

NOTE: This is a pre-publication manuscript version of a published book chapter. It is not the copy of record and may not exactly replicate the authoritative document published in the book.

Pathogens, Personality, and Culture

Damian R. Murray
Tulane University

Mark Schaller
University of British Columbia

(2017)
In A. T. Church (Ed.), *The Praeger handbook of personality across cultures* (Vol. 3, pp. 87-116).
Santa Barbara CA: Praeger.

“The most important relationship in each of our lives is with germs.”
- Tetro, “The Germ Code” (2013, p. ix)

Personality styles vary widely across cultures, as Volume 1 of this work attests. On average, New Zealanders report higher extraversion than Nigerians; Chileans report higher openness to experience than Chinese (e.g., McCrae et al., 2005). Similarly, when comparing small-scale societies, the Wolof tend to be more self-restrained than the Warrau; the Aztec more restrained than the Amahuaca (Barry, Josephson, Lauer, & Marshall, 1976). But why does this variation exist? Is it simply stochastic noise, or ethnographic dazzle? Or do these cultural differences reflect real, adaptive responses to differing ecological and social demands between cultures? In this chapter, we focus on one specific ecological variable—the threat posed by infectious disease—and its implications for cultural variation in personality.

Broad Conceptual Background

Ecological Variation and Animal Behavior

The implications of ecological variation for differences in animal behavioral dispositions (or, to use the term loosely, “personalities”) has long been a focus of enquiry within the biological sciences. The basic logic underpinning this work is *adaptive variation*: Animals will tend to adaptively calibrate their behavioral tendencies in ways that increase their probability of surviving and successfully reproducing. Animals that risk predation when they search for food, for example, forage less when they perceive the threat of predation to be especially high (e.g., Dugatkin & Godin, 1992). Of course, chronic predation risk also varies between groups, and this variation leads to the evolution of different systems of behavioral tendencies. “Predator inspection” behavior between groups of guppies offers a fruitful example. Predator inspection is a beneficial behavior for the female guppy because it allows for identification of potential predators. However, for females this behavior also carries potential reproductive costs. Males of this species have developed a covert mating strategy—“sneaky matings”—which involves sneaking up behind a female and inseminating her while she is otherwise preoccupied. Of course, the benefits of predator inspection are greater in ecologies characterized by higher threat of predation, and should be especially likely to outweigh the costs of potentially being sneakily mated in these environments, which leads to the prediction that females should spend more time

on predator inspection in ecologies characterized by higher predation threat. This is exactly what is found: Females in predator-rich ecologies spend more time on predator inspection (and lower the risk of predation), but pay the cost of more frequent sneaky matings (Magurran, 1999).

Just as the threat of predation leads to the evolution of behavioral systems, so too does the threat of parasitic attack. In certain species of leafcutter ants, for example, the threat posed by parasitic flies has led to the evolution of a strategically clever behavioral solution. Leafcutter ants are most defenseless when carrying leaf pieces back to their nests, at which time—for some groups of ants—a parasitic fly will descend upon the ant and lay its eggs in the ant's neck. These eggs hatch, the larvae within eat the ant's neck muscles, and the ant is eventually decapitated. Where this parasite is endemic, however, ants have evolved a counter-strategy. As one ant carries a leaf piece home, another ant sits atop the leaf, and physically vanquishes any parasitic flies that attempt an attack (Feener & Brown, 1997). Although it literally halves the overall productivity of the ants, in groups where the parasitic threat is sufficiently high, this ride-catching behavior has anti-parasite benefits that outweigh the productivity costs.

Ecological Perspectives on Human Cross-Cultural Differences

Just as biologists often invoke ecological explanations to (at least partly) explain variation in animal behavior, so too have psychologists more recently begun to invoke ecological explanations for cultural variation in human behavior and personality. (For the purposes of this paper, “ecological” refers to characteristics of the natural environments inhabited by humans). Indeed, there is reason to believe that human behavior may be especially responsive to differing ecological contexts; human adaptation to nearly every corner of the globe has necessitated the development of a diverse suite of culture-specific behaviors and social systems. Specific behaviors necessary for survival in one ecology may involve seal-hunting, fishing, and building shelters from ice and snow (e.g., the Inuit, see Stefansson, 2004), whereas survival in another ecology may depend crucially upon knowledge of edible plants and means of root and tuber extraction (e.g., aboriginal peoples of central Australia, see O’Dea et al., 1991). Different populations have developed different behavioral norms and practices in response to the different demands of their local ecologies.

Much work suggests that ecological variation can have implications for the most psychologically fundamental of cultural differences. Even basic perceptual processes appear to be influenced by ecological demands. Perceptual susceptibility to the well-known Müller-Lyer optical illusion, for example, varies cross-culturally and may do so in part because of differences in the geometric properties of local architecture—inhabiting environments in which architectural right angles are common is associated with being more susceptible to the illusion (Segall, Campbell, & Herskovits, 1966).

Another line of work has focused on ecological differences that may have contributed to the emergence of cultural differences in holistic perception and thought (e.g., Nisbett, Peng, Choi, & Norenzayan, 2001). This perspective suggests that differential modes of subsistence should be amenable to different ways of cognitively sorting one's environment. This idea is supported by results showing that, compared to herders, farmers and fishermen show greater levels of holistic perception and thought (Uskul, Kitayama, & Nisbett, 2008). Similarly, more recent work has documented the psychological implications of agricultural economies based on the cultivation of wheat versus rice. Talhelm and colleagues (2014) predicted that rice cultivation would favor individuals with dispositional tendencies towards cooperation and interdependence, given the higher cooperative demands between adjacent plots of rice cultivation relative to wheat

cultivation. Indeed, comparing regions within mainland China, they found that individuals in rice-growing regions were relatively more interdependent and more prone to holistic thought.

Other work has focused on the implications of climate and ambient temperature for value systems, and posits that poor cultures inhabiting more climatically “demanding” ecologies should develop norms and values that restrict freedoms, whereas rich cultures inhabiting climatically demanding ecologies should develop norms and values that encourage freedoms, and cultures inhabiting temperate climates should develop norms that lie somewhere between these endpoints, regardless of wealth (Van de Vliert, 2013; Chapter 5, this volume).

Although the ecological perspectives summarized above may not focus on personality *per se*, they highlight a fundamental point: Ecological variation is instrumental to understanding cultural variation in human cognition and behavior. This point applies to personality too. (Throughout this chapter we characterize personality in its broad sense—as dispositional tendencies towards certain behavioral, cognitive, and affective patterns; Mischel, Shoda, Smith, & Mischel, 2004). We turn now to the specific linkage between ecological variation in the prevalence of infectious diseases and cultural variation in personality traits and other behavioral dispositions.

Pathogen Prevalence and Cross-Cultural Variation in Personality

Logical Underpinnings of a Link between Disease Threat and Behavioral Dispositions

Research that empirically addresses the implications of ecology for personality is underpinned by a simple premise: Many behaviors—and their associated psychological processes—will have differential costs and benefits across different ecologies. This differential cost/benefit ratio will result in cultural or genetic selection for different sets of behaviors and cognitions, which, over time, will lead to the development of cultural differences in personality.

Within the domain of ecological challenges, there is much reason to believe that infectious diseases may represent an especially potent problem, with especially important implications for behavioral dispositions. Parasites have posed a threat to the welfare of the ancestors of modern humans for roughly a billion years (e.g., Zimmer, 2001). The infectious diseases caused by parasites have represented one of the largest threats to survival throughout human history; even today, within populations lacking sophisticated medical systems, infectious diseases are one of the most common causes of death, and remain the central driver of local genetic adaptation (Fumagalli et al., 2011; Inhorn & Brown, 1990).

One set of mechanisms designed to mitigate the threat posed by infectious disease comprises the physiological immune system. At a basic level, this system operates by detecting invading parasites in the body, notifying the appropriate antibodies, and activating the appropriate physiological response. Although this highly sophisticated system is generally effective, it suffers from at least three shortcomings. First, this cascade of defenses only becomes operative *after* infection; pathogens may wreak significant damage during even this short latency period. Second, this system is more effective at eliminating pathogens with which it has already been in contact; although the number of unique antibodies possessed within any given person numbers in the billions (e.g., Fanning, Connor, & Wu, 1996), the immune system lacks the specific antibodies required for novel pathogens, which further increases the latency time between detection and elimination. Third, these physiological defenses are costly. Immunological responses to bacterial infections, for example, typically involve an increase in body heat (experienced as fever), which potentiates immune responses and creates a challenging environment for the invading pathogen (e.g., Nesse & Williams, 1995). But this fever response

is energetically costly: A 13 percent increase in metabolic activity increases human body temperature by just 1° Celsius (Dantzer, Kent, Bluthe, & Kelley, 1991).

