16

Infectious Diseases and the Evolution of Cross-Cultural Differences

MARK SCHALLER and DAMIAN R. MURRAY

We'll begin with a prediction: Years from now it will become obvious to observe that cross-cultural differences result substantially from regional differences in the prevalence of infectious diseases.

Does that sound presumptuous? Perhaps even preposterous? Maybe. For many readers, our prediction may seem like a provocation that we've made up out of thin air. That's not quite so. The scientific literature has, for years, documented cultural differences that are predicted by the prevalence of pathogens (e.g., Gangestad & Buss, 1993; Low, 1990; Quinlan, 2007; Sherman & Billing, 1999). But these findings tend to fly under the radar of the vast majority of social scientists who concern themselves with culture and cultural variation.

Why has there been so little attention paid to the potentially profound role that infectious diseases might play in the creation of cross-cultural differences? One reason, perhaps, is that much cultural scholarship (e.g., cultural anthropology, cultural psychology) is concerned primarily with *descriptions* of cultural differences or with the *consequences* that these cultural differences have for individual behavior. Less attention has been paid to the *origins* of cultural differences in the first place. Another reason may lie in the fact that, in the occasional articles that do link pathogen prevalence to cultural outcomes, those outcomes have been relatively narrow in scope (pertaining specifically to food preparation, for instance, or to mating behavior). These findings may strike readers as interesting curiosities but perhaps not diagnostic of cultural differences more broadly. A third reason may be that there really hasn't been much reason to expect that infectious diseases should have any sort of wide-ranging impact on culture. Only recently has there emerged a body of theory and research identifying specific psychological mechanisms that are responsive to the perceived threat of infectious diseases and that may play an important role in the construction of many different kinds of cross-cultural differences. With that context in mind, this chapter has three objectives.

First, we want to address the question of *why* disease prevalence might be expected to predict a broad range of cultural outcomes. To do so, we present a conceptual framework that draws explicitly on an evolutionary analysis. We discuss the negative fitness consequences of contracting infectious diseases, and we identify specific kinds of behavioral strategies that may limit exposure to infectious diseases. We also consider the fact that, in addition to conferring specific kinds of fitness benefits (i.e., reduced exposure to diseases), these same behavioral strategies may have specific costs as well. Through the logic of an evolutionary cost-benefit analysis, this framework implies that these behavioral strategies may vary in their functional utility, depending on the extent to which infectious diseases actually pose a prevalent threat in the immediate environment. This in turn implies a causal link between regional variability in disease prevalence and cross-cultural variability in attitudes and values that are relevant to those behavioral strategies.

Second, we want to address the question of whether disease prevalence does, in fact, predict important cross-cultural differences. We summarize a variety of ways in which the general theoretical framework can be applied to deduce hypotheses about specific kinds of cross-cultural differences that may result from regional variation in disease prevalence. In each case, we summarize empirical results supporting these predictions. It turns out that worldwide variation in disease prevalence predicts a remarkably wide range of cross-cultural differences, pertaining not only to overt cultural customs (e.g., food preparation) but also to many more subtle differences operating at a psychological level of analysis—including cross-cultural differences in basic personality traits (e.g., extraversion) and values (e.g., individualism versus collectivism). Furthermore, as a consequence of these effects on fundamental psychological variables, regional differences in disease prevalence may also lead to persistent differences operating at the societal level of analysis as well.

Third, we want to consider exactly *how* these interesting relationships might have emerged. We raise, and discuss, several important questions about the actual evolutionary mechanisms that might underlie links between regional variation in disease prevalence and cultural variation in human behavior. By doing so, we highlight some of the thorny conceptual issues that inevitably arise when applying an evolutionary perspective to human cultural variation—issues that can be resolved only with rigorous and sustained research efforts.

WHY THE PREVALENCE OF DISEASE CAN HAVE CULTURAL CONSEQUENCES

So why might cultural outcomes be influenced by the prevalence of infectious diseases in the local ecology? There are at least two different lines of reasoning.

Cultural Practices as Socially Constructed Defenses Against Disease

One reason is based on the premise that cultural practices can be promulgated as rational responses to the prospects and perils posed by immediate ecological circumstances. Coastal communities develop rituals and practices pertaining to boat building and fishing, for instance, whereas landlocked communities don't. Similarly, given the threat that infectious diseases have posed to human populations, some kinds of cultural practices may have been invented to serve as barriers to the transmission of those diseases. Such practices would be especially likely to be invented and sustained under ecological circumstances in which infectious diseases pose an especially substantial threat.

