3

PATHOGEN PREVALENCE AND GEOGRAPHICAL VARIATION IN TRAITS AND BEHAVIOR

DAMIAN R. MURRAY AND MARK SCHALLER

Extensive geographical variation exists in personality traits, value systems, and human behavior. For example, people in Bulgaria report higher levels of Extraversion than people in Botswana (McCrae & Terracciano, 2005), and people in France tend to conform more in laboratory studies than do people in Finland (Bond & Smith, 1996). Why does this geographical variation exist? Might specific features of a local geography foster specific behavioral patterns and personality profiles? Here, we summarize and discuss a growing body of evidence demonstrating that geographical variation in behavior, personality, and values is due, at least in part, to regional variation in the prevalence of infectious diseases (or, as we term it here, *pathogen prevalence*).

Investigating the antecedents of geographical differences in human psychology is an enormous enterprise. These antecedent variables do not operate exclusively and, in addition, can change over time as a result of natural

http://dx.doi.org/10.1037/14272-004
Geographical Psychology: Exploring the Interaction of Environment and Behavior, P. J. Rentfrow (Editor)

circumstances and human intervention. This chapter, therefore, is offered as an introduction to this topic and to some of the broad implications of pathogen prevalence.

PATHOGENS AND PSYCHOLOGY

Disease-causing pathogens have posed a substantial threat to survival and reproduction throughout human history. In fact, infectious diseases have likely accounted for more deaths than all wars, noninfectious diseases, and natural disasters combined (Inhorn & Brown, 1990). Infectious diseases have thus imposed immense selective pressure on human physiology and behavior (e.g., Ridley, 1993). Not surprisingly, humans have evolved elaborate defenses that serve to mitigate the harmful effects of pathogens. One such defense involves the suite of complex physiological mechanisms that compose the immune system, which identifies disease-causing organisms within the body and responds with a set of biochemical and cellular defenses designed to eliminate the parasitic threat. These physiological immune responses are adaptive, but they are costly as well. For example, an inflammatory response produces fever that helps to kill bacterial infections, but to raise body temperature by just 1°C (a very modest fever) requires as much as a 13% increase in metabolic activity (Dantzer, Kent, Bluthe, & Kelley, 1991). Along with these metabolic costs, immunological responses can also invoke behavioral responses (e.g., lethargy) that are temporarily debilitating and that prevent one from performing other adaptive activities such as acquiring resources or caring for kin (Klein & Nelson, 1999). Thus, although activation of the immune system is beneficial when it becomes absolutely necessary, it is even more beneficial to engage this system as infrequently as possible.

For this reason, immunological defenses against pathogens are complemented by behavioral responses that serve to minimize contact with infectious agents in the first place. Evidence of such behavioral defenses against pathogens is rife across the animal kingdom: Chimpanzees react with unusual violence to ingroup members infected with polio (Goodall, 1986), rodents avoid mating with other rodents who produce olfactory cues connoting disease (Kavaliers & Colwell, 1995), and bullfrog tadpoles avoid swimming in the vicinity of other infected tadpoles (Kiesecker, Skelly, Beard, & Preisser, 1999).

Humans too are equipped with a suite of psychological mechanisms that promote behavioral defense against pathogens—a sort of *behavioral immune system* (Schaller, 2011; Schaller & Park, 2011). Broadly, these mechanisms are designed to detect potential pathogen cues within the immediate

environment and trigger specific affective and cognitive responses that promote specific kinds of behavioral reactions that, in turn, reduce the likelihood of pathogen transmission. Much evidence now implicates these mechanisms across a gamut of human psychological phenomena, including implications for attention (Ackerman et al., 2009), emotion (Oaten, Stevenson, & Case, 2009), prejudice and person perception (e.g., Faulkner, Schaller, Park, & Duncan, 2004; Park, Schaller, & Crandall, 2007), conformity (Murray & Schaller, 2012), and interpersonal behavior in general (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010).

PATHOGEN PREVALENCE AND THE EMERGENCE OF GEOGRAPHIC VARIATION IN HUMAN PSYCHOLOGY

Although disease-causing pathogens have posed a serious threat throughout history, the magnitude of this threat varies geographically (see Figure 3.1). Many pathogens thrive in warm, wet conditions; the