Given the necessary constraints of the physiological immune system, it follows that it may be beneficial to engage this system as infrequently as possible. One means of minimizing the burden placed upon the immune system is by adopting behavioral patterns that strategically minimize exposure to infectious disease in the first place. These behavioral strategies can be thought of as serving as a first line of defense against pathogens. These psychologically-motivated strategies operate by detecting potential disease-connoting cues within the local environment and responding with a cascade of cognitive, affective, and behavioral reactions designed to facilitate avoidance of pathogens (Murray & Schaller, in press; Schaller, 2016).

Just like broader ecological perspectives on animal behavior, specific behavioral strategies that minimize exposure to infectious diseases have long been studied within the biological sciences. Avoidance behaviors may be directed against pathogenic substances (such as selective feeding away from fecal matter, e.g., Michel, 1955) as well as potentially infectious group members. Caribbean spiny lobsters discriminately avoid conspecifics suffering from viral infections (Behringer, Butler, & Shields, 2006); bullfrog tadpoles detect chemically-transduced cues signaling parasitic infection in other tadpoles, and respond by selectively swimming away from the infected conspecifics (Kiesecker, Skelly, Beard, & Preisser, 1999). Phylogenetically closer to home, disease has likely been one of the most important ecological influences in the evolution of primate behavior, given its frequent role in illness and mortality in free-living primates (Freeland, 1976).

Although pathogens—and the diseases they cause—pose a threat to people worldwide, the magnitude of this threat and the welfare costs they impose vary geographically. Most pathogens thrive in warm, wet conditions; the prevalence and diversity of pathogens is therefore a predictable function of latitude and other relatively stable geographical characteristics (Cashdan, 2014; Guernier, Hochberg, & Guégan, 2004). Thus, if indeed the behavioral dispositions of individuals are adapted to the demands of their local ecological circumstances, the implication is that ecological variation in the prevalence of pathogens may predict cultural variation in behavioral dispositions.

The use of spices in food preparation offers one such example. Spices are natural antibiotics; they contain toxins that kill many of the potentially harmful bacteria that can be found in otherwise palatable food. This antibiotic effect is noticeable even in modern nation-states today: A recent prospective study of almost 500,000 Chinese found that higher spice consumption was linked with significantly lower mortality risk, and that this effect was at least partly due to lower mortality risk from bacterial infections and infectious respiratory diseases (Lv et al., 2015). The use of spices in the preparation of food, then, can be beneficial as a defense against bacterial infections. Of course, the luxury of spice-use incurs practical costs as well: The cultivation of spices consumes time and arable resources that might otherwise be spent cultivating more nutritious foods. Consequently, the use of culinary spices would most likely emerge and persist as a cultural practice in regions where the benefits of this practice are especially likely to outweigh the costs—under circumstances in which there is a high likelihood of bacterial infestation in food. Sherman and Billing (1999) reasoned that warmer ambient temperatures would increase the probability of bacterial infestations in food, and analyzed the cuisines of dozens of countries worldwide to test the hypothesis that in geographical regions that are especially hot (meteorologically speaking), the cuisines are spicily hot as well. And this is

exactly what they found. Cultural variation in the use of spices appears to be rooted, at least in part, in the differential ecological prevalence of pathogens.

The same cost/benefit logic that underlies the link between pathogen prevalence and cultural differences in culinary practices also applies to cultural differences in personality traits and other behavioral dispositions. In the following sections, we summarize a series of conceptual hypotheses articulating specific applications of this logical analysis, and empirical research bearing on those hypotheses.

Methodological Considerations

Before proceeding to review the relevant evidence, however, it may be useful to identify some of the inferential issues bearing on that evidence, and to discuss methods that may be useful in addressing these issues.

Units of analysis. First, just *defining* which cultures should be considered functional units of analysis is a challenge in this research enterprise. Several of the investigations reviewed below use modern geopolitical entities—mostly countries—as units of analysis. Using these units has drawbacks (such as non-independence and heterogeneity; Nettle, 2009; Pollet, Tybur, Frankenhuys, & Rickard, 2014), and few would argue that country is synonymous with culture. However, political borders offer both a convenient and a geographically objective means of dividing up the worldwide human population into culture-like categories, and empirical evidence suggests that they serve as useful proxies for cultural boundaries (e.g., Schwartz, 2004).

To be more inferentially compelling, however, research employing countries as units of analysis can be buttressed by conceptually parallel investigations using alternate units of analysis, be those units small-scale societies, world regions, or regions within the same country. Some of the investigations reviewed below have used these additional units of analysis to complement cross-national comparisons.

Causal inference. As with most cross-cultural research, these investigations employ correlational methods, and so we cannot enjoy the inferential comfort of controlled experiments. (One cannot randomly assign participants to a country or to a culture, and pathogen prevalence cannot be experimentally manipulated between cultures.) Many other country- or culture-level variables may be correlated with pathogen prevalence, and some of these variables might be expected to independently predict particular cross-cultural differences. These other putatively-predictive variables must be statistically controlled when testing whether pathogen prevalence actually predicts the cross-cultural difference of interest. Compelling support for any hypothesis about the effects of pathogen prevalence emerges only when pathogen prevalence uniquely predicts cross-cultural outcomes even when controlling for these additional variables.

In addition, even when correlations persist after controlling for potential "third variables" (as is the case in most the research reviewed below), these correlations alone offer little evidence of causal direction. In the absence of additional results, even large correlations between pathogen prevalence and cultural outcomes cannot tell us whether ecological variation in pathogen prevalence might be a cause, rather than a consequence, of cultural variation. Certain methodological and analytical tools can be used to complement simple correlations in order to clarify the causal relationships lurking in cross-cultural data. Temporal precedence is one important inferential ally. To infer that pathogen prevalence exerts a causal influence on culture (and not the reverse), it helps to obtain a measure of pathogen prevalence at a period of time substantially prior to the measure of the cultural outcome variable. It can be even more inferentially compelling if contemporary cultural differences are predicted more strongly by a

measure of historical pathogen prevalence than by a measure of contemporary pathogen prevalence.

Assessment of pathogen prevalence. Of course, creating a reliable and representative index of *historical* disease prevalence is no easy task. Global epidemiological record-keeping is a relatively recent practice; institutional initiatives such as the Center for Disease Control did not exist before the mid twentieth century (www.cdc.gov/about/history), so obtaining reliable epidemiological estimates before this time is challenging.

For our cross-national research—which we summarize below—we employed a methodological strategy adapted from Gangestad and Buss (1993), who followed an approach used by Low (1990). Low used historical epidemiological atlases to code the prevalence of seven infectious diseases in small-scale societies that are part of the Standard Cross-Cultural Sample (Murdock & White, 1969). Gangestad and Buss (1993) developed a similar country-level measure for 29 nation states in order to investigate the relationship between disease prevalence and preferences for attractiveness in a mate. (They found that pathogen prevalence positively predicted the importance that people place upon the attractiveness of a potential mate.) We extended this approach to cover a more complete set of 230 geopolitical regions worldwide (Murray & Schaller, 2010). Most of these regions are countries (e.g., Libya), whereas others are territories or protectorates (e.g., Guam) or culturally distinct regions within a nation (e.g., Hong Kong). For the sake of expository ease, we use the word "country" to refer to all of these regions. The 9 infectious diseases coded were leishmania, schistosoma, trypanosoma, leprosy, malaria, typhus, filaria, dengue, and tuberculosis. With one exception (tuberculosis), the prevalence of each disease was informed by epidemiological atlases and additional epidemiological information compiled in either the late 19th or early 20th centuries (from Rodenwaldt & Bader, 1952-1961; Simmons, Whayne, Anderson, & Horack, 1944). For the majority of countries (N = 160), prevalence data on all 9 diseases was available, allowing the computation of a standardized 9-item index of historical pathogen prevalence (Cronbach's $\alpha = .84$). For all 230 countries, a standardized index of historical pathogen prevalence was computed based on data from either 6 or 7 infectious diseases. Results reported in Murray and Schaller (2010) attest to the construct validity of this measure.

This coding strategy was also re-employed to create a more comprehensive disease index for the small-scale societies comprising the Standard Cross-Cultural Sample. Cashdan, Steele, and Murray (2014) coded the prevalence of eight pathogens: leishmanias, trypanosomes, malaria, schistosomes, filariae, dengue, typhus, and plague; the authors also added from Low's (1990) original codings for spirochetes and leprosy. (The choice of pathogens was determined largely by whether or not source materials contained adequate global coverage. These ten pathogens reflect only a small proportion of the total number of pathogens worldwide; however, these are also especially prevalent and representative pathogens, see Cashdan et al., 2014). This index for small-scale societies parallels the country-level index and provides opportunities for comparative investigations of these samples.

