

Parasite-stress promotes in-group assortative sociality: The cases of strong family ties and heightened religiosity

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Abstract: Throughout the world people differ in the magnitude with which they value strong family ties or heightened religiosity. We propose that this cross-cultural variation is a result of a contingent psychological adaptation that facilitates in-group assortative sociality in the face of high levels of parasite-stress while devaluing in-group assortative sociality in areas with low levels of parasite-stress. This is because in-group assortative sociality is more important for the avoidance of infection from novel parasites and for the management of infection in regions with high levels of parasite-stress compared with regions of low infectious disease stress. We examined this hypothesis by testing the predictions that there would be a positive association between parasite-stress and strength of family ties or religiosity. We conducted this study by comparing among nations and among states in the United States of America. We found for both the international and the interstate analyses that in-group assortative sociality was positively associated with parasite-stress. This was true when controlling for potentially confounding factors such as human freedom and economic development. The findings support the parasite-stress theory of sociality, that is, the proposal that parasite-stress is central to the evolution of social life in humans and other animals.

Keywords: assortative sociality; collectivism; family ties; *Homo sapiens*; individualism; infectious disease; parasites; religion; religiosity; sociality

1. Introduction

Across the world people vary in the magnitude with which they value strong family ties and extended families (Alesina & Giuliano 2007; Gelfand et al. 2004); and people adopt religion and exhibit religious commitment to different degrees across the world in patterns strikingly similar to those of family ties (McCleary & Barro 2006; Norris & Inglehart 2004). In this target article, we argue that the reason some people devalue family ties or eschew religion while others prioritize and embed themselves in family relationships and religion, rests on a central phenomenon of social life called in-group assortative sociality. Such sociality refers to the preferential association among similar individuals who compose an in-group versus out-group or dissimilar others. Phenotypic features such as dress and formal costumes, tattooing and scarification, culinary preference, language and dialect, religion and other belief systems, normative behavior, social displays, rituals, and body-scent mark in-group similarity. Assortative sociality's three general social components are (1) limited dispersal for reproduction from the natal locale, (2) in-group favoritism, and (3) out-group dislike and avoidance – in humans, the three are referred to as

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philopatry, ethnocentrism, and xenophobia, respectively (Fincher & Thornhill 2008a; 2008b). Recent theory – the parasite-stress theory of sociality – and its empirical testing tie the patterns of these three phenomena fundamentally to varying levels of parasite-stress experienced by people, both within a region and across geographic space. We first review this research linking in-group assortative sociality to parasite-stress and then expand it, conceptually and empirically, to include family ties and religious affiliation and commitment. We conduct our analyses both cross-nationally and within a single polity, the United States of America.

2. The parasite-stress theory of sociality

2.1. Foundations

Established knowledge of the ecology and evolution of parasitic disease (=infectious disease = pathogenic disease) provides a foundation for the parasite-stress theory of sociality. Infectious diseases were a major source of morbidity and mortality, and hence of natural selection, in human evolutionary history (Anderson & May 1991; Dobson & Carper 1996; Ewald 1994; McNeill 1998; Wolfe et al. 2007). Human adaptations that defend against parasites comprise the biochemical, cellular, and tissue-based *classical immune system*, as well as the *behavioral immune system* that includes (a) anti-parasite psychology and behavior (Schaller & Duncan 2007), and (b) psychology and behavior that manages infectious diseases when they occur. The behavioral immune system is comprised of ancestrally adaptive feelings, attitudes, and values about and behaviors toward out-group and in-group members, caution about or unwillingness to interact with out-group people, and prejudice against people perceived as unhealthy, contaminated, or unclean (Curtis 2007; Curtis et al. 2004; Faulkner et al. 2004; Fincher et al. 2008; Navarrete & Fessler 2006; Oaten et al. 2009; Park et al. 2003; 2007; Schaller & Duncan 2007; Thornhill et al. 2010). The behavioral immune system also includes the same types of bias against contact with nonhuman animals that pose human infectious disease threats (Prokop et al. 2010a; 2010b).

Hosts and their parasites coevolve in antagonistic and perpetual races with adaptation, counter-adaptation, and counter-counter-adaptation for both hosts and parasites (Ewald 1994; Haldane 1949; Ridley 1993; Thompson 2005; Tooby 1982; Van Valen 1973). In the human case, this dynamic, enduring, antagonistic interaction is illustrated by the observation that, despite the huge somatic allocation made to the immune system, people still get sick and even small reductions in immunocompetence increase vulnerability to infectious disease.

Furthermore, host-parasite races are geographically localized across the range of a host species, creating a co-evolutionary mosaic that involves genetic and phenotypic differences in host immune adaptation and corresponding parasite counter-adaptation across a host's range (Thompson 2005). An important outcome of this is that host defense works most effectively against the *local* parasite species, strains, or genotypes, and not against those evolving in nearby host groups. Hence, out-groups may often harbor novel parasites that cannot be defended against by an individual or his or her immunologically similar

in-group members (Fincher & Thornhill 2008a; 2008b). Out-group individuals pose the additional infectious-disease threat of lacking knowledge of and therefore violating local customs or norms, many of which, like hygiene and methods of food preparation, may prevent infection from local parasites (Fincher et al. 2008; Schaller & Neuberg 2008). Norms of many types – culinary, linguistic, moral, sexual, nepotistic, religious, dress-related, and so on – are used by people both to portray in-group affiliation and associated values and to distinguish in-group from out-group members. Norm differences between groups are often the basis of intergroup prejudice and hostility (i.e., xenophobia). Likewise, norm similarity is the basis of positive valuation and altruism among people (Norenzayan & Shariff 2008; Park & Schaller 2005).