An example is provided by research documenting worldwide variation in the use of culinary spices (Sherman & Billing, 1999). Spices are natural antibiotics; they contain toxins that kill many of the potentially harmful bacteria that can be found in the food we eat. Thus the use of spices in the preparation of food can be very beneficial as a defense against bacterial infections. Of course, there may be costs as well. The cultivation of spices consumes resources that might otherwise be spent to obtain more nutritious foods. There may also be physiological costs associated with the ingestion of spices, as they do contain toxins. Consequently, the use of culinary spices would most likely emerge and persist as a cultural practice under ecological circumstances in which the benefits of this practice are especially likely to outweigh the costs: under circumstances in which there actually is a high likelihood of bacterial infestation in food. Sherman and Billing (1999) reasoned that the risk of bacterial infestation is fundamentally a product of ambient temperature (the hotter the ambient temperature, the more likely that foodstuffs will be contaminated by bacterial infestations). They proceeded to analyze the cuisines of dozens of countries worldwide and tested the hypothesis that in geographical regions that are especially hot (meteorologically speaking), the cuisines are spicily hot as well. This is indeed the case. Meals in Mexico and Ethiopia are spicier than those in Mongolia and Estonia, and these culinary differences aren't just random cultural quirks. They are part of a broader worldwide pattern of cross-cultural differences in food preparation. This pattern of cultural differences appears to be rooted, at least in part, in the differential prevalence of pathogens.

This particular relation between disease prevalence and cultural outcomes may not reflect an evolutionary process per se. More likely, it implies the operation of cultural transmission processes that are analogous to evolutionary processes (see chapters by Dutton and Heath and by Rozin in this volume). These cultural transmission processes certainly operate on cultural rituals and practices that—like food preparation—are explicitly imitated, taught, and learned. But it's not clear just how broadly they apply to many other, more subtle facets of culture. Therefore, it's important to consider an additional line of reasoning that links disease prevalence to cross-cultural differences. This line of reasoning explicitly draws on speculations about evolutionary adaptations that influence human cognition and their further implications for human culture.

The "Behavioral Immune System" and Its Cultural Implications

Infectious diseases pose a substantial threat to reproductive fitness. Examples abound. Tens of millions of European peoples succumbed to the so-called Black

Death during the Middle Ages, enormous numbers of aboriginal Americans died from bacterial diseases introduced by colonial Europeans, and so forth (Guerra, 1993; Lippi & Conti, 2002; McNeill, 1976). And these are just recent examples. Infectious diseases have been important agents of disability and mortality within human (and prehuman) populations for far longer than that (Wolfe, Dunavan, & Diamond, 2007) and have exerted very strong selection pressures on these populations. Therefore, it's no surprise that humans (like many other species) are characterized by an extraordinarily sophisticated suite of mechanisms—the immune system—that evolved the capacity to identify and defend against harmful pathogens when those pathogens come into contact with our bodies. Of course, we pay a price whenever we actually use our immune system (e.g., fever and other debilitating symptoms; the consumption of caloric resources). Therefore it's also no surprise that humans (and many other species) are equipped with a "behavioral immune system" that serves as a first crude line of defense against potentially harmful pathogens.

Provide reference for Wolfe, Dunavan, & Diamond, 2007.

This system operates by facilitating the behavioral avoidance of pathogens and the conspecifics that carry them (Kiesecker, Skelly, Beard, & Preisser, 1999; Schaller, 2006; Schaller & Duncan, 2007). In humans, this system is sensitive to threats (including people) in the immediate environment that appear, superficially, to represent some sort of contagion risk. When these threats are perceived, aversive emotions and cognitions are automatically activated, facilitating avoidant behavioral reactions. Of course, there may be functional costs as well as benefits associated with the activation of these aversive reactions. Consequently, the behavioral immune system is likely to have evolved in such a way as to be flexibly engaged, depending on additional information indicating the relative ratio of benefits to costs in the immediate environment. Aversive reactions to potential contagion risks are expected to be especially profound when additional information indicates that an individual is especially vulnerable to disease (Schaller & Duncan, 2007).

Several recent lines of research have applied this conceptual framework toward a deeper understanding of specific interpersonal aversions and intergroup prejudices (Park, Faulkner, & Schaller, 2003; Park, Schaller, & Crandall, 2007; Schaller & Duncan, 2007). One line of work has focused on xenophobia and ethnocentrism. Historically, contact with foreign peoples may have posed an increased contagion risk. (There are at least two reasons for this risk: Foreign peoples may introduce novel pathogens; foreign peoples may also violate local customs—such as those pertaining to food preparation—that serve as barriers to disease transmission.) Consequently, the behavioral immune system may be hypersensitive to superficial cues connoting foreignness, and the perception of foreign peoples may trigger aversive emotional, cognitive, and behavioral responses. Moreover, these xenophobic responses are likely to be variable across persons and contexts, depending on the extent to which perceivers are vulnerable (or merely perceive themselves to be vulnerable) to the transmission of infectious diseases. Recent research reveals that this is the case. People who are more chronically worried about disease show stronger negative responses to subjectively foreign (but not familiar) ethnic groups (Faulkner, Schaller, Park, & Duncan, 2004; Navarrete & Fessler, 2006). Xenophobic and ethnocentric responses are also exaggerated among people whose immunological defenses are temporarily compromised (Navarrete, Fessler, & Eng,

2007) and are amplified by contextual cues that make the risk of disease temporarily salient (Faulkner et al., 2004).