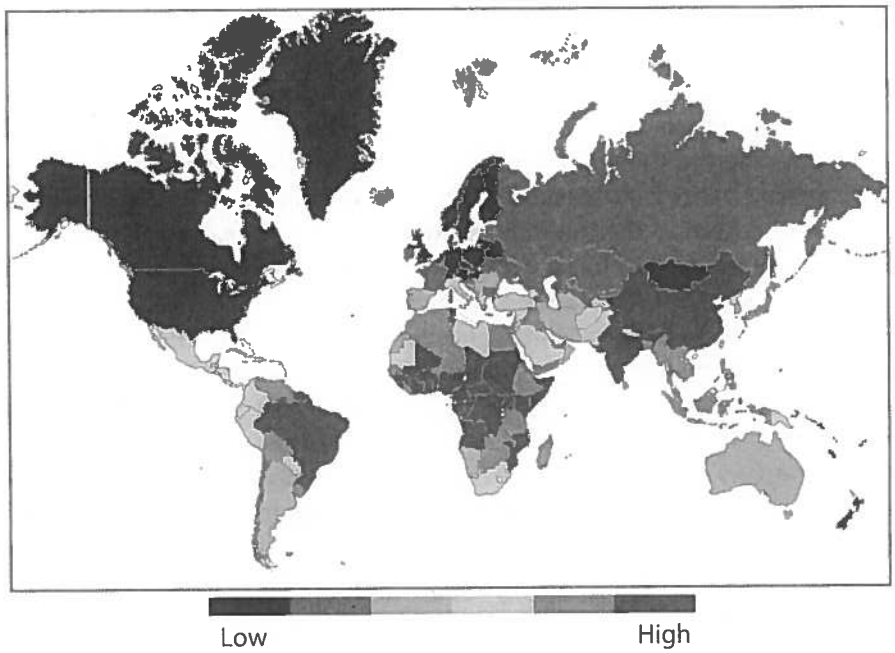

Figure 3.1. Global pathogen prevalence, ~1900 A.D. World map of the historical prevalence of infectious disease (by country).

prevalence and diversity of pathogens are therefore predictable functions of latitude and additional geographical characteristics of a place (Guernier, Hochberg, & Guégan, 2004). The substantial geographical variation that exists in the prevalence of pathogens has obvious implications for regional differences in health outcomes; less obviously, it also predicts regional differences in psychological outcomes.

Exactly why might geographical variation in pathogen prevalence predict variation in psychological outcomes? A cost–benefit framework is useful for addressing this question. The logical analysis proceeds as follows: Any behavioral tendency that inhibits contact with pathogens has the benefit of reducing the likelihood of pathogen-related illness or mortality. However, it may have costs as well. Thus, this behavioral tendency will be functionally adaptive only when its disease-mitigating benefits outweigh its costs. The benefits will be especially high in geographical regions where pathogens are most highly prevalent, and so it is also in these regions that the benefits are more likely to outweigh costs. The logical upshot is that any behavior that serves to reduce the likelihood of pathogen transmission should be most prevalent among populations inhabiting high-disease geographical regions and least prevalent among populations in low-disease regions. Conversely, any behavior that increases exposure to pathogens (but that has unrelated adaptive benefits) should be least prevalent in high-disease regions and most prevalent in low-disease regions.

Geographical variation in mate preferences offers an illustrative example. Although physical attractiveness in a mate is universally valued, regional differences exist in the relative value placed on physical attractiveness relative to other desired traits (Buss, 1989). Interestingly, subjective appraisals of physical attractiveness are influenced by a variety of features—clear skin, bilateral symmetry, morphological typicality—that are associated with health and genetically heritable immunocompetence (Rhodes, 2006; Thornhill & Gangestad, 1999; Weeden & Sabini, 2005). Thus, preferences for physically attractive mates are beneficial insofar as they increase the likelihood of choosing a disease-free mate and the likelihood of producing immunocompetent offspring.

However, a preference for attractive mates is not without some potential costs. Mate preferences often involve trade-offs; by placing a relatively higher priority on physical attractiveness, people may place relatively lower value on other beneficial traits, such as wealth or intelligence (Gangestad & Simpson, 2000). It follows that individuals may be most likely to place a high value on physical attractiveness under conditions in which the benefits associated with physical attractiveness are most pronounced, such as when there is greater threat posed by infectious diseases. Consistent with this logic is experimental evidence showing that when the threat of disease is made

temporarily salient, people show an exaggerated tendency to judge symmetrical faces to be more highly attractive (Little, DeBruine, & Jones, 2011). A conceptually similar effect emerges when comparing different geographical regions: In an analysis of data on mate preferences collected from 29 countries worldwide, the historical prevalence of disease-causing pathogens within a country positively predicted the value that people within that country placed on the physical attractiveness of a mate (Gangestad & Buss, 1993; see also Gangestad, Haselton, & Buss, 2006). This effect occurred for both men and women and was robust when controlling for other socioeconomic variables.

This example illustrates a conceptual cost–benefit analysis that has been applied to deduce many additional hypotheses linking pathogen prevalence to geographic variation in psychological phenomena. Before proceeding to summarize these hypotheses and the evidence that supports them, it is useful to identify some of the thorny methodological and inferential issues inherent in these types of investigations.

One obvious inferential problem stems from the fact that empirical studies of this sort are necessarily correlational. Researchers studying the relation between ecological variation in pathogen prevalence and geographic variation in psychological outcomes do not have the luxury of experimental control or random assignment. Thus, although a nonzero relationship between pathogen prevalence and a psychological trait may be consistent with a causal hypothesis, this relationship alone cannot provide convincing evidence that varying pathogen prevalence truly caused geographical variation in the trait.