For further comparative purposes, it can be inferentially informative to employ a measure of contemporary pathogen prevalence. In these investigations, these contemporary measures are most often taken from the Global Infectious Disease & Epidemiology Network (GIDEON). GIDEON is a frequently updated, subscription-based online database of human infectious diseases available to the medical community and researchers. If historical, rather than contemporary, pathogen prevalence emerges as a stronger predictor of a variables of interest, this is consistent with disease threat being a cause, rather than a consequence, of cultural differences.

Given the precision and comprehensiveness of the GIDEON database, it has been used as a basis for the development of several additional measures that assess the prevalence of specific kinds of infectious diseases that vary in terms of their mode of transmission (e.g., Thornhill, Fincher, Murray, & Schaller, 2010). Of particular relevance are separate indices assessing the prevalence of non-zoonotic diseases (many of which are transmitted via human-to-human contact) versus the prevalence of zoonotic (animal-to-human) diseases. Given that many facets of personality dictate behavioral tendencies in the realm of sociality and interpersonal interaction, one might expect that non-zoonotic (compared to zoonotic) diseases to be especially strongly predictive of cross-cultural differences in personality.

Pathogen Prevalence and Big Five Personality Traits

The most straightforward starting point in illustrating the implications of disease threat for personality involves relationships between pathogen prevalence and well-validated personality constructs. As recently as a decade ago such an investigation would not have been possible but, thanks to recent large-scale personality projects, several extensive cross-cultural personality comparisons now exist. These investigations have employed assessments of the Big Five personality traits—a factor structure that largely generalizes across cultures and has been independently found in languages such as German, Portuguese, Hebrew, Chinese, Korean, and Japanese to name a few (e.g., McCrae & Costa, 1997). These investigations have documented important cultural differences along each of the Big Five personality traits.

To investigate relations between pathogen prevalence and the Big Five personality traits, Schaller and Murray (2008) employed the results of three of these large-scale personality investigations. McCrae (2002) summarized results from multiple independent studies that used the NEO-PI-R questionnaire (Costa & McCrae, 1992) to assess the self-reported personality traits in 33 different countries. In a separate study, McCrae and an international team of collaborators obtained observer reports on the NEO-PI-R questionnaire from almost 12,000 individuals in 50 different countries (McCrae et al., 2005). In a third international study, Schmitt and his colleagues assessed self-reports on the Big Five Inventory (John & Srivastava, 1999) from almost 18,000 individuals in 56 different countries (Schmitt et al., 2007). Each investigation produced a set of country-level scores on each of the Big Five personality traits for dozens of countries around the globe, and documented extensive cross-cultural variation in average personality profiles.

Of course, given the questionnaire-based research strategies employed, some of the differences in country-level personality scores may be attributable to noise or methodological artifacts, such as non-equivalent translations or reference group effects. Nevertheless, to the extent that there is at least some validity associated with these country-level personality scores, they offer the potential to test conceptual hypotheses about the links between pathogen prevalence and cross-cultural differences in fundamental personality traits.

Extraversion. Highly extraverted personalities imply a wider circle of acquaintances and social contacts and an increased frequency of contact with those people. These social contacts have the potential to expose individuals to interpersonally transmitted pathogens. Indeed, empirical evidence suggests that highly extraverted personalities are associated with an enhanced risk of disease transmission and a higher frequency of acute infections (Hamrick, Cohen, & Rodriguez, 2002; Nettle, 2005).

However, extraversion is associated with many positive outcomes as well, including higher levels of leadership effectiveness and increased opportunities for sexual reproduction (Berry & Miller, 2001; Silverthorne, 2001). These benefits of extraversion are likely to

outweigh the disease-related costs under conditions in which the disease-related costs are relatively minimal: In ecological settings characterized by low levels of interpersonally transmitted pathogens. However, as pathogen prevalence increases, there is increased likelihood that the disease-related costs of extraversion will begin to outweigh the benefits. It is worth noting that these costs of extraversion are likely to accrue not only to extraverts themselves, but also to anyone (even an introvert) in the local population who happens to interact with an extravert. Therefore, in places characterized by high pathogen prevalence, one might expect that individuals will not only be less extraverted themselves, but will also devalue extraversion more generally. In any case, the hypothesis is straightforward: Regional variation in pathogen prevalence is expected to be inversely related to cultural variation in extraversion.

Schaller and Murray (2008) conducted multiple tests of this hypothesis, using the results from the three different cross-national surveys of the Big Five personality traits summarized above (McCrae, 2002; McCrae et al., 2005; Schmitt et al., 2007). As predicted, across every measure, regional differences in Extraversion were negatively correlated with historical pathogen prevalence. These relationships remained even when controlling for additional country-level variables (e.g., GDP, income inequality, individualistic versus collectivistic values, etc.). Further, consistent with the causal relation specified by the hypothesis, Extraversion was more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence. Additional results reveal that cultural variation in Extraversion is especially strongly predicted by the prevalence of non-zoonotic pathogens that are transmitted through human interaction (Thornhill et al., 2010).

For 2 of the 3 cross-national surveys—those that employed the NEO-PI-R questionnaire—facet scores were reported (McCrae, 2002, and McCrae & Terracciano, 2008). Ancillary analyses revealed that pathogen prevalence was consistently negatively associated with the facets warmth, gregariousness, activity, and positive emotions; it was not reliably associated with assertiveness or excitement seeking. Given the number of facets, coupled with the exploratory nature of these analyses, these facet-level results might best be interpreted with some caution.

Openness to Experience. Although perhaps less intuitively appealing than the inverse relation between pathogen prevalence and extraversion, a similar cost/benefit analysis suggests a similar inverse relation between pathogen prevalence and openness to experience. Openness is associated with creativity, willingness to deviate from established norms and tradition, and attraction to novel experiences (e.g., Larsen & Buss, 2014). These behavioral dispositions can be associated with certain kinds of fitness benefits, in that they encourage innovation and adaptive problem solving. But these dispositions also connote potential fitness costs specific to pathogen transmission. Many social and cultural norms are protective—particularly in domains such as food preparation, personal hygiene and public health—and actually serve as buffers against pathogen transmission. To the extent that individuals deviate from these accustomed norms (e.g., experiment with novel methods of food preparation, or take creative approaches to hygiene), those individuals expose themselves and others within their ingroup to an increased risk of pathogen transmission. These particular kinds of costs are likely to be greater (and more likely to outweigh the benefits associated with open personalities) under conditions of greater pathogen prevalence. Thus, regional variation in pathogen prevalence is expected to be inversely related to cultural variation in openness to experience.

Schaller and Murray (2008) conducted multiple tests of this hypothesis using the same source materials summarized above. Again, across every measure, cross-cultural differences in

openness to experience were negatively correlated with historical pathogen prevalence. These negative relationships remained even when controlling for other country-level variables that might be associated with openness. Consistent with the causal relation specified by the hypothesis, openness to experience was more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence. Also, as with extraversion, follow-up results revealed also that cultural variation in openness was especially strongly associated with the prevalence of non-zoonotic (compared to zoonotic) diseases (Thornhill et al., 2010).

At the facet level, across both measures pathogen prevalence was negatively associated with fantasy, feelings, and values, and marginally negatively associated with ideas. It was not consistently associated with either actions or aesthetics. Again, however, one must exercise caution when drawing inferences from these facet-level findings.

Other Big Five traits. In addition to testing hypotheses linking pathogen prevalence to cross-cultural differences in extraversion and openness, Schaller and Murray (2008) also conducted additional analyses to explore whether there might be any relationships with the other three Big Five factors: agreeableness, conscientiousness, and neuroticism. No consistent patterns emerged across the various measures, although there was some evidence that pathogen prevalence may predict more narrowly defined facets of these additional factors. For instance, at a cross-cultural level, pathogen prevalence was consistently positively correlated with measures of deliberation (a facet of conscientiousness), and negatively correlated with measures of impulsiveness (a facet of neuroticism). One must be cautious when interpreting results on these underlying facets. That said, it is worth noting that the findings on deliberation and impulsiveness fit neatly within the conceptual analysis that gave rise to the hypothesis pertaining to openness.

There is some useful inferential value associated with the negligible relations between pathogen prevalence and these additional three Big Five factors (agreeableness, conscientiousness, neuroticism). These negligible relations suggest that the conceptually interesting results on extraversion and openness are unlikely to be due to response biases (e.g., acquiescence bias) or other methodological artifacts that affect all traits assessed by the personality questionnaires. This improves confidence that the observed correlations involving pathogen prevalence and personality are truly meaningful.