An analogous phenomenon might exist at a cultural level of analysis. If aversive responses to foreigners are affected by differences in individuals' perceived vulnerability to infectious diseases, it's no stretch to suppose that xenophobia and ethnocentrism might also be affected by ecological factors that render some populations, more than others, to be chronically vulnerable to infectious diseases. Within geographical regions in which infectious diseases have historically been more prevalent, one might expect greater levels of xenophobia within the local population. In other words, worldwide variation in disease prevalence may predict cultural differences in xenophobic attitudes.

Is this actually so? To our knowledge, no empirical research has rigorously addressed the hypothesis, but a quick secondary analysis of data already in the scholarly literature suggests some provisional support. Recently (within the context of research described more fully later) we developed an index indicating the historical prevalence of infectious diseases in dozens of countries worldwide (Fincher, Thornhill, Murray, & Schaller, 2008; Schaller & Murray, 2008). This index can be used to predict country-level measures of xenophobia. One might employ results from an item, as one crude country-level indicator of xenophobia, on the World Values Survey that assesses the percentage of people in each country who explicitly indicate that they wouldn't want "people of a different race" as their neighbors. Are the two variables related? Yes. Across a sample of 67 countries, the correlation is substantially positive and statistically significant ($r = .43$, $p < .001$). Ecological variability in disease prevalence does seem to predict cross-cultural variability in xenophobia.

Need to provide a reference for the World Values Survey?

Now, we don't want to make too much of this one empirical result. After all, it's just one correlation, and it reflects just a single indicator of cross-cultural differences in xenophobic attitudes. And we don't want to suggest that xenophobia is a defining cultural characteristic. We present this result here simply to illustrate a fundamental point: The evolutionary cost-benefit analysis that informs our understanding of the behavioral immune system not only implies specific ways in which individuals' psychological responses differ within different everyday contexts but also implies specific ways in which cultural outcomes may differ under different ecological circumstances. Many attitudes, values, and traits may dispose people to be either more or less vulnerable to infectious diseases. These dispositions are likely to be cross-culturally variable, contingent on the prevalence of infectious diseases within the local ecology.

DISEASE PREVALENCE PREDICTS MANY KINDS OF CROSS-CULTURAL DIFFERENCES

Exactly what kinds of characteristics might dispose people to be more vulnerable to infectious diseases? Conversely, what kinds of characteristics might help people avoid infectious diseases? At a cultural level of analysis, are these characteristics predicted by regional variability in the prevalence of disease? Here are some answers to those questions.

Mate Preferences and Mating Strategies

Many diseases may be transmitted via intimate physical contact of the sort associated with sexual behavior. Because of this, animals of various species are sensitive to superficial characteristics indicating the contagion risk posed by potential mates, and they selectively avoid mating with those who demonstrate these characteristics (e.g., Kavaliers, Fudge, Colwell, & Choleris, 2003). Human mate preferences are also likely to be influenced by superficial physical traits connoting the presence of (or potential resistance to) contagious parasites. One such trait is physical (un)attractiveness. In many species, bilateral symmetry may be a cue indicating both the current absence of disease and a strong immune system in general (Møller, 1996). In humans, bilateral symmetry in facial features contributes to the subjective impression of physical attractiveness (Thornhill & Gangestad, 1999). Therefore, subjective impressions of physical attractiveness may serve as a heuristic cue indicating both the absence of and the resistance to infectious diseases. It follows that not only will physical attractiveness be a highly prized feature in a mate but it will be especially prized within cultures with historically high prevalence of infectious diseases. Exactly such a result was reported by Gangestad and Buss (1993; see also Gangestad, Haselton, & Buss, 2006). Disease prevalence strongly predicted cross-cultural differences in the value placed on the physical attractiveness of a potential mate.

Provide reference for Kavaliers, Fudge, Colwell, & Choleris, 2003? Is a reference for Kavaliers, Colwell, Braun, & Choleris, 2003.

In addition to hypotheses about cross-cultural differences in the characteristics that people value in a mate, we can also deduce additional hypotheses about mating behavior more broadly. Because sexual intimacy puts people at an increased risk of contracting infectious diseases, there may be fitness costs associated with any chronically incautious (e.g., promiscuous or unrestricted) approach to mating. These costs must be weighed against the potential fitness benefits that might accrue as a result of incautious mating strategies (among men especially, promiscuous mating strategies may produce more offspring). This cost-benefit ratio is likely to vary depending on the prevalence of infectious diseases in the immediate ecology: Within high-disease places, the costs associated with unrestricted mating strategies are most likely to outweigh the benefits. Consequently, in high-disease places, people are expected to exhibit a more cautious, restricted approach to sexual relations.

