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Original Article

Zoonotic and Non-Zoonotic Diseases in Relation to Human Personality and Societal Values: Support for the Parasite-Stress Model

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Abstract: The parasite-stress model of human sociality proposes that humans' ontogenetic experiences with infectious diseases as well as their evolutionary historical interactions with these diseases exert causal influences on human psychology and social behavior. This model has been supported by cross-national relationships between parasite prevalence and human personality traits, and between parasite prevalence and societal values. Importantly, the parasite-stress model emphasizes the causal role of *non-zoonotic* parasites (which have the capacity for human-to-human transmission), rather than *zoonotic* parasites (which do not), but previous studies failed to distinguish between these conceptually distinct categories. The present investigation directly tested the differential predictive effects of zoonotic and non-zoonotic (both human-specific and multihost) parasite prevalence on personality traits and societal values. Supporting the parasite-stress model, cross-national differences in personality traits (unrestricted sexuality, extraversion, openness to experiences) and in societal values (individualism, collectivism, gender equality, democratization) are predicted specifically by non-zoonotic parasite prevalence.

Keywords: collectivism, democracy, gender equality, infectious diseases, sociosexual orientation, zoonosis.

Introduction

The parasite-stress model of human sociality implies that parasitic diseases (i.e., infectious diseases) are causal, both proximately and ultimately, in shaping major features of human psychology and behavior. Throughout evolutionary history, human ancestors faced adaptive problems caused by infectious diseases' negative effects on morbidity, mortality, and reproductive fitness. This selection history is demonstrated by the many adaptations that have evolved for defenses against these negative effects. These include mechanisms that detect and neutralize parasitic infection of the body (i.e., mechanisms that comprise the classical immune system), and additional mechanisms—the behavioral immune system—that facilitate behavioral avoidance of parasite transmission in the first place, as well as mechanisms that function to manage local parasitic infections. The behavioral immune system, like the classical immune system, manifests conditionally in a predictable set of affective and cognitive responses to local levels of parasite stress, which have additional implications for cross-national variation in human behavioral dispositions (i.e., personality traits) and value systems basic to important features of human social life.

Parasite Prevalence and Worldwide Variation in Human Personality

Many behavioral dispositions have the potential to increase individuals' exposure to infectious diseases. However, the fitness costs associated with contacting disease must be weighed against the potential fitness benefits associated with those behavioral dispositions. Sexual behavior offers an obvious example. Compared to "restricted" forms of sexual behavior (e.g., monogamous mating), "unrestricted" sexual behavior is associated with greater exposure to socially transmitted diseases. But unrestricted sexual behavior can confer reproductive benefits as well (Thornhill and Gangestad, 2008). Consequently, there are adaptive advantages associated with context-dependent phenotypic plasticity in the domain of sexual behavior, with a more restricted approach to mating occurring under ecological conditions in which the threat of parasite transmission is greater, and a more unrestricted approach occurring when the threat of parasite transmission is reduced. Worldwide data on human populations support this hypothesis: in countries with a higher prevalence of infectious diseases, people report a dispositional tendency toward greater sexual restrictedness, and these cultures are defined also by more conservative and traditional values, both sexual and otherwise (Schaller and Murray, 2008; Thornhill, Fincher, and Aran, 2009). This cross-national positive relationship between prevalence of infectious disease and sexual restrictiveness is stronger for women than for men.

This same logic applies to other human behavioral tendencies. A dispositional tendency toward gregariousness with a diversity of people and extraversion is associated with specific kinds of interpersonal benefits—e.g., larger social networks, including mating pools—but also implies greater exposure to infectious diseases (Nettle, 2005). To the extent that there evolved a capacity for contingent plasticity in dispositional tendencies toward extraversion, it follows that human populations are likely to be characterized by extraversion primarily under ecological conditions of low parasite prevalence, whereas a more introverted personality style is more likely to emerge when the prevalence of parasites is high. This prediction has been supported by cross-national data describing the personality traits of tens of thousands of people in dozens of countries worldwide (Schaller and Murray, 2008).

Similarly, specific kinds of fitness benefits may accrue to individuals who are curious, adventurous, and generally "open" to unfamiliar experiences and new ideas. For several reasons, however, dispositional openness also may be associated with increased risk of parasite transmission. Individuals who are curious and adventurous may be more likely to violate rituals and norms (such as those pertaining to hygiene and food preparation; e.g., Sherman and Billing, 1999) that serve as buffers against contact with local parasites. In addition, dispositional openness, in ways similar to extraversion, is associated with increased contact with out-group members and other unfamiliar peoples who may be hosts to novel parasites to which the immune defenses of one's self, one's family, and one's fellow group members are not adapted. Host–parasite coevolutionary races are localized on a geographical scale. Thus, defenses of both the classical and behavioral immune systems are most suited to local infectious diseases, but not those outside one's in-group or typical social milieu (Fincher and Thornhill, 2008; also, Tanaka, Kumm, and Feldman, 2002). In short, neophobia reduces risk of parasite-based morbidity and mortality, whereas neophilia increases risk of contracting infectious diseases. To the extent that there is contingent plasticity in dispositional tendencies toward openness, it follows that human populations are expected to have higher levels of dispositional openness (neophilia) within ecologies characterized by low parasite prevalence, and will have lower levels of openness (neophobia) within ecologies characterized by higher prevalence of parasites. Empirical evidence across many countries of the world also supports this prediction (Schaller and Murray, 2008).

