Henry C. Harpending

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BIOGRAPHICAL *Memoirs*

A Biographical Memoir by
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HENRY COSAD **HARPENDING**

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Elected to the NAS, 1996

Henry Harpending

By Alan R. Rogers

Henry Harpending grew up in the small town of Dundee, New York, where his ancestors had lived since 1811. He finished high school at age 17, graduated from Hamilton College at age 20, and then took his time in Harvard graduate school, finishing his Ph.D. at age 28. He is hard to categorize: a population geneticist, but also a demographer, an ethnographer, and a sociobiologist. He made fundamental contributions that continue to shape several disciplines.

Henry did a total of 43 months of fieldwork, from 1967 through 1992, in the Kalahari Desert of Botswana and Namibia. He worked first with the Ju/'hoansi (formerly known as the !Kung) and later with the Herero. Many of his most innovative ideas grew out of these field experiences.

As a graduate student in the 1960s, he was part of the Harvard Kalahari Project. He travelled widely across the Kalahari, studying populations of Ju/'hoansi. Some were mobile foragers; others, who lived near cattle posts, were sedentary. The ecological differences between mobile and sedentary Ju/'hoansi would eventually shape much of Henry's career. At the time, however, his focus was on their genetics and demography.

Population Genetics in the 1970s

It was a time of enthusiasm within human population genetics. During the 1960s, the method of electrophoresis had made it easier to assay genetic variation. Computers had made it feasible to study the larger data sets that resulted, and theoreticians had developed new models describing how evolution and demography shape the geographic distribution of genes. In response to these opportunities, several research groups started field projects in different parts of the world to assay human genetic variation. One of these took Henry to the Kalahari Desert.

Truck trouble in the Kalahari, 1969. Irven DeVore, John Yellen, Henry Harpending, and Kachitambo (also known as ≠Gau).

During the early 1970s, this research led to two principal discoveries, one of which involved the relationship between ecology and human genetic variation. Genetic group differences tend to be large among tropical-forest horticulturalists (Friedlaender, 1975; Neel and Ward, 1972) but small among foragers (Harpending and Jenkins, 1974; Yellen and Harpending, 1972). Henry and others also showed that this pattern reflects differences in intergroup mobility, which tends to be low among tropical-forest horticulturalists but high among foragers. It was not clear, however, which of these patterns characterized early human populations. Modern foragers survive only in habitats where agriculture is hard. Early foragers in richer habitats might have been more densely settled, more warlike, and less mobile. If so, genetic differences between local groups would have been larger than those among modern Ju/'hoansi. This is still an open question.

Henry's early research on population genetics also helped establish the close relationship between genetics and geography. Genetic differences between groups tend to mirror the geographic distance between them, so that a map of genetic distances looks like a geographic map (Harpending and Jenkins, 1973). Henry developed methods for studying this relationship that are still in use.

These projects established Henry's reputation within anthropological genetics, yet he himself was critical of the whole endeavor. As he put it in 1974:

> *The central difficulty underlying all studies of the genetic structure of small populations was given by Morton...when he remarked that they maximize the ratio of noise to signal. They are simply too small to detect most systematic forces, and they are too small and homogeneous to make studies of drift really interesting. (1974, p. 240)*

He went on to speculate that in the future we would learn more about evolutionary history from species-wide data at a large sample of loci. Henry then withdrew from research on population genetics. He didn't return until the 1990s, when large samples of mitochondrial DNA sequence data attracted his interest once again.

Population ecology in the 1970s

Meanwhile, Henry's Kalahari field experience also motivated an interest in population ecology. Humans cope with variation in resource supply either by storage (averaging over time) or by mobility and sharing (averaging over space). These strategies are mutually exclusive. Those who store must defend their stored resources against others who would like to share them. Conversely, an ethic of sharing makes storage impossible. The contrast between the mobile and the sedentary Ju/'hoansi in Henry's sample therefore represented a fundamental shift in strategy.

Henry studied how these alternative strategies affect the spatial structure of populations (Harpending and Davis, 1977) and also their dynamics in time (Harpending and Bertram, 1975). One might expect that complex societies would be less vulnerable to environmental variation than would simple ones, but this is only partly so. Jorde and Harpending (1976) showed that although complex societies are less vulnerable to short-scale variation, they are more vulnerable to variation at time scales of a generation or two.