Evidence for geographically localized host–parasite coevolutionary races is convincing. On the parasite side of the race, parasite geographical mosaics were found, for example, in recent research on the important human parasite *Leishmania braziliensis*. Rougeron et al. (2009) described the high genetic diversity and subdivided population structure of this parasite across both Peru and Bolivia. They found high levels of microgeographic variation identifiable by at least 124 highly localized, physiologically and genetically distinct strains. The strains showed strong evidence of high degrees of close inbreeding and thus resembled genetic clones. This extremely fine-grained geographic mosaic in *L. braziliensis* implies a similar microgeographic population and genetic mosaic in human hosts. This type of spatial variation in host adaptation against local parasites, or, said differently, in host immune maladaptation against out-group-typical parasites, is a general pattern in the animal and plant infectious disease literature (e.g., Corby-Harris & Promislow 2008; Dionne et al. 2007; Kaltz et al. 1999; Thompson 2005; Tinsley et al. 2006). Human cases showing this include the caste-specific infectious diseases and corresponding specific immunity among sympatric Indian castes (Pitchappan 2002). Indeed, McNeill (1998) and Mattausch (in press) have suggested that the castes of India formed in part from differential cultural responses to parasite-stress. Another case is found in the village-specific immune defenses against leishmania parasites in adjacent Sudanese villages (Miller et al. 2007). In particular cases the localization is so fine-grained that human hosts inbreed, risking the potential costs of inbreeding depression, in order to maintain coadapted gene complexes important for their offsprings' defense against local parasite infection, as Denic and colleagues have found for malaria (Denic & Nicholls 2007; Denic et al. 2008a; 2008b; also Hoben et al. 2010).

Further evidence of localized immunity derives from events where humans from isolated groups interact with novel groups by conquest or trade and infectious disease transmission ensues, sometimes with drastic effects. This has occurred after intra- and inter-continental movement of individuals brought about inter-group contact (Diamond 1998; Dubos 1980; Good 1972; Jenkins et al. 1989; McNeill 1998). Other human examples of localized immunity are reviewed in Fincher and Thornhill (2008a) and Tibayrenc (2007). Final evidence for local host adaptation to parasites is found in the literature showing that the hybridization between adjacent, closely related conspecific populations results in hybrid offspring with reduced

immunocompetence (e.g., house mice: Sage et al. 1986; cottonwood trees: Floate et al. 1993; also see Thompson 2005 for other examples).

Because of localized host immune adaptation in an ecological setting of high disease stress, xenophobia, ethnocentrism, and reduced dispersal are adaptive preferences/values and behaviors for avoidance of novel parasites contained in out-groups and the management of local infectious disease. Philopatry – the absence or low level of dispersal away from a natal area for reproduction – reduces contact with out-groups and their habitats that may contain new parasites. Likewise, xenophobia – the avoidance and dislike of out-group members – discourages contact with out-groups and their likely different parasites. Ethnocentrism – in-group favoritism and embeddedness entailing nepotism toward both nuclear and extended family, as well as altruism toward unrelated, yet immunologically similar, in-group members – focuses prosociality among in-group members, and fosters the supportive social networks for coping with present infections in members of the in-group. Thus, philopatry, xenophobia, and ethnocentrism – elements of in-group assortative sociality – are predicted to be strongly held values in areas of high parasite-stress (also see Fincher et al. 2008; Thornhill et al. 2009).

Parasite-stress is not the same across the globe nor has it been the same across time. Humans have experienced parasite gradients throughout history and continue to do so today (Crawford 2007; Dobson & Carper 1996; Guernier et al. 2004; Lopez et al. 2006; Low 1990; McNeill 1980; 1998; Smith et al. 2007; Wolfe et al. 2007). Hence, we expect that the benefits and costs of in-group assortative sociality will shift along the parasite-stress gradient such that in some areas (of high parasite-stress) high levels of in-group assortative sociality will be more beneficial than in other areas (of low parasite-stress). As parasite-stress declines, the infectious-disease contagion risks to individuals from interaction with out-groups decrease. Consequently, for individuals in areas that are relatively low in parasite-stress, out-group contacts and alliances may provide greater benefits than costs. The benefits of out-group interactions include gains through intergroup trade, new and better ideas and technology, and diversified and larger social networks for marriage and other social alliances (Fincher et al. 2008; Thornhill et al. 2009).

McElreath et al. (2003) and Nettle (1999) argued that assortative sociality could cause cultural isolation and, hence, cultural divergence and emergent new cultures in the absence of geographic barriers (e.g., unfavorable habitats or unsurpassable mountain ranges) that fractionate a culture's distribution. Building on this, we argued that given the ecological localization of host defenses against parasites, the three components of assortative sociality – limited dispersal, ethnocentrism, and xenophobia – fractionate populations and thereby cause their cultural and evolutionary independence (Fincher & Thornhill 2008a; 2008b). Therefore, the parasite-stress model includes a theory about the genesis of cultural or ethnic diversity, and some of the predictions related to this aspect of the model have been empirically supported. We have shown that endemic religion diversity (both major religions and ethnoreligions), as well as indigenous language diversity, across contemporary countries worldwide are related strongly and positively to parasite-stress (Fincher & Thornhill 2008a; 2008b). Also consistent with the

ethnogenesis aspect of the parasite-stress model was Cashdan's (2001a) finding for traditional peoples in the ethnographic record that high parasite-stress regions have more ethnic groups than low parasite-stress regions.

The parasite-stress theory of sociality posits an adaptive (ancestrally) condition-dependent adoption of in-group and out-group social tactics by individuals dependent on local parasite-stress. This condition-dependent adaptation requires local variation in morbidity and mortality from parasite severity, as the selection that acted historically in favoring contingent assortative-sociality behavioral and psychological adaptations. The evolution of conditional response as an important feature of assortative sociality's design, rather than exclusive fixity of localized genetically distinct adaptations, is consistent with knowledge about infectious diseases. The dynamics of an infectious disease can generate high variation in incidence, prevalence, transmissibility, and pathogenicity of the disease agent across the range of its host species, as well as on a very fine-grained, local scale. Factors affecting this variability at a single locale are temporal changes in host group size, climate and weather, disease-vector abundance and behavior, and the number and dynamics of the different infectious diseases infecting a host (Anderson & May 1991; Corby-Harris & Promislow 2008; Ewald 1994; Guernier et al. 2004; Prugnolle et al. 2005). The dynamic nature of host-parasite coevolution itself creates localized variation across generations in parasite-stress (Hamilton & Zuk 1982).

