

# Historical Evidence and Human Adaptations

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Phylogenetic information is often necessary to distinguish between evolutionary scenarios. Recently, some prominent proponents of evolutionary psychology have acknowledged this, and have claimed that such evidence has in fact been brought to bear on adaptive hypotheses involving complex human psychological traits. Were this possible, it would be a valuable source of evidence regarding hypothesized adaptive traits in humans. However, the structure of the Hominidae family makes this difficult or impossible. For many traits of interest, the closest extant relatives to the human species are too phenotypically different from humans for such methods to provide meaningful data. While phylogenetic information can be useful for testing adaptive hypotheses in humans, these generally involve traits that are (a) not widely shared in the species or (b) fairly widely shared in the Hominidae family, and hence likely of a lower order of complexity than the sorts of traits evolutionary psychology has so far been interested in.

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**1. Introduction: Adaptations, Adaptationism, Evidence, and Humans.** The primary focus of the current debates surrounding ‘adaptationism’ seems to be resolving into questions about the sorts of evidence necessary for an adaptive (or a non-adaptive, for that matter) hypothesis to be considered well-supported (see e.g. Griffiths 1996; Brandon and Rauser 1996; Rose and Lauder 1996 and cites there; Pigliucci and Kaplan 2000 and cites therein); what requirements are accepted as legitimate will obviously have serious implications for the success of evolutionary psychology meeting

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its stated goal of providing strong empirical support for the adaptive hypotheses put forward (see Lloyd 1999; Lewontin 1998). There are a number of different kinds of evidence that can be brought to bear on hypotheses surrounding how and why a particular phenotypic trait (or traits) arose, spread within a population, and has been maintained within that population. These include laboratory and ecological field studies of the consequences of phenotypic manipulations of that trait (or those traits), laboratory evolution experiments designed to test adaptive and non-adaptive hypotheses (such as those involving constraints, or the robustness of proposed pathways), optimization analyses of various sorts, regression analyses of the trait and fitness consequences, and analyses of the phylogeny of the populations involved; in general, more than one type of evidence will need to be gathered for an adaptive (or again, a non-adaptive) hypotheses to be adequately tested against reasonable competitors (see Pigliucci and Kaplan 2000).

In this paper, I explore the extent to which the various techniques used to test adaptive hypotheses in non-human populations can be and have been successfully applied to testing adaptive hypotheses in the context of human populations. While evolutionary psychology's main proponents' focus on complex psychological traits as well as on supposedly universal human adaptations will be revealed to be deeply problematic from the standpoint of putting forward testable hypotheses, it will be suggested that other approaches less focused on these arenas might prove to be promising.

**2. Testing Adaptive and Non-Adaptive Hypotheses in Humans: The Impossible and the Difficult.** Unfortunately, many of the techniques commonly used to test adaptive hypotheses in other organisms are of little use in testing purported human adaptations. Obviously, experimental manipulations designed to reveal fitness consequences of modifications of putatively adaptive traits, both in laboratory and in natural populations (see Sinervo and Basolo 1996 and cites therein) fall into this category because using these techniques on humans is in general ethically impossible. Partial exceptions are provided by 'natural' experiments, in which phenotypic traits are 'manipulated' accidentally (either because of e.g. traumatic injury or genetic mutations), but in these cases it is very hard to control for related variables. In the case of hypothesized human *psychological* adaptations, the manipulations necessary to properly test adaptive hypotheses by phenotypic manipulation might well be beyond the current state-of-the-art in e.g. neuropsychology, even if they were not ethically impossible. Similarly, laboratory evolution experiments designed to, for example, falsify alternate hypotheses (such as those involving constraints and allometry, see Schlichting and Pigliucci 1998) or to test the repeatability of adaptive pathways (see Rose, Nusbaum, and Chippindale 1996, and cites

therein) can be rejected as all-but impossible in the human case, for both ethical and practical reasons.

