

Constraints on Speciation in Human Populations: Phenotypic

Diversity Matters

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ABSTRACT:

A phenotype is an expression of a genotype interacting with a component of an environment. Phenotypic diversity can be generated by mutation, physiological mechanisms, developmental processes, or learning (reinforcing and aversive stimulus-response effects). Causes and consequences of lifetime reproductive success can be partitioned into one or another of the previous mechanisms of phenotypic diversity. This article highlights, in particular, the ways in which behavioral diversity including cultural rules, enhances a phenotype's relative reproductive success. Expanding Frank's (2013) theoretical framework, it is argued that, while a diverse (e.g., "modular") human phenotype may broaden a phenotype's success in a given landscape, byproducts are produced that increase gene flow between populations, limiting the potential for population divergence and reproductive isolation. The mechanisms discussed herein are not necessarily dependent upon conscious and aware operations.

Key words: *Homo sapiens; Behavioral flexibility; Collaboration; Cooperation; Fitness landscape; Gene flow; Multilevel societies; Open groups; Phenotypic diversity*

INTRODUCTION:

In the Order Primates, thirteen extant genera are represented by a single species (Groves, 2001; Wilson & Reeder, 2005), indicating that mechanisms and processes characteristic of those taxa have delayed, interrupted, or prevented speciation events. Our own species, *Homo sapiens*, is one of the thirteen. A review of each genus in the set of thirteen reveals few commonalities. With the notable absence of insectivores, virtually all dietary strategies are represented (omnivore, frugivore-insectivore, folivore-frugivore, granivore). No pattern is detected when the thirteen single-species genera are compared for alpha- (α : within-habitat), beta- (β : between-habitat), or, gamma- (γ : geographic)-diversity (Pimm & Gittleman, 1992; Jones, 1997), the overwhelming ecological dominance of humans is unique. Four of the thirteen genera (31%) are nocturnal, and a mix of crepuscular, arboreal, and terrestrial habits is exhibited. Similarly, a broad range of socio-sexual structures is represented among these primate genera, for example, "solitary" (*Mirza*, giant mouse lemur), "monogamous" (*Symphalangus*, siamang), polygynous

(*Erythrocebus*, patas monkey), multimale-multifemale (*Oreonax*, yellow-tailed woolly monkey), and “multi-level” (*Theropithecus*, gelada; humans).

Eight of the thirteen species (62%) are typically found in one habitat type or demonstrate a strong preference for same. The remaining taxa, including, humans, have been observed in several habitat types, making them good candidates for a number of comparative analyses (genomics, physiology, and behavior, as well as, population, community, and ecosystem ecology), . Significantly, cooperatively-breeding primates are not represented among the subset of thirteen (but, see, *Allocebus*, hairy-eared dwarf lemur). On the other hand, several genera, are distinguished by elaborate vocal repertoires (e.g., *Lemur*, ring-tail lemur; siamang; *Homo*), and all have one or more exaggerated anatomical or morphological features (e.g., pelage, coloration, genital structures), suggesting evolution by sexual selection, a controversial mechanism of speciation (“macroevolution”: Servedio & Kopp, 2012). Insufficient empirical data exist on the relative significance of historical geographical barriers to gene flow that might have facilitated the speciation process (Jones, 1987; Groves, 2001) or of the roles played by habitat specificity (“habitat selection”: Jones, 1997; but, see *Erythrocebus*) in limiting a genus to a single species, a condition obscuring patterns that may exist in Nature.

In the present paper, humans are highlighted in an attempt to identify both general and specific features constraining differentiation of their populations into interbreeding, reproductively-isolated units (“the biological species concept”: see Rundle & Boughman, 2010). Such analyses may contribute to our understanding of *Homo sapiens* as a “weedy”, invasive species, the most geographically and ecologically successful taxon among terrestrial vertebrates. Though many aspects of human biology are relatively well-known, the capacity of technological societies to maintain high population densities (high α -diversity), to successfully invade virtually all global habitats (high β -diversity), to modify their areal ranges (high γ -diversity), to utilize effective mechanisms of niche invasion and expansion (e.g., cooperation, social learning, fire, tools, migration, war), and to impose profound, deleterious effects on global biogeochemistry demand systematic treatments of hominin ecology, phylogeny, and evolution (Hill *et al.*, 2011). Herein, a tentative attempt is made to identify selected human characteristics associated with interruption, delay, or prevention of reproductive (genetic) barriers (e.g., incompatible habitats, “isolation by distance”, pre- or post-copulation mate selection, or geographic barriers such as rivers, mountains, and soil gradients) sufficient to transition from between-population gene