Several strategies can be used to help address the various alternative causal explanations that might be offered to account for predicted correlations. First, other variables that might create spurious correlations (because they are themselves related both to pathogen prevalence and to the outcome variable) can be measured and statistically controlled for. In their research linking pathogen prevalence to mate preferences, for example, Gangestad and Buss (1993) controlled for a variety of such "third variables." Conclusions about the causal influence of pathogen prevalence require that pathogen prevalence remains a unique predictor of outcome variables when controlling for plausible third variables. Second, in order to logically infer that pathogen prevalence actually caused geographical variation in psychological phenomena (rather than vice versa), it is useful to use a measure of pathogen prevalence that temporally precedes the outcome measures of interest.

In our own research, we have employed methods modeled after those described by Gangestad and Buss (1993), who used old epidemiological atlases to estimate country-level prevalence of seven kinds of pathogens across 29 countries. We expanded on this strategy and computed an index on the basis of the historical prevalence of nine different kinds of pathogens

(trypanosomes, schistosomes, leishmanias, typhus, dengue, malaria, tuberculosis, filariae, and leprosy), mostly from data aggregated near the end of the 19th century. These pathogens are characterized by an acute stage of infection, with the possibility of either death, long-term debilitation, or recurrence of acute episodes. This index represents only a small subset of debilitating infectious pathogens; however, it serves as a useful and diagnostic indicator of relative geographical differences in the historical prevalence of disease-causing pathogens (for a detailed discussion of computation and validity of this index, see Murray & Schaller, 2010). This index is available for over 160 geopolitical regions worldwide. It can be especially informative to compare the predictive strength of this measure of historical pathogen prevalence with the predictive strength of indices that assess contemporary pathogen prevalence. If pathogen prevalence is a consequence rather than a cause of the psychological outcome variable, then the outcome variable should be more strongly related to contemporary rather than historical pathogen prevalence. If instead historical prevalence more strongly predicts the outcome variable, the reverse causal explanation is less plausible.

Another inferential issue arises from the fact that many contemporary geographical comparisons of psychological outcomes use countries as units of analysis. Countries cannot be assumed to be statistically independent (ideas, cultural norms, and people flow freely across geopolitical boundaries), and this has important implications for statistical inference based on country-level analyses (Nettle, 2009). Therefore, it can be useful to supplement comparisons between countries with additional comparisons between world regions that, historically, have been more culturally distinct (e.g., Africa, Eastern Eurasia). When individual-level data are available from individuals within countries, multilevel modeling approaches may also be especially informative (e.g., Van Leeuwen, Park, Koenig, & Graham, 2012).

These inferential issues are worth keeping in mind as we summarize results from recent studies identifying a variety of links between pathogen prevalence and geographical differences in human personality, values, and behavioral tendencies.

Sociosexual Attitudes

We begin with an investigation of geographical differences in dispositional tendencies toward restricted versus unrestricted sexual behavior (Schaller & Murray, 2008). Sexual behavior provides much opportunity for disease transmission. This risk exists both for infections spread exclusively through sexual contact and infections spread through nonsexual contact. The implication is simple: The more "unrestricted" (e.g., sexually promiscuous) individuals are, the more they put themselves at risk of contracting diseases

and spreading these diseases to others. However, unrestricted sexual attitudes 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 on the prevalence of disease-causing pathogens. Where pathogen prevalence is higher, the costs of unrestricted sociosexuality 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 sociosexually restricted attitudes.

To test this hypothesis, we employed the results of a cross-national study (Schmitt, 2005) that assessed responses on a Sociosexual Orientation Inventory (SOI; Simpson & Gangestad, 1991) from over 14,000 people in 48 different countries and reported mean male and female SOI scores for each country. High SOI scores indicate unrestricted sexual attitudes and behavior, whereas low SOI scores indicate more restricted attitudes and behavior. The hypothesis predicts a negative relationship between these SOI scores and historical pathogen prevalence, and that is what we found: In places with a higher level of historical pathogen prevalence, both men and women reported more restricted attitudes toward sexual relations (*r*'s for men and women were –.27 and –.62, respectively; Schaller & Murray, 2008).

This effect is stronger for female SOI 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.

Additional analyses revealed that historical pathogen prevalence predicted these sociosexuality measures better than did a contemporary (and much more precise) measure of pathogen prevalence. Plus, the effect (among women only) persisted even when controlling for a variety of plausible third variables. These results are consistent with the hypothesized causal relationship and are inconsistent with alternative causal explanations.

Extraversion and Openness

An individual's proclivity to engage in restricted versus unrestricted sexual behavior is a type of personality trait. However, it is a very specific trait. Might pathogen prevalence predict variation in more fundamental

personality traits as well? Several research projects have gathered data on the Big Five personality traits (Extraversion, Openness, Agreeableness, Conscientiousness, and Neuroticism) from tens of thousands of individuals from dozens of countries worldwide. These studies produced country-level scores on each of the five fundamental dimensions of personality and have revealed cross-national differences in each of the five traits. These scores provide a useful tool for investigating geographic variation in two of these fundamental personality traits—Extraversion and Openness—that, on the basis of cost–benefit analyses, can be predicted to vary in response to pathogen prevalence.