Within-culture variation on Big Five traits. The cost/benefit logic linking higher pathogen prevalence to lower Openness also implies that there may be a relationship between pathogen prevalence and the magnitude of between-person trait variability within a culture. A higher level of within-culture trait variation indicates that individuals' dispositional tendencies deviate more greatly from local dispositional norms. In essence, it indicates a greater tendency to be "non-normal." Thus, just as pathogen prevalence is inversely related to cultural variation in mean levels of openness to experience, it might be expected also to inversely predict within-culture personality variation across countries. Using results reported previously by McCrae (2002)—who, in addition to computing country-level means on 30 facets of the NEO-PI-R, also reported standard deviations around those means—Murray, Trudeau, and Schaller (2011) tested this prediction, and that is exactly what they found.

Authoritarianism and Other Conformist Dispositions

The logic bearing on openness and within-culture dispositional variation also applies to conformist attitudes more generally. One such construct is the "authoritarian personality." Adorno and his colleagues (Adorno, Frenkel-Brunswick, Levinson, & Sanford, 1950) developed a questionnaire—the "F Scale"—to assess individual differences in traits and attitudes that define

the authoritarian personality (e.g., conventionalism, authoritarian submission, ethnocentrism), and this F scale has been validated in both Western and non-Western cultures (e.g., Kool & Ray, 1983). Meloen (1996) compiled results obtained from over 30,000 individuals worldwide who completed the F Scale, and reported mean standardized F Scale scores for individuals living within each of 31 countries. Murray, Schaller, and Suedfeld (2013) examined the relationship between historical pathogen prevalence and authoritarian personality scores across countries and found, as predicted, a strong positive relationship between these two measures. Pathogen prevalence exerted a unique predictive effect on authoritarian personality scores even when controlling for other variables that plausibly covary with authoritarianism, such as wealth, inequality, level of education, and other threats to human welfare.

There are other fruitful ways for assessing conformist dispositions too. Murray et al. (2011) found that historical pathogen prevalence positively predicts cross-national variation in the effect sizes observed in social psychological experiments on conformity behavior, and also predicts cross-national variation in the extent to which people place importance on raising children with obedient dispositions. These relationships were not accounted for by other country-level variables, such as GDP, population density, or other threats within the environment.

The relationship between pathogen prevalence and conformist traits is found not only in comparisons of contemporary countries, it has also been found in comparisons of the small-scale societies that comprise the ethnographic database of the Standard Cross-Cultural Sample. Using the new pathogen codes developed by Cashdan et al. (2014), Cashdan and Steele (2013) found that historical pathogen prevalence positively predicted cross-cultural variation in the emphasis that parents place on the development of “obedient” traits in children, and negatively predicted emphasis on the development of “self-reliant” traits. These relationships were robust when controlling for variables such as latitude, population density, and political integration.

Dispositional Inclinations Regarding Sexual Promiscuity

Sexual behavior provides much opportunity for disease transmission, and more sexually promiscuous behavior is associated with an increased risk of contracting diseases and spreading these diseases to others. However, unrestricted sexual behavior can also have specific kinds of adaptive benefits—providing, for example, the opportunity to produce more offspring. These benefits must be weighed against the disease-related costs, and this cost/benefit ratio varies depending upon the prevalence of disease-causing pathogens. Where pathogen prevalence is higher, the costs of unrestricted sexuality are more likely to outweigh the benefits, whereas in places characterized by lower pathogen prevalence the benefits are more likely to outweigh the costs. This logic leads to the hypothesis that greater pathogen prevalence predicts more sexually restricted attitudes.

Cross-national evidence provides some support for this hypothesis (Schaller & Murray, 2008). In places with a higher level of historical pathogen prevalence, both men and women report being more sexually restricted (r 's for men and women were $-.27$ and $-.62$, respectively). This effect is stronger for female scores, and this sex difference in effect sizes fits with the cost/benefit framework. Men have a lower minimum level of parental investment than do women; thus, the fitness benefits associated with unrestricted sexual behavior are likely to be greater among men than among women. Therefore, for men only, these benefits may outweigh the costs (disease transmission) even at relatively high levels of pathogen prevalence. Among women, however, the benefits of unrestricted sexuality are relatively minimal, and so are more likely to be outweighed by disease-related costs as pathogen prevalence increases. Consistent with the conceptual framework, additional results revealed that cross-national variation in

women's unrestricted sexual attitudes were predicted especially strongly by the prevalence of human-transmitted non-zoonotic diseases, compared to the prevalence of zoonotic diseases (Thornhill et al., 2010).

Xenophobic and Ethnocentric Attitudes

Xenophobic personality traits have costs, including reduced opportunities for trade and coalitional alliances. But dispositional wariness of outsiders may also have disease-relevant benefits. The human immune system is highly localized; even outgroup members from neighboring communities are more likely to harbor exotic pathogens (e.g., Miller et al., 2007), which are especially virulent to individuals with no prior exposure to them. Outgroup members are also more likely to be ignorant of local norms that buffer against pathogen transmission. These disease-specific benefits of xenophobic values are likely to be greater in regions of higher pathogen prevalence.

Some work supports the link between pathogen prevalence and markers of xenophobic traits. For example, individuals are more likely to indicate that they would not want “someone of a different race” as a neighbor in regions of higher disease prevalence (Schaller & Murray, 2010). Other work is obliquely supportive of this logic as well. Fincher, Thornhill, Murray, and Schaller (2008) investigated the relationship between pathogen prevalence and measures of individualist and collectivist values across cultures. Relative to individualism, collectivism is characterized by higher wariness of outsiders and sharper ingroup/outgroup boundaries (it is also characterized by higher emphasis on conformity to group norms, consistent with the conceptual logic bearing upon conformist traits). As predicted, pathogen prevalence strongly positively predicted two measures of collectivism and negatively predicted two measures of individualism. Historical pathogen prevalence was a stronger predictor than was contemporary pathogen prevalence, and further analyses revealed that this relationship between pathogen prevalence and collectivistic values was unique to non-zoonotic diseases (Thornhill et al., 2010).

A tendency towards higher wariness of outgroups is often associated with tighter relationships within groups—with especially tight relationships among family members and other close allies, as indicated by values promoting exchange of resources among family and other allies. Although there are costs associated with this obligatory expenditure of resources, reciprocal benefits of obligatory prosociality accrue whenever one (or one's immediate kin) requires aid from others. These benefits are likely to be especially pronounced under conditions characterized by high levels of pathogen prevalence. As Navarrette and Fessler put it, “Since networks of alliances are the only health insurance policy available in small-scale societies, it follows that, when the likelihood of illness increases, individuals should be motivated to ensure both that their premiums are paid and that their coverage is extensive” (2006, p. 272). Fincher and Thornhill (2012) investigated whether pathogen prevalence predicts this type of prosociality. They created a country-level index of “strength of family ties” based upon five responses obtained from the World Values Survey (e.g., the percentage of respondents who indicated that one of their goals in life was to “make their parents proud”). Consistent with the hypothesis, geographic variation in strength of family ties was positively predicted by pathogen prevalence at both the country and world-region levels of analysis. This relationship remained after controlling for possible confounds such as economic development and human freedoms. These findings were further replicated with independent analyses that used American states as units of analysis.

Moral Values

According to moral foundations theory (e.g., Haidt, 2012), the many different kinds of moral values can be located within two foundational categories: Some moral values are considered to be "individualizing" whereas others are considered to be "binding." Binding moral foundations are relevant to concerns such as group loyalty, respect for authority, and purity. These binding aspects of morality have obvious implications for a variety of individual differences (e.g., ethnocentrism, obedience, cleanliness) that may serve as buffers against disease transmission. Therefore, individuals' endorsement of "binding" moral values may be more common in places characterized by a greater threat of pathogen infection.

Van Leeuwen and colleagues (2012) tested this hypothesis on data obtained from over 120,000 people in 147 countries. Results showed that historical pathogen prevalence was a significant predictor of cross-national variation in individuals' endorsement of binding moral values (but not their endorsement of individualizing moral values). This predictive effect of historical pathogen prevalence was greater than the effect of contemporary pathogen prevalence—a finding that is inconsistent with a reverse causal explanation. These effects emerged even when controlling for other purported causes of variation in moral values. This result emerged not only from analyses that treated countries as units of analysis, but also from multilevel analyses on individual responses.

Our own analyses suggest that these results are buttressed by additional results from analyses of Pew survey data from 40 countries (www.pewglobal.org/2014/04/15/global-morality) pertaining to the tendency to place moral sanctions on sexual behaviors. The tendency to moralize sexual behavior varies widely across cultures. (97% of Indonesians say that premarital sex is wrong whereas 11% of Italians do; 15% of Canadians say homosexuality is morally wrong whereas 61% of Chinese do). Historical pathogen prevalence strongly predicts the percentage of people within a country who state that premarital sex is morally wrong ($r = .65, p < .001$), as well as the percentage who state that homosexuality is morally wrong ($r = .67, p < .001$). Contemporary pathogen prevalence is also highly correlated with these percentages; however, only historical pathogen prevalence remains a significant predictor of both of these measures in multiple regressions that include both pathogen prevalence measures.