exchange, to (genetic) differentiation of populations (“population divergence”), to the creation of genetic barriers and a completed process of speciation. Behavior and social organization are likely to interest a significant proportion of this journal’s readers. Thus, the present discussion emphasizes phenotypic diversity and population structure, as well as, learning to explain the systematic status of *Homo sapiens*. This paper introduces a novel interpretation and application of the single-species status of extant *Homo* inferred from Frank’s (2013) treatment of the mechanisms “smoothing” a “rugged” fitness landscape. Questions regarding the nature of sub-species or racial identities in *Homo sapiens* are referred to Anthropologists.

Genetic differentiation within and between human populations: incipient speciation?

Genetic differentiation and, possibly, incipient speciation of human populations have been documented. Numerous studies exist identifying clusters (“neighborhoods”) of “single-nucleotide polymorphisms” (SNPs) in human populations, a pattern of results suggesting a past, possibly, continuing, process of adaptation to local abiotic (e.g., soil gradient) or biotic (e.g., plant gradient) regimes (“local adaptation”), a phenomenon similar to “habitat selection”. For example, Xing *et al.* (2009; also, see ISWG, 2001) identified “shared [genetic] variation” among 27 human populations in Africa, Asia, and Europe, including, “caste and tribal samples” in India, demonstrating a degree of genetic continuity across geographical regions. Further statistical analyses of “SNP microarrays” (“haplotypes”: closely-associated alleles on one chromosome), however, revealed genetic structure between sampled sites, and notably, most individual subjects were accurately assigned to the correct population. All individuals were accurately mapped to continents, though genetic structure was not detected for some “closely-related populations”. Xing *et al.* (2009) concluded that their results confirmed a statistically significant association between geography and genetics, including social sub-groups (“caste and tribal” sub-populations). Despite the strong patterns revealed by the previous study, it is important to note that the authors’ findings pertain to differences in genetic structure within and between populations, and do not specify the functions (genotypes expressed as phenotypes) of those discernible genotypes.

What mechanisms might determine genetic structuring and differentiation of human populations?

Fowler *et al.* (2011; also, see Henry *et al.*, 2011; Brent *et al.*, 2013) considered “genetic stratification” within and between human populations to be a function of mate selectivity or kin

preferences. These authors investigated whether or not variations in specific genes were associated with social networks of “friends”, where friendship was defined as “stable, non-reproductive [non-sexual] unions”. Using microarray analyses, Fowler *et al.* (2011) demonstrated that one allele, DRD2, was associated with homophily (assortment of similar types), while, another allele, CYP2A6, was associated with heterophily (assortment of different types). The aforementioned study assessed virtually every possible interpretation and implication of the report, concluding, that “phenotypic similarities between individuals connected in a social network are reflected in their genotypes”. This hypothetical construct, derived from empirical data, advanced the idea that some social traits are correlated with genotype, an association requiring some direct or indirect mechanism of individual recognition. A straightforward extension of the Fowler *et al.* (2011; also, see Fu *et al.*, 2012) report is that, where (genetically-correlated) homophily recurs over time, reproductive isolation of similar genotypes is expected to occur, that, left unimpeded, has potential to induce barriers to gene flow decreasing likelihoods of genetic “mixing” within and between populations. The latter scenario proposes a necessary, though not sufficient, condition for speciation to occur. The present paper addresses some of the behavioral mechanisms and processes limiting reproductive isolation and preventing speciation in *Homo sapiens*, emphasizing the ways in which human technology and other innovations (e.g., tools, fire, language, ritualized warfare) have ameliorated the potentially disruptive effects of “rugged” landscapes that might enhance a process leading to speciation. The aforementioned extension of the research reported by Fowler *et al.* (2011) provides a plausible explanation for the latter authors’ findings as well as for the findings of Xing *et al.* (2009). The extension is amenable to quantitative (“individual”- or “agent-based”) modeling as well as empirical testing with opportunistic, “natural experiments” of concurrent mate choice/genotype trait analyses using human subjects in natural conditions. The “green beard effect” is a possible candidate as a sexually-selected mechanism of homophily, including, interindividual recognition (Brooks & Griffith 2010; Gardner & West, 2010), possibly an element of a primate social “toolkit”. For example, suggesting a mechanism for a “greenbeard effect”, Mahajan *et al.* (2011) identified “inter-group bias” (homophily) in Rhesus macaques (*Macaca mulatta*). These monkeys, residing in semi-natural conditions, discriminated between in-group and out-group members, demonstrating a reliable choice for particular individuals in their social groups.