Extraversion

The logic that underlies a potential link between pathogen prevalence and Extraversion is similar to its relationship with sociosexuality. Although being sexually unrestricted is associated with a higher variety and frequency of intimate interpersonal contact, Extraversion too is associated with a higher variety and frequency of (nonintimate) contact with others. These social contacts have the potential to expose individuals to interpersonally transmitted pathogens. (In fact, empirical evidence does suggest that dispositional Extraversion is associated with enhanced risk of disease transmission; Nettle, 2005.) However, Extraversion is also associated with many benefits. More highly extraverted individuals report higher levels of happiness, are more effective leaders, and enjoy more opportunities for sexual reproduction (Berry & Miller, 2001; Silverthorne, 2001). These benefits of Extraversion are more likely to outweigh the disease-related costs under ecological conditions in which these costs are relatively minimal—in places characterized by low levels of interpersonally transmitted pathogens. Conversely, in areas characterized by high pathogen prevalence, the disease-related costs of Extraversion may outweigh its benefits. This cost–benefit analysis suggests that regional variation in pathogen prevalence should be inversely related to population-level variation in Extraversion.

We (Schaller & Murray, 2008) conducted multiple tests of this hypothesis using results from three different cross-national surveys of the Big Five personality traits (McCrae, 2002; McCrae & Terracciano, 2005; Schmitt, Allik, McCrae, & Benet-Martinez, 2007). As predicted, across every measure regional differences in Extraversion were negatively correlated with historical pathogen prevalence. These relationships remained even when controlling for a variety of additional country-level variables (e.g., GDP, individualistic vs. collectivistic values). Further, consistent with the causal relation specified by the hypothesis, Extraversion was more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence. Finally (and consistent with our analysis of the specific kinds of costs associated with

Extraversion), a follow-up investigation revealed that geographic variation in Extraversion is especially highly predicted by the prevalence of a specific subset of pathogens—those that are transmitted through human interaction (Thornhill, Fincher, Murray, & Schaller, 2010).

Openness

A similar cost–benefit analysis also suggested that regional variation in pathogen prevalence may help account for geographic differences in Openness to Experience. Dispositional Openness is characterized by creativity, attraction to novelty, and a willingness to try new and unfamiliar things (Larsen & Buss, 2005). These behavioral dispositions can be beneficial in that they encourage innovation and adaptive problem solving. These dispositions can also be costly: Many traditional ways of doing things (particularly in domains such as food preparation, personal hygiene, and public health) serve as buffers against pathogen transmission. (In fact, in many technologically "primitive" small-scale societies of the sort traditionally studied by ethnographers, the majority of social norms may operate as prescriptions to avoid illness in some way [Fabrega, 1997].) To the extent that individuals deviate from these accustomed norms (e.g., experiment with novel or idiosyncratic approaches to hygiene or food preparation), those individuals expose themselves and others in their community to an increased risk of pathogen infection. These particular kinds of costs are greater (and more likely to outweigh benefits associated with Openness) under conditions of greater pathogen prevalence. Thus, regional variation in pathogen prevalence is expected to be inversely related to population-level variation in Openness to Experience.

We conducted multiple tests of this hypothesis using exactly the same source materials as we used in our investigations of Extraversion (Schaller & Murray, 2008). 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 additional country-level variables. Again, consistent with the causal hypothesis, Openness to Experience was more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence.

We also performed analyses on the three remaining fundamental personality traits (Agreeableness, Conscientiousness, and Neuroticism). Across measures, results revealed no appreciable or consistent relationships between pathogen prevalence and these personality traits. These results, when taken in concert with the consistent significant relationships obtained for Extraversion and Openness, suggest that the significant results for Extraversion and Openness were not due to response biases or other methodological artifacts that often pose issues for cross-national investigations, and increase confidence in a conclusion that the results obtained reflect truly meaningful causal

relationships. It is also worth noting that convergent significant results for both Openness and Extraversion (as well as negligible results for the remaining variables) have been documented using world regions as the units of analysis (e.g. Schaller & Murray, 2012).

Individualism and Collectivism

Adaptive logic suggests that the influence of pathogen prevalence should have implications for cultural value systems as well. Although there are many forms of cultural values, the value constructs of individualism and collectivism have been subjected to more rigorous scientific inquiry than any other (Heine, 2008). At least three characteristics of individualism/collectivism suggest that geographic variation along this dimension may have been causally influenced by pathogen prevalence.

First, collectivistic (compared with individualistic) value systems imply a more rigid psychological distinction between ingroup and outgroup (Gelfand, Nishii, & Raver, 2006), which manifests in higher levels of ethnocentrism and xenophobia. Higher levels of xenophobia have costs, including reduced opportunities for trade and coalitional alliances. But xenophobia may also have disease-relevant benefits. Outgroup members are more likely to harbor exotic pathogens, 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 xenophobia are likely to be greater in regions of higher pathogen prevalence.