We recently tested this hypothesis (Schaller & Murray, 2008). To do so, we employed the results of a massive cross-cultural study reported by Schmitt (2005). Schmitt administered the *Sociosexual Orientation Inventory* (SOI; Simpson & Gangestad, 1991) to over 14,000 people living in 48 different countries. (Low SOI scores indicate a restricted approach to sexuality; higher SOI scores indicate a more unrestricted approach—including greater chronic interest in new sexual partners and greater comfort with casual sexual encounters.) Schmitt (2005) reported mean standardized SOI scores for each country, among other results. Separately, using methods modeled after previous investigations (e.g., Gangestad et al., 2006; Low, 1990), we computed an index indicating the historical prevalence of infectious diseases in each of these countries. Did regional variation in disease prevalence predict cross-cultural variation in the SOI? Yes. The correlation was negative: In places with a higher prevalence of disease, both men and women tend to report a more restricted approach to sexual relations.

Interestingly, this effect was substantially stronger for SOI scores for females than for SOI scores for males, and it was only on SOI scores for females that the effect remained statistically significant even after statistically controlling for other country-level variables (e.g., GDP per capita, life expectancy, absolute latitude, mean annual temperature). This makes sense within the overall conceptual framework described earlier. Because of differential reproductive investment, the fitness benefits of an incautious approach to sexual relations are likely to be greater among men than among women. For men, these benefits may actually outstrip the costs even at relatively high levels of disease prevalence, and previous research indicates that this may indeed be the case (e.g., Low, 1990). Among women, however, the benefits of unrestricted sexuality behavior are lower and so may more readily be outweighed by the costs (disease transmission) when diseases are highly prevalent.

Fundamental Personality Traits

Behavior need not be sexual to increase the risk of disease transmission. Broader behavioral dispositions (i.e., those that are not specific to the domain of sexual behavior) can also affect the risk of exposure to disease-causing pathogens. Any interaction that places an individual in close proximity to other people may expose that individual to socially transmitted pathogens. Thus, a dispositional tendency toward gregariousness and extraversion may be associated with an enhanced risk of disease transmission (Hamrick, Cohen, & Rodriguez, 2002; Nettle, 2005)—particularly under ecological circumstances in which diseases are highly prevalent. This implies a predictable cross-cultural difference in dispositional extraversion: In regions characterized by high levels of diseases, there are likely to be generally lower levels of extraversion within the local population.

Only some diseases are transmitted through direct social interaction. Many others are transmitted indirectly as a result of contaminated water supplies, inexpertly prepared foods, and so forth. And, as we discussed earlier, many cultural norms serve as barriers against these forms of transmission (e.g., cultural practices that proscribe the placement of latrines near sources of drinking water or that prescribe the appropriate spicing of meats). To the extent that individuals violate these cultural conventions, they may expose themselves and others to infectious diseases—especially within regions in which the prevalence of disease is high. This has an implication for cross-cultural differences in dispositional tendencies toward curiosity, experimentation, and willingness to deviate from the status quo—the sorts of traits signaled by the fundamental personality trait that is sometimes called "openness to experience." In regions characterized by high levels of diseases, there are likely to be generally lower levels of openness within the local population.

Would it be helpful to list all of the Big Five personality traits?

Extraversion and openness are two of the "Big Five" personality traits—the dimensions of personality that are considered fundamental to an understanding of individual differences (John & Srivastava, 1999). It follows that variation along these same traits may be fundamental to the perception of overall dispositional differences between cultural populations. Several recent cross-cultural research projects have administered personality questionnaires to thousands of people in dozens of countries worldwide and as a result have documented cross-cultural differences along each of the Big Five personality traits, including extraversion and openness (McCrae, 2002; McCrae et al., 2005; Schmitt et al., 2007). Using the same index that we used in the aforementioned investigations, we found that the historical prevalence of diseases indeed predicts cross-cultural variation along the two hypothesized personality dimensions: Disease prevalence is negatively correlated with country-level mean scores on both extraversion and openness (Schaller & Murray, 2008).

Additional analyses ruled out various alternative explanations for these effects. A reverse causal explanation is rendered implausible by several considerations, including the fact that contemporary personality scores were more strongly predicted by our index of historical disease prevalence than by an analogous index based on contemporary epidemiological data. Additional analyses revealed that the relations between disease prevalence and personality traits persisted even when controlling for other variables (e.g., GDP per capita, life expectancy, absolute latitude, mean annual temperature), thus ruling out a variety of alternative causal explanations. The results suggest that cross-cultural differences in personality style may indeed result, in part, from regional differences in the prevalence of disease.