In-group assortative sociality is an example, we argue, of adaptive phenotypic plasticity, that is, of a conditional strategy with multiple contingent tactics (Fincher et al. 2008; Schaller & Murray 2008; Thornhill et al. 2009). Such plasticity in traits is favored when phenotypic change allows the individual to modify phenotypic expression in directions that give higher inclusive fitness than that achieved by a single phenotype. Conditional strategies in behavior, psychology, development, and physiology are very common across animal taxa (West-Eberhard 2003). Socially learned or cultural behavior in humans is a category of behavioral and psychological plasticity that evolved, at least in part, as a solution to the evolutionary historical fitness problem of local social complexity and change (Alexander 1979; Flinn 1997; Flinn & Coe 2007). We have argued that a significant part of this complexity and change likely arose from local people's adjustments in in-group and out-group oriented behavior to deal adaptively with temporally varying parasite problems (Thornhill et al. 2009).

The characterization of human in-group assortative sociality as a contingent, "plastic" phenotype includes cultural transmission via social learning that is conditional on local optima in values. Accordingly, culture is not evoked and transmitted passively, but instead is actively evoked and transmitted by psychological adaptations for enculturation that discriminate cultural elements incorporating the elements that have local utility and discarding elements that do not. We hypothesize that the ontogeny of people includes design by Darwinian selection to choose ideas, ways of thinking, and attitudes – that is, choose values – that correspond to routes of ancestrally adaptive social navigation in their community/local culture. The recognition that individuals choose their values is quite old in the sociological and psychological literature (see Jost et al. 2009). We add to this traditional

sociological view with our proposal that the choices are by evolved design and, specifically in regard to values of assortative sociality, they are guided by psychological adaptations dedicated to the function of value acquisition to meet ecological adversity and demands pertaining to infectious-disease stress (for views compatible with this hypothesis for cultural acquisition, see Alexander 1979; Billing & Sherman 1998; Boyd & Richerson 1985; Gangestad et al. 2006b; Henrich & Henrich 2010; Schaller 2006).

However, we do not restrict application of the parasite-stress theory of sociality only to humans and other cultural animals. Therefore, we include in our article aspects of the behavioral immune system that can be considered even in acultural species.

Furthermore, our emphasis on adaptive contingency in the expression and adoption of human assortative sociality does not imply that we expect no region-specific variation across human societies in genetic adaptation for assortative sociality. Culture-gene coevolution may produce genetically differentiated cross-cultural variation in the values and behaviors of assortative sociality. For example, in areas of high parasite prevalence, cultural practices of philopatry, ethnocentrism, and xenophobia may effectively select for alleles affecting psychological features that promote the learning and use of these practices (Fincher et al. 2008). Our argument is that infectious disease problems are locally variable, and hence, significant conditionality will be favored and maintained by selection even in the presence of region-specific genetic adaptation functioning in local adoption and use of values and behaviors. Boyd and Richerson (1985), Cavalli-Sforza and Feldman (1981), and Lumsden and Wilson (1981) treat culture-gene coevolution in detail. There is evidence that it may play a role in cross-national variation in the value dimension *collectivism-individualism* (Chiao & Blizinsky 2010), a dimension related importantly to topics in this article. That genetically distinct adaptations for coping with an ecological problem and condition-dependent adaptation for the same problem domain can co-occur, is well established in the literature of alternative reproductive tactics (see recent review in Oliveira et al. 2008).

A considerable body of research supports the hypothesis of an evolved contingent assortative sociality in people that functions against infectious disease. For example, Faulkner et al. (2004) and Navarrete and Fessler (2006) provide evidence, based on numerous and diverse Western samples, that scores among individuals on scales that measure the degree of xenophobia and ethnocentrism correspond to chronic individual differences in perceived vulnerability to infectious disease; those who perceive high disease risk are more xenophobic and ethnocentric than those who perceive low disease risk. This research also shows that xenophobia and ethnocentrism within individuals increases under experimental primes of greater disease salience in the current environment. A related recent study (Schaller et al. 2010) reports that research subjects who observed slides of people with disease symptoms (e.g., pox, skin lesions, sneezing) immediately mounted a classical immune response. Their white blood cells produced elevated amounts of inflammatory cytokine-interleukin-6 when exposed to bacterial antigens. This immune response was not seen in research subjects who viewed control slides, including slides depicting a person pointing a gun directly at the viewer. Hence, the immune response was not a general reaction to danger or threat, but

was specific to cues of other people with symptoms of parasitic infection (Schaller et al. 2010).

Moreover, a recent study by Mortensen et al. (2010) reports that subjects viewing slides with disease-salient cues immediately exhibited greater feelings promoting between-person avoidance (reduced extraversion and openness to experiences) in comparison to these subjects' feelings upon viewing control slides. These researchers also found that subjects with high scores on perceived vulnerability to disease showed greater feelings of interpersonal avoidance than did subjects with low scores on the same scale. Finally, this same paper reports that viewing parasite-salient slides resulted in increased avoidant arm movements when subjects viewed facial photos of strangers, especially for subjects high in perceived vulnerability to disease. In sum, the studies by Schaller et al. (2010) and Mortensen et al. (2010) reveal that visually perceiving cues pertinent to risk of parasitic infection generates an immediate immune response and a change in perceptions of one's own personality and behavioral actions that defend against or avoid infectious people. Hence, such cues markedly activate the classical immune system as well as the behavioral immune system.

In sum, there is considerable evidence of both inter-individual chronic differences as well as within-individual conditionality in xenophobic and ethnocentric values and related personality features and behaviors, and that both the inter-individual consistency and within-individual contingency are caused by infectious-disease problems in the local environment.