Interindividual recognition of the sort reported by Mahajan *et al.* (2011) probably characterizes all primates whose brains categorize and compartmentalize information into simpler units (Sporns, 2011). Thus, it is no surprise that environmental patterns are classified systematically by a variety of rules, including similarity, proximity, or other assortative features (e.g., psychophysical operations: Matsuno & Fujita, 2009). Recent work by Yun *et al.* (2012) demonstrates another possible “green beard” (interindividual recognition) mechanism: synchrony of motor patterns between interacting individuals (e.g., gestures: Pollick & DeWaal, 2007; also, see Brooks & Griffith, 2010, Nagasaka *et al.* 2013). “Greenbeard” traits may be genetically correlated, and the latter in addition to other features (e.g., skin color, morphology) may have facilitated speciation in one genus (*Macaca*), but interrupted the process in humans, depending upon differential genotype x environment and phenotype x phenotype interactions..

For example, human groups may be more permeable than non-human primate groups, or humans may use a broader range of characters when making decisions about who to associate with. Furthermore, on average, humans may receive greater benefits from associating with different types compared to speciose primate genera. The latter case might be expected where intra-group competition is more intense than inter-group competition (West *et al.*, 2002). Peculiar features of our species, then, may have broadened the areal effect of an individual’s reproductive success in “rugged” landscapes (“fitness landscape”), and phenotypes bearing these features are proposed to have directly or indirectly promoted gene flow within- and between-groups, -populations, and -regions limiting the potential for population divergence, reproductive isolation, and speciation. Other primate genera characterized by a single species are presumed to exhibit traits that spread because of their success in managing thresholds of intra-group competition, subsequently decreasing the likelihood of speciation events by facilitating gene flow, preventing reproductive isolation.

Notwithstanding evidence for clustering of genotypes within and between populations, human behavioral diversity appears to enhance gene flow

Using Frank’s (2011) theoretical framework, I posit that numerous genetically correlated or uncorrelated behavioral and social traits characteristic of human phenotypes mediated genotype-environment and phenotype-phenotype interactions (“reaction norms”). Human technological and other innovations (e.g., language, metacognition) are proposed to have increased the proportional area on an idealized (theoretical, multidimensional: Frank, 2013) or realized (a 3-

dimensional abiotic and biotic environment: this paper) “landscape” upon which a genotype, expressed as a phenotype, is more reproductively successful relative to the mean lifetime reproductive success of other genotypes in a population. This perspective can be visualized by imagining a grid superimposed on a space subdivided into areas defined by shared features (e.g., a habitat, a watering hole, a grove of fruiting trees, other singular or clumped resources).

Frank’s (2011) treatment allows us to conceptualize a landscape on which reproductively successful phenotypic innovations generated and spread by mutation, developmental plasticity, or learning increased the proportion of cells on the grid upon which a phenotype is effectively successful. In other words, an individual’s “fitness landscape” will be, proportionally, increased relative to the mean fitness of others in a population not exhibiting the successful traits. In Frank’s (2011) terminology, the aforementioned process is a “smoothing” operation reflecting a phenotype’s capacities to decrease stressful environmental events where degrees of stress can be conceptualized as the extent to which the landscape approximates a very rugged (challenging) or a relatively even (less challenging) space in which to survive and reproduce.