Second, collectivist cultural values are characterized by a higher expectation of prosocial behavior among family members and other individuals within a local social alliance. There are costs associated with the obligatory expenditure of resources. Reciprocal benefits of this obligatory prosociality accrue whenever one (or one's immediate kin) is in need of assistance from others. These benefits are likely to be especially pronounced under conditions characterized by high levels of threat to health and welfare. Thus, because of the emphasis on obligatory prosociality among group members, collectivistic value systems are likely to be relatively more advantageous under conditions of greater pathogen prevalence.

A third relevant feature of collectivistic value systems is *tightness*: A strong premium is placed on conforming to ingroup norms, and a lack of tolerance exists for individuals who deviate from those norms (Gelfand et al., 2006). Individualistic value systems, however, place a premium on individual rights and are more tolerant of deviance. Thus, the cost–benefit implications are similar to those discussed for Openness to Experience: Although there are costs associated with vigilant adherence to established norms (e.g., decreased

innovation), the pathogen-mitigating characteristics of many of these norms makes adherence beneficial too. These benefits are more likely to outweigh the costs in geographical regions of high disease prevalence.

Overall, these multiple distinct lines of deduction converge on a hypothesis linking pathogen prevalence to geographic variation in individualistic versus collectivistic values: Pathogen prevalence should negatively predict measures of individualism and positively predict indicators of collectivism.

We conducted four tests of this hypothesis using two different country-level measures of individualism and two country-level measures of collectivism (Fincher, Thornhill, Murray, & Schaller, 2008). The results were clear across all four sets of analyses: Consistent with the hypothesis, geographical variation in historical pathogen prevalence was significantly negatively correlated with individualism (r's = –.69 and –.71) and significantly positively correlated with collectivism (r's = .73 and .63, all p's < .001). These results were further corroborated using world regions as the units of analysis (in fact, correlations tended to be even stronger when using these larger units of analysis). Additional analyses revealed that the predictive effect of pathogen prevalence remained even when controlling for a variety of additional variables that might plausibly have a causal influence on individualistic/collectivistic value systems (e.g., GDP, inequality, other threats to health and morality). Consistent with the causal relation specified by the hypothesis, individualism/collectivism was more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence. Similar sets of analyses have since been performed using American states as the unit of analysis (Fincher & Thornhill, 2012) and have produced inferentially identical results.

These results provide compelling evidence for a causal relationship between pathogen prevalence and cultural value systems. Individualism and collectivism are, however, multifaceted constructs, comprising several conceptually distinct kinds of values (pertaining to intergroup relations, family dynamics, conformity to norms, etc.). Evidence bearing on this broad construct does not speak to whether pathogen prevalence specifically relates to geographic variation in xenophobia, obligatory prosociality, conformity pressure, or any other specific facet underlying the individual/collectivism dimension. Disentangling which of these relationships contributes to the relationship between pathogen prevalence and individualism/collectivism requires additional analyses on additional measures of geographic variation.

Conformity Pressure

We recently conducted a series of analyses designed to focus specifically on the hypothesis that regional differences in pathogen prevalence predict

worldwide geographic differences in conformity pressure (Murray, Trudeau, & Schaller, 2011). In testing this prediction, we used a methodologically diverse set of four country-level measures of conformity pressure. One measure was taken from a meta-analysis of dozens of behavioral conformity experiments performed worldwide (Bond & Smith, 1996), which allowed us to compute mean conformity effect sizes for individual countries. A second measure was obtained from the World Values Survey (http://www.worldvaluessurvey.org/) and pertained to attitudes toward obedience: the percentage of respondents within each country who indicated that obedience was an important trait for children to learn. A third measure follows from the logical implication that, in populations characterized by stronger conformity pressure, there is less tolerance for deviation from established norms. One way to measure this tolerance for deviation is through the mean level of within-population variability on personality traits (reduced tolerance for nonconformity should result in reduced variability). Exactly such a measure of within-country personality variability was reported by McCrae (2002). The fourth measure was the percentage of individuals within a country who are left-handed. The logic underlying this measure arises from the fact that right-handedness is normative, and so, in regions characterized by conformity pressure, it is more likely that naturally left-handed people will be compelled to become right-handed (Porac & Martin, 2007; Triandis, 1995). Thus, the percentage of left-handers serves as an indirect indicator of tolerance for behavioral nonconformity.

Our results revealed that each of these four measures of conformity pressure was predicted by pathogen prevalence. The historical prevalence of pathogens correlated significantly positively with behavioral conformity effect sizes and the value placed on obedience (r's = .49 and .48) and significantly negatively with personality variation and the percentage of left-handers (r's = −.52 and −.73). Additional analyses revealed that pathogen prevalence remained a significant predictor when controlling for additional variables that might be conceptually linked to conformity (e.g., level of agriculture, life expectancy, population density). Analyses performed at the world-region level produced correlations that were even higher in magnitude than those obtained at the country level. Historical pathogen prevalence was a stronger predictor of these conformity variables than was contemporary prevalence. These results all support the proposed causal link between pathogens and conformity.