Parasite Prevalence and Worldwide Variation in Societal Values

The prevalence of parasites in the local ecology not only has implications for human personality, but also—perhaps more profoundly—for the cultural value systems and political ideologies that define human societies.

To the extent that value systems encourage adherence to existing traditions and norms, and place constraints on individuals' inclinations to deviate from those norms through unwillingness to accept new ideas and ways that arise within or outside the group, these value systems provide a buffer against parasite transmission. To the extent that value systems encourage xenophobic responses to unfamiliar peoples, these value systems limit exposure to novel parasites harbored by out-groups (Fincher, Thornhill, Murray, and Schaller, 2008; Navarrete and Fessler, 2006). To the extent that value systems encourage philopatry, and impose limits on the dispersal from natal locales, they also limit exposure to novel parasites (Fincher et al., 2008). The relative benefits of these value systems—as opposed to value systems encouraging individualism, dispersal, innovation and xenophilia—would be especially great under ecological conditions in which infectious parasites are especially prevalent. The implication is that these value systems, and their manifest behavioral patterns, are likely to be especially common in populations characterized by a high prevalence of infectious diseases. This prediction has been supported empirically across multiple studies, using a variety of empirical indicators of social values. One study focused specifically on dispersal. Across a large sample of traditional societies in the ethnographic record, geographic dispersal (measured as home range size) was related negatively with parasite prevalence (Fincher and Thornhill, 2008). Another study examined multiple measures of "collectivism" and "individualism." Collectivistic value systems are defined, in part, by ethnocentric attitudes, adherence to existing traditions, behavioral conformity, and neophobia; individualistic values are defined by higher levels of intergroup contact, encouragement of innovation, tolerance for idiosyncratic behavior, and neophilia (Gelfand, Bhawuk, Nishii, and Bechtold, 2004; Triandis, 1995). Across a worldwide sample of contemporary countries, parasite prevalence was strongly, negatively associated with two different measures of individualism, and strongly, positively associated with two additional measures of collectivism (Fincher et al., 2008).

These effects generalize to political ideologies and associated political systems as well. Autocracy, the antipole of democracy, arises, in part, from societal values promoting widespread obedience to authority, conformity and neophobia. In contrast, democratic ideologies and political structures are associated with more individualistic value systems and the specific behaviors associated with them (e.g., greater trust of, altruism toward, and interaction with out-groups) (Thornhill et al., 2009). According to the parasite-stress model, variation among contemporary nations' political structures is therefore expected to correspond to ecological variation in parasite prevalence. Recent evidence indicates that this is so. In analyses involving most of the world's countries, parasite prevalence was inversely correlated with four different measures of democratization (Thornhill et al., 2009).

For similar reasons, parasite prevalence also is expected to predict other forms of political liberalism. For example, democratization is accompanied by the liberation of women from the tradition of masculine social control, which manifests in an increase in women's civil rights and political representation (Inglehart, 2003; Wejnert, 2005; Welzel, 2007). It follows from the parasite-stress model that this form of liberalism should be more pronounced within populations that have a relatively low prevalence of parasites. It is. Across many countries of the world, parasite prevalence correlates negatively with national indicators of gender equality (Gangestad, Haselton, and Buss, 2006; Thornhill et al., 2009).

Robustness of these Cross-national Relationships

These empirical findings provide provocative and wide-ranging support for the parasite-stress model of human sociality. Furthermore, additional findings have largely ruled out alternative explanations for these significant relationships between parasite prevalence and cross-national differences in personality and values.

For example, previous research has assessed and statistically controlled for a wide variety of potential confounding variables. These include variables pertaining to economic development (e.g., gross domestic product per capita, income inequity), climate (e.g., mean annual temperature), social demographics (e.g., population density), and non-disease-related threats to human welfare. The predictive effects of parasite prevalence have persisted even when these variables are controlled, thus rendering many potential alternative explanations untenable (for details, see Fincher et al., 2008; Fincher and Thornhill, 2008; Schaller and Murray, 2008; Thornhill et al., 2009).

Additional analyses have addressed the possibility that the magnitude and/or significance of the cross-national results might be artificially inflated by statistical non-independence. Although a considerable amount of cross-cultural research indicates that geopolitical boundaries (i.e., national borders) can serve as useful proxies for cultural boundaries (e.g., Schwartz, 2004), it can be argued that the personality styles and societal norms of geographically proximal nations may not be truly independent—that they may be descriptively similar not merely because of similar ecologies, but also because of shared cultural histories (e.g., Mace and Pagel, 1994; Nettle, 2009; Rogers and Cashdan, 1997; Ross and Homer, 1976). One way to test whether there is a predictive relationship between parasite prevalence and cultural outcomes, and to assure that this relationship is not merely an artifact of statistical non-independence, is to compute parasite-prevalence, personality traits, and societal value scores for larger culturally-distinct world regions (e.g., the six world cultural regions identified by Murdock, 1949), and to treat those cultural regions (rather than nations) as the unit of statistical analysis. Fincher et al. (2008) reported exactly such analyses, and found that parasite prevalence still predicted cultural differences in individualism and collectivism. Although not previously reported, analogous analyses have been done on the other trait and value variables too, and in all cases these world-region analyses have produced results replicating the nation-level effects. For example, in analyses treating Murdock's six world regions as the unit of analysis, the mean historical prevalence of parasites within a region (computed from nation-level scores reported by Murray and Schaller, 2010) strongly predicts mean contemporary levels of extraversion, openness, and democratization (*r*s exceed -0.75 in magnitude, *p*s < 0.05, one-tailed). These results are inconsistent with any alternative explanation based on statistical non-independence of nation-level data.