You have to be healthy to look sick and other paradoxes

Diseases need time to cause lesions on bone. If the infected individual dies quickly, no lesion will form, and the skeleton will look healthy. Lesions form only if the infected individual is healthy enough to survive for an extended period. Lesions on ancient bone may therefore imply that the population was healthy!

The demographic component of Henry's Kalahari fieldwork would also echo throughout his career. In demography, as in much of science, there is a quality-quantity tradeoff. One can collect cursory information about a large sample or detailed information about a small one. Outside of anthropology, demographers tend toward the former extreme, and analyses are often carried out at the level of entire nations. Within anthropology, the opposite tradition prevails. Anthropological demographers often collect detailed information about a small sample from a local population. Henry took an intermediate approach, sampling widely among the Ju/'hoansi populations of Botswana.

This regional sample included sedentary as well as mobile Ju/'hoansi and thus allowed Henry to test the hypothesis that sedentism promoted population growth by increasing fertility (Binford, 1968). Contrary to this hypothesis, mobile and sedentary Ju/'hoansi did not differ in fertility. They did, however, differ in childhood mortality, which was much lower among sedentary than among mobile populations (Harpending and Wandsnider, 1982). Not only did this finding contradict the prevailing view, it also seemed to contradict the evidence of Henry's own eyes: children in mobile camps seemed "uniformly healthy, well-nourished, and active," whereas those in sedentary villages were "plagued with eye and respiratory diseases" and seemed "less vital and active than the children in the bush" (Harpending, 1976,p. 150). Harpending and Wandsnider (1982) attributed this to better nutrition among the sedentary Ju/'hoansi. Paradoxically, the sedentary populations looked sicker because they had sufficient nutrition to survive disease.

Henry and his colleagues used the same idea a decade later to discuss signs of disease in skeletal samples from archaeological sites. Diseases need time to cause lesions on bone. If the infected individual dies quickly, no lesion will form, and the skeleton will look healthy. Lesions form only if the infected individual is healthy enough to survive for an extended period. Lesions on ancient bone may therefore imply that the population was healthy! This idea is part of the "osteological paradox" (Wood, et al., 1992).

Henry's demographic work also contributed to archaeology in another way. Paleodemographers use the age distribution of skeletal samples to reconstruct the demography of ancient populations. When the mean age at death increases across the levels of an archaeological site, it is tempting to attribute this to declining mortality. Yet as Sattenspiel and Harpending (1983) showed, no such conclusion is warranted. Births contribute to a single age class, whereas deaths occur at all ages. Consequently, the distribution of skeletal ages is much more sensitive to fertility than to mortality. Increasing age at death is more likely to reflect declining fertility than declining mortality.

Sociobiology in the 1980s

In the 1970s, as Henry's interest in genetic data waned, he began developing population genetic models of social evolution. He overturned 40 years of conventional wisdom by showing that group selection works best not when groups are isolated but when they are strongly connected by gene flow (1980, pp. 58-59; Harpending and Rogers, 1987). When gene flow is restricted, successful mutants cannot spread beyond the initial group, and group selection stalls.

He developed a model of kin selection (1979) and used it to study the evolution of sharing under diminishing marginal returns to consumption (1980, pp. 54-56). His theory explained why meat from large animals is often shared widely rather than targeted to close relatives, whereas plant foods are shared mainly with close relatives.

Alongside these quantitative models of social evolution Henry also pursued a more qualitative approach in a series of papers during the 1980s. The most influential of these was his work with Patricia Draper (Draper and Harpending, 1982). They distinguish between "father-present" and "father-absent" households. In father-present households, the father plays an active role in provisioning and educating children. In father-absent households, he does not.

Draper and Harpending document consistent differences in the behavior of children raised in these different types of household. Boys from father-absent households tend to be aggressive, to denigrate femininity, and to take an exploitative attitude toward females. On cognitive tests, their verbal scores often exceed their quantitative ones. Girls from father-absent households show precocious sexuality, tend to derogate masculinity and males, and have difficulty maintaining stable pair bonds with men. In all these respects, children from father-present households are just the opposite.

They also show that these generalizations hold not only within societies but also between them. In technologically advanced societies, father-absent households are more common in lower socioeconomic groups and are seen as deviant and inferior. On the other hand, father absence is the norm in many parts of the world. Yet none of this seems to matter. In spite of immense variation in social context, the correlates of father absence are the same everywhere (Draper and Harpending, 1982, p. 256).