'Transplant' experiments, a variation of experimental manipulations wherein supposed adaptations to local conditions (e.g. hypotheses about the significance of particular ecotypes) are tested by physically *moving* the organisms in question to other locales and observing the fitness consequences (see Reznick and Travis 1996 and cites therein; see Wilson 1994 and cites therein), can only be 'done' with humans in a very limited way (e.g. following people or peoples that move), and generally with a self-selecting and likely atypical sample. Again, properly controlling for correlated variables is difficult in these cases. So far, attempts to use these techniques to study human adaptations have been rare.

Optimization arguments that take historical contingencies into account (see for example Sober 1996; Orzack and Sober 1996; Lauder 1996; Seger and Stubblefield 1996, and cites therein) seem a more promising avenue for research into human adaptations, as they primarily involve *observation* rather than manipulation.<sup>1</sup> Similarly, techniques making use of broadly historical evidence about the genesis and spread of the trait in question should be one of the more plausible approaches to testing adaptive hypotheses in humans. Indeed, this latter kind of evidence, has been explicitly mentioned as relevant by prominent evolutionary psychologists; Miller, for example, has noted that "examining the distribution of traits across related species with known phylogenies" can be used to "discern when and where evolutionary innovations occurred" (1998, 117; see also Buss 1999, 54-64).

While these techniques are not impossible (or nearly so) in the way that, for example, most phenotypic manipulations of humans would be, there are still important questions about how successful one should expect such techniques to be at developing evidence that can be used to support or contradict adaptive hypotheses in humans. Below I argue that these techniques have been applied with at least moderate success, and adaptive hypotheses have been well-supported, in the case of human adaptations similar to ecotypes. However, despite the claims of some of evolutionary psychology's proponents, I argue here that such evidence is rarely available in the case of purported 'universal' human psychological adaptations. The very limited information available on the environments in which key

1. In some optimization analyses the historical information is not explicitly dealt with—for example, when analyzing potential foraging strategies, the range of options and the problem to be solved are often held constant. As long as the behavioral adaptation under consideration is fairly local in evolutionary time, this presents few problems. In the case of purported universal human adaptations, however, neither the *specific* problem to be solved nor the range of options available to solve it can be assumed to have been constant.

aspects of human evolution took place<sup>2</sup> make optimization techniques difficult to apply here. Further, while in some cases phylogenetic information about Hominidae may provide evidence relevant to adaptive hypotheses in humans, nature and history have ‘conspired’ to make the task much more difficult with humans than it is in many other species. These difficulties, combined with the above-outlined difficulties with hypotheses in humans, continue to doom many of the hypotheses of interest to evolutionary psychology’s most prominent proponents to having to make do with inadequate evidence.

**3. Human Adaptations: Discovery and Evidence.** In the case of (some) *physical* adaptations in humans, there is in general agreement regarding, at least, what needs to be explained, and how well supported current explanations are. For example, while human bipedalism seems to most researchers to be a fact in need of explanation, there seems general agreement that no current hypothesis (adaptive or otherwise) is so well supported by the evidence as to exclude all reasonable competitors (see Tattersall 1995 for discussion). The massive increase in brain size during human evolution is in a similar position—there is agreement that it stands in need of explanation, but no agreement on what that explanation is. While many possible explanations have been proposed, none are generally considered well supported, nor is there agreement on a plausible research program for solving this problem.

Famously, the high prevalence of alleles associated with sickle-cell anemia (the HbS alleles) in certain populations is a fact in need of explanation; unlike the other cases, however, there is agreement on what the correct explanation is (at least in outline). The sickle-cell allele is an adaptation for partial malaria resistance; the alleles associated with sickle-cell anemia in homozygotes are associated with resistance to malaria in heterozygotes. Evidence for this adaptive hypothesis comes from many sources; the alleles associated with sickle-cell anemia are relatively prevalent only in populations recently exposed to environments where malaria is a problem (in addition, work done on the history of populations vis-a-vis migrations, prevalence of HbS allele, and the prevalence of malaria show a clear relationship); finally, reasonable estimates of the fitness of the HbS versus ‘normal’ alleles in various environments correlate fairly well with actual