Pathogens, Personality, and Their Broader Cultural Consequences

The results reviewed above suggest that pathogen prevalence may be responsible, at least in part, for contemporary cross-cultural variation in individuals' dispositions. Some of these results reflect actual behavioral observations (e.g., cultural differences in behavioral conformity), but many results are based on self-report measures of traits, attitudes, and values. Given enduring concerns about the extent to which individual differences predict actual behavior (e.g., Higgins, 2000; Mischel, 1968), it is worth asking: Does pathogen prevalence predict variation on society-level outcomes that may reflect individual-level behavioral decision-making? Some evidence indicates that the answer is "yes."

One such piece of evidence comes from comparative work on political systems. Just as authoritarian personalities are characterized by conventionalism, authoritarian submission, and ethnocentrism, authoritarian political systems are characterized by concentrated power structures that repress dissent and emphasize submission to authority, social conformity, and hostility towards outgroups (Adorno et al., 1950; Altemeyer, 1996). The implication is that authoritarian forms of governance are especially likely to emerge and to persist in cultures inhabiting regions of relatively higher pathogen prevalence. In support of this hypothesis, Thornhill, Fincher, and Aran (2009) found that cross-national variation in contemporary pathogen prevalence was

positively associated with cross-national variation in the extent that governments repress individual rights and freedoms, and was negatively associated with liberalism and democratization. Additional results reveal that these outcomes are even more strongly predicted by a measure of historical pathogen prevalence (Murray & Schaller, 2010).

These results, combined with the authoritarian personality results reported earlier, logically compel a further question: Do authoritarian personality traits encourage the development of authoritarian political systems, or vice-versa? Murray, Schaller, and Suedfeld (2013) tested these competing causal models. Results revealed that country-level mean values of individuals' scores on measures of the "authoritarian personality" mediated the relationship between pathogen prevalence and measures of authoritarian governance. Conversely, variation in authoritarian governance did not mediate the relationship between pathogen prevalence and individual-level authoritarianism. These results are consistent with the explanation that pathogen prevalence has implications for country-level differences in individuals' authoritarian dispositions, and these dispositional differences have downstream behavioral consequences for the systems of governance and emerge and persist within societies.

In a complimentary study, Murray et al. (2013) investigated the relationship between pathogen prevalence and twelve different markers of authoritarian political structures that have been observed by ethnographers across the dozens of small-scale societies that comprise the Standard Cross-Cultural Sample. Results revealed that pathogen prevalence was positively associated with all twelve measures of authoritarian governance. Moreover, this relationship remained significant when controlling for other ecological threats that might also be expected to exert an effect on political structures.

In addition to their downstream consequences for political structures, the dispositional consequences of pathogen prevalence might also be expected to have downstream consequences for geographical variation in innovation. Assuming that novel discoveries are more likely to emerge, and to spread, within populations characterized by greater openness to new ideas and less conformity to existing traditions (e.g., Herbig & Dunphy, 1998), it follows that ecological variation in pathogen prevalence will be inversely predictive of cultural variation in technological innovation.

Murray (2014) tested this hypothesis using five different country-level markers of scientific and technological innovation (indices of Global Innovation, Technological Achievement, Innovative Capacity, as well as measures of patent applications per capita and Nobel laureates per capita). Consistent with predictions, each of these variables was negatively associated with historical pathogen prevalence. These relationships remained when controlling for other important drivers of innovation—including country-level measures of wealth, life expectancy, and resources devoted to education—and were replicated using world regions as units of analysis. Further analyses revealed that this relationship was partially mediated by cross-national variation in conformist dispositions.

The implications of pathogen prevalence for xenophobic attitudes may also have further downstream consequences. Fincher and Thornhill (2008), for example, found that there is less contact between different ethnic groups in regions and countries of higher pathogen prevalence. This lower level of intergroup contact and mixing also appears to manifest in a higher frequency of intrastate conflict and civil war in countries of higher pathogen prevalence (Letendre, Fincher, & Thornhill, 2010).

There also may be society-level behavioral norms that emerge in response to the implications that pathogen prevalence has for reduced extraversion and more cautious

dispositional approaches to interpersonal interaction. Using data coded from the ethnographic observations that comprise the Human Relations Area Files (hraf.yale.edu/online-databases/ehraf-world-cultures), Murray, Fessler, Kerry, White, and Marin (2015) found that higher levels of historical pathogen prevalence were associated with lower levels of physical contact during culture-specific greeting rituals. For example, within cultures characterized by low pathogen prevalence, individuals are more likely to embrace or kiss their greeting partner; but within cultures characterized by higher levels of pathogen prevalence, individuals are more likely to simply touch shoulders or to bow.

Mechanisms, Monomania, and Other Musings

Underlying Causal Mechanisms

If we are to tentatively accept the growing body of evidence that ecological variation in pathogen prevalence is partly responsible for cross-cultural variation in personality, an important question arises: *How* exactly does this causal process operate? By what mechanism, or mechanisms, does the local prevalence of infectious disease influence cultural personalities? Multiple mechanisms are possible, which are reviewed in turn below.

Cultural transmission processes. Humans have extensive cognitive capacities that allow them to learn beneficial behavior efficiently based upon environmental feedback, to communicate this information effectively to others, and to adopt others' behavioral dispositions based upon its perceived benefits. Cultural transmission processes provide a plausible means through which disease might influence cultural variation in personality. Cultural transmission provides a relatively quick means for adapting to a wide range of ecologies and environmental changes. An explanation based upon wholly cultural processes is also compatible with evidence documenting relatively rapid changes in values (i.e., changes observed over the course of a generation or two) associated with immigrant populations who migrate from ecologies of high disease threat to ecologies with substantially lower disease threat (e.g., Hardyck, Petrinovich, & Goldman, 1976). Humans are also equipped with cognitive tools and biases which are compatible with a cultural transmission explanation, such as perceptual hypervigilance to cues connoting the presence of threat, selective communication about threat, and social learning of avoidant responses to threat (Cook & Mineka, 1990; Öhman, Flykt, & Esteves 2001; Schaller & Conway, 1999). There are also some studies that suggest hypervigilance to disease-connoting cues in particular (e.g., Miller & Maner, 2012).

However, there is no empirical work that directly tests the hypothesis that cultural transmission processes might mediate any of the observed relationships between pathogen prevalence and cultural differences in personality. While logically compelling, the role that cultural transmission processes play in shaping cultural variation requires further direct investigation.

Genetic evolution. Genes that predispose individuals to specific kinds of personality traits may be differentially likely to proliferate within different ecologies. Just as alleles promoting post-weaning production of lactase have been differentially selected for (and consequently have become relatively more common) within populations that domesticate milk-producing animals (Durham, 1991), alleles promoting protective traits (e.g., low extraversion, low openness, restrictive sexuality) may have been differentially selected for within ecologies characterized by higher levels of disease threat.

The plausibility of such a process requires that the pertinent personality variables have some genetic basis. This appears to be the case for the personality traits and other behavioral

dispositions discussed above. Extraversion and openness to experience are moderately heritable (Henderson, 1982; Jang, Livesley, & Vernon, 1996; Loehlin et al., 1998; Riemann, Angleitner, & Strelau, 1997); there is also evidence of genetic influence on dispositional tendencies towards traditionalism, xenophobia, and conformity (Bouchard & McGue, 2003). The plausibility of such a process is also buttressed by evidence of relatively rapid evolution of different gene frequencies within populations inhabiting ecologies that differ in pathogenic threat (Williamson, Hubisz, Clark, Payseur, Bustamante, & Nielson, 2007). Other research suggests that particular genetic polymorphisms that confer greater susceptibility to infectious diseases are also associated with more disease-avoidant personality traits. MacMurray, Comings, and Napolioni (2014) investigated a cytokine-related gene variant which is associated with a higher susceptibility to certain infectious diseases (the A vs T allele of *INFG* +874); they found that individuals with the higher-susceptibility gene variant scored higher on individual difference measures of Harm Avoidance and lower on Big Five Extraversion. A similar study found that participants with the C* allele on the *ACPI* gene—which has been linked to higher susceptibility to certain infectious diseases—were lower in dispositional Big Five Extraversion and Openness (Napolioni, Murray, Comings, Peters, Gade-Andavolu, & MacMurray, 2014).

Only one study provides evidence bearing directly on the possibility that population-level differences in gene frequencies might help to account for the relationships between pathogen prevalence and cultural variation in personality. Chiao and Blizinsky (2010) reported that, across several dozen countries worldwide, the relative frequency of short 5-HTTLPR alleles is positively associated with country-level indices of pathogen prevalence and also positively associated with country-level values of collectivism; even more intriguingly, the relative frequency of 5-HTTLPR alleles partially mediated the relationship between pathogen prevalence and collectivism.