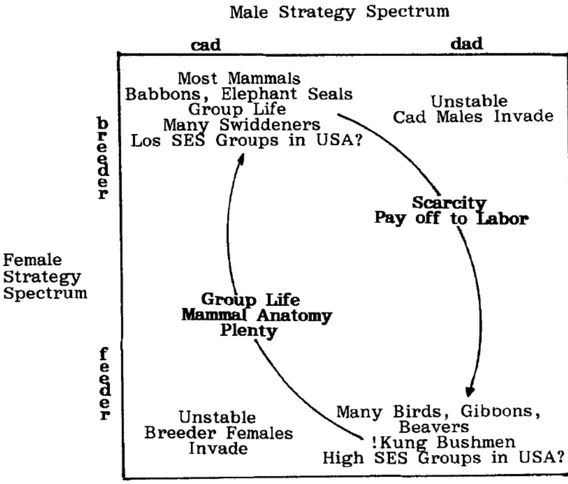
Although these correlates show up in adolescence, they are not a response to father absence at that age. Children are apparently most sensitive to father absence during the first few years of life (Draper and Harpending, 1982, p. 258).

Draper and Harpending proposed an evolutionary theory to explain these facts. Male parenting styles differ greatly among populations, and in these different contexts, selection should favor different behaviors:

> *A male in trying to reproduce can play any mix, combination, or compromise of putting his reproductive effort into mating or into parenting—that is, into being a cad or being a dad. Females have a choice too, although it seems somewhat more restricted than that of males. On the one hand*

> *a female can selectively find a mate who will provision her before she undertakes to reproduce—the feeder strategy—or she can ignore and forswear male provisioning and manage her own resource acquisition and apportionment—the breeder strategy—Harpending and Draper, 1986, pp. 48–49.*

The optimal strategy for each sex depends on the behavior of the other sex: feeders are selected against if cads are common, and dads are selected against if breeders are common. Thus, the only stable strategy pairs are "cad/breeder" and "dad/feeder," as illustrated in Fig. 2. But payoffs in this evolutionary game also depend on subsistence economy. If women cannot provision themselves and their offspring without assistance, then the "cad/breeder" corner of Fig. 2 is not feasible, and we are left with "dad/feeder." Draper and Harpending argue that this is true of the Ju/'hoansi, and other mobile foragers in marginal habitats. Among swidden agriculturalists, on the other hand, female labor is more productive, and men can afford to do less work. The theory thus predicts that such populations will be more likely to fall into the "cad/breeder" equilibrium, as in fact they seem to do.



Model of reproductive strategy options of the two sexes (Harpending and Draper, 1986, Fig. 2)

Although this theory is couched in Darwinian terms, Harpending and Draper do not see genetic evolution as the engine that accounts for variation within and among societies. Instead, they suggest a facultative adaptation: humans have "evolved the ability to sense household structure in infancy" and to alter their developmental trajectories in response to what is learned during this early critical period (1980, p. 63).

This theory provided a coherent explanation for apparently disparate phenomena across a wide range of societies. It has been influential in several disciplines and continues to motivate research (DelPriore et al., 2017).

Demography in the 1980s and early 1990s

Henry returned to the Kalahari during 1987-88 to work with the Herero, a group of pastoralists who live in many of the same areas where he had studied Ju/'hoansi during the '60s and '70s. Demography was the focus of this research, but Henry's view of that subject was broad: "the Darwinian metric of success is the fitness of individuals, and demography is really the study of fitness and the covariates of fitness" (Pennington and Harpending, 1993, p. 3). For Henry, demography, ecology, and evolutionary genetics were a single subject.