Individualism and Collectivism

Underlying many specific cross-cultural differences lies a fundamental distinction between individualistic and collectivistic value systems (Hofstede, 2001; Triandis, 1995). Indeed, it has been suggested that the individualism–collectivism dimension "may ultimately prove to be the most important dimension for capturing cultural variation" (Heine, 2008, p. 189). But why exactly are some cultures individualistic and others collectivistic? Disease prevalence may provide an important part of the answer to this question.

There are at least two reasons to suspect a causal link between disease prevalence and individualism and collectivism, each of which focuses on a specific component of the multifaceted systems of values to which the terms *individualism* and *collectivism* refer. First, compared to individualistic value systems, collectivistic value systems are defined in part by an especially sharp distinction between ingroup and out-group and by the corollary tendency to be especially wary of outgroup members (Gelfand, Bhawuk, Nishii, & Bechtold, 2004; Sagiv & Schwartz, 1995). The same deductive logic that implies a positive correlation between disease prevalence and xenophobia also implies a positive correlation between disease prevalence and collectivism. Second, collectivism is defined in part by a strong value placed on tradition and conformity, whereas individualism is characterized by a greater tolerance for (and encouragement of) deviation from the status quo (Oishi, Schimmack, Diener, & Suh, 1998). The same deductive logic that implies a negative correlation between disease prevalence and openness also implies a positive correlation between disease prevalence and collectivism. Thus, for multiple reasons, one might expect that worldwide variation in disease prevalence will predict cultural variation along the individualism–collectivism dimension.

This relationship is exactly what the empirical data show (Fincher et al., 2008). Across multiple country-level indices of individualism and/or collectivism (Gelfand et al., 2004; Hofstede, 2001; Kashima & Kashima, 1998; Suh, Diener, Oishi, & Triandis, 1998), our index of disease prevalence correlated positively with collectivism and negatively with individualism. These correlations were exceptionally strong.

And, just as with differences in personality style, these effects remained statistically significant even after controlling for a variety of other country-level variables (e.g., GDP per capita). In fact, our results indicate that a substantial part of the often-observed relation between GDP and individualism is attributable more directly to pathogen prevalence than to economic development. It appears that the scholarly literature on individualism and collectivism may have overestimated economic influences while underestimating the causal influence of pathogens.

The Political, Civil, and Spiritual Fabric of Society

Because cultural value systems (of the sort implicated by individualism and collectivism) have profound implications for how individuals think, feel, and behave in relation to one another, they inevitably have implications that manifest in the systematic workings of societal institutions—governments, economies, legal systems, and so forth. Within any culture that prizes tradition and conformity, certain kinds of civil liberties and individual rights (e.g., freedom of speech) may be perceived to pose a greater threat to the common good. Consequently, authoritarian governmental regimes may be more likely to emerge and persist, and individual liberties and rights may be systematically repressed by legal and/or political means (Conway, Sexton, & Tweed, 2006). It follows, therefore, that disease prevalence may predict legislated restrictions on individual civil liberties and political rights. And, more generally, disease prevalence may place limits on the democratization of societies. New research by Randy Thornhill and his colleagues provides support for these hypotheses (Thornhill, personal communication).

Provide date (month, day, year) for this personal communication?

Conformity to cultural traditions is facilitated not only by legislated repression of dissent but also by the kinder, gentler sort of interpersonal interactions through which people learn to adopt, and reproduce anew, those cultural traditions. Much of this socialization and acculturation occurs during childhood, within the context of familial interactions. But the family is by no means the only social context through which cultural indoctrination occurs. Religion also serves this community function (Atran & Norenzayan, 2004; see also the chapter in this volume by Shariff, Norenzayan, & Henrich). Indeed, by invoking the specter of omniscient and powerful supernatural beings, religious teachings provide an especially potent set of mechanisms through which individuals learn to uphold cultural traditions and to fear the consequences of violating those traditions. One might expect, therefore, that when diseases pose an especially substantial problem (and ritualized behavioral practices provide a more consequential buffer against that problem), religiosity will be more prevalent as well. Again, preliminary empirical results indicate that this is the case (Fincher & Thornhill, 2008).

We should be careful not to overinterpret findings such as these. They are, after all, just correlations, and they reflect just a few of the many variables that must be assessed to rigorously document relations between disease prevalence and societal outcomes. Still, these findings are consistent with—and contribute to—the increasingly plausible conclusion that a considerable chunk of cross-cultural variability, across many different domains of social life, results from regional variability in the prevalence of infectious diseases.

GENES, DEVELOPMENT, COGNITION, AND CULTURE

Even if we allow ourselves to draw that conclusion, we are still a long way from truly understanding the actual mechanisms through which disease prevalence influences cultural outcomes. There are different kinds of mechanisms (operating over different timescales) that might plausibly account for a causal relationship between disease prevalence and cultural norms.