Strength of Family Ties

The strength of family ties—which is associated with obligatory prosociality toward extended family members—is an integral part of collectivist (vs. individualist) value systems. Recently, Fincher and Thornhill (2012)

investigated whether pathogen prevalence predicts this specific facet of collectivism. They created a country-level index of "strength of family ties" on the basis of 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"; http://www.worldvaluessurvey.org/). 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. Fincher and Thornhill replicated these findings with independent analyses that used American states as units of analysis. These convergent results support the hypothesized causal link between pathogen prevalence and geographic variation in values pertaining to family ties and obligatory prosociality.

Xenophobia and Ethnocentrism

Several results provide some support for a link between pathogen prevalence and regional variation in ethnocentrism and xenophobia. For instance, pathogen prevalence is positively correlated with the percentage of people in a country who indicate that they would not want "people of a different race" as neighbors (Schaller & Murray, 2010). High pathogen prevalence is also associated with population-level outcomes that indirectly indicate reduced levels of contact between ethnic groups (e.g., Fincher & Thornhill, 2008). The frequency of intrastate conflict and civil war is also positively correlated with pathogen prevalence—a relationship that is conceptually consistent with higher levels of xenophobia and ethnocentrism within pathogen-prevalence regions (Letendre, Fincher, & Thornhill, 2010).

"Binding" Moral Values

The preceding findings all suggest intriguing relations between pathogen prevalence and fundamental cultural value systems. Values are conceptually linked to moral judgments and moral behavior, suggesting that geographic differences in morality might also be predicted by pathogen prevalence. One recent investigation examined the possibility that regional differences in pathogen prevalence may help to explain worldwide geographic variation on a particular subset of moral values (Van Leeuwen et al., 2012). According to moral foundations theory, 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 attitudes and behaviors (e.g., ethnocentrism, obedience, cleanliness) that, as we have already discussed, may serve as buffers against disease transmission. It follows, therefore, that binding moral values will be endorsed more fervently 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. The results showed that historical pathogen prevalence was a significant predictor of binding moral values but not of individualizing moral values. The 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 a variety of additional variables that can influence moral values, thus eliminating a variety of alternative explanations. Also, importantly, this result emerged not only from analyses that treated countries as units of analysis but also from multilevel analyses on individual responses.

Political Ideology

Just as cultural values have implications for morality, they also have implications for political ideology, and this can have important consequences. Economic and political outcomes within a country are influenced substantially by the political ideologies held by its citizens. A culture that prizes tradition and conformity, for example, may perceive specific kinds of individual rights and freedoms (e.g., freedom of speech) to pose a threat. Consistent with this analysis is evidence that cultural tightness and collectivism are highly associated with the existence of authoritarian governments and legalized repression of civil liberties and individual freedoms (Conway, Sexton, & Tweed, 2006). The overall upshot is that cross-national differences in political systems and style of governance may result, in part, from regional differences in pathogen prevalence.

In support of this hypothesis, Thornhill, Fincher, and Aran (2009) found that a measure of contemporary pathogen prevalence significantly predicted a variety of country-level measures of political ideologies and additional outcomes pertaining to governance—including positive correlations with measures that assess repression of individual rights and freedoms, negative correlations with additional measures of social and political liberalism, and negative correlations with democratization in general. These relations persist even when controlling for a variety of potential confounds. Follow-up analyses revealed that these outcomes pertaining to political ideology and governance are even more strongly predicted by historical pathogen prevalence (Murray & Schaller, 2010).

IMPLICATIONS AND FUTURE DIRECTIONS

Taken together, these findings support a range of conceptual hypotheses that link pathogen prevalence to geographical variation in traits, values, behaviors, and societal outcomes. These findings also provide a more complete understanding of previously documented relationships between psychological outcomes that vary geographically. For example, it has been previously observed that regional differences in Extraversion are linked to regional differences in individualistic value systems, and discussions of this relationship have centered on the possible causal influence of cultural value systems on individual dispositions, or vice versa (e.g., Hofstede & McCrae, 2004). Our analyses reveal, however, that the relationship between Extraversion and individualism disappears when statistically controlling for pathogen prevalence (Fincher et al., 2008; Schaller & Murray, 2008). Therefore, it appears that there is no meaningful causal relationship between Extraversion and individualism; their relation may be a result of both variables being consequences of lower pathogen prevalence.

Another example is latitude, which has been cited as a strong predictor of many cross-cultural differences (e.g., Hofstede, 2001). Of course, a latitude value is an abstract cartographic convention; it has no meaningful causal influence on human psychology. Any correlation between latitude and psychological phenomena requires explanations that focus on additional variables that vary geographically and that actually do have an impact on human experience and psychological functioning. Pathogen prevalence is one such variable, and it may be an integral part of any causal explanation for a relationship between latitude and psychological outcomes.

The prevalence of pathogens within any geographic region is not immutable, however; as mentioned at the outset of this chapter, it can change over time, both as a result of natural circumstances and as a result of human intervention. Consequently, public health initiatives (e.g., vaccination campaigns) may have consequences that extend far beyond epidemiological morbidity and mortality; efforts designed to reduce the prevalence of infectious diseases may also lead to meaningful changes in personality, cultural values, intergroup relations, political practices, and many other aspects of human life. A reduction in pathogen prevalence may, for example, lead to a higher tolerance for nonconformity, thereby facilitating artistic creativity and technological innovation. It is worth noting here, perhaps, that the number of Nobel laureates per capita within a country is strongly negatively predicted by historical pathogen prevalence ($r = -.59$, $p < .0001$), and this relationship remains robust when controlling for variables such as economic development (Murray, 2013). Rigorous longitudinal investigations will be needed to test whether temporal variation in pathogen prevalence does indeed lead to changes in these kinds of psychological and societal outcomes.