Frank’s (2011) treatment suggests that phenotypic diversity will be induced by novel (e.g., disappearance of a limiting resource) or extreme (e.g., severe drought) environmental events and that responses may be genetic (mutation), cellular (physiological and developmental), or learned (by trial-and-error or by “Hebbian” association). Applied to humans, the present treatment posits that characteristics such as cooperation, tool use, the application of fire for processing food, the manufacture of clothing, language, long-distance dispersal, social learning, and the like, effectively switched an environment (“landscape”) from a stressful (difficult, dangerous, risky, extreme, novel), “rugged” one, to a less stressful, more even, or “smoother” one. Reproductively successful innovative human phenotypes, it is proposed, extended networks within- and between-groups and –populations, connecting networks to one or more resource patches, including, other human individuals and groups, thereby, broadening the effective spaces of phenotypes, decreasing deleterious consequences of environmental challenges for (relative) individual reproductive rates, growth rates of groups, and mean fitness of populations..

Traits characteristic of non-human primates and humans interrupt or prevent population divergence

Empirical examples drawn from the primate literature characterize Frank’s (2011) concept of mechanisms functioning to “smooth” a challenging (“rugged”) landscape. Analyzing species

distribution patterns of black howler monkeys (*Alouatta pigra*) and Central American spider monkeys (*Ateles geoffroyi*) in Belize, Jones & Jost (2007) showed that black howlers, but not spider monkeys, had successfully traversed the Mayan Mountains/Cockscombe Range in southern Belize. Howler monkeys are adapted to a folivorous diet, an evenly distributed supply of food compared to fruit upon which spider monkeys are heavily dependent. As a consequence of the heterogeneous and often unpredictable availability of their food supplies, *Ateles* is expected to be more sensitive to environmental perturbations (Terborgh & Winter, 1980). The ability to consume old leaves is thought to facilitate colonization (Jones & Jost, 2007), providing a relatively accessible food resource in most habitats, allowing flexible “switching” from howlers’ preferred diet (new leaves, flowers, fruit) to less nutritious and physiologically stressful foods (mature leaves) during periods when favored food items are unavailable or scarce (Milton, 1980; Crockett, 1998; Hamilton, 2010).

On the other hand, a diet of fruit presents many challenges because of its low nutritional value and patchy distribution (Terborgh & Winter, 1980; Fleming *et al.*, 1987), factors that may limit or retard the geographical spread of species if appropriate food types or habitats are not encountered. This comparison demonstrates one behavioral mechanism, enhanced niche width, whereby the configuration of landscapes is modified by spatiotemporal effects. The capacity to process old leaves facilitated construction of a comparatively “smooth” landscape for the widely distributed, speciose, hardy genus, *Alouatta*. Another “smoothing” effect occasioned by a folivorous diet may be reduction of costs from predation, since toxins ingested from leaves may decrease the palatability of howler tissues, a hypothesis supported by one study’s findings that human hunters considered spider monkeys (frugivores) a tastier meat than that of howlers (Jones & Jost, 2007). Differential attractiveness, then, may “smooth” prey landscapes while increasing the ruggedness of predators’. However, the speciose genus, *Alouatta*, is considered to have differentiated *via* a process of dietary and geographical partitioning, or, possibly, hybridization (Bicca-Marques *et al.*, 2008). Human adaptations, combined with learning capacities, including cultural exchange, presumably avoided many dietary challenges (e.g., fire, tools, weapons), outweighing deleterious effects, including, tradeoffs, that might have been associated with the innovations (e.g., increased inter-group competition).