2. Space considerations preclude a lengthy discussion of our (lack of) knowledge about the relevant environments in which key aspects of human evolution took place. Briefly, however, we do not know *where* (in the world) the various key evolutionary innovations that led to *Homo sapiens* took place (see e.g. Templeton 1999 and cites therein) nor *when* these innovations took place (see e.g. Tattersall 1998 and cites therein); given this, even if we knew what the environment was like at each place and in each time (which we don’t), we still would not have sufficient information to use the comparative method.

distributions (see Griffiths et al. 1996; Das 1995, and cites therein). There are still any number of questions to be answered in the sickle-cell case, and some fascinating work being done on the extreme heterogeneity of the clinical manifestation of sickle-cell disease,<sup>3</sup> but the basic adaptive claim seems reasonably well supported. While there has been some research suggesting that other diseases caused by single recessive genes (such as CF) may be the result of alleles with similar adaptive roles (in the case of CF, possibly resistance to typhoid; see Pier et al. 1998), as yet none have gathered evidence strong enough to have been generally accepted. Similarly, a promising research avenue involves attempts to explain particular genetic variations through the testing of particular adaptive hypotheses more generally, such as the work being done attempting to link the prevalence of the apparently recent spread of the CCR5?32 'HIV resistance allele' in populations of European descent to outbreaks of Black Death in Europe (see Stephens et al. 1998).

Other phenotypic traits in humans for which adaptive explanations have been offered and seem reasonably well-supported include skin color (fair skin for diets poor in vitamin D in locales with low levels of sunlight), and some variations in body size and shape between populations in radically different climates (see for example Cavalli-Sforza and Cavalli-Sforza 1995; Lewontin 1995). There are undoubtedly others. What is startling, though, is that even basic phenotypic features (such as our large brains, bipedalism, opposable thumbs, relative-hairlessness, etc.) that are generally agreed to have arisen after the lineage that gave rise to humans diverged from those lineages that gave rise to the great apes have in general *not* been explained by hypotheses (adaptive or otherwise) that have gained wide acceptance (see Tattersall 1995 and 2000 for a review). This is certainly *not* a feature of adaptive explanations shared with other species; for many species with species-typical phenotypic traits there are adequate adaptive explanations for these traits. Why then have acceptable explanations even for such banal human traits as our bipedal stance been so hard to come by in the human case?

**4. Phylogenetic Histories and Bad Luck.** The basic difficulty with testing adaptive hypotheses for widely-shared human traits stems from an unfortunate feature of our phylogenetic history. Our closest living relatives are the great apes; however, as these things go, they aren't really all that close.

3. Some preliminary work may point toward the existence of 'co-mutations' inherited with the HbS allele providing partial protection against sickle-cell disease, even in the homozygotic case (see Guasch et al 1999 and cites therein). As yet, it is not known when these (putatively) protective mutations arose and spread compared to the HbS mutations.

It is widely agreed that the most recent common ancestor we share with the great apes was at the very least 6 m.y.a., and possibly rather longer (see Tattersall 1995, 218; Goodman et al. 1998). Nor do those apes themselves represent a particularly diverse range of species; only the two extant species of chimpanzee share a relatively recent common ancestor with another extant species (Tattersall 1995, 218; Goodman et al. 1998); although some have suggested that DNA evidence implies that orangutans may be best thought of as representing two distinct species, having diverged perhaps 1.7 m.y.a. (see Gragneux et al. 1999). There are, then, perhaps 7 or so species in the 'Hominini' tribe, that (perhaps) share a common ancestor on the order of 10–14 m.y.a. or so, and perhaps another few species of 'lesser apes' in the Hominidae family, sharing a common ancestor with the great apes on the order of 18 m.y.a. or so (see Goodman et al. 1998; Gragneux et al. 1999).