Proximate mechanisms by which individuals assess local parasite-stress – and thereby ontogenetically and contingently express the locally adaptive degree of defensive assortative sociality – may include immune system activation (such as, the frequency of infection; Stevenson et al. 2009) and social learning of local disease risks, as well as direct observation of parasite threat (as evidenced in the studies mentioned just above). All of these mechanisms may act in combination and account for both the inter-individual and within-individual variation in values affecting in- and out-group behavioral preferences comprising assortative sociality. The recent research by Stevenson et al. (2009) reports that people with high contamination sensitivity and disgust sensitivity, which are thought to be emotional defenses against parasitic infection, had fewer recent infectious diseases than people with low sensitivities, providing evidence of a protective function of these emotions against these diseases. These researchers also found that high contamination sensitivity, in particular, was associated positively with a person's history of contracting infectious diseases (but not with recency of infections), implying that an ontogeny and conditionality of repeated activation of the classical immune system may underlie the adoption of the values associated with assortative sociality.

2.2. Cross-cultural evidence for the parasite-stress theory of sociality

We mentioned in section 2.1 that the parasite-stress theory of sociality led to the discovery of global patterns in the diversity of religions and languages. The theory has been tested and supported by additional, recent cross-cultural studies, which we describe next.

The parasite-stress model predicts that philopatry should be positively associated with infectious disease stress. We tested this prediction by examining human societal range size (a measure of dispersal) in relation to parasite-stress for a large sample of traditional societies in the anthropological record (339 societies), and found that range size was smaller where pathogen stress was higher, indicative of adaptive philopatry as defense against parasites (Fincher & Thornhill 2008b). It is possible that the reduced range size in high pathogen-stress regions is due to the malaise and inactivity of parasitized individuals. However, this apparently is not the case. According to our analysis in Fincher and Thornhill (2008b), people in traditional societies move more often but over shorter distances in high parasite-stress areas than do people in low parasite-stress areas.

High xenophobia and ethnocentrism correspond to the Western value system referred to as conservatism, whereas low xenophobia (i.e., high xenophilia toward out-groups) and restricted ethnocentrism (i.e., focus on nuclear family) correspond to more liberal values (see Navarrete & Fessler 2006; Thornhill et al. 2009). Furthermore, conservatism–liberalism overlaps considerably with the well-studied cross-cultural value system referred to as “collectivism–individualism” by cross-cultural sociologists and psychologists. Conservatism and collectivism are similar in their heightened xenophobia and ethnocentrism inclusive of the extended family and other in-group members with similar conformist and traditional values, whereas liberalism and individualism are similar in nuclear-family-focused nepotism and relatively high xenophilia (Barnea & Schwartz 1998; Fincher et al. 2008; Gelfand et al. 2004; Georgas et al. 2001; Oishi et al. 1998; Sagiv & Schwartz 1995; Schwartz 2004; Triandis 1995). In contemporary societies, collectivists and individualists differ significantly in their view of the social structure of the society in which they reside. Collectivists emphasize the boundary between in-group and out-group and are distrusting of and unwilling to contact out-group members; individualists make less distinction between in- and out-groups, and are more trusting of and show more willingness to contact out-groups (Gelfand et al. 2004; Oishi et al. 1998; Sagiv & Schwartz 1995).

Fincher et al. (2008) showed that the unidimension of collectivism–individualism across many countries of the world is predicted strongly by infectious disease prevalence. High parasite-stress is associated with high collectivism (low individualism), and low infectious disease risk with low collectivism (high individualism). Murray et al. (2011) showed that cultural emphasis on conformity was positively related to pathogen prevalence across many countries. Other recent cross-national studies showed that collectivism, autocracy, traditional gender roles (women’s subordination relative to men’s higher status), and women’s traditional sexual restrictiveness and continence are values that positively covary with one another, and occur in nations with high prevalence of infectious disease. The assortative sociality adaptations of xenophobia and ethnocentrism link these values to avoidance and management of parasites. Also, the antipoles of each of the values – individualism (hence, liberalism), democracy, and women’s political rights, freedom, and increased participation in casual sex – are a positively covarying set of values and are found in countries with relatively low parasite-stress (Gangestad

et al. 2006a; Murray & Schaller 2010; Schaller & Murray 2008; Thornhill et al. 2009).

Moreover, Schaller and Murray (2008) found that important components of personality seem to be part of assortative sociality and associated behavioral immunity. They reported that extraversion versus introversion and openness versus closedness to new experiences and ideas correlated with variation in parasite prevalence across many countries of the world. People in high-parasite-stress nations showed cautious personalities conducive to avoiding exposure to contagion from conspecifics – high introversion scores and low scores on interest in new ideas and experiences – whereas people in low-parasite-stress nations showed high extraversion and openness to novelty.

In addition, Thornhill et al. (2010) have shown that, across countries, the relationships between parasite-stress and democratization, gender relations, sexual restrictiveness, and collectivism–individualism are much more strongly correlated with human infectious diseases that are *transmissible* between humans (called nonzoonotics) than with those that are not transmissible between humans (zoonotics). This is a strong test of the parasite-stress theory of sociality because only nonzoonotic human diseases can be contracted from conspecifics; and hence, assortative sociality and related values should be designed to respond primarily to these diseases.

The cross-national patterns we mentioned that support the parasite-stress theory of sociality, depending on the particular analysis, statistically controlled for potential confounders, including Murdock’s (1949) six world regions (see sect. 4.6), a particular region’s history of colonization and conquest, and the respective countries’ latitude, Gross Domestic Product (GDP) *per capita*, wealth disparity, population size, land area, and extent of democratization. The cross-cultural study of philopatry in traditional societies controlled for population size, big-game hunting, world region, and other variables. Relatedly, we reported that across a large sample of contemporary countries, collectivism is positively correlated with philopatry measured as adults remaining throughout life in their natal region (Fincher & Thornhill 2008b).

In sum, we and others have argued that parasite-stress generated past selection that crafted the assortative-sociality psychological adaptation of humans. Accordingly, this adaptation has a condition-dependent functional design, resulting in the contingent expression by the individual of ancestrally adaptive degrees of in-group assortative sociality – arising from its three basic components, philopatry, xenophobia, and ethnocentrism – along a gradient of experienced parasite-stress. Individuals who experience relatively high levels of parasite-stress show greater in-group assortative sociality than those who experience relatively lower levels of parasite-stress (Fincher & Thornhill 2008a; 2008b; Fincher et al. 2008; Murray & Schaller 2010; Schaller & Duncan 2007; Schaller & Murray 2008; Thornhill et al. 2009; see also Freeland 1976; 1979; Loehle 1995 for earlier discussion of related ideas).

