waterholes, or n!ore, on the Kalahari, are more often called big men, and are more likely to have families by more than one wife (Cashdan, 1980; Lee, 1979). Across the ethnological and archaeological records, more sedentary foragers are more polygynous foragers. Hunter-gatherers along waterways and coastal strips, where continentality is low, climates are consistent, and resources are lush, tend to be less egalitarian than foragers further inland. But most hunter-

gatherers track resources in small groups, and movement is a way of life (Dyson-Hudson & Smith, 1977; Keeley, 1988; Keen, 2006; Kelly, 2007).

In the same way, shifting cultivators and livestock breeders in richer, less variable habitats are more likely to be polygynous. In the Orinoco River Basin lowlands, where it’s easier to plant gardens and find game, disgruntled Yanomamö are more reluctant to walk away. So their villages are bigger than in the highlands, and their headmen marry more women (Chagnon, 1974, 1979a, 1979b, 1988). Across cultures, gardeners and herders may be less egalitarian in habitats with high dispersal costs. Pacific islands are cases in point (Boone, 1992; Kirch, 1984).

Subsistence intensification is made possible by sedentism. In *H. sapiens*, as in other social animals, from termites to beetles to ants, full-time farming probably followed a settled life (Flannery, 1973; Mueller, Gerardo, Aanan, Six, & Schultz, 2005). As Robert Carneiro once famously summed up, the first states rose up in lake or river valleys rich in resources, but set off by mountains, seas, or deserts, so that “escape in every direction” was blocked (Carneiro, 1970:345). The land between the Tigris and Euphrates Rivers is bordered to the east by the Zagros Mountains and to the west by the Syrian Desert. The hieroglyph for Egypt, km.t, represented the “Black Land” of the Nile Valley, and the hieroglyph for the desert, dSrt.t, represented the “Red Land” of the Sahara that stretched across Africa to the east and west. China’s Middle Kingdom, Zhongguo, flourished in the loess that collected along the Yellow River. Empires centered on the Indus and Ganges were bordered by the Himalayas to the northeast and by the Hindu Kush to the northwest. The lakes in the Valley of Mexico are surrounded by mountains and volcanoes that reach up to 5000 m above sea level. And valleys in the Andes are bordered by ranges over 7000 m high. In every one of those cradles of civilization, subsistence intensified, and reproductive specialization increased.

For thousands of years, civilization in the West looked a lot like civilization in the East. Emperors and other well-to-do men in Greece or Rome were monogamously married to just one wife at a time, but had sexual access to as many slaves as they could afford (Betzig, 1992a; 1992b; 2010; Scheidel, 2009, 2011). Lords in the Middle Ages had sexual access to hundreds of dependent *servi*, or serfs; and householders in early modern Northwest Europe had sexual access to servants, with up to a fifth of the population “in service” at once (Betzig, 1995, 2002).

Over the last several centuries, the Western societies that have spread out around the globe, and their colonies, have tended back toward monogamy. In prescriptively monogamous cultures, demographer after demographer has found evidence that suggests higher variance in men’s reproductive success, though the differences between men and women have always been small (e.g., Alvard & Gillespie, 2004; Bereczkei and Csanaky, 1996; Betzig & Weber, 1993, 1995; Betzig, 1988; Boone, 1986, 1988; Brown & Hotra, 1988; Clark, 2007; Fieder & Huber, 2007; Flinn, 1986; Helle,

Lummaa, & Jokela, 2008; Hopcroft, 2006; Hughes, 1986; Jokela, Rotkirch, Rickard, Pettay, & Lummaa, 2010; Low, 1989, 1991; Nettle & Pollett, 2008; Pettay, Kruuk, Jokela, & Lummaa, 2005; Quinlan & Flinn, 2005; Roskaft, Wara, & Viken, 1992; Scott & Duncan, 1999, 2000; Turke & Betzig, 1985; Voland, 1988, 1990; compare Strassmann & Gillespie, 2003 on prescriptive monogamists and polygamists, where male reproductive variance is greater).

The collapse in power, and reproductive variance, is more recent than many of us remember. And it seems, tentatively, to have something to do with our renewed freedom to move (Betzig, 1996, 1997, 2009b, 2011). Across species, reproductive “skew” is often an effect of ecological constraints (Alexander, Noonan, & Crespi, 1991; Emlen, 1982, 1995; Vehrencamp, 1980, 1983; Wilson & Hölldobler, 2005). It may be for humans, too.

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