The problem with such a sparsely populated clade is that the basic techniques that permit one to figure out how putative adaptations relate to selective regimes are difficult if not impossible to assess without reasonably large numbers of reasonably close relatives. To get good evidence that a trait was subject to strong selective forces, and figure out what those forces were (and hence what the trait might be an adaptation for), requires comparing phylogenetic histories of the populations and traits in question to ecological field studies (or work through experimental manipulations) of the fitness consequences of the traits in questions (see for example Griffiths 1996; Larson and Losos 1996; Sinervo and Basolo 1996; Leroi et al. 1994). These techniques are only plausible if there are available variations on the traits to test against the known histories of the lineages.

This evidence is not at all impossible to come by in other species, even for 'species typical' adaptive traits. For example, Sinervo and Basolo (1996) describe the research that was done to test the hypothesis that the 'sword' of the sword-tailed fish (*Xiphophorus*) is an adaptation to female preference for male fish with swords. Phenotypic manipulations, mainly the addition or subtraction of swords, were used both to measure the strength of the female preference for swords (and hence the fitness consequences of being 'sword-ed') in current populations, and, in combination with phylogenetic information about *Xiphophorus* and related genera (such as the closely related *Pirapella*), to try to unravel the history of the trait and preference. The studies suggest that the female preference for swords arose prior to the swords, that is, that the primitive trait is a female preference for swords but sword-less males. This, they suggest, supports the hypothesis that the swords are an adaptation to female preference (Sinervo and Basolo 1996, 173–175). These tests were possible *because* a reasonable phylogeny exists for fish of these types; the genus *Xiphophorus* itself comprises several dozen species, the males of which have sword-tails

(of varying lengths), and the females all have a preference for swords. The females of some closely related genera (such as *Pirapella*) share the preference for swords, even where none of the males of their species are sworded; since evidence suggests that sword-less-ness is the primitive trait, the adaptive hypothesis is well-supported (see Sinervo and Basolo 1996, 172). While Sinervo and Basolo point out that many questions still remain to be answered, this sort of research into putative adaptations certainly addresses many of the problems with ‘adaptationism’ that, for example, Gould and Lewontin pointed towards (Gould and Lewontin 1979).

The problem is that this sort of evidence just isn’t available in the case of putative universal human adaptive traits; we have no extant relatives which are suspected of sharing similar selective regimes and that can therefore be used to test the fitness consequences of the supposed adaptations. If all or most of the estimated dozen or so extinct hominid species (comprising, perhaps two or three genera) still existed, phylogenetic studies would certainly be easier, and might well be useful for distinguishing between competing hypotheses about the spread and maintenance of phenotypic traits of interest. Unfortunately for testing adaptive hypotheses in humans, all the other hominids are extinct, and so comparisons between the groups, with special attention to the fitness consequences of differences in key traits, are impossible.<sup>4</sup>

The best place to look for testable human adaptations, then, is either for traits widely shared in the hominoid (or larger) clade (hence, not uniquely human traits) *or* for traits that are of local adaptive significance (such as the HbS mutation or the CCR5 $\Delta$ 32 mutation). However, there is very little known systematic diversity within the genus *Homo*, either at the level of meaningful phenotypes or at the genetic level. Indeed, current DNA evidence points to humans having far less genetic diversity even than the other great apes, despite the relatively old age of our clade (Gagneux et al. 1999, 5081).<sup>5</sup> This *may* mean that there will be relatively few signifi-

4. Little is known about the details of the environmental (including social) conditions under which human evolution took place (see note 3, above); without such details, analyzing the fitness consequences of traits is at best difficult. It has been argued that since there are no reliable phylogenies of the hominini line, linking changes in phenotypes to changes in environment will prove difficult or impossible (see Collard and Wood 2000 and cites therein).

5. The suggestion that the most likely explanation for the low level of genetic diversity in *Homo* is that at some point, the “lineage leading to humans must have experienced a lower genetic effective population size” (Gagneux et al. 1999, 5080) has intriguing implications for non-adaptive explanations of widely shared human traits; small effective population sizes could result in the fixing of particular phenotypic traits through non-adaptive forces such as drift (see e.g. Futuyma 1998). This would recommend caution in explaining universal uniquely human traits as adaptive.

cant local variations to be found; however, more work needs to be done looking for such variation before any such claims could be supported.