3. Extending the theory to family ties and religiosity

Thus far, research indicates that parasite-stress is an important correlate of the values of in-group assortative

sociality as reflected in the cross-cultural elements of democracy, collectivism-individualism, conformity, dispersal behavior, and the personality components, openness and extraversion. Two other important elements of social life that appear to represent in-group assortative sociality are strong family ties and religiosity. Neither of these two topics has been placed, we feel, in the appropriate context of their causation by parasite-stress generating adaptive in-group assortative sociality. In the next sections, we develop hypotheses to explain the global patterns for these two phenomena based on relative variation in parasite-stress and then demonstrate, through empirical analyses involving most of the countries of the world as well as interstate comparisons within the United States, the centrality of parasite-stress for explaining the cross-cultural patterns of family ties and religiosity.

3.1. Strength of family ties

No one is without parents; but individuals do differ in the amount that they rely on or invest in their parents and other members of their family. Some people invest only in themselves or maybe at most in their nuclear family (spouse and children), while others consider themselves completely interdependent on a much larger extended family that includes not only spouses and children but also their parents, siblings, grandparents, cousins, uncles, aunts, nieces and nephews, and so on. Why this variation exists has been frequently discussed by scholars and it is generally attributed to differences in relative economic prosperity. For example, Inglehart and Baker (2000) provided evidence suggesting that countries that have relatively low wealth are also characterized by people who generally rely on their extended families; whereas people who live in countries with high levels of wealth are more able to strike out on their own because of the greater opportunities associated with greater wealth (see also Gelfand et al. 2004).

Intense loyalty and interdependence on the family (i.e., strong family ties) are generally considered important components of the cross-cultural dimension of collectivism-individualism, with collectivism positively associated with strong family ties in multiple cross-cultural studies (e.g., Alesina & Giuliano 2007; Gelfand et al. 2004). Often, collectivism is indexed by measuring the relative importance of the family. For example, Vandello and Cohen (1999) developed a measure of collectivism for each of the states in the USA that includes scores for family loyalty and interdependence. The distribution of collectivism-individualism across the globe has been explained by the distribution of wealth across the world in the form of GDP with the highest levels of collectivism associated most strongly with lowest levels of societal wealth (Hofstede 2001; Kashima & Kashima 2003; Triandis 1995). This is consistent with the argument that prosperity can explain patterns of family interdependence.

There is an alternative view, however (Fincher et al. 2008). Along with an emphasis on interdependence, collectivistic attitudes are generally associated with an unwillingness to contact or otherwise interact with out-group members (Gelfand et al. 2004; Oishi et al. 1998; Sagiv & Schwartz 1995). As described in section 2.2, Fincher et al. (2008) argue that this reflects the importance of avoiding out-group members, who may carry infectious

diseases that an individual is not able to cope with. Relatedly, collectivism is adaptive under high levels of parasite-stress by providing the benefits of disease avoidance and management, while widespread individualism under low levels of parasite-stress provides benefits in terms of increased out-group interaction (e.g., increased sharing of goods and innovations). Our studies of multiple, separate but conceptually related measures of collectivism-individualism support this view (Fincher et al. 2008; Thornhill et al. 2010). We make a similar argument for the importance of strong family ties – in areas with high levels of parasite-stress people will value strong family ties more than in regions with low parasite-stress. This reflects the importance of xenophobia for the avoidance of out-group members and of ethnocentrism for the development and maintenance of supportive in-group networks in the face of parasite-stress.

Current evidence that supports this comes from studies of traditional societies. To paraphrase Navarrete and Fessler (2006), in human evolutionary history, when under parasite attack, in-group members were the only health insurance one had, and it was adaptive to have always paid your premiums – in terms of social investment and loyalty toward in-group allies that buffer an individual and his or her family against the morbidity and mortality of infectious disease. The support and loyalty toward in-group members was an individual's defense against the morbidity and mortality effects of parasites (Navarrete & Fessler 2006; Sugiyama 2004; Sugiyama & Sugiyama 2003). Sugiyama (2004) reported that among the Shiwiari, an Amazonian society without ready access to modern medicine, health care in the forms of food and other assistance from in-group members to persons suffering from infectious diseases was a major factor in lowering the mortality rate. This pattern, in general, seems to characterize numerous traditional human societies in the ethnographic record (Gurven et al. 2000; Hill & Hurtado 2009; Sugiyama 2004; Sugiyama & Sugiyama 2003).

Thornhill et al. (2010) show as well that parasite-stress was positively associated with a measure of family ties across modern countries. In this target article we explore a new measure of the strength of family ties at the cross-national level, using updated World Values Survey files from a recently produced, public dataset which was unavailable at the time of Thornhill et al. (2010). We also provide a novel empirical examination of parasite-stress in relation to a measure of collectivism across the states of the United States of America (Vandello & Cohen 1999) and to a component of this measure that taps family-ties specifically.

3.2. Religiosity

Participation in a religion has certain costs for the participant, which include the time and effort involved in learning a religion and practicing it, the loss of opportunity to engage in other beneficial activities (opportunity costs), and risks such as the avoidance of modern medical care or extended fasting (Sosis et al. 2007). To learn the emotionality and associated language of a religion requires a long developmental (ontogenetic) exposure to the belief system. Opportunity costs include the inability to associate with other groups because one's specific beliefs may be considered irrational or contra-evidentiary to out-group

members. (On irrationality as a functional component of religiosity, see Irons 2008).