One possible mechanism is natural selection, through which different genes are selectively favored under different ecological circumstances. Consider, for instance, cross-cultural differences in fundamental personality traits. Well-established research shows that these traits are heritable (e.g., Jang, Livesley, & Vemon, 1996), and research has begun to identify specific genetic markers associated with specific personality traits (e.g., Savitz & Ramesar, 2004; Stein, Schork, & Gelernter, 2004). Also clear is that infectious diseases can pose a powerful selective force on gene frequencies within different human populations (Sabeti et al., 2002; Williamson et al., 2007). It is plausible that among populations living in chronically disease-ridden regions of the world, natural selection has favored alleles that are probabilistically associated with introversion rather than extraversion and with dispositional caution rather than curiosity and openness to experience. Moreover, if we assume that there is some heritable genetic contribution to other attitudes and dispositions (e.g., dispositional tendencies toward collectivism), a natural selection process can be extended to explain cross-cultural variability along those characteristics too.

This is by no means the only explanation. A causal link between disease and culture might also operate through an entirely different kind of evolved mechanism. Genes associated with specific traits and dispositions may be widespread across all human populations but may be differentially expressed depending on the prevalence of infectious diseases within the local ecology. Phenotypic differences often emerge from the differential expression of common genes; a gene's expression often depends on input from the immediate environment, and this context-contingent phenotypic plasticity is often adaptive (Carroll, 2005; Ridley, 2003). Consider personality traits again. Because these traits may confer either fitness costs or benefits, and these costs and benefits vary under different circumstances (Nettle, 2007), the expression of genes associated with these traits may have evolved to be sensitive to informational inputs signaling the prevalence of infectious diseases. The consequence of such an evolutionary process is that even genetically identical populations may, under different ecological circumstances, have different overall levels of extraversion, openness, and other traits.

This sort of phenomenon is sometimes called "evoked culture" (Gangestad et al., 2006; Tooby & Cosmides, 1992), a label emphasizing the important point that cultural differences may reflect universal human capacities that are differentially evoked under different ecological circumstances. Of course, even if we suggest that cultural differences might be evoked as the result of context-contingent gene expression, we have still just barely begun to elucidate the mechanisms through which this occurs (Schaller, 2006). To more fully elaborate on this phenomenon, one must articulate specific developmental and psychological processes. For instance, one might hypothesize that in high-disease environments, genes associated with introversion may be expressed early in individuals' development, with the phenotypic result that these individuals develop personalities characterized by a chronic tendency toward introversion. Or, somewhat differently, one might hypothesize that evolved developmental processes produce individuals who aren't chronically introverted or extraverted per se but are instead chronically sensitive to disease-relevant inputs from the environment; when those inputs are received, these individuals respond by being temporarily introverted or extraverted, depending on the nature of those inputs.

It is also possible that disease prevalence may produce these many cross-cultural differences through mechanisms that have nothing directly to do with genes at all. Some of these effects might be explained by the kind of social construction and cultural transmission processes that, earlier, we illustrated with cross-cultural differences in the use of culinary spices. In regions characterized by persistently high levels of disease, cultural learning and transmission processes may selectively sustain values that advise against extraversion, openness, individualism, and other potentially costly dispositional tendencies. These kinds of cultural processes don't render "real" evolutionary processes irrelevant. (After all, cultural transmission processes depend on evolved cognitive and behavioral capabilities.) They do, however, relegate these evolutionary processes to a role that is somewhat more distant from, and less specific to, observed cultural differences.

These different kinds of explanatory mechanisms are conceptually independent and are not mutually exclusive. Even if specific genes associated with specific traits are differentially pervasive across different human populations, the actual expression of those genes may still vary depending on immediate ecological circumstances. And even if there are evolved genetic mechanisms contributing directly to cultural differences in personality, cultural transmission processes may play a role as well. Each of these possible mechanisms has unique empirical implications. Many different kinds of research programs may prove useful in testing these implications. With advances in genomics, the coming years are likely to reveal many specific genetic markers for personality traits, attitudes, and values. This may allow direct tests of the possibility (which at this point is purely hypothetical) that infectious diseases have exerted selection pressures on the genetic bases of these traits, attitudes, and values. Similarly, advances in genetics and developmental biology may allow more direct tests of the possibility that cross-cultural differences result, in part, from the differential expression of these genes. Other research strategies can be pursued immediately. Useful insights might be gained by the careful longitudinal study of the behavioral dispositions of immigrants and their offspring. (Perhaps especially informative will be studies of immigrants who relocate from low-disease regions to places characterized by a much higher prevalence of pathogens.) It might also be informative to conduct analog studies on nonhuman animals, in which the developmental context (e.g., the prevalence of infectious diseases in laboratory populations) might be carefully manipulated so as to test for possible consequences on dispositional tendencies. And, of course, some of the hypothesized implications might be tested with experimental methodologies of the sort that have been used to document other consequences of the behavioral immune system (e.g., Navarrete et al., 2007; Park et al., 2003, 2007). Variations on these methods might be used to test whether the temporary salience of (or vulnerability to) infectious diseases affects the activation of collectivistic values into working memory or the temporary inhibition of extroverted behavioral tendencies. Other variations might test whether a temporary feeling of vulnerability influences the transmission and/or learning of specific values, traits, or dispositional tendencies.