The implication is that national differences in personality and values are predicted by parasite prevalence, and that these relations cannot easily be attributed to alternative causal explanations. Nevertheless, some additional conceptual and empirical limitations remain unaddressed by previous research.

Zoonotic Versus Non-Zoonotic Diseases as Differential Predictors of Human Variation

One limitation results from the fact that these previous investigations employed relatively crude measures of pathogen prevalence. One measure (employed by Fincher et al., 2008, and Schaller and Murray, 2008) estimated overall parasite prevalence (number of cases of disease) on the basis of data pertaining to a diverse set of nine human infectious diseases represented in epidemiological atlases that refer back to the early 1900s. A second measure (employed by Fincher et al., 2008, and Thornhill et al., 2009) estimated overall parasite prevalence (number of cases) on the basis of data pertaining to a diverse set of 22 human infectious diseases, obtained in 2007 from an online database of contemporary human infectious diseases (GIDEON, see below). Statistical analyses attest to the reliability and validity of these measures (e.g., Fincher et al., 2008; Murray and Schaller, 2010; Thornhill et al., 2009), but these measures are only indicators of overall parasite prevalence. These measures fail to discriminate between conceptually distinct categories of parasites defined by different modes of transmission.

Parasitologists and epidemiologists classify human diseases into three distinct categories based on their modes of transmission: zoonotic, multihost, and human-specific (Smith, Sax, Gaines, Guenier, and Guégan, 2007). Zoonotic parasites develop and reproduce entirely in non-human hosts (e.g., livestock, wildlife) and can infect humans as well, but are not transmitted directly from human to human. Multihost parasites can use both non-human and human hosts to complete their life cycle, and may be transmitted directly from human to human as well as through inter-species transmission. Human-specific parasites are transmitted only from human to human (although ancestrally they often have had a zoonotic transmission origin; see Pearce-Duvet, 2006).

These categorical distinctions matter in the present theoretical context. The cross-national differences discussed above—differences in personality traits and societal values—are predicted by a parasite-stress model of human *sociality* that emphasizes especially the potential infection risks associated with interactions with conspecifics. The risks associated with unrestricted sociosexuality and extraversion, for instance, refer specifically to the risk of human-to-human transmission. The infection risks associated with openness are not quite so specific, but many of the specific forms of behavior associated with openness (e.g., increased contact with out-group members) do imply a higher risk of human-to-human transmission. The same logic applies to the societal value dimensions of individualism and collectivism (given that collectivism is defined, in part, by ethnocentrism and philopatry) as well as to democratization and liberalism in general (given that socially and politically liberal attitudes are also defined, in part, by a greater tolerance for, liking of, and contact with unfamiliar peoples).

The implication is clear. According to the parasite-stress model of human sociality, worldwide differences in the domains of human personality and societal values are unlikely to correlate with the presence of zoonotic parasites (which cannot be transmitted from human to human), but should correlate strongly with the presence of non-zoonotic parasites (which have the capacity for human-to-human transmission). Empirical evidence consistent with this prediction would provide unique and novel support for the parasite-stress model of human sociality.

Materials and Methods

The unit of analysis used throughout the current investigation is that of a geopolitical region. In most cases, these regions are nations. In some cases, these regions are geographically separate colonies or territories (e.g., Guam), or culturally distinct regions within a country (e.g., Hong Kong). For the sake of expository efficiency, the term "country" will hereafter refer to all units of analysis.

Given that previous results (described above) have shown already that parasite prevalence predicts cultural outcomes regardless of whether country or broader cultural region is treated as the unit of analysis, we do not report cultural-region-level analyses here. Furthermore, our objective is to test whether these previously documented effects are differentially predicted from the prevalence of zoonotic versus non-zoonotic parasites. This objective requires analyses with sufficient statistical power to test for differential effects. Nation-level analyses satisfy this requirement; world-region-level analyses do not.

Three Indices of Parasite Richness: Zoonotic, Multihost, Human-Specific

For each of 227 countries, we computed three indices of parasite richness, based on the presence or absence of every human infectious disease cataloged in the GIDEON database. GIDEON is a frequently updated, subscription-based online database of human infectious diseases available to the medical community and researchers. GIDEON data have been used extensively in prior research on the global distribution of infectious diseases (e.g., Guernier, Hochberg, and Guegan, 2004; Smith et al., 2007; Thornhill et al., 2009). Our indices were generated from data obtained from GIDEON in 2008.

We classified each human infectious disease as either zoonotic, multihost, or human-specific, according to Smith et al.'s (2007) classification scheme, with updates based on more recent epidemiological information in GIDEON and in other sources. These updates are as follows. Ten new diseases have been added to the GIDEON database since Smith et al. was published. Thirty-five diseases have changed names since Smith et al.'s paper. Four diseases were reclassified by us, because of error by Smith et al. and/or recent information about transmission provided by GIDEON or other sources. Data on the number of each of the three disease types per country are available from the corresponding author upon request. This classification has 154 diseases as zoonotic (e.g., rabies, plague, hantavirus), 40 diseases as multihost (e.g., leishmaniasis, Chagas disease, Dengue fever), and 117 diseases as human-specific (e.g., measles, cholera, filariasis). For each country, we computed separately the sums of all zoonotic diseases, multihost diseases, and human-specific diseases that GIDEON listed as having a presence within that country. These three sums represented three distinct indices of parasite richness. Across all countries, the mean parasite richness scores were as follows: zoonotic: $M \pm SD = 53.92 \pm 10.40$ (*range* = 38–87); multihost: $M \pm SD = 23.59 \pm 2.81$ (*range* = 20–32); human-specific: $M \pm SD = 102.33 \pm 2.96$ (*range* = 98–110).