This premise – that religious participation has costs – is a basis for studying religiosity from both the economic and the evolutionary science perspectives. From the economics viewpoint, Azzi and Ehrenberg (1975) presented an analysis of individual religiosity as a function of the maximization of household allocation of time and found that people were attempting to rationally engage in religious behaviors such that they maximized the return on their time investments. Iannaccone has done much to formalize this economic investigation of religiosity (e.g., Iannaccone 1990; 1994, among others). Iannaccone (1990) used economic theory to show that people employ sophisticated cost-benefit analyses often maximizing their investments when engaging in religious behaviors. Iannaccone (1994) used rational choice theory to examine the relationship between a church's religious strictness and its strength or permanence, and concluded that, "Strictness reduces free riding. It screens out members who lack commitment and stimulates participation among those who remain" (p. 1204). In other words, paying-in indicates commitment but it also precludes desertion to other churches, because it is too costly to desert and then develop the same level of embeddedness in a new church. Therefore, individuals in strict churches exhibit higher rates of participation because they are assured, in comparison to individuals in less strict churches, a higher level of return on their investment through the reduction of free-riders and a higher level of investment by other individuals in the church. Iannaccone (1994) observed that there is variation among churches in strictness and hence in the average religiosity among its members. That same research established that the strictest churches, those that require the highest costs for continued membership, have the tightest and most permanent collectives.

Many researchers have applied evolutionary costly-signaling theory to the understanding of religion and religious behavior (Bulbulia 2004a; 2004b; Cronk 1994; Henrich 2009; Irons 1996; 2001; Johnson 2008; Sosis 2000; 2003; 2005; Sosis & Alcorta 2003; Sosis & Bressler 2003; Sosis & Ruffle 2003; Steadman & Palmer 2008; Wilson 2002). This approach builds on the same foundation as the economic study of religious behavior – that religious participation has costs. Evolutionary science deepens our knowledge by providing methods that can pinpoint not only how benefits are maximized currently (also called the proximate-level of understanding), but also how benefits were maximized historically (also called ultimate-level of understanding). Through adaptationist study, evolutionary science has the ability to discover the historical setting in which a phenotypic feature that is an evolved adaptation, yielded net reproductive benefits (inclusive fitness) to its bearers (Andrews et al. 2002; Thornhill 1990; Williams 1966). The researchers using costly-signaling theory propose that membership in a religious group is necessary for individuals to accrue certain social benefits not accessible independently, and that engaging in religious behavior is a signal of in-group allegiance to other individuals (both in-group and out-group individuals). The greater the costs of religious participation, the more honestly the participation signals allegiance to the religious in-group. The high costs of religiosity mentioned above are ideal for honestly signaling

embeddedness in and commitment to an in-group with a particular spiritual belief system. Religion is often defined as a value system that is based on supernatural phenomena (Boyer 2001). This defining feature of religiosity has the high cost of displaying belief in the power of supernatural phenomena – phenomena that are generally considered antithetical to the empirical data humans gather from sensory experience (Irons 2008). Religious groups adopt their own distinct costly versions of supernatural beliefs in order to heighten costs of participation and distance themselves from out-groups.

Sosis (2000) and Sosis and Bressler (2003) provided supportive evidence for the costly-signaling theory of religion by studying the longevity of 19th century United States communes. Sosis (2000) found that religious communes in comparison to secular ones had longer life spans, and Sosis and Bressler (2003) found that longevity for religious communes was positively related to the magnitude of the costly acts required for membership within a commune (e.g., restriction from alcohol and sex). A logical prediction from the costly-signaling perspective, put in evolutionary theoretical terms, is that the adaptive value of religious signaling to signalers, and hence the magnitude and associated costs of the signal, will vary from place to place based on the underlying ecological necessity of in-group assortativeness for inclusive fitness maximization (also see, Sosis et al. 2007). According to the parasite-stress model, this ecological necessity is determined by parasite-stress variation across regions.

We argue that the maintenance of in-group assortativeness by practiced and signaled religious allegiance provides two benefits: (a) the protective barrier provided by separation from out-group individuals who may harbor novel infectious diseases and/or perform non-normative behavior; and (b) in-group embeddedness that reduces the morbidity and mortality caused when infectious disease invades the in-group. Hence, measures of the importance of religion for people in an area (religiosity) should be predictable based on the area's position along the parasite gradient, reflecting the average infectious disease stress experienced by people in the region. Therefore, we hypothesized that religious participation and commitment, indicating the importance of in-group assortative sociality, would be positively related to parasite-stress across regions.

One of the assumptions of our hypothesis is that there is a positive relationship between religiosity and out-group dislike or in-group preference. Evidence supporting this is found in a few studies. For example, Jackson and Hunsberger (1999) conducted a study of the relationships between individuals' religiosity and their prejudicial attitudes toward religious and non-religious others. They found that the religious participants showed significant positive attitudes towards in-group-religious others but negative attitudes towards non-religious others. As well, the magnitude of the prejudice was correspondent to the individual's own level of religiosity. That is, a participant who scored highly on religious fundamentalism also scored highly on out-group prejudice. In a separate study, Bulbulia and Mahoney (2008) demonstrated that New Zealand Christians were more altruistic toward Canadian Christians than were New Zealand citizens to other New Zealand citizens. Similarly, Widman et al. (2009) showed that individuals with strong Christian

beliefs were more likely to rate others displaying a symbol of Christianity (a cross) as more kind and moral than others not displaying such a symbol. These studies support our assumption. They also suggest, on the one hand, the importance of religiosity as a marker of in-group membership, and, on the other hand, an underlying mental mechanism within individuals to measure religious similarity. Such a mechanism was indicated by Park and Schaller (2005), who found that when people experienced attitudinal similarity with others, they considered them more like family than when attitudes were dissimilar. Furthermore, there is convincing evidence that religious prosociality is primarily in-group altruism (Norenzayan & Shariff 2008).