The take-home message is this: It has become increasingly apparent through the application of an evolutionary perspective on human culture that important cross-cultural differences may result from regional differences in the prevalence of infectious diseases. But the exact causal mechanisms remain unclear. Future research must rise to this empirical challenge if we wish to truly understand the evolutionary origins of cross-cultural differences.

ACKNOWLEDGMENTS

This research was supported in part by research grants from the University of British Columbia Hampton Fund and the Social Sciences and Humanities Research Council of Canada.

REFERENCES

Atran, S., & Norenzayan, A. (2004). Religion's evolutionary landscape: Counterintuition, commitment, compassion, communion. *Behavioral and Brain Sciences*, *27*, 713–770.

Carroll, S. B. (2005). *Endless forms most beautiful*. New York: Norton.

Conway, L. G., III, Sexton, S. M., & Tweed, R. G. (2006). Collectivism and governmentally initiated restrictions: A cross-sectional and longitudinal analysis across nations and within a nation. *Journal of Cross-Cultural Psychology, 37*, 20–41.

Faulkner, J., Schaller, M., Park, J. H., & Duncan, L. A. (2004). Evolved disease-avoidance mechanisms and contemporary xenophobic attitudes. *Group Processes and Intergroup Behavior*, *7*, 333–353.

Fincher, C. L., & Thornhill, R. (2008). *Infectious disease prevalence and the worldwide distribution of religiosity and religions*. Paper presented at the Evolutionary Psychology Pre-Conference, Society for Personality and Social Psychology. Albuquerque, NM.

Provide month of meeting?

Fincher, C. L., Thornhill, R., Murray, D. R., & Schaller, M. (2008). Pathogen prevalence predicts human cross-cultural variability in individualism/collectivism. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 1279–1285.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology*, *14*, 89–96.

Gangestad, S. W., Haselton, M. G., & Buss, D. M. (2006). Evolutionary foundations of cultural variation: Evoked culture and mate preferences. *Psychological Inquiry*, *17*, 75–95.

Gelfand, M. J., Bhawuk, D. P. S., Nishii, L. H., & Bechtold, D. J. (2004). Individualism and collectivism. In R. J. House, P. J. Hanges, M. Javidan, P. W. Dorfman, & V. Gupta (Eds.), *Culture, leadership, and organizations: The GLOBE study of 62 societies* (pp. 437–512). Thousand Oaks, CA: Sage.

Guerra, F. (1993). The European–American exchange. *History and Philosophy of the Life Sciences*, *15*, 313–327.

Hamrick, N., Cohen, S., & Rodriguez, M. S. (2002). Being popular can be healthy or unhealthy: Stress, social network diversity, and incidence of upper respiratory infection. *Health Psychology*, *21*, 294–298.

Heine, S. J. (2007). *Cultural psychology*. New York: Norton.

Hofstede, G. (2001). *Culture's consequences* (2nd ed.). Thousand Oaks, CA: Sage.

Jang, K. L., Livesley, W. J., & Vemon, P. A. (1996). Heritability of the Big Five personality dimensions and their facets: A twin study. *Journal of Personality*, *64*, 577–592.

John, O. P., & Srivastava, S. (1999). The Big Five trait taxonomy: History, measurement, and theoretical perspective. In L. A. Pervin & O. P. John (Eds.), *Handbook of personality: Theory and research* (2nd ed., pp. 102–138). New York: Guilford.

Kashima, E. S., & Kashima, Y. (1998). Culture and language: The case of cultural dimensions and personal pronoun use. *Journal of Cross-Cultural Psychology*, *29*, 461–486.

Kavaliers, M., Colwell, D. D., Braun, W. J., & Choleris, E. (2003). Brief exposure to the odour of a parasitized male alters the subsequent mate odour responses of female mice. *Animal Behaviour*, *65*, 59–68.

Ensure this reference is cited in the text.

Kiesecker, J. M., Skelly, D. K., Beard, K. H., & Preisser, E. (1999). Behavioral reduction of infection risk. *Proceeding of the National Academy of Sciences*, *96*, 9165–9168.

Lippi, D., & Conti, A. A. (2002). Plague, policy, saints and terrorists: A historical survey. *Journal of Infection*, *44*, 226–228.

Low, B. S. (1990). Marriage systems and pathogen stress in human societies. *American Zoologist*, *30*, 325–339.

McCrae, R. R. (2002). NEO-PI-R data from 36 cultures: Further intercultural comparisons. In R. R. McCrae & J. Allik (Eds.), *The five-factor model of personality across cultures* (pp. 105–126). New York: Kluwer Academic/Plenum.