Concepts advanced by Frank (2011) are implicit in field research conducted in Mexico by Chaves and his colleagues (2012; also, see Scherbaum & Estrada, 2013). These authors studied

Ateles geoffroyi in two conditions of rainforest habitat, continuous canopy and fragmented patches, in order to compare and contrast utilization of available food resources. Consistent with expectation, niche width of monkeys inhabiting fragmented forest was wider than that for monkeys in undisturbed forest, including a higher proportion of leaves. Chaves *et al.* (2012, pp 109-111) concluded, “It is unlikely that [small fragment size] can maintain viable populations in the long term, they may function as *stepping-stones* [italics added], facilitating inter-fragment movements and, ultimately, enhancing seed dispersal in fragmented landscapes.” Combined, where necessary, with descent from trees and ground movement, increased niche breadth enhances the behavioral repertoire of spider monkeys, facilitating “initial survival of a genotype in response to novel or extreme environmental challenges, providing an opportunity for subsequent adaptation.” (Frank, 2011, pp 2318-2319). Additionally, variations in other non-human primate traits may function to “smooth” landscapes in feeding and foraging contexts, for example, body size (Wheatley, 1982), “time-energy [“fitness”] budgets” (Grueter *et al.*, 2012), “decision and choice” (Scherbaum & Estrada 2012), social behavior among females (Hanya *et al.*, 2008), “co-residence patterns” and other hunter-gatherer features (Hill *et al.*, 2011), “egalitarian” and other prosocial tendencies (Gavrilets, 2012).

The previous paragraphs in this section presage human habits serving similar functions. Jones & Young (2004), for example, surveyed hunters in Belize, demonstrating that, among non-volant terrestrial or semi-terrestrial vertebrates, niche width varied with food availability, implying an opportunistic (“utilitarian”) strategy based on a hierarchy of preferences. Thirty-four hunters ranked their favorite prey, yielding eight vertebrate species, with paca (*Agouti paca*) reported to be the most favored bushmeat, “hicatee”, the Central American river turtle (*Dermatemys mawii*), the least. Prey characteristics (predominantly medium-sized, crepuscular or diurnal, and terrestrial) suggested that energetic factors influenced hunting behavior by Creole men at this site, possibly influenced by gustatory preferences, as suggested above. Indeed, paca’s rich, non-“gamey”-tasting flesh, is considered a national delicacy. Hunting practices of indigenous Belizeans are strongly influenced by cultural practices, in addition to economic ones (Jones & Young, 2004; also, see Wilkie & Godoy, 2001), consistent with Frank’s (2011) emphasis on phenotypic variation (e.g., niche breadth) and learning (e.g., imitation, observational learning, cultural rules) as factors “smoothing a fitness landscape with multiple peaks and valleys”. Combined with spatial “concentration and dispersion” of human populations facilitating the

evolution of multilevel population structure, phenotypic diversity in humans broadens a phenotype's success in a given landscape, while, concurrently, increasing gene flow between populations, effects limiting the potential for population divergence and reproductive isolation.

Humans benefit from phenotypic diversity and learning

Following Frank's (2011) conceptual framework, the present article posits that numerous traits characterizing *Homo sapiens* served to decrease environmental challenges deleterious to lifetime reproductive success of individuals. These technological and other innovations, once spread through groups, populations, and regions *via* sex and social learning increased social and breeding networks, mitigating environmental and social challenges. Tanaka's (1976) studies of the ≠Kade San ("bushmen"), hunter-gatherers in the Kalahari (southern African desert) clearly demonstrate ways in which a cultural innovation limits mortality and, by extension, enhances reproductive success. The ≠Kade San, comprised of mobile and mobile-subsistence units, inhabit a "marginal" environment characterized by drought (Tanaka, 1976, Fig. 4.1, p 105) and seasonal patterns of food availability (Tanaka, 1976, Fig. 4.2, p 108), a spatiotemporal regime not unlike the heterogeneous environments in which humans are thought to have evolved (Hill et al., 2011). On one occasion, Tanaka (1976) observed chacma baboons (*Papio ursinus*) foraging in the Kalahari, noting that this primate's home range was limited by their inability to cross arid land. This researcher compared the monkeys' habits with those of the ≠Kade San, capable of inhabiting the extreme desert environment as a result of digging through the soil surface to locate and utilize the limiting resource. This cultural practice permits a "band" to expand inherent capacities, "smoothing" effects decreasing likelihoods of sub-lethal or lethal outcomes, and increasing the likelihood of contacts with other "bands" (see below). Such phenotypic diversity is expected to impact individual life-histories (survival and mortality), enhancing mean fitness of populations via increased reproductive rates (Frank, 2011), with consequent effects on higher levels of ecological organization (communities, ecosystems, biomes).