These parasite indices do not distinguish between certain aspects of disease transmission—e.g., vector-borne vs. those that require direct contact—nor need they. Whether a disease transmitted between people is carried through the air by way of a mosquito or by expelled mucus droplets is not relevant to our main hypothesis about differences between nonzoonotic and zoonotic influences. Similarly, the taxon of the disease—e.g., fungi, viral, helminth, etc.—is not relevant to this hypothesis.

We should note that these measures of parasite *richness* are only indirect measures of the *severity* of stress that parasites impose on human populations. Nevertheless, there is abundant evidence that parasite richness covaries substantially with parasite severity (Fincher et al., 2009; Fincher and Thornhill, 2008); consequently, these measures of parasite richness can be used to test hypotheses derived from the parasite-stress model of human sociality.

Measures of Human Personality Traits

Female Sociosexual Orientation. The Sociosexual Orientation Inventory (SOI; Simpson and Gangestad, 1991) is a self-report instrument commonly used to assess a behavioral disposition toward unrestricted sexuality (e.g., willingness to engage in sexual relations in the absence of a long-term commitment). Based on data collected from 14,059 adults worldwide, Schmitt (2005) reported sex-specific mean SOI scores for nearly 50 countries. Using this data, Schaller and Murray (2008) found that parasite prevalence predicted both male and female mean SOI scores, although only the relation with female SOI scores remained statistically significant after controlling for additional variables (also see similar results in Thornhill et al., 2009). Consequently, our analyses here focus exclusively on mean female SOI (high SOI scores indicate a more unrestricted approach to sexual behavior).

Extraversion. The NEO-PI-R questionnaire is the most widely employed and well-validated instrument available for assessing the five fundamental trait dimensions that account for most of the variability in human personality (see McCrae, 2002). Extraversion is one of these dimensions. Two different investigations have employed the NEO-PI-R questionnaire to assess and describe worldwide differences in extraversion. McCrae (2002) summarized results from several dozen independent investigations that used the NEO-PI-R questionnaire to assess the self-reported personality traits in about 30 different countries. Separately, McCrae et al. (2005) used the NEO-PI-R questionnaire and an observer-report methodology to assess the personality traits of 11,985 individuals living in about 50 different countries. Both investigations produced average extraversion scores for each country included in their analyses. Schaller and Murray (2008) found that parasite prevalence significantly and negatively predicted both measures of extraversion.

Openness to Experience. Openness to experience is also one of the five fundamental trait dimensions assessed by the NEO-PI-R questionnaire. McCrae (2002) and McCrae et al. (2005) reported mean openness scores for each country included in their analyses. Schaller and Murray (2008) found that parasite prevalence significantly and negatively predicted measures of openness from both studies.

Measures of Societal Values

Individualistic and Collectivistic Values. The values unidimension of individualism/collectivism has been a major research focus in cross-cultural psychology, as it is widely felt to describe important cultural differences across countries of the world (e.g., Gelfand et al., 2004). Fincher et al. (2008) reported significant correlations between parasite prevalence and four different numerical indicators of the extent to which a country is characterized by collectivistic or individualistic values. Two different (but highly overlapping) measures of individualism were taken from Hofstede (2001) and Suh, Diener, Oishi, and Triandis (1998); two different (but highly overlapping) measures of collectivism were taken from Gelfand et al. (2004) and Kashima and Kashima (1998). (A complete description of these measures can be found in Fincher et al., 2008.) As an additional indicator of collectivistic values, we conducted analyses on the strength of "family ties" within each country—measured as a numerical composite variable of multiple self-report items included in the World Values Survey. Allegiance to extended family is a defining feature of collectivistic value systems (Alesina and Giuliano, 2007; Gelfand et al., 2004), and the family ties variable correlates very highly with other measures of individualism/collectivism (for evidence and further discussion, see Thornhill et al., 2009). See Table 2 for sample sizes (number of countries) associated with the five value systems of individualism/collectivism.

*Democratization.*Thornhill et al. (2009) reported significant correlations between pathogen prevalence and four measures commonly employed by scholars to describe the nature of political systems across the globe. Two measures were developed by Vanhanen (2003) on the basis of quantifiable data. One is Vanhanen's Index of Democracy, which reflects the extent to which people in a country participate in elections, as well as the extent to which there exists opportunities allowing competition for political power and opposition to heads of states. Vanhanen's other measure, the Resource Distribution index, assesses the mean level to which five valuable resources (e.g., money, property ownership, educational opportunities) are distributed widely and equitably across the people in the country. Vanhanen's two indices are highly positively correlated. Both indices are scored such that higher values reflect higher levels of democratization within a country. Two additional measures of democratization assess the extent to which people of a country have various political rights and civil liberties, and are based on subjective judgments of political scientists, legal scholars and other experts. The Human Freedom Index, obtained from the *World Christian Encyclopedia* (Barrett, Kurian, and Johnson, 2001), offers a composite score of several variables related to political rights and civil liberties. Higher scores correspond to greater levels of individual freedom. The organization Freedom House (www.freedomhouse.org) provides two ratings reflecting restrictions on individual freedoms—one rating assessing restrictions on political rights, and another rating assessing restrictions on civil liberties (see Karatnycky, 1998 for a discussion of rating methods). The two Freedom House ratings are highly correlated (r = 0.94). Higher ratings correspond to higher restrictions. Therefore, for our analyses, we summed the Freedom House ratings into a single index reflecting restrictions on democratization rights.