McCrae, R. R., Terracciano, A., & 78 members of the Personality Profiles of Cultures Project. (2005). Universal features of personality traits from the observer's perspective: Data from 50 cultures. *Journal of Personality and Social Psychology*, *88*, 547–561.

McNeill, W. H. (1976). *Plagues and peoples*. New York: Anchor Books.

Møller, A. P. (1996). Parasitism and developmental instability of hosts: A review. *Oikos*, *77*, 189–196.

Navarrete, C. D., & Fessler, D. M. T. (2006). Disease avoidance and ethnocentrism: The effects of disease vulnerability and disgust sensitivity on intergroup attitudes. *Evolution and Human Behavior*, *27*, 270–282.

Navarrete, C. D., Fessler, D. M. T., & Eng, S. J. (2007). Elevated ethnocentrism in the first trimester of pregnancy. *Evolution and Human Behavior*, *28*, 60–65.

Nettle, D. (2005). An evolutionary approach to the extraversion continuum. *Evolution and Human Behavior*, *26*, 363–373.

Nettle, D. (2007). Individual differences. In R. I. M. Dunbar & L. Barrett (Eds.), *Oxford handbook of evolutionary psychology* (pp. 479–489). Oxford, UK: Oxford University Press.

Oishi, S., Schimmack, U., Diener, E., & Suh, E. M. (1998). The measurement of values and individualism–collectivism. *Personality and Social Psychology Bulletin*, *24*, 1177–1189.

Park, J. H., Faulkner, J., & Schaller, M. (2003). Evolved disease-avoidance processes and contemporary anti-social behavior: Prejudicial attitudes and avoidance of people with physical disabilities. *Journal of Nonverbal Behavior*, *27*, 65–87.

Park, J. H., Schaller, M., & Crandall, C. S. (2007). Pathogen-avoidance mechanisms and the stigmatization of obese people. *Evolution and Human Behavior*, *28*, 410–414.

Quinlan, R. J. (2007). Human parental effort and environmental risk. *Proceedings of the Royal Society B*, *274*, 121–125.

Ridley, M. (2003). *The agile gene*. New York: HarperCollins.

Sabeti, P. C., Reich, D. E., Higgins, J. M., et al. (2002). Detecting recent positive selection in the human genome from haplotype structure. *Nature*, *419*, 832–837.

Sagiv, L., & Schwartz, S. H. (1995). Value priorities and readiness for out-group contact. *Journal of Personality and Social Psychology*, *69*, 437–448.

Savitz, J. B., & Ramesar, R. S. (2004). Genetic variants implicated in personality: A review of the more promising candidates. *American Journal of Medical Genetics Part B: Neuropsychiatric Genetics, 131B,* 20–32.

Schaller, M. (2006). Parasites, behavioral defenses, and the social psychological mechanisms through which cultures are evoked. *Psychological Inquiry*, *17*, 96–101.

Schaller, M., & Duncan, L. A. (2007). The behavioral immune system: Its evolution and social psychological implications. In J. P. Forgas, M. G. Haselton, & W. von Hippel (Eds.), *Evolution and the social mind: Evolutionary psychology and social cognition* (pp. 293–307). New York: Psychology Press.

Schaller, M., & Murray, D. R. (2008). Pathogens, personality, and culture: Disease prevalence predicts worldwide variability in sociosexuality, extraversion, and openness to experience. *Journal of Personality and Social Psychology*, *95*, 212–221.

Schmitt, D. P. (2005). Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Sciences*, *28*, 247–311.

Schmitt, D. P., Allik, J., McCrae, R. R., Benet-Martinez, V., et al. (2007). The geographic distribution of Big Five personality traits: Patterns and profiles of human self-description across 56 nations. *Journal of Cross-Cultural Psychology*, *38*, 173–212.

Sherman, P. W., & Billing, J. (1999). Darwinian gastronomy: Why we use spices. *BioScience*, *49*, 453–463.

Simpson, J. A., & Gangestad, S. W. (1991). Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Social Psychology*, *60*, 870–883.

Stein, M. B., Schork, N. J., & Gelernter, J. (2004). A polymorphism of the beta1-adrenergic receptor is associated with low extraversion. *Biological Psychiatry*, *56*, 217–224.

Suh, E., Diener, E., Oishi, S., & Triandis, H. C. (1998). The shifting basis of life satisfaction judgments across cultures: Emotions versus norms. *Journal of Personality and Social Psychology*, *74*, 482–493.

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, *3*, 452–460.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 19–136). New York: Oxford University Press.

Triandis, H. C. (1995). *Individualism and collectivism*. Boulder, CO: Westview.

Williamson, S. H., Hubisz, M. J., Clark, A. G., Payseur, B. A., Bustamante, C. D., & Nielsen, R. (2007). Localizing recent adaptive evolution in the human genome. *PloS Genetics*, *3*(6), e90. doi:10.1371/journal.pgen.0030090.