If changes in pathogen prevalence do have the downstream effects that we suggest, another question that arises is when these effects might become evident. This "when" question is largely dependent on another scientific factor that requires much more investigation: the mechanism by which pathogen prevalence might produce these geographic differences in the first place. At least four such mechanisms are possible. One possibility is that these differences are created through facultative cognitive mechanisms, wherein individuals detect disease cues within their immediate environment and respond by emitting appropriate disease-mitigating behaviors. Alternatively, these differences may be more genetically based, whereby historical geographical variation in pathogen prevalence has led to differential selection for genes associated with behaviors that have implications for pathogen transmission. A different type of genetic mechanism—an epigenetic mechanism—is also a possibility, wherein genes associated with traits such as collectivism and conformity are more likely to be developmentally expressed in regions of higher disease. Finally, these cultural differences may have arisen through cultural transmission, wherein information about the most locally adaptive sets of traits, behaviors, or practices is selectively communicated across generations.

The time frame whereby changes in disease prevalence lead to cultural change will provide clues as to which of these mechanisms is at play: Any cultural change that transpires within days or weeks of disease outbreak (or disease eradication) would indicate the operation of facultative mechanisms; changes that occur one generation after a disease outbreak are more likely to implicate an epigenetic process; and changes that accumulate across multiple generations would be more indicative of a cultural transmission process or even a genetic process. (For a more substantive discussion of these mechanisms, and the evidence bearing on each of them, see Schaller & Murray, 2011.)

Investigating the antecedents of geographical differences in human psychology is an enormous enterprise. These antecedent variables do not operate exclusively, and only now are we beginning to appreciate the complex interplay between the variables that contribute to the geographical differences we see today. Much work remains to be done in investigating the mechanisms by which these variables operate, the interactions that exist between them, and their implications.

REFERENCES

Ackerman, J. M., Becker, D. V., Mortensen, C. R., Sasaki, T., Neuberg, S. L., & Kenrick, D. T. (2009). A pox on the mind: Disjunction of attention and memory in processing physical disfigurement. *Journal of Experimental Social Psychology, 45*, 478–485. doi:10.1016/j.jesp.2008.12.008

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. doi:10.1006/jrpe.2000.2304

Bond, R., & Smith, P. B. (1996). Culture and conformity: A meta-analysis of studies using Asch's line judgment task. *Psychological Bulletin, 119*, 111–137. doi:10.1037/0033-2909.119.1.111

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12*, 1–14. doi:10.1017/S0140525X00023992

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. doi:10.1177/0022022105282293

Dantzer, R., Kent, S., Bluthe, R. M., & Kelley, K. W. (1991). Cytokines and sickness behaviour. *European Neuropsychopharmacology, 1*, 377–379. doi:10.1016/0924-977X(91)90576-G

Fabrega, H. (1997). Earliest phases in the evolution of sickness and healing. *Medical Anthropology Quarterly, 11*, 26–55. doi:10.1525/maq.1997.11.1.26

Faulkner, J., Schaller, M., Park, J. H., & Duncan, L. A. (2004). Evolved disease-avoidance mechanisms and contemporary xenophobic attitudes. *Group Processes & Intergroup Relations, 7*, 333–353. doi:10.1177/1368430204046142

Fincher, C. L., & Thornhill, R. (2008). Assortive sociality, limited dispersal, infectious disease and the genesis of the global pattern of religious diversity. *Proceedings of the Royal Society: B. Biological Sciences, 275*, 2587–2594. doi:10.1098/rspb.2008.0688

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. doi:10.1017/S0140525X11000021

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. doi:10.1098/rspb.2008.0094

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology, 14*, 89–96. doi:10.1016/0162-3095(93)90009-7

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. doi:10.1207/s15327965pli1702_1

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences, 23*, 573–644. doi:10.1017/S0140525X0000337X

Gelfand, M. J., Nishii, L. H., & Raver, J. L. (2006). On the nature and importance of cultural tightness-looseness. *Journal of Applied Psychology, 91*, 1225–1244. doi:10.1037/0021-9010.91.6.1225

Goodall, J. (1986). Social rejection, exclusion, and shunning among the Gombe chimpanzees. *Ethology and Sociobiology*, *7*, 227–236. doi:10.1016/0162-3095(86)90050-6

Guernier, V., Hochberg, M. E., & Guégan, J.-F. (2004). Ecology drives the worldwide distribution of human diseases. *PLoS Biology*, *2*, 740–746. doi:10.1371/journal.pbio.0020141

Heine, S. J. (2008). *Cultural psychology*. New York, NY: Norton.