We also included a fifth measure of democratization not presented in prior analyses. The Economist Intelligence Unit (EIU; www.eiu.com) computed a cross-national Democracy Index based on 60 indicators assessing five defining components of democratization (electoral process and political pluralism, civil liberties, the functioning of the government, political participation, and political culture). We employed the EIU Democracy Index for 2008; higher scores reflect higher levels of democratization. See Table 3 for sample sizes associated with the democratization variables.

Gender Equality. An index of gender equality for 93 countries is provided by the Gender Empowerment Measure, reported in the United Nations Human Development Report (http://hdrstats.undp.org/indicators/280) in 2007. This index provides a composite measure of gender equality in political and economic participation, and in power over economic resources. High scores indicate higher levels of gender equality within a country. Thornhill et al. (2009) found that this measure of gender equality correlated positively with democratization and correlated negatively with both collectivism and parasite prevalence (also see Gangestad et al., 2006).

Results

For each outcome variable, we computed correlations (Pearson *r*s) with each of the three parasite-richness indices (zoonotics and each of the two non-zoonotic indices). In addition, because the three indices of parasite richness were positively intercorrelated (*r*s ranged from 0.56 to 0.66), we conducted additional regression analyses to more rigorously assess the unique predictive effects associated with each index.

Correlations Between Parasite Richness Indices and Personality Traits

Female Sociosexual Orientation. Across 45 countries, female SOI was correlated negatively with indices of both human-specific parasite richness ($r = -0.38$, $p = 0.01$) and multihost parasite richness ($r = -0.47$, $p < 0.001$). The relation with zoonotic parasite richness was negligible and non-significant ($r = -0.12$, $p = 0.44$). When all three parasite-richness indices were entered simultaneously as predictors of female SOI in a follow-up regression analysis, only the multihost index remained a statistically significant predictor ($p = 0.02$).

Extraversion. Table 1 reports correlations between each parasite richness index and the two measures of extraversion. A clear pattern is evident: extraversion was predicted most strongly by human-specific parasite richness, somewhat less strongly by multihost parasite richness, and least strongly by zoonotic parasite richness. In follow-up regression analyses that included all three parasite-richness indices as simultaneous predictors of each extraversion measure, only the human-specific indices remained a statistically significant predictor (for the McCrae, 2002, and McCrae et al., 2005 measures of extraversion, *p*s = 0.02 and 0.001, respectively). There were negligible unique effects associated with the other two indices (*p*s > 0.18).

Openness to Experience. A similar pattern emerged in the correlations between the parasite-richness indices and the two measures of openness, although the correlations involving the human-specific and multihost indices were not substantially different in magnitude (see Table 1). In follow-up regression analyses that included all three parasite-richness indices as simultaneous predictors of each openness measure, none of the three indices was a significant predictor (all *p*s > 0.20). Given the uninformative results of these regression analyses, an additional set of regression analyses was created in which the human-specific and multihost parasite-richness indices were summed to create a broader index of non-zoonotic parasite richness; this non-zoonotic index was entered along with the zoonotic index as predictors of openness. The results revealed that the non-zoonotic index was a significant predictor of the McCrae et al. (2005) openness measure ($p = 0.03$) and a near-significant predictor of the McCrae (2002) openness measure ($p = 0.10$). In contrast, zoonotic parasite richness exerted no predictive effect whatsoever (beta's = 0.00 and 0.04, *p*s > 0.85).

Table 1. Correlations (Pearson *r*s, accompanied by *p*-values) between each index of parasite richness and each measure of extraversion and openness to experience (*N* = the number of countries in each analysis).

	Index of Parasite Richness						
	Human	*p*	Multihost	*p*	Zoonotic	*p*	*N*
Extraversion (McCrae, 2002)	-0.58	0.001	-0.49	0.006	-0.28	> 0.10	30
Extraversion (McCrae et al., 2005)	-0.54	< 0.001	-0.34	0.02	-0.31	0.03	48
Openness (McCrae, 2002)	-0.43	0.02	-0.35	0.06	-0.29	> 0.10	30
Openness (McCrae et al., 2005)	-0.31	0.03	-0.28	0.06	-0.11	> 0.10	48

Relations Between Parasite Richness Indices and Societal Values

Individualism and Collectivism. Each of the two individualism measures correlated substantially negatively with both human-specific and multihost parasite richness; in contrast, they correlated only weakly with zoonotic parasite richness (see Table 2). Analogously, each of the two collectivism measures, as well as the measure of family ties, showed moderate to strong positive correlations with both human-specific and multihost parasite richness, and weaker correlations with zoonotic parasite richness. Follow-up regression analyses included all three parasite richness indices as predictors. The results revealed that the predictive effects associated with human-specific parasite richness remained significant on two of the five outcome measures (the Suh et al. individualism measure, and the family ties measure; both *p*s < 0.001), and marginally significant on two other measures (the Hofstede individual measure, and the Gelfand collectivism measure; *p*s = 0.09 and 0.12, respectively). The predictive effects of multihost parasite richness remained significant on three of the five outcomes measures (both individualism measures, as well as the Kashima and Kashima pronoun-drop measure of collectivism; all *p*s < 0.001) and marginally significant on one additional measure (the Gelfand collectivism measure; *p*

