

wrong. It is time to move on to more dynamic models that incorporate regional and temporal diversity.

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Eswaran models a mechanism for correlating adaptive change across the entire species range. His model explains one possible mode of multiregional evolution for Pleistocene humans, but it is important not to overstate its importance either by presenting it as a *unique* mode of change or by implying that the observed course of events in the Late Pleistocene necessarily requires a *unique* explanation.

Multiregional evolution (as described by Relethford 2001; Templeton 1997, 2002; Wolpoff 1989; Wolpoff, Hawks, and Caspari 2000) is a theory relying on well-understood forces of evolution to explain the pattern of variation and change for Pleistocene human evolution by resolving the apparent contradiction between specieswide changes and regional continuities of local features. Local variation is promoted by differences in selection as well as isolation by distance and unequal reciprocal gene flow¹ in the absence of selection. Clinal distributions are created by balances of gene flow (mostly from the center to the edges of the human range) and selection or drift. Features defining common evolutionary trends can disperse throughout the species when reciprocal gene flow is predominantly directional, for instance, the largely center-to-edge pattern originally identified as a key element of multiregional evolution. Dispersal is more rapid when the characteristics are promoted by selection or when they respond to cultural changes that spread. In either case some unique local variations persist for shorter or longer periods because there are no instances of complete population replacement everywhere (Wolpoff et al. 2001).

A significant issue in multiregional evolution is how new features, in particular, features that come to characterize the whole species, disperse together. One would expect that a dispersing population mixing with other populations would break apart and attenuate the package. This is one reason that many multiregionalists argue that new features had independent origins and appeared together only after they had dispersed individually and that other researchers, convinced that complexes of features have dispersed together, turn to a population *replacement* explanation for it such as the Eve theory.

Eswaran uses Wright's adaptive-landscape model for a new insight, to explain how a complex of features might disperse together as a diffusion wave through popula-

tions without any population movement. His explanation focuses on the spread of "modernity."

The model predicts a successful diffusion wave within a limited range of parameters: strong selection promoting the dispersing gene complex and limited intermixture. Eswaran suggests that the source of this strong selection is a reduction of birth mortality. He cites Rosenberg's (1992) discussion of the evolution of human birthing difficulties in support of his argument, but Rosenberg notes that birthing difficulties can be inferred more than a million years before the modern humans whose new morphology presumably "solves" them. Further, the enlarged pelvic inlets and outlets characteristic of "modernity" that make births easier are found in female Neandertal (Rosenberg 1998) and earlier pelvises (Arsuaga et al. 1999). Two Neandertal populations (Krapina [Wolpoff 1979] and Sima de los Huesos [Bermúdez de Castro and Nicolás 1997]) have high childhood mortality and low adult survivorship, which means that they could not also have had high birthing mortality because they would not have had enough surviving children to persist. As it is, Wolpoff (1979) calculated that the live births at Krapina must have been spaced very close together for the Krapina "population" size to have been stable.

A more significant question is whether "modernity" is actually a unique complex of features and even whether it can be validly defined apart from the description that modernity depicts people as they are today and in the recent past. If modern humans were a new species or an overwhelmingly superior anatomical and/or behavioral variant they should have a package of unique, distinct features, but repeated attempts to identify such a package (Day and Stringer 1982, 1991) fail to include all recent (Wolpoff 1986) or living (Brown 1990) people. This suggests that modernity is not a morphological complex but a perspective created by the fact that we view the past from the present.

Questioning whether this particular explanation of a diffusion wave is valid does not affect the issue of whether multiregional evolution works. It does address how it *might* work, but there is nothing in the multiregional hypothesis implying that only one mechanism has been operative in dispersing features. With pleiotropy and hitchhiking when there is selection, a number of models could explain the simultaneous adaptive spread of more than one trait. How many traits must disperse together before simpler selective models are no longer adequate?