However, genetic evolutionary processes can provide only a partial explanation of the observed phenomena. Genetic evolution certainly cannot account for changes in cultures that often occur over the course of just one or two generations. Further, unlike physiological immunocompetence, which is highly heritable (De Craen et al., 2005), sensitivity to disease cues appears to be only minimally heritable (Rozin & Millman, 1987). A genetic evolution explanation must be considered in conjunction with other plausible explanatory processes (see also Chapter 2, this volume).

Epigenetic processes. Differential environmental inputs lead to selective expression of certain genes. Gene expression is profoundly influenced—typically in functionally adaptive ways—by the ecological circumstances within which an individual organism develops. This context-contingent epigenetic process may result in regional and individual variation in personality traits (Gangestad, Haselton, & Buss, 2006).

The plausibility of an epigenetic explanation rests upon a large body of evidence documenting gene-by-environment interactions in human cognition and behavior (e.g., Cole, 2009). Its plausibility is further supported by an extensive literature in the biological sciences bearing on the evolutionary advantages associated with phenotypic plasticity, and the innumerable ways phenotypic plasticity manifests in the natural world (e.g., Ridley, 2003). Among many mammal species these epigenetic processes begin before birth. Among meadow voles, for example, the placental transfer of melatonin (a chemical signal diagnostic of the length of the day) signals to the fetus which season to “expect”; as a developmental consequence, infants are born with thicker coats as winter approaches (Lee & Zucker, 1988).

Human personality development may be similarly influenced by the placental transfer of chemical signals that are produced maternally when mothers are exposed to ecological threats such as pathogens. These chemical signals include corticosteroids and other hormones associated with stress and immune response. In research with non-human mammals, prenatal exposure to maternal corticosteroids has been linked to dispositional tendencies later in life, including lower levels of sexual aggression, reduced social interaction, and less exploratory behaviors in novel environments (see Edwards & Burnham, 2001, for review). In one particularly notable study, pregnant mice who were exposed to pathogen-infected conspecifics produced higher levels of corticosterone and produced offspring who, as adults, were meeker and less socially aggressive than controls (Curno, Behnke, McElligot, Reader, & Barnard, 2009). Analogously, among humans, pregnant mothers treated with a stress hormone (dexamethasone) gave birth to children who at age five, compared to controls, were relatively shyer and less sociable (Trautman, Meyer-Bahlburg, Postelnek, & New, 1995).

These developmental results neatly parallel the cross-cultural research linking pathogen prevalence to lower extraversion and openness, and more restrictive sexual dispositions, and thus give some credence to an explanation based upon the effects of pathogen prevalence on genetic expression. But this evidence is indirect at best; more compelling tests of this explanation must focus more specifically on human development, and must consider a broader range of personality traits and behaviors that have been linked to ecological threats.

Situational influences on behavior. Discussion of mechanisms influencing cultural variation would not be complete without also considering situational factors that may also contribute to behavior. It is possible, for example, that some of the cultural variation captured in the dozens of surveys reported here is not wholly due to personality variation but to situation-specific behavioral and attitudinal plasticity. Just as animals will forage less when the immediate threat of predation is higher (e.g., Dugatkin & Godin, 1992), so too may humans respond to disease-connoting stimuli in the immediate environment with affective and cognitive responses that facilitate disease-avoidant behavior (Murray & Schaller, in press; Schaller, 2015).

There is a growing body of work suggesting that cues connoting the temporary salience of disease have implications for situational variation in several of the domains discussed above. The salience of infectious diseases also leads to lower self-reported extraversion and to behavioral withdrawal from social stimuli (Mortensen et al., 2010). Other laboratory experiments reveal higher behavioral and attitudinal conformity when the threat of disease is experimentally made salient (Murray & Schaller, 2012; Wu & Chang, 2012). Dispositionally germ-averse individuals report more restrictive sexual attitudes when the threat of disease is made immediately salient (Murray, Jones, & Schaller, 2013). Other research suggests that under conditions in which the threat of infection is either especially high or temporarily salient, people respond by reporting more xenophobic and ethnocentric attitudes toward foreigners (Faulkner et al., 2004; Navarette, Fessler, & Eng, 2007).

However, situational factors cannot solely account for cultural variation in behavior and attitudes for at least a few reasons. First, many of the situational effects of temporary disease salience are interactive—they operate in coordination with relatively stable personality traits. Second, the psychological and behavioral consequences of situational cues appear rapidly; thus, if the cross-cultural differences of pathogen prevalence were due solely to the operation of neurocognitive mechanisms, one would expect contemporary measures of pathogen prevalence to predict cultural outcomes more strongly than historical measures. In fact, the opposite is true. Further, one would expect immigrants to show a virtually instantaneous change in dispositions

and values upon migrating to a novel ecological niche, and this is rarely the case. Situational factors too must be considered in conjunction with other causal mechanisms.

The overall implication is that no single explanatory process is likely to satisfactorily account for the full range of outcomes linking pathogen prevalence to cultural differences. Multiple causal mechanisms—operating at multiple levels of analysis—are required to explain the many documented relations between ecological variation in infectious diseases and cultural variation in personality.

Limited Utility of One-Factor Accounts of Personality Variation

Although the work reviewed above suggests that pathogen prevalence may have important implications for cross-cultural variation in human dispositions, this existing body of research represents just one piece in a much bigger puzzle pertaining to the origins of cultural variation in personality. Although these results highlight the predictive utility of pathogen prevalence, they are mute in regard to the complicated causal relations between pathogen prevalence and other variables that may also contribute to cross-cultural variations.

Many of the analytic models within these investigations sacrifice ecological validity in favor of statistical strategy: Multiple regressions, for example, provide information about the unique effects of independent predictor variables. But real ecologies aren't structured that way. Pathogen prevalence doesn't vary independently of climate or population density, nor is it unaffected by social factors such as wealth. As noted earlier, several other compelling ecological perspectives exist that may account for cross-cultural variation in human psychology and behavior (e.g., Van de Vliert, 2013; see also Chapter 5, this volume). Each of these explanations need not operate at the exclusion of others. In order to provide a more complete and fully coherent understanding of cultural variability, it will be necessary to develop more complex structural models of the interrelationships between plausibly causal ecological variables and their impact on cultural outcomes.

Some of this work is underway: Conceptually, parasite stress and climate-economic theories fit together nicely: Some of the relationships between thermal demands and cultural outcomes may be partially mediated by pathogen prevalence (Murray, 2013). Indeed, Van de Vliert and Murray (under review) found that an integrative model combining the interactive effects of climatic demands, wealth, and human-transmitted pathogen prevalence was by far the best model for accounting for cross-cultural variation in creativity and innovation. Another recent result suggests that patterns of voluntary settlement and pathogen prevalence may work in tandem to predict nonconformist voting in the United States (Varnum, 2012). Still other work suggests that the degree to which cultures are considered “tight” is due to the multilevel influence of many interrelated factors, such as ecological threats, population density, resource availability, and territorial conflict (Gelfand et al., 2011; see also Chapter 8, this volume). Such integrative models will eventually provide more complete and realistic accounts of the causal chains underlying personality variation across cultures.

Envoi

Just as our physiology has been shaped by our billion-year relationship with pathogens, so has our personality. This relationship appears to account for at least some of the cross-cultural differences in personality we see today. This also raises the possibility that significant changes in pathogen prevalence incurred by worldwide health initiatives may actually have implications for personality profiles around the globe—in effect, by changing our ecology we may be changing who we are as well.