In a study supportive of the proposal we present (albeit this study was not designed to test the parasite-stress model), Saroglou et al. (2004) conducted a meta-analysis of the relationships between Schwartz's model of 10 cross-culturally stable, core values (Schwartz 1992) and religiosity. Saroglou et al.'s (2004) meta-analysis focused on 21 samples from 15 countries (total $n = 8551$ people). They discovered that religious people favored values that promoted social order (mainly the values *Tradition* and *Conformity*) but disliked values that promoted openness to change and autonomy (*Stimulation* and *Self-Direction*). This was true across a variety of religions (i.e., Christians, Jews, and Muslims) and countries from Europe, North America, and the Middle East. Interestingly, the positive correlation between religiosity and "conservation" (=conservative) values (*Conformity*, *Tradition*, and *Security*) and the negative relationship between religiosity and openness to change and autonomy (*Stimulation* and *Self-Direction*) showed greater effect sizes in a sample of Mediterranean countries in contrast to a sample of Western European countries. Mediterranean countries have greater levels of parasite-stress than Western European countries (Fincher & Thornhill 2008b; Guernier et al. 2004).

The question may be raised: If a signal such as religious identity is strong enough to function as a social boundary, then why are multiple signaling modalities (e.g., language and religion) used to indicate in-group allegiance? Signaling systems across species typically show redundancy across components or modalities (Searcy & Nowicki 2005). This is thought to enhance communication, given that each signal is imperfect in information content but, combined, they provide greater accuracy. Redundancy is seen in human signaling of in-group affiliation and boundary. A combination of signals involving religiosity, language or dialect, word use, dress, music, smell, and so on comprise a redundant suite of honest signals about one's group membership and embeddedness.

3.2.1. Other models to explain cross-cultural differences in religiosity.¹ McCleary and Barro (2006) have explored the validity of the secularization hypothesis that economic development causes lower levels of religiosity among individuals. Inglehart and Baker (2000) and Norris and Inglehart (2004) have suggested that individuals reduce religiosity when conditions of living are benign but become religiously embedded under dire conditions of hardship and high mortality salience (i.e., the existential security hypothesis). In both models, people are less religious in areas where they have less "need" of a religion and the benefits that it offers. We refer collectively to

the secularization hypothesis and the existential security hypothesis as the "conditions-of-living" model. The conditions-of-living model has been tested and supported, in part, by examining the relationships between religiosity and economic conditions across countries. McCleary and Barro (2006) focused on GDP *per capita* as the most indicative marker of economic development, demonstrating significant negative relationships between economic development and religiosity. Norris and Inglehart (2004) showed large differences in religiosity between wealthy and poor nations, providing positive support for their hypothesis that people living in poor conditions also show greater religiosity. More recent tests found support for the conditions-of-living model: Rees (2009) discovered a positive relationship between income inequality (used as a proxy for personal insecurity) and religiosity across many nations, and Delamontagne (2010) found that social inequality (measured by inequalities in education, income and race) was highly, positively predictive of religiosity in the United States.

There is clearly overlap between the conditions-of-living model and our proposed framework because high levels of infectious diseases are a component of "dire conditions" and low economic development. Indeed, both Inglehart and Baker (2000) and McCleary and Barro (2006) mention disease differences across countries and explicitly try to treat disease in their analyses by including a country's latitude (latitude is negatively correlated with infectious disease stress; e.g., Guernier et al. 2004). Our approach is different in that it incorporates the evolutionary history of *Homo sapiens* into the research framework for generating hypotheses and predictions. Our model relies on specific aspects of the biology of infectious diseases and incorporates these processes into the hypothesized design of the human mind and human behavior by Darwinian selection acting in the context of parasite-stress. 334.3n9i52mplcorBtw436523.3(predictio)-9.9ed,use43-684

then, a positive relationship between the strength of family ties and parasite-stress across nations and across the states of the United States of America.

4.1.1. Cross-national²: Strength of Family Ties. We compiled a new measure of the strength of family ties which assesses the importance of family loyalty and interdependence. It is similar to that used by the GLOBE project (House et al. 2004), and by Alesina and Giuliano (2007) and Thornhill et al. (2010), but is more encompassing and updated. Data for the five items comprising our index came from the 1981–2007 pooled dataset of the World Values Survey across 72 countries (see the *Electronic Supplement 1.A* [ES 1.A], which can be viewed at <http://www.journals.cambridge.org/bbs2012001>). All five components were summed to become our measure, *Strength of Family Ties*. Larger values indicate stronger family ties while smaller values indicate weaker family ties. The data are provided in the *Electronic Supplement 2* (ES 2) which can be viewed at <http://www.journals.cambridge.org/bbs2012002>.

4.1.2. United States³: Collectivism and Strength of Family Ties USA. In order to investigate family ties in the United States we used a measure of state-level collectivism compiled and validated by Vandello and Cohen (1999) because collectivism includes strong family ties; it also includes preferential assortment with in-group members outside the extended family (Fincher et al. 2008; Gelfand et al. 2004; Hofstede 2001; Thornhill et al. 2009; Triandis 1995). Vandello and Cohen (1999) measured collectivism (referred to here as *Collectivism*) across the U.S. states by standardizing and summing eight items obtained from state data archives (ES 1.B). Larger values indicate greater collectivism (or less individualism) while smaller values indicate lower levels of collectivism (or more individualism). We extracted from the same sources data for the three components that specifically address family ties as described by Vandello and Cohen (ES 1.B). The three items were combined to become the variable *Strength of Family Ties USA*. Larger values indicate stronger family ties while smaller values indicate weaker family ties. The data are provided in the *Electronic Supplement 3* (ES 3) which can be viewed at <http://www.journals.cambridge.org/bbs2012003>.

4.2. Religiosity

We predicted a positive association between religiosity and parasite-stress cross-nationally and across the states of the United States of America. To test this we indexed religiosity with two measures: (a) religious affiliation, and (b) religious participation and value. In the next sections, we describe how these variables were constructed for the cross-national and interstate analyses.

4.2.1. Religious affiliation. According to the parasite-stress model, people in areas with more parasite-stress will adhere to local religious systems to a greater extent than individuals in areas with low parasite-stress. This is because the values of people in areas with low parasite-stress provide them with greater flexibility in whether they adhere to a religion or not, or they may make up their own system of secular beliefs. The benefits of

heightened in-group assortative sociality are predicted to be higher in high parasite-stress areas than in low parasite-stress areas. Hence, we predict that the proportion of religionists in an area would be positively correlated with parasite-stress because higher levels of parasite-stress can potentially increase the costs of nonconformity to in-group values and norms. We describe next our measures of religious affiliation for both the cross-national and the United States analyses.