I am not opposed in principle to the idea that a package of related features could have spread around the world, presumably from a single source—this is the assumption of the (poorly named) "assimilation"² explanation of multiregional evolution proposed by Smith, Falsetti, and Donnelly (1989), and a single-source explanation is favored by Relethford (2001). But the fossil evidence has never provided much support for the idea as an expla-

1. Gene flow refers to the movements of genes, which may or may not involve the movements of peoples but in either case is reciprocal and requires interbreeding between people from different groups—variously called mixture, admixture, assimilation, or hybridization.

2. All explanations of how multiregional evolution works necessarily involve gene flow, which implies interbreeding, and therefore all are "assimilation" models.

nation of modern human origins. Still, there is no question that in some form or other Eswaran's diffusion-wave model is quite likely a valid explanation for the multi-regional pattern of any one of a number of specieswide events in human evolutionary history. It is a significant and particularly insightful description of how multiregional evolution might be expected to work when a specieswide change involves a package of characteristics that have a single origin but are related only by the common adaptation they promote.

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A popular interpretation of the results of genetic studies of the origins of modern humans is that no Neandertal genes survive among today's Europeans. This interpretation is in turn used to argue for the total replacement of anatomically archaic Eurasian populations by anatomically modern groups migrating out of Africa. Eswaran's "diffusion-wave" model shows that those present-day genetic patterns can be more parsimoniously explained through the operation of such ordinary population biology mechanisms as demic diffusion and admixture. In fact, the model suggests that such patterns are better explained by hybridization than by total replacement and that hybridization "could have been the principal reason for the disappearance of the archaic morphology."

I cannot but agree with these conclusions, since I have been arguing along similar lines (Zilhão 2001a:72):

It is quite likely that between 100,000 and 40,000 years ago a large majority of all the planet's human beings lived in Africa, where the modern morphological form evolved. If these African groups also had a higher fertility, as is commonly the case with warm climate populations of the same species when compared with those from colder climates, we can plausibly explain what happened [the "extinction" of Neandertals through assimilation by moderns]. When Africa became "full" of Africans, Africans started to disperse into the neighboring regions. . . . Given enough time, even a very small difference in fertility would put the much smaller and more scattered populations of Neandertals at a demographic disadvantage, especially if interbreeding was common.

This quotation highlights where it is that I disagree with Eswaran. His model requires two assumptions: that a strong adaptive advantage for the "modern" genotype exists and that the rate of interbreeding between demes is low. He also suggests that the advantage may have lain in the particular features of anatomical modernity, for instance, in bringing about reduced childbirth mortality: "an increase in fertility due to this advantage is sufficient to explain the modern transition." He also assumes that population density is constant across time and space,

which entails making all group-demes of the same size and each made up of a single genome.

There are a few problems with these assumptions. First, as is pointed out by Eswaran himself, in order for the model to work, the magnitude of the difference need be no greater than archaic populations' having 7 children per mother versus modern ones' having 7.5. Such differences in fertility, however, are of the same order of magnitude as those between warm-temperate and arctic populations of contemporary hunter-gatherers (Binford 1983), all of which are anatomically modern. Consequently, the selective advantage assumed by Eswaran is not necessarily related to body morphology, and the model cannot be used to support the notion that moderns had reduced childbirth mortality because of "a decrease of the anterior-posterior diameter of the modern cranium" and "concomitant modifications of the pelvis."

Second, one of the simulation's basic mechanisms, the mating procedure, is probably realistic. Under Eswaran's rules, for the model to work mating inside the deme (which, if I understand him correctly, is a hunter-gatherer band of normal size, i.e., ca. 25 people) must be much more common than mating outside it; as he points out, "the interbreeding rate between human groups would need to have been very constrained to allow the spread of complex advantageous genotypes." However, this condition contradicts the rules of exogamy, which, as Wobst (1974, 1976; see also Smith 1992) has shown, are demographically obligatory to secure a group's reproduction in the long run. Important aspects of lithic technology are widespread in the late Lower and the early Middle Paleolithic, implying information exchange networks encompassing vast areas. Such networks must have functioned as overlays on the exchange of individuals between demes in the framework of exogamic mating, whose rules, therefore, must have been in place well before the worldwide spread of anatomical modernity.