References

- Adorno, T., Frenkel-Brunswick, E., Levinson, D., & Sanford, R. (1950). *The authoritarian personality*. New York, NY: Harper & Row.
- Altemeyer, B. (1996). *The authoritarian specter*. Cambridge MA: Harvard University Press.
- Behringer, D. C., Butler, M. J., & Shields, J. D. (2006). Avoidance of disease by social lobsters. *Nature*, *441*, 421. doi:10.1038/441421
- Barry, H., Josephson, L., Lauer, E., & Marshall, C. (1976). Traits inculcated in childhood: Cross-cultural codes 5. *Ethnology*, 83-106.
- Berry, D. S., & Miller, K. M. (2001). When boy meets girl: Attractiveness and the Five-Factor Model in opposite-sex interactions. *Journal of Research in Personality*, *35*, 62-77.
- Bouchard Jr, T. J. & McGue, M. (2003). Genetic and environmental influences on human psychological differences. *Journal of Neurobiology*, *54*, 4-45.
- Cashdan, E. (2014). Biogeography of Human Infectious Diseases: A Global Historical Analysis. *PLoS ONE*, *9*, e106752.
- Cashdan, E., & Steele, M. (2013). Pathogen prevalence, group bias, and collectivism in the Standard Cross-Cultural Sample. *Human Nature*, *24*, 59-75.
- Cashdan, E., Steele, M., & Murray, D. New Pathogen Codes for the Standard Cross-Cultural Sample. *PLoS ONE*, *9*. doi:10.1371/journal.pone.0106752.s001
- Chiao, J. Y., & Blizinsky, K. D. (2010). Culture-gene coevolution of individualism-collectivism and the serotonin transporter gene. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 529-537.
- Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology: Animal Behavior Processes*, *16*, 372-389.
- Curno, O., Behnke, J. M., McElligott, A. G., Reader, T., & Barnard, C. J. (2009). Mothers produce less aggressive sons with altered immunity when there is a threat of disease during pregnancy. *Proceedings of the Royal Society B*, *276*, 1047-1054.
- Dantzer, R. Kent, S., Bluthe, R. M., & Kelley, K. W. (1991). Cytokines and sickness behaviour. *European Neuropsychopharmacology*, *1*, 377-379.
- De Craen, A. J. M., Posthuma, D., Remarque, E. J., Van Den Biggelaar, A. H. J., Westendorp, R. G. J., & Boomsma, D. I. (2005). Heritability estimates of innate immunity: An extended twin study. *Genes and Immunity*, *6*, 167-170.
- Dugatkin, L. A., & Godin, J. G. J. (1992). Predator inspection, shoaling and foraging under predation hazard in the Trinidadian guppy, *Poecilia reticulata*. *Environmental Biology of Fishes*, *34*, 265-276.
- Durham, W. H. (1991). *Coevolution: Genes, culture and human diversity*. Stanford CA: Stanford University Press.
- Edwards, H. E., & Burnham, M. (2001). The developing nervous system: A series of review articles. *Pediatric Research*, *50*, 433-440.
- Fanning, L. J., Connor, A. M., & Wu, G. E. (1996). Development of the immunoglobulin repertoire. *Clinical Immunology and Immunopathology*, *79*, 1-14.
- Feener, D. H., & Brown, B. V. (1997). Diptera as parasitoids. *Annual Review of Entomology*, *42*, 73-97.

- Fincher, C. L., & Thornhill, R. (2008). Assortative sociality, limited dispersal, infectious disease and the genesis of the global pattern of religious diversity. *Proceedings of the Royal Society B*, 275, 2587-2594.
- Fincher, C. L., & Thornhill, R. (2012). Parasite-stress promotes in-group assortative sociality: The cases of strong family ties and heightened religiosity. *Behavioral and Brain Sciences*, 35, 61-79.
- 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*, 275, 1279-1285.
- Freeland, W. J. (1976). Pathogens and the evolution of primate sociality. *Biotropica*, 8, 12-24.
- Fumagalli, M., Sironi, M., Pozzoli, U., Ferrer-Admetlla, A., Pattini, L., & Nielsen, R. (2011). Signatures of environmental genetic adaptation pinpoint pathogens as the main selective pressure through human evolution. *PLoS Genetics*, 7, e1002355.
- 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., Raver, J. L., Nishii, L., Leslie, L. M., Lun, J., Lim, B. C., ... & Yamaguchi, S. (2011). Differences between tight and loose cultures: A 33-nation study. *Science*, 332, 1100-1104.
- Guernier, V., Hochberg, & Guégan, J.-F. (2004). Ecology drives the worldwide distribution of human diseases. *PloS Biology*, 2, 740-746.
- Haidt, J. (2012). *The righteous mind: Why good people are divided by politics and religion*. USA: Pantheon.
- 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.
- Hardyck, C., Petrinovich, L., and Goldman, R. (1976). Left handedness and cognitive deficit. *Cortex*, 12, 266-278.
- Henderson, N. D. (1982). Human behavioral genetics. *Annual Review of Psychology*, 33, 403-440.
- Herbig, P., & Dunphy, S. (1998). Culture and innovation. *Cross Cultural Management: An International Journal*, 5, 13-21.
- Higgins, E. T. (2000). Does personality provide unique explanations for behaviour? Personality as cross-person variability in general principles. *European Journal of Personality*, 14, 391-406.
- Inhorn, M. C., & Brown, P. J. (1990). The anthropology of infectious disease. *Annual Review of Anthropology*, 19, 89-117.
- Jang, K. L., Livesley, W. J., & Vernon, 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 perspectives. In L. A. Pervin & O. P. John (Eds.), *Handbook of personality: Theory and research* (2nd ed., pp. 102-138). New York: Guilford.
- Kiesecker, J. M., Skelly, D. K., Beard, K. H., & Preisser, E. (1999). Behavioral reduction of infection risk. *Proceedings of the National Academy of Sciences*, 96, 9165-9168.

- Kool, V.K., & Ray, J.J. (1983). *Authoritarianism across cultures*. Bombay: Himalaya Publishing House.
- Larsen, R. J., & Buss, D. M. (2014). *Personality psychology (5th Ed.)*. New York, NY: McGraw-Hill.
- Lee, T. M., & Zucker, I. (1988). Vole infant development is influenced perinatally by maternal photoperiodic history. *American Journal of Physiology*, *255*, 831-838.
- Letendre, K., Fincher, C. L., & Thornhill, R. (2010). Does infectious disease cause global variation in the frequency of intrastate armed conflict and civil war? *Biological Reviews*, *85*, 669-683.
- Loehlin, J. C., McCrae, R. R., Costa, P. T. Jr., & John, O. P. (1998). Heritabilities of common and measure-specific components of the big five personality factors. *Journal of Research in Personality*, *32*, 431-453.
- Low, B. S. (1990). Marriage systems and pathogen threat in human societies. *American Zoologist*, *30*, 325-339.
- Lv, J., Qi, L., Yu, C., Yang, L., Guo, Y., Chen, Y., ... & Li, L. (2015). Consumption of spicy foods and total and cause specific mortality: Population based cohort study. *BMJ*, *351*, h3942. doi: <http://dx.doi.org/10.1136/bmj.h3942>
- MacMurray, J., Comings, D. E., & Napolioni, V. (2014). The gene-immune-behavioral pathway: Gamma-interferon (IFN- γ) simultaneously coordinates susceptibility to infectious disease and harm avoidance behaviors. *Brain, Behavior, and Immunity*, *35*, 169-175.
- Magurran, A. E. (1999). The causes and consequences of geographic variation in antipredator behavior: Perspectives from fish populations. In S. A. Foster & J. A. Endler (eds.), *Geographic variation in behavior: Perspectives on evolutionary mechanisms* (pp. 139-163). New York: Oxford University Press.
- 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., & Costa Jr, P. T. (1997). Personality trait structure as a human universal. *American Psychologist*, *52*, 509-516.
- McCrae, R. R., & Terracciano, A. (2008). The five-factor model and its correlates in individuals and cultures. In F. J. R. van de Vijver, D. A. van Hemert, & Y. Poortinga (Eds.), *Individuals and cultures in multi-level analysis* (pp. 247-281). Mahwah, NJ: Erlbaum.
- McCrae, R. R., Terracciano, A., & 79 members of the Personality Profiles of Cultures Project. (2005). Personality profiles of cultures: Aggregate personality traits. *Journal of Personality and Social Psychology*, *89*, 407-425.
- Meloan, J. (1996). Authoritarianism, democracy, and education: A preliminary empirical 70-nation global indicators study. In R. F. Farnen, H. Dekker, R. Meyenberg, & D. B. German (eds.), *Democracy, socialization and conflicting loyalties in East and West* (pp. 20-38). UK: St. Martin's Press.
- Michel, J. F. (1955). Parasitological significance of bovine grazing behaviour. *Nature*, *175*, 1088-1089.
- Miller, E. N., Fadl, M., Mohamed, H. S., Elzein, A., Jamieson, S. E., ... & Blackwell, J. M. (2007). Y chromosome lineage- and village-specific genes on chromosomes 1p22 and 6q27 control visceral leishmaniasis in Sudan. *PLoS Genetics*, *3*, 679-88.
- Miller, S. L., & Maner, J. K. (2012). Overperceiving disease cues: The basic cognition of the behavioral immune system. *Journal of Personality and Social Psychology*, *102*, 1198-1213.