"Bands" of "bushmen" from a variety of cultural groups share the desert environment, sometimes interacting with one another (cf. Lee, 1976, Map 3.2, p 85; Map 3.3, p 87; Map 3.4, p 93; also, see Tanaka, 1976; Hill *et al.*, 2011). These flexible land-use patterns ("spatial organization"), limited by availability of water, are one component of a "rugged landscape", ensuring relatively frequent contact with other cultural groups. As Tanaka's (1976; also, see Lee's chapter in the same volume) chapter highlights, fluid patterns of interaction increase

potential for conflicts which the bands prevent or resolve via cultural innovations such as reciprocity, cooperation, common ceremonies, and the like, minimizing conflict and aggression, permitting shared access to resources, cooperative manufacture of tools and weapons, and overlapping ranges. Though Tanaka's (1976) report does not address the nature of intimate relations among "bands" (see Lee, 1976), transfer of individuals between groups and opportunities for sexual congress probably occurred, leading to gene flow sufficient to prevent reproductive isolation and speciation events. This scenario is consistent with the interpretations of hunter-gatherer data reviewed by Hill *et al.* (2011).

The evolution of human prosocial behaviors and constraints on speciation

Two recent papers provided a detailed empirical review of "co-resident patterns in hunter-gatherer societies" (Hill *et al.*, 2011) and a preliminary quantitative (mathematical) treatment of "the egalitarian syndrome" characterizing *Homo sapiens* (Gavrilets, 2012; see Crook, 1971). Hill *et al.* (2011) analyzed datasets for 32 extant hunter-gatherer societies with a mean "band" size of 28.2 individuals. These authors documented a profile including bisexual dispersal from natal groups, similar to other apes and Neotropical Atelines. Though opposite-sex [adult] siblings resided, with some frequency, in the same reproductive unit, group membership comprising non-kin prevailed across "bands". Patterns of kinship and group architecture resulting from dispersal, resulted in nested networks of relatives and non-relatives from "bands" embedded in local ("patch") contexts to higher levels of sociosexual organization. These "multilevel" ("hierarchical") societies exhibited relatively "open" structures, permitting selective immigration and emigration, and have been described for other mammalian taxa (e.g., some cetaceans, elephants, geladas; Hamadryas baboons, *Papio hamadryas*).

In "hierarchical" and other complex societies, problems associated with temporal and spatial coordination and control must be managed, and the theoretical literature on "scheduling" indicates that such challenges are solved via within- and between-group "queuing" (Andrews, 2004; also, see Alberts *et al.*, 2003; Fruteau *et al.*, 2013). Within- and between-levels, hunter-gatherers exhibit a broad array of mechanisms, effectively, (1) increasing the similarity of shared fitness optima ("fitness-sharing": Sareni & Krähenbühl, 1998) and (2) decreasing asymmetries ("egalitarian syndrome": Gavrilets, 2012). Hill *et al.* (2011), and most other students of human behavior and social organization (e.g., Crook, 1971; 1972; Eibl-Eibesfeldt, 1989; West *et al.*, 2006), characterize these mechanisms as one or another manifestation of "cooperation" (and/or

collaboration). However, despite the benefits provided by cooperation, queuing, and similar features in many conditions, limits on “prosocial” behavior in humans must, also be addressed (Jones, 2005a, b; Burton-West *et al.*, 2006; Chelley & West, 2013).

The two aforementioned mechanisms are consistent with Frank’s (2011) “smoothing” paradigm, operating to “solve” environmental challenges, to repress selfishness and competition, to enhance access to resources, and to decrease inter-individual and inter-group conflicts. In these instances, social traits benefiting a conspecific’s fitness are posited to limit morbidity and mortality, as well as to enhance relative reproductive rates compared to benefits that might accrue from alternative, selfish interactions (e.g., “non-damaging” and “damaging” aggression). Discussing hunter-gatherer “spatial organization”, Lee (1976) employed maps to show how patterns of “concentration and dispersion” promote inter-unit cooperation (“reciprocal access to resources”), flexible access to abundant and scarce resources *via* communication networks, and conflict-management *via* “social” separation. Lee (1976) found that “concentration and dispersion” increased unit size, on average, an effect that he showed was correlated with higher rates of population increase.