However, if differential fertility is related not to an advantageous genotype but to cultural-environmental constraints, as suggested by the ethnographic data, the need to constrain the interbreeding rate disappears. Moreover, this rate is also likely to have been extremely variable, for example, low in situations in which mutual avoidance was possible, high in geographical culs-de-sac (Zilhão 2001b). My question, therefore, is whether the same outcome (i.e., the disappearance of archaics through their assimilation into moderns dispersing out of Africa) might not be obtained assuming an imbalance in population density and population size between the core area of the world's population of humans, occupied by moderns, and the peripheral areas, occupied by archaics. Although this biogeographical scenario remains to be modeled, it seems empirically more realistic than Eswaran's. I compliment him on an elegant demonstration but would welcome similar quantitative testing of alternative mechanisms.

comment) we are sure that the *marked* changes⁴ in these features that accompanied the archaic/modern transition really did not impact childbirth mortality. A single parameter such as the pelvis/cranium ratio can be only a rough indicator of birth difficulty, especially if this ratio remained constant across the archaic-modern transition as Rosenberg suggests it did.⁵ It is likely that, when more complete information on archaic female pelvises⁶ and infant crania is obtained, the passage of the latter through the former will need to be modeled before definite conclusions can be drawn.

There has presumably been a continuous pelvic adaptation to human childbirth for the past 2 million years because of the selection pressure of increasing neonate cranium size. Thus enlarged pelvises in Neandertals and other late archaic humans are only to be expected. I have merely suggested that some co-adapted changes in the pelvis and the cranium further eased the birth process for modern humans and significantly decreased childbirth mortality in yet another step in a continuously evolving “solution” to the childbirth problem.⁷ Finally, I have no doubt that the Neandertal live birth rate was adequate to sustain their population, for otherwise they would not have lasted 200,000 years. But natural selection chooses among competing phenotypes, and the anatomically modern one may have been better—in terms of offering greater childbirth survivability—than the Neandertal one.

I hope that more data and further study will resolve this issue. At the very least this hypothesis, by suggesting that modern anatomical features were adaptive, cautions against jumping to conclusions regarding the conspecificity of archaic and modern humans from the morphological differences between them.

Finally, I emphasize that the diffusion-wave theory is based on a modified version⁸ of the three-phase shifting-balance theory of Wright (1932). This is significant because Wright’s process, if it operates, could increase the pace and scope of the evolution of a species beyond what is attainable by Fisherian mass selection alone. This may help to explain the uniqueness of human adaptation and intelligence. We can speculate that the evolution of humans was largely determined by the small-deme, low-interbreeding social structure required for Wright’s process. Thus the invocation of Wright’s theory in human evolution has rich consequences in need of further in-

vestigation. It allows us to go beyond the problem of modern human origins to the whole of human evolution.

Indeed, I believe that two other disciplines—evolutionary psychology and historical linguistics—should perhaps spare a glance at this theory, for, apart from the increased scope of evolution offered by Wright’s process, an evolutionary environment dictated principally by life in small competitive demes is likely to have had a profound effect on the evolution of the human mind and emotions, with implications that would bear investigation. As for historical linguistics, the correspondence of the pattern of diffusion waves (fig. 1) with the pattern of language families is striking and—apart from suggesting the need for a radical reassessment of the age of language families—may offer explanations for the existence of the linguistic superfamilies that have been proposed and have been the subject of much controversy for the past half-century.

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4. The differences between archaic and modern infant crania have been thought sufficient to be at the species level (Stringer and McKie 1996:88). There were also significant differences between Neandertal and modern pelvises (Rak 1990)

5. But see Tague (1992:19), who suggests that Neandertals had a less favorable cephalo-/maternal-pelvic relationship and so would have had more difficult childbirth than modern humans.

6. The only known complete Neandertal pelvis (from Kebara) is presumed to be male.

7. Which is still not completely “solved,” for natural childbirth in humans remains the most difficult among the primates. Even after the modern transition, the disappearance of browridges, etc., may have been driven by selection pressure to decrease childbirth mortality still further.

8. For it insists on mobile demes.

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