The Herero project revealed a surprising sex difference in rates of juvenile mortality. Herero boys were three times as likely as girls to die as infants and twice as likely to die in childhood (Pennington and Harpending, 1993, p. 59). Yet

> *Herero informants of both sexes and all ages denied that there was any preference for a child of either sex. They agreed that all children were gifts of God, they were precious, and the idea of favoring one sex or the other was abhorrent. (Pennington and Harpending, 1993, p. 69)*

Meanwhile, the

> *!Kung Bushmen neighbors of the Herero reported that the Herero "took their daughters to their hearts" and "refused their sons." Several !Kung were quite indignant about Herero mistreatment of males and said that the way that Herero treated their little boys was a "disgrace." One informant said that she surreptitiously fed a Herero neighbor's male toddler and claimed that without her care he would have died of malnutrition. (Pennington and Harpending, 1993, p. 70)*

By age five, Herero boys begin tending cattle, and these duties often involve missing meals. Thus, it makes sense that Herero boys might be thinner than girls after age five, and skin-fold measurements show that this is so (Pennington and Harpending, 1993, Fig. 3.3). It remains mysterious, however, that Herero girls gain fat just after weaning, whereas boys lose fat.

The Herero demography project also shed new light on the low fertility of Kalahari Ju/'hoansi.

> *The low fertility of the !Kung became incorporated into an anthropological legend about the Bushmen—that they were affluent, cheerful, and*

> *gentle people who ate a lot of high fibre natural foods, lactated a long time, and got a lot of exercise. This way of life led to "natural" fertility control, according to the ideology, so that they had near zero population growth and were in long term balance with their environment. The natural state was lost when Herero and other pastoralists moved into their range. !Kung settled with Herero, began drinking milk and eating grain, quit walking long distances to forage, and their fertility increased dramatically through shorter birth intervals. (Pennington and Harpending, 1993, p. 200)*

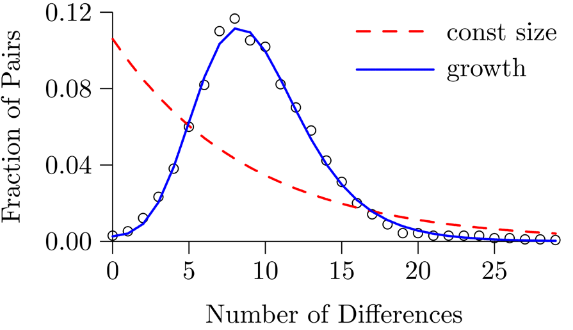
It turned out, however, that early in the twentieth century the fertility of sedentary Herero was even lower than that of mobile Ju/'hoansi. In the 1950s, as Ju/'hoansi began settling near Herero cattle posts, Ju/'hoan fertility went down rather than up. The fertility of both groups began to rise only after mobile medical clinics began dispensing antibiotics in the area. This suggests that the low Ju/'hoan fertility was not an adaptation to mobile foraging. Instead, it probably resulted from sexually transmitted diseases, which reduced fertility throughout the region (Pennington and Harpending, 1993, Ch. 8).

Molecular population genetics

In the late 1980s, studies based on large samples of human mitochondrial DNA sequence data began appearing in the literature (Cann, et al., 1987). Henry e-mailed me about a puzzling result. In sequence data from the Ju/'hoansi (Vigilant, et al., 1989), there were very few distinct mitochondrial sequences, or "haplotypes." This suggested a small population size. Yet those haplotypes that did exist differed from each other in many places, and this seemed to imply a large population. How could the Ju/'hoan population be both large and small?

This sort of question would not have arisen in classical population genetics, because genetic variants were either the same or different—you couldn't measure the magnitudes of differences. With DNA sequence data, such measurements became possible, and it turned out that the differences accumulate gradually over time. This gave population genetics a clock (Rogers, 2014).

Henry and I studied the "mismatch distribution," one of which is shown in Fig. 4. The graph shows the fraction of pairs of DNA sequences that differ at 0 sites, 1 site, 2 sites, and so on, in the worldwide sample of Cann, et al. (1987). We first tried a model of constant population size (the dashed red line), which didn't fit well at all. Then we fit a model that allowed for one episode of growth (the blue line), which fit remarkably well. The fitted parameter values implied a massive increase in population size that coincided roughly with the origin of



Two models fit to an empirical mismatch distribution from a worldwide sample. Open circles show the empirical distribution. The dashed red line assumes constant population size. The solid blue line assumes roughly 100-fold growth 7.2/2u generations ago, where u is the mutation rate per sequence per generation (Rogers and Harpending, 1992).

modern humans (Rogers and Harpending, 1992). This was the first method for inferring the history of population size from genetic data, and it is still widely used.