= 0.10). In contrast, the modest relations with zoonotic parasite richness actually reversed in sign when controlling for shared variance with the other parasite-richness measures. For the two individualism measures, the reversal in sign actually resulted in significant *positive* relations with zoonotic parasite richness (both *p*s < 0.002), in direct contrast with the significant *negative* relations with human-specific and multihost parasite richness. Additional regression analyses that included the zoonotic index and the non-zoonotic composite index as predictors revealed a clear distinction: non-zoonotic parasite richness was a unique negative predictor of individualism (both *p*s < 0.001), and a unique positive predictor of collectivism and family ties (all three *p*s < 0.001); zoonotic parasite richness had no consistent unique effect, and any effect at all (on the two individualism measures) was exactly opposite to that indicated by the correlations in Table 2.

Table 2. Correlations (Pearson *r*s, accompanied by *p*-values) between each index of parasite richness and each measure of individualism/collectivism (*N* = the number of countries in each analysis).

	Index of Parasite Richness						
	Human	*p*	Multihost	*p*	Zoonotic	*p*	*N*
Individualism (Hofstede, 2001)	-0.60	< 0.001	-0.70	< 0.001	-0.17	> 0.10	67
Individualism (Suh et al., 1998)	-0.58	< 0.001	-0.61	< 0.001	-0.20	> 0.10	57
Collectivism (Gelfand et al., 2004)	0.51	< 0.001	0.51	< 0.001	0.27	0.04	57
Collectivism (Pronoun-drop; Kashima and Kashima, 1998)	0.35	0.003	0.45	< 0.001	0.19	> 0.10	70
Family Ties (World Values Survey)	0.58	< 0.001	0.50	< 0.001	0.26	0.02	78

*Democratization.*Across all five democratization measures, there emerged a clear pattern in the relative magnitude of correlations (see Table 3). Human-specific parasite richness had the strongest correlations, followed by multihost parasite richness; all these correlations were statistically significant. In contrast, zoonotic parasite richness had relatively weaker relations with democratization measures. In follow-up regression analyses, with all three parasite richness indices entered simultaneously as predictors, human-specific parasite richness remained a robust and statistically significant predictor of all five outcome measures (all *p*s < 0.001). These regression analyses revealed a unique effect of multihost parasite richness on one of the five democratization measures (Vanhanen's resource distribution measure; *p* = 0.05). These same analyses revealed that any apparent effect of zoonotic parasite richness disappeared entirely or, if anything, reversed in sign. Zoonotic parasite richness was significantly *positively*, rather than negatively, correlated with the EIU democracy index, and with both of Vanhanen's indices, when controlling for shared variance with the other parasite richness indices; *p*s < 0.005.

Table 3. Correlations (Pearson *r*s, accompanied by *p*-values) between each index of parasite richness and each measure of democratization (*N* = the number of countries in each analysis).

	Index of Parasite Richness						
	Human	*p*	Multihost	*p*	Zoonotic	*p*	*N*
Democracy Index (EIU, 2008)	-0.48	< 0.001	-0.26	0.001	-0.02	> 0.10	163
Index of Democracy (Vanhanen, 2003)	-0.55	< 0.001	-0.30	< 0.001	-0.02	> 0.10	168
Resource Distribution (Vanhanen, 2003)	-0.70	< 0.001	-0.43	< 0.001	-0.08	> 0.10	168
Human Freedom Index (Barrett et al., 2001)	-0.51	< 0.001	-0.41	< 0.001	-0.39	< 0.001	214
Restrictions on Rights† (Freedom House, 2007)	0.43	< 0.001	0.32	< 0.001	0.22	0.002	190

† Freedom House measure is scored such that higher scores represent greater restriction on civil liberties and political rights.

Gender Equality. Across 93 countries, gender equality was correlated negatively with indices of both human-specific parasite richness (r = -0.52, p < 0.001) and multihost parasite richness (r = -0.35 p < 0.001). The relation with zoonotic parasite richness was negligible and non-significant (r = -0.09, p = 0.37). In a follow-up regression analysis with all three parasite richness indices simultaneously entered as predictors of gender equality, only the human-specific index remained a statistically significant predictor (p < 0.001).

Ancillary Analyses: Zoonotics, Non-Zoonotics and Livestock. The preceding analyses suggest that relations linking parasite prevalence to human personality and societal values (documented in previous publications) are attributable primarily to the prevalence of non-zoonotic parasites (human-specific and multihost parasites). Compared to the effects of non-zoonotic parasite richness, any effects associated with zoonotic parasite richness were negligible.

Before conclusively ruling out the contribution of zoonotic parasites to these world-wide differences in personality and values, it is important to consider an alternative explanation, based on differential measurement error. It is possible that epidemiologists and health agencies are especially attentive to diseases that are transmitted from human to human, whereas the presence of zoonotic parasites may be relatively poorly recorded. If so, then simply for reasons of differential measurement error, zoonotic parasite richness would be expected to correlate less strongly than non-zoonotics with any outcome variable.