Hofstede, G. (2001). *Culture's consequences. Comparing values, behaviors, institutions, and organizations across nations* (2nd ed.). Thousand Oaks, CA: Sage.

Hofstede, G., & McCrae, R. R. (2004). Personality and culture revisited: Linking traits and dimensions of culture. *Cross-Cultural Research*, *38*, 52–88. doi:10.1177/1069397103259443

Inhorn, M. C., & Brown, P. J. (1990). The anthropology of infectious disease. *Annual Review of Anthropology*, *19*, 89–117. doi:10.1146/annurev.an.19.100190.000513

Kavaliers, M., & Colwell, D. D. (1995). Discrimination by female mice between the odours of parasitized and non-parasitized males. *Proceedings of the Royal Society: B. Biological Sciences*, *261*, 31–35. doi:10.1098/rspb.1995.0113

Kiesecker, J. M., Skelly, D. K., Beard, K. H., & Preisser, E. (1999). Behavioral reduction of infection risk. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 9165–9168. doi:10.1073/pnas.96.16.9165

Klein, S. L., & Nelson, R. J. (1999). Influence of social factors on immune function and reproduction. *Reviews of Reproduction*, *4*, 168–178. doi:10.1530/ror.0.0040168

Larsen, R. J., & Buss, D. M. (2005). *Personality psychology* (2nd ed.). New York, NY: McGraw-Hill.

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 of the Cambridge Philosophical Society*, *85*, 669–683.

Little, A. C., DeBruine, L. M., & Jones, B. C. (2011). Exposure to visual cues of pathogen contagion changes preferences for masculinity and symmetry in opposite-sex faces. *Proceedings of the Royal Society: B. Biological Sciences*, *278*, 2032–2039. doi:10.1098/rspb.2010.1925

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, NY: Kluwer Academic/Plenum. doi:10.1007/978-1-4615-0763-5_6

McCrae, R. R., & Terracciano, A. (2005). Personality profiles of cultures: Aggregate personality traits. *Journal of Personality and Social Psychology*, *89*, 407–425. doi:10.1037/0022-3514.89.3.407

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. doi:10.1177/0956797610361706

Murray, D. R. (2013). *The implications of pathogen prevalence for scientific and technological innovation*. Manuscript submitted for publication.

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. doi:10.1177/0022022109349510

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. doi:10.1002/ejsp.863

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. doi:10.1177/0146167210394451

Nettle, D. (2005). An evolutionary approach to the extraversion continuum. *Evolution and Human Behavior, 26*, 363–373. doi:10.1016/j.evolhumbehav.2004.12.004

Nettle, D. (2009). Ecological influences on human behavioral diversity: A review of recent findings. *Trends in Ecology & Evolution, 24*, 618–624. doi:10.1016/j.tree.2009.05.013

Oaten, M., Stevenson, R, J. & Case, T. I. (2009). Disgust as a disease-avoidance mechanism. *Psychological Bulletin, 135*, 303–321. doi:10.1037/a0014823

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. doi:10.1016/j.evolhumbehav.2007.05.008

Porac, C., & Martin, W. L. B. (2007). A cross-cultural comparison of pressures to switch left-handed writing: Brazil versus Canada. *Laterality: Asymmetries of Body, Brain and Cognition, 12*, 273–291. doi:10.1080/13576500701269462

Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology, 57*, 199–226. doi:10.1146/annurev.psych.57.102904.190208

Ridley, M. (1993). *The red queen: Sex and the evolution of human nature*. New York, NY: Penguin Books.

Schaller, M. (2011). The behavioural immune system and the psychology of human sociality. *Philosophical Transactions of the Royal Society: B. Biological Sciences, 366*, 3418–3426. doi:10.1098/rstb.2011.0029

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. doi:10.1037/0022-3514.95.1.212

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, NY: 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.

Schaller, M., & Park, J. H. (2011). The behavioural immune system (and why it matters). *Current Directions in Psychological Science*, *20*, 99–103. doi:10.1177/0963721411402596

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. doi:10.1017/S0140525X05000051

Schmitt, D. P., Allik, J., McCrae, R. R., & Benet-Martinez, V. (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. doi:10.1177/0022022106297299

Silverthorne, C. (2001). Leadership effectiveness and personality: A cross cultural evaluation. *Personality and Individual Differences*, *30*, 303–309. doi:10.1016/S0191-8869(00)00047-7

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. doi:10.1037/0022-3514.60.6.870

Thornhill, R., Fincher, C. L., & Aran, D. (2009). Parasites, democratization, and the liberalization of values across contemporary countries. *Biological Reviews of the Cambridge Philosophical Society*, *84*, 113–131. doi:10.1111/j.1469-185X.2008.00062.x

Thornhill, R., Fincher, C. L., Murray, D. R., & 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.

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, *3*, 452–460. doi:10.1016/S1364-6613(99)01403-5

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

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. doi:10.1016/j.evolhumbehav.2011.12.005

Weeden, J., & Sabini, J. (2005). Physical attractiveness and health in Western societies: A review. *Psychological Bulletin*, *131*, 635–653. doi:10.1037/0033-2909.131.5.635