4.2.1.1. Cross-national: Proportion of Religionists. To construct this variable, we extracted the proportion of non-religionists for the year 2000 from the World Christian Encyclopedia (Barrett et al 2001), an oft-used and highly regarded resource in religious scholarship (Grim & Finke 2006). Non-religionists include the two forms of nonbelievers: agnostics and atheists. The proportion of non-religionists within nations ranged from 0 (e.g., Afghanistan) to 55.6% (Democratic People's Republic of Korea) ($n = 230$ countries). The proportion of non-religionists was subtracted from 1 to yield our analytical variable, *Proportion of Religionists*, which was arcsine-square-root transformed.

4.2.1.2. Cross-national: Proportion of Believers. For the *Proportion of Believers* we used the inverse of the “proportion of nonbelievers in God” as presented in Lynn et al (2009; this is a tabulation of data described in Zuckerman 2007). This measure relies in part on values from the World Christian Encyclopedia (Barrett et al. 2001) but incorporates many other survey sources and likely provides more reliable estimates. The proportion of nonbelievers ranged from .5% (e.g., Cameroon) to 81% (Vietnam) ($n = 137$ countries). The values were subtracted from 1 to represent the *Proportion of Believers*, which was arcsine-square-root transformed. The *Proportion of Religionists* and the *Proportion of Believers* were positively correlated ($r = .67$, $n = 137$, $p < .0001$).

4.2.1.3. United States: Proportion of Religionists USA. The 2001 American Religious Identification Survey (ARIS; Kosmin et al 2001) was a telephone survey of 50,281 households. The survey asked, “What is your religion, if any?” From this, we obtained the proportion of respondents that indicated “no religion” for each state (Hawaii and Alaska were not included in the ARIS 2001). The “no religion” proportion/state value was subtracted from 1 to represent the *Proportion of Religionists USA*, and then arcsine-square-root transformed.

4.2.1.4. United States: Proportion of Religious Adherents. The Association of Statisticians of American Religious Bodies conducted a study of 149 religious bodies in the United States over the years 1999–2001 to assess the number of congregations in each state within the USA. The study produced a measure of the total adherents of each congregation providing a comprehensive measure of the total religious adherents in each state. These data comprised our interstate variable, *Proportion of Religious Adherents* (ES 1.C), which was arcsine-square-root transformed. The *Proportion of Religious Adherents* was correlated positively with the *Proportion of Religionists USA* ($r = .66$, $n = 48$, $p < .0001$).

4.2.2. Religious participation and value. We predicted that the magnitude of time and effort dedicated to religious practice and the value placed on religious practice and ideals would be positively correlated with parasite-stress. We describe next our measures of religious participation and value cross-nationally and within the United States.

4.2.2.1. Cross-national: Religious Participation and Value. We created an index of *Religious Participation and Value* based on items contained in the World Values Survey collected in 1981–2007 from about 344,000 individuals in 95 countries (ES 1D). The data are in the ES 2. Also, we created a variable, *Proportion that Prayed Every Day*, from the same survey (ES 1.D). The *Proportion that Prayed Every Day* was correlated positively with *Religious Participation and Value*, $r = .93$ ($n = 59$, $p < .0001$). And, *Religious Participation and Value* was correlated positively with the *Proportion of Religionists* ($r = .74$, $n = 90$, $p < .0001$) and the *Proportion of Believers* ($r = .83$, $n = 82$, $p < .0001$). Furthermore, the *Proportion that Prayed Every Day* was correlated positively with the *Proportion of Religionists* ($r = .64$, $n = 57$, $p < .0001$) and the *Proportion of Believers* ($r = .85$, $n = 51$, $p < .0001$).

4.2.2.2. United States: Religious Participation and Value USA. The Pew Forum on Religion and Public Life produced the report “US. Religious Landscape Survey, Religious Affiliation: diverse and dynamic (February 2008).” We collected data for eight items from this survey and generated the variable *Religious Participation and Value USA* (ES 1.E). The data are in the ES 3. *Religious Participation and Value USA* was positively correlated with the *Proportion of Religionists USA* and the *Proportion of Religious Adherents* (religionists: $r = .56$, $n = 44$, $p < .0001$; adherents: $r = .42$, $n = 45$, $p = .0041$).

4.3. In-group assortative sociality

There is considerable conceptual overlap between religiosity and family ties that, we argue, reflects the importance of in-group assortative sociality within societies (e.g., the cross-national *Religious Participation and Value* was positively correlated with *Strength of Family Ties*, $r = .79$, $n = 72$ countries, $p < .0001$). Because of this conceptual overlap, we generated synthetic in-group assortative sociality variables, one cross-national, which we called *In-Group Assortativeness*, and one for the states of the USA, which we called *In-Group Assortativeness USA*, to capture the common variation among our multiple dependent variables tapping in-group assortative sociality (ES 1.F). The cross-national data are in ES 2 and the interstate data are in ES 3.

4.4. Parasite-stress

4.4.1. Cross-national: Infectious Disease DALY. We used the World Health Organization (WHO) variable *Infectious Disease DALY*, a cross-national measure of morbidity and mortality (Disability Adjusted Life Years; DALY) attributed to 28 different “infectious and parasitic diseases” for the year 2002 (e.g., tuberculosis, measles, leprosy, dengue; WHO 2004). The DALY measure combines the

time lived with disability and the time lost due to premature mortality. One “Infectious Disease DALY” is equivalent to one lost year of healthy life, with the burden of infectious disease as a measurement of the gap between current health status and an ideal situation where everyone lives into old age free of disease and disability (ES 1.G).

4.4.2. Cross-national: Nonzoonotic versus Zoonotic Parasite Prevalence.

An important element of the parasite-stress theory of sociality is the costs associated with acquiring diseases from out-group humans. Thus, infectious diseases that are transmissible between humans are predicted to be more important for assortative sociality than human infectious diseases that are not transmitted between