These results seemed to support one side of the debate about modern human origins—the "replacement hypothesis," which held that all modern humans descend from a population that arose in the late Pleistocene and then spread throughout the world, replacing earlier humans as it went (Stringer and Andrews, 1988). The alternative "multiregional hypothesis" envisioned evolution within a worldwide network of regional populations, loosely connected by gene flow (Wolpoff, 1989). Our results seemed to contradict the multiregional hypothesis, because the initial population was too small to span the globe, and the episode of growth was consistent with a geographic range expansion. Throughout the 1990s Henry (along with most population geneticists) favored the replacement model of human origins (Harpending, et al., 1993, 1998; Harpending, 1994a,b; Harpending, et al., 1998; Sherry, et al., 1994; Vigilant, et al., 1991).

Near the end of the 20th century, large-scale studies of nuclear DNA began to appear, and these undermined support for the replacement hypothesis (Harding, et al., 1997). There was still evidence of a late-Pleistocene bottleneck in the size of Eurasian populations, but this bottleneck seemed to be much milder than the mitochondrial evidence had implied (Marth, et al., 2002). Harpending and Rogers (2000) pointed out that evidence for a bottleneck was weakest in portions of the nuclear genome that code for protein and suggested that widespread balancing selection might underlie this pattern. Since then, evidence for balancing selection has accumulated (Bamshad, et al., 2002; Andrés et al., 2009).

Henry was also among the first geneticists to argue for admixture between modern humans and archaic populations such as Neanderthals. His interest in the subject began in 2002, when he received a manuscript from Vinayak Eswaran, an engineer who was interested in the possibility that modern humans had interbred with archaic hominins as they expanded across Eurasia. Henry arranged for Vinayak to spend a year in Utah developing that idea. That work provided the first genetic evidence for admixture between moderns and archaics (Eswaran, et al., 2005). A year later, Henry and others published another paper arguing for archaic admixture (Hawks, et al., 2006). That idea is well established now but was controversial then.

Adaptive evolution

Henry's interest in adaptive evolution never waned. In 2006 he copublished a controversial paper arguing that a single cause underlies two apparently unrelated phenomena: the high IQ scores of Ashkenazi Jews and the elevated frequencies of several genetic diseases within this population (Cochran, et al., 2006). He and his coauthors argued that both result from selection for intelligence during 800–1600 C.E. They argued that (a) history indicates that throughout this period most Ashkenazi Jews worked as money lenders and tax farmers—occupations that demand intelligence—and that successful individuals had large families; (b) furthermore, Ashkenazi Jews were segregated from surrounding populations, which would have limited gene flow; (c) the high heritability of IQ implies that it would have responded rapidly to selection; (d) selection on a given trait often reduces fitness because of deleterious side-effects, and Ashkenazi genetic diseases may represent such side effects; (e) several of these diseases are associated with high intelligence; (f) these diseases cluster in a small number of metabolic pathways, which is inconsistent with the hypothesis that they arose through genetic drift during a bottleneck in population size; moreover, (g) high Ashkenazi heterozygosity refutes any hypothesis of a severe bottleneck. It is now necessary to qualify the last of these points, because Carmi, et al., (2014) infer an Ashkenazi bottleneck beginning 32 generations ago. However, their bottleneck is so mild that it does not compromise the argument of Cochran, et al. (2006).[1]

In 2009, Henry and Gregory Cochran published a monograph, T*he 10,000 Year Explosion*, which describes adaptive evolution during the last few millennia of human evolutionary history (Cochran and Harpending, 2009). People used to think that genetic evolution had been unimportant since the origin of modern humans, tens of thousands of years ago. It is now clear this isn't so. Cochran and Harpending tell the story of the discoveries that made this clear—how selection shaped our bodies, brains, and immune systems in response to gene flow from Neanderthals, to climate, to agriculture, and to the organization imposed by states.

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[1] The Ashkenazi population was apparently reduced to size 250, then grew exponentially at rate 0.16 per generation for 32 generations. This implies only a slight (~1%) reduction in heterozygosity.)

Summary

Henry's research was so multifaceted that most of us probably knew only a piece of it. He was a population geneticist for some, a sociobiologist for others, and so on. We knew him as the blind men knew the elephant. But these disparate interests were connected. Much of his career was about genetics and population history, and the rest was about adaptive evolution. His research on adaptive evolution developed out of a fascination with two sets of contrasting ecologies: that between sedentary and mobile Ju/'hoansi, and that between societies in which men do and do not provision and educate their children.

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