The plausibility of this alternative explanation is undermined by evidence that many zoonotic diseases are monitored by the Centers for Disease Control and Prevention and other relevant agencies worldwide, as zoonotics are thought to be an important source of emerging human infectious diseases (e.g., bird flu; Greger, 2007; Jones et al., 2008). Some zoonotics, however, may escape surveillance by these agencies (e.g., Maudlin, Eisler and Welburn, 2009). One way to address this alternative explanation empirically is to show that the zoonotic parasite-richness index is measured with sufficient fidelity to predict additional outcome variables to which it is conceptually related—such as the presence of livestock within a country. Many zoonotic diseases are contracted from livestock, and so we should observe an especially strong relationship between livestock and zoonotic parasite richness—but only if the index of zoonotic parasite richness is measured with a high degree of validity and reliability.

For 205 countries, we computed the total number of avian and mammalian livestock over the period from 2000 to 2004 (data obtained from the *Global Livestock Atlas* of the World Agricultural Information Center; http://www.fao.org/index_en.htm). To correct for skew and kurtosis, this value was log-transformed prior to analyses. Correlations with the three parasite richness indices were as follows: human-specific, $r = 0.31$; multihost, $r = 0.44$; zoonotic, $r = 0.78$ (all ps < 0.001). In a follow-up regression analysis with all three parasite-richness indices simultaneously entered as predictors, only zoonotic parasite richness remained significantly, positively related to the total number of livestock ($p < 0.001$).

These results reveal that the zoonotic parasite-richness index is measured with sufficient accuracy to be a uniquely powerful predictor in domains of conceptual relevance. Differential measurement error, therefore, is unlikely to account for the fact that non-zoonotic parasite richness predicted cross-national variability in human personality and societal values to a much greater extent than did zoonotic disease richness. The data for each of the analyses in this article are available upon request from the corresponding author.

Discussion

Although there is a substantial body of evidence linking the prevalence of human infectious diseases to human social behavior, prior investigations have been limited by the fact that (a) previous indices of human parasite prevalence represented only a small fraction of the hundreds of infectious diseases that affect human health, and (b) these indices failed to distinguish between different disease categories defined by the mode of transmission. To address these limitations, in this study we employed data bearing on more than 300 different human infectious diseases, we computed separate indices assessing the prevalence of three functionally distinct categories of these diseases (human-specific, multihost, zoonotic), and we examined the extent to which each index uniquely predicted cross-national differences in personality traits and societal values. The results were striking.

Both human-specific and multihost parasite richness predicted uniquely cross-national differences in personality traits and social values. Zoonotic parasite richness contributed little, if at all, to previously documented cross-national relationships between parasite prevalence and sociality. Thus, to the extent that worldwide variation in sociality is predicted by parasite prevalence, this variation appears to be attributable almost entirely to the prevalence of *non*-zoonotic diseases.

Several cross-national differences were especially strongly predicted by human-specific parasite richness. For example, only human-specific parasite richness (but not multihost parasite richness) uniquely predicted differences in extraversion. This highly specific effect fits the functional logic that informs the parasite-stress model of sociality, given that extraversion is defined by behavioral interactions with other humans, but has little bearing on the broader range of behaviors that may expose individuals to inter-species pathogen transmission. Cross-national differences in democratization and gender equality also were more strongly predicted by human-specific rather than multihost parasite richness. This effect may reflect the fact that one fundamental consequence of democratic, egalitarian ideologies is increased proximity to and behavioral contact between a wider range of peoples.

In contrast, human-specific and multihost parasite richness were approximately equally predictive of openness to experience, and of individualistic/collectivistic values. These findings also conform to the functional logic of the parasite-stress model, as both openness and individualism/collectivism have consequences for a broad range of behaviors, including behaviors with implications for interpersonal contact (e.g., approach versus avoidance of unfamiliar peoples), as well as behaviors with implications for inter-species transmission of pathogens (e.g., violation versus conformity to cultural norms pertaining to hygiene).

Intriguingly, there was also one cross-national difference that was predicted especially strongly by multihost (compared to human-specific) parasite richness: female sociosexual orientation. This is the only finding observed here that is not immediately interpretable within our functional framework.

More generally, interpretation of the sociosexuality findings is complicated by a complex set of causal relations involving social value systems, sexual behavior, and parasite transmission. We have seen that as prevalence of non-zoonotic diseases declines, there is greater liberalization of social attitudes and values in general, and of sexual attitudes in particular. In turn, sexual liberalization facilitates transmission of sexually transmitted parasites, and is correlated positively with the prevalence, diversity and virulence of sexually transmitted parasites (Barber, 2008; Celentano, Sifakis, Go, and Davis, 2008; Ewald, 1994). One implication of our results is that female sexual liberalization accompanies a reduction in non-zoonotic (especially multihost) diseases, *in spite of* the fact that this sexual liberalization produces an increase in the threat posed specifically by sexually transmitted diseases. In order to more completely untangle this complicated set of causal relations, it may be necessary to develop even more nuanced parasite-stress measures (e.g., country-level measures specific to sexually transmitted parasites that assess temporal changes in prevalence, variety and virulence).

In contrast to the effects of non-zoonotic disease richness, we found that (when controlling for shared variance with non-zoonotic disease richness) zoonotic disease richness actually related positively with several democracy measures. The direction of this relation is in the direction opposite that expected if zoonosis causes human social psychology and behavior. We can only speculate as to the reason for this positive relation. One possibility is that this relation may reflect the broader trade policies and associated openness to agricultural importation in democratic countries compared to autocratic countries.