Clustering of “bands” at “patchy” sources of water and food may have induced social competition, leading to social selection favoring the evolution of collaboration, cooperation and behavioral diversity (e.g., social learning, imitation, tool use). Increased inter-individual contact with associated gene flow would be a byproduct of this model, discussed using primate examples, by Crook (1971, 1972; also, see Lee, 1976; Tanaka, 1976; Yellin, 1976). As a result, likelihoods of gene flow between reproductive units (“bands”) would increase, decreasing rates of population divergence and opportunities for speciation events. The fitness strategies discussed in this paragraph constitute adaptive mechanisms responding to environmental challenges, transforming a rugged landscape to a smoother one, enhancing lifetime reproductive success of individuals. Interpretations of the literature advanced in this article are testable empirically and quantitatively, and initial agent-based treatments might be conducted employing the data presented in Hill *et al.* (2011). It would also be beneficial to compare populations and regions exhibiting high, moderate, and low degrees of genetic differentiation in an attempt to discern similarities and differences among humans and their networks in each condition. For instance, is network strength greater or lesser across these conditions, and do these conditions

and their features correlate with measures of success (e.g., income, education, rules governing immigration and emigration).

DISCUSSION

Frank's (2011) treatment of the ways in which phenotypic diversity and phenotypic novelty serve individual interests by facilitating lifetime reproductive success provides a schema that can be applied to most human tactics and strategies. In particular, the model permits researchers to evaluate the extent to which human responses to environmental challenges promote problem-solving in a variety of ways. The mechanisms addressed herein, as well as other responses not discussed (altruism, spite, role-reversal, facultative division-of-labor), are expected to facilitate the individual's avoidance, circumvention, delay, or confrontation with challenges sufficiently severe, risky, rare, or difficult to compromise lifetime reproductive success, including, the effects of morbidity and mortality. Mortality records for extant hunter-gatherers require quantitative treatments since humans are iteroparous breeders with a typical litter-size of one, characteristics associated with predictable environments in which adult survivorship is uncertain (Stearns, 1982; Millar & Zammuto, 1983). Breeding positions of individuals in mammal groups with the aforementioned characteristics are generally precarious (Millar & Zammuto, 1983), and the diverse phenotypic adaptations and novelties reviewed herein may increase environmental predictability by increasing individuals' abilities to cope with stressors.

Following Hill (1976), humans appear to combine iteroparity with a high fertility rate and notably high "reproductive effort". This combination of traits is not usually associated with mammals in heterogeneous ("rugged") regimes (Millar & Zammuto, 1983). Similarly, most mammals are poor colonizers, and social mammals are generally constrained by their dependence upon conspecifics and group life (Cody, 1986), challenges that humans have overcome via the "concentration and dispersion" spatiotemporal patterns and multilevel societies described by Lee (1976), Tanaka (1976), Yellin (1976), and others (Hill *et al.* 1976), in combination with rule-governed repression of selfish behavior ("culture"). Investigating patterns of juvenile and female mortality should reveal relative survivorship, indicating whether or not "bet-hedging" strategies were featured among early *Homo*. This information, once modeled, may expose in greater detail thresholds of reproductive benefits that may have accrued to humans from responses designed to solve problems presented in lethal or sub-lethal regimes, mechanisms with byproducts decreasing likelihoods of reproductive isolation and the potential

for speciation. Finally, students of mammalian taxa exhibiting noteworthy phenotypic diversity (e.g., mammals exhibiting multilevel social organization) must bear in mind that “plastic” traits will not yield the highest relative fitness in many regimes (Jones, 2005a, 2005b; Pigliucci, 2010, Frank, 2011, pp 2312-2313). Thus, differential reproductive costs and benefits of genotype x environment interactions require systematic investigation for the human case.

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