**5. Giving Up on Universal and Unique Features: What's Left for Evolutionary Psychology?** Insofar as it is the goal of many of the most vocal proponents of evolutionary psychology to explain 'human nature' as a collection of adaptive traits unique to humans (see Cosmides, Tooby, and Barkow 1992, 5), the unfortunate structure of our clade, combined with the ethical constraints on human research, seems very problematic.<sup>6</sup> Evidence relating to other related goals, however, is more plausibly obtainable.

Wilson, for example, has noted that evolutionary psychology has not dealt seriously with the possibility of studying adaptive phenotypic variation between human populations; he argues that there are both theoretical and empirical reasons to suspect that such variation might exist (Wilson 1994). And some of the critical difficulties in gathering evidence relevant to claims regarding universal uniquely human adaptations don't apply to gathering evidence relevant to more local, population-level adaptations. For example, when population-level psychological adaptations are suspected, adoption studies (if properly executed) *might* provide 'natural' transplant experiments. It is possible that studies of immigrants to new locales could also shed some light on hypothesized population-level adaptations. And regression analyses done on populations where the selective pressures are known (or suspected) could provide quantitative assessments of the strength of particular selective pressures and perhaps even 'catch' adaptation in action (see Lande and Arnold 1983; see also Schlichting and Pigliucci 1998, 166ff. and cites therein for more recent developments). Of course, gathering such evidence would likely be difficult. Not only would it require cross-cultural field work, but it would also require careful work on adoption and immigration practices in order to attempt to deal with the large number of confounding (cultural, etc.) factors.<sup>7</sup>

Another approach is to deal not with hypothesized adaptive traits that are uniquely human, but rather with adaptive traits shared by at least some

6. Cosmides and Tooby have been most active in arguing this position; see Tooby and Cosmides 1989; Tooby and Cosmides 1990, 1992, 2000. Buss makes the same argument in his (1995), as does Pinker in his (1999) and Symons (1995). Miller (2000) accepts the argument with respect to 'ordinary' adaptations but rejects it for those traits involved in sexual selection, which are his primary interest.

7. Indeed, while it seems in principle possible to test population-level adaptive hypotheses in the human case, it may in practice prove to be impossible in many cases due to the inability to control for confounding factors or to gather sufficient evidence to adequately support either the acceptance or the rejection of adaptive hypotheses. However, insofar as this is a serious problem for population-level adaptations, it is even more of a problem for universal adaptations.

of our close relatives. For example, Sterelny and Griffiths point out that it seems like it should be possible to do good work on the origin of those emotions widely shared within the Hominidae lineage (1999, chapter 14). While little of that work has been done, hypotheses about the origins and adaptive significance of some aspects of our emotions might be tested by comparisons to related species which share problems (and solutions?) of varying similarity. Similarly, the work done testing theories regarding sperm competition show at least a good (albeit still very problematic) start (see Futuyma 1998, 359, 588–589 for an introduction to some of the higher quality research that has been done on this subject).<sup>8</sup> While shared psychological traits will likely be less complex than uniquely human psychological traits, testing their adaptive significance may be possible.

Evolutionary psychology has not yet developed the tools necessary to uncover our “shared human nature” (if such there is—see Dupré 1998) any more than physical anthropology has been able to uncover the specifics even of such clear human adaptations as our bipedalism. It is obvious that our brains were subject to selective pressures during our evolutionary history; it is not at all obvious what those pressures were. Rather than over-reaching by attempting to uncover the historical causes of psychological features shared by all and only humans, evolutionary psychology might be better off attempting to develop ways of adequately testing possible adaptive traits of a less ambitious nature, either because they are widely shared outside our species, or shared only by specific ‘eco-types’ within our species.

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8. See Miller 2000 (231–232 and cites therein) for some *very* speculative suggestions regarding the implications of this work for the human case. Many standard techniques, such as phylogenetic correction (see Bohning-Gaese and Oberrath 1999 and cites therein), have not yet been performed, nor has sufficient attention been paid to e.g. the ancestral condition. But these observations merely point out that this topic presents a plausible research program.

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