- Mischel, W. (1968). *Personality and assessment*. New York: Wiley.
- Mischel, W., Shoda, Y., Smith, R. E., & Mischel, F. W. (2004). *Introduction to personality*. University of Phoenix: John Wiley & Sons.
- Mortensen, C. R., Becker, D. V., Ackerman, J. M., Neuberg, S. L., & Kenrick, D. T. (2010). Infection breeds reticence: The effects of disease salience on self-perceptions of personality and behavioral tendencies. *Psychological Science, 21*, 440-447.
- Murdock, G. P., & White, D. R. (1969). Standard cross-cultural sample. *Ethnology, 8*, 329-369.
- Murray, D. R. (2013). Adaptations to the differential threats posed by hot versus cold climates. *Behavioral and Brain Sciences, 36*, 33-34.
- Murray, D. R. (2014b). Direct and indirect implications of disease threat for scientific and technological innovation. *Journal of Cross-Cultural Psychology, 45*, 971-985.
- Murray, D. R., Fessler, D. M. T., Kerry, N., White, C., & Marin, T. (2015). Does pathogen prevalence predict less physical interpersonal contact in small scale societies? Manuscript in preparation.
- Murray, D. R., Jones, D. N., & Schaller, M. (2013). Perceived threat of infectious disease and its implications for sexual attitudes. *Personality and Individual Differences, 54*, 103-108.
- Murray, D. R., & Schaller, M. (2010). Historical prevalence of disease within 230 geopolitical regions: A tool for investigating origins of culture. *Journal of Cross-Cultural Psychology, 41*, 99-108.
- Murray, D. R., & Schaller, M. (2012). Threat(s) and conformity deconstructed: Perceived threat of infectious disease and its implications for conformist attitudes and behavior. *European Journal of Social Psychology, 42*, 180-188.
- Murray, D. R., & Schaller, M. (in press). The behavioral immune system: Implications for social cognition, social interaction, and social influence. *Advances in Experimental Social Psychology*.
- Murray, D. R., Schaller, M., & Suedfeld, P. (2013). Pathogens and politics: Further evidence that parasite prevalence predicts authoritarianism. *PLoS ONE, 8*, e62275.
- Murray, D. R., Trudeau, R., & Schaller, M. (2011). On the origins of cultural differences in conformity: Four tests of the pathogen prevalence hypothesis. *Personality and Social Psychology Bulletin, 37*, 318-329.
- Napolioni, V., Murray, D. R., Comings, D. E., Peters, W. R., Gade-Andavolu, R., & MacMurray, J. (2014). ACP1*C allele and the gene-immune-behavioral pathway: At the crossroads of extraversion, past-malarial morbidity and fertility. *Infection, Genetics, and Evolution, 26*, 267-273.
- 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.
- Nesse, R., & Williams, G. (1995). *Why we get sick: The new science of Darwinian medicine*. USA: Vintage books.
- Nettle, D. (2005). An evolutionary approach to the extraversion continuum. *Evolution and Human Behavior, 26*, 363-373.
- Nettle, D. (2009). Ecological influences on human behavioural diversity: A review of recent findings. *Trends in Ecology & Evolution, 24*, 618-624.
- Nisbett, R. E., Peng, K., Choi, I., & Norenzayan, A. (2001). Culture and systems of thought:

- Holistic versus analytic cognition. *Psychological Review*, 108, 291-310.
- O'Dea, K. (1991). Traditional diet and food preferences Of Australian aboriginal hunter-gatherers. *Philosophical Transactions of the Royal Society of London B*, 334, 233-241.
- Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General*, 130, 466–478.
- Pollet, T. V., Tybur, J. M., Frankenhuys, W. E., & Rickard, I. J. (2014). What can cross-cultural correlations teach us about human nature? *Human Nature*, 25, 410-429.
- Ridley, M. (2003). *The agile gene*. New York: HarperCollins.
- Riemann, R., Angleitner, A., & Strelau, J. (1997). Genetic and environmental influences on personality: A study of twins reared together using the self- and peer report NEO-FFI scales. *Journal of Personality*, 65, 449–475.
- Rodenwaldt, E., & Bader, R. E. (1952-1961). *World-atlas of infectious diseases*. Hamburg, Germany: Falk-Verlag.
- Rozin, P., & Millman, L. (1987). Family environment, not heredity, accounts for family resemblances in food preferences and attitudes: A twin study. *Appetite*, 8, 125-134.
- Schaller, M. (2016). The behavioral immune system. In D. M. Buss (Ed.), *Handbook of evolutionary psychology, 2nd Edition* (pp. 206-224). New York: Wiley.
- Schaller, M., & Conway, L. G., III (1999). Influence of impression-management goals on the emerging contents of group stereotypes: Support for a social-evolutionary process. *Personality and Social Psychology Bulletin*, 25, 819-833.
- 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*, 93, 212-221.
- Schaller, M., & Murray, D. R. (2010). Infectious diseases and the evolution of cross-cultural differences. In M. Schaller, A. Norenzayan, S. J. Heine, T. Yamagishi, & T. Kameda (Eds.), *Evolution, culture, and the human mind* (pp. 243-256). New York: Psychology Press.
- Schaller, M., & Murray, D. R. (2011). Infectious disease and the creation of culture. In M. Gelfand, C.-y. Chiu, & Y.-y. Hong (Eds.), *Advances in culture and psychology* (Vol. 1, pp. 99–151). New York, NY: Oxford University Press.
- 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.
- Schwartz, S. H. (2004). Mapping and interpreting cultural differences around the world. In H. Vinken, J. Soeters, & P. Ester (Eds.), *Comparing cultures: Dimensions of culture in a comparative perspective* (pp. 43 – 73). Leiden, The Netherlands: Brill.
- Segall, M. H., Campbell, D. T., & Herskovits, M. J. (1966). *The influence of culture on visual perception*. Indianapolis: Bobbs-Merrill.
- Sherman, P. W., & Billing, J. (1999). Darwinian gastronomy: Why we use spices. *Bioscience*, 49, 453-463.
- Silverthorne, C. (2001). Leadership effectiveness and personality: A cross cultural evaluation. *Personality and Individual Differences*, 30, 303-309.
- Simmons, J. S., Wayne, T. F., Anderson, G. W., & Horack, H. M. (1944). *Global epidemiology*. Philadelphia: J. B. Lippincott.
- Stefansson, V. (2004). *My life with the Eskimo*. USA: Kessinger Publishing.

- Talhelm, T., Zhang, X., Oishi, S., Shimin, C., Duan, D., Lan, X., & Kitayama, S. (2014). Large-scale psychological differences within China explained by rice versus wheat agriculture. *Science*, *344*, 603-608.
- Tetro, J. (2013). *The germ code: How to stop worrying and love the microbes*. Canada: Doubleday.
- Thornhill, R., Fincher, C. L. & Aran, D. (2009). Parasites, democratization, and the liberalization of values across contemporary countries. *Biological Reviews*, *84*, 113–131.
- Thornhill, R., Fincher, C. L., Murray, D. M., & Schaller, M. (2010). Zoonotic and non-zoonotic diseases in relation to human personality and societal values: Support for the parasite-stress model. *Evolutionary Psychology*, *8*, 151-169.
- Trautman, P. D., Meyer-Bahlburg, H. F. L., Postelnek, J., & New, M. I. (1995). Effects of early prenatal dexamethasone on the cognitive and behavioral development of young children: Results of a pilot study. *Psychoneuroendocrinology*, *20*, 439-449.
- Uskul, A. K., Kitayama, S., & Nisbett, R. E. (2008). Ecocultural basis of cognition: Farmers and fishermen are more holistic than herders. *Proceedings of the National Academy of Sciences*, *105*, 8552-8556.
- van Leeuwen, F., Park, J. H., Koenig, B. L., & Graham, J. (2012). Regional variation in pathogen prevalence predicts endorsement of group-focused moral concerns. *Evolution and Human Behavior*, *33*, 429-437.
- Van de Vliert, E. (2013). Climato-economic habitats support patterns of human needs, stresses, and freedoms. *Behavioral and Brain Sciences*, *36*, 465-480.
- Van de Vliert, E., & Murray, D. R. (under review). Climate and creativity: Cold and heat trigger invention and innovation in richer populations.
- Varnum, M. E. W. (2012). Frontiers, germs, and nonconformist voting. *Journal of Cross-Cultural Psychology*. doi:10.1177/0022022112466591
- 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*, e90. doi:10.1371/journal.pgen.0030090
- Wu, B. P., & Chang, L. (2012). The social impact of pathogen threat: How disease salience influences conformity. *Personality and Individual Differences*, *53*, 50-54.
- Zimmer, C. (2001). *Parasite rex: Inside the bizarre world of nature's most dangerous creatures*. USA: Simon and Schuster.
- Zuckerman, M., Kuhlman, D. M., Joireman, J., Teta, P., & Kraft, M. (1993). A comparison of the structural models for personality: The Big Three, the Big Five, and the Alternative Five. *Journal of Personality and Social Psychology*, *65*, 757-768.

Acknowledgement

This work was supported by grants from the Social Sciences and Humanities Research Council of Canada.