The dependent variables that we used span several prior decades. Value systems and parasite stress tend to be regionally stable in general (Fincher et al., 2008; Murray and Schaller, 2010; Thornhill et al., 2009). In large part, the stability of parasite stress is stable because of parasites' adaptation to ecological factors such as temperature and rainfall (Guernier et al., 2004). When parasite stress declines dramatically as a result of increased hygienic and medical infrastructure and technology in a region, there is evidence that values also show the changes predicted by the parasite-stress theory of sociality (see below on the social revolution in the West). Also, our research shows that the contemporary parasite measures we used have the same patterns of covariation across dependent variables, regardless of when the dependent variables were tabulated by prior researchers.

Most broadly, our results have many implications for future research exploring relations between infectious diseases and human sociality. For instance, in addition to investigations that have tested the parasite-stress model of sociality on cross-national data, there are additional studies that have identified correlates of parasite stress across small-scale societies (Low, 1990; Quinlan, 2007). The results of these studies are—like previous cross-national inquiries—limited by the fact that parasite-stress measures did not distinguish between functionally distinct categories of disease (e.g., human-specific, multihost, zoonotic). Therefore, just as our analytic methods allowed a more nuanced interpretation of cross-national results, interpretation of the small-scale society results also is likely to benefit from a similar analytic approach. As well, an important, broad implication of our findings is that investigations into the interactions between parasites and sociality in organisms outside of humans will benefit from considering the distinction between infectious agents that are transmitted between conspecifics versus those that are not.

There are additional implications for processes operating at other levels. It has been argued that ontogenetic infection experiences or lack thereof may be proximate causes that track individuals into collectivism or individualism, respectively, and that other cues of local contagion risk during ontogeny also may be proximate causes (Fincher et al., 2008; Thornhill et al., 2009). Cross-national consequences of parasite prevalence may result from even more subtle ontogenetic processes operating on individuals. For instance, research on non-human mammals reveals that maternal exposure to parasites has effects on offspring social behavior (e.g., Curno, Behnke, McElligott, Reader, and Barnard, 2008), implying epigenetic consequences on individuals' social development. Given our results, one might speculate that these effects are more pronounced under conditions of maternal exposure to non-zoonotic, rather than zoonotic, pathogens. A separate line of research on human cognition reveals that the perceived threat posed by infectious diseases has consequences for prejudicial attitudes and other forms of social cognition (e.g., when the threat of disease is more salient, people express more xenophobic attitudes and less extraverted behavioral inclinations; Faulkner, Schaller, Park, and Duncan, 2004; Mortensen, Becker, Ackerman, Neuberg, and Kenrick, in press). These effects also may be specific to the perceived threat of non-zoonotic, rather than zoonotic, diseases.

There are also implications for predicting effects of public health policy on societal change. Thornhill et al. (2009) noted that the predictions of the parasite-stress model are consistent with the marked increase in the liberalization of social values that began to occur in the West in the 1960s and 1970s (e.g., civil rights, women's rights, gay and lesbian rights, anti-authoritarianism, etc.). In the West, but not outside of it, infectious-disease prevalence was reduced dramatically a generation or two earlier as a result of widespread availability of antibiotics, child vaccination programs, food- and water-safety practices, increased sanitation and vector control (see Thornhill et al., 2009 for documentation). Notably, these public health programs were especially successful in combating non-zoonotic rather than zoonotic diseases. This observation, buttressed by the results reported here, suggests that public health initiatives are most likely to have additional consequences for societies (e.g., promotion of civil liberties and egalitarian value systems) to the extent that those initiatives are effective in reducing the prevalence of non-zoonotic, rather than zoonotic, diseases.

Our proximate model for how humans get their value system and personality is based on condition-dependent psychology. This implies the presence of both low and high infectious-disease stress in the deep-time past generations of humans. Hence, we are not saying that humans are primarily individualistic, nor are they basically collectivistic. Fundamentally, they are both, and which track is taken depends on ontogenetic experiences pertaining to parasite stress in the local ecological setting. The conditionality is not negated by evidence of genetic differences in value systems across countries (Chiao and Blizinsky, 2010). The literature on alternative reproductive tactics in animals reveals that adaptive conditionality, i.e., adaptive phenotypic plasticity, typically is a part of genetically distinct adaptations across populations and species (Oliveira et al., 2008).

Conclusion

The parasite-stress model of human sociality provides an evolutionarily informed explanation of why specific human populations inhabiting different parts of the planet (northern Europe versus southern Europe, for instance) are often described by different traits, different values, and different cultural norms. More strikingly perhaps, it also helps explain why some populations inhabiting different parts of the planet (e.g., equatorial South America and southeast Asia) actually have many cultural traits in common. Thus, in addition to prototypically cultural processes that are sometimes used to explain commonalities among nations (e.g., cultural transmission processes), our research implies that many important cultural commonalities—just like many cultural differences—are attributable partially to evolved processes through which universal psychological tendencies are evoked in response to features in the natural ecology (Gangestad et al., 2006). Further, this work suggests that, among those ecological features, the prevalence of disease-causing parasites exerts a particularly important influence on human psychology and culture. And finally, as we show here, the parasites that seem to have mattered most to cultural outcomes are *not* the zoonotic diseases. Rather, as predicted by the parasite-stress model of human sociality, the parasites that have mattered most are those with non-zoonotic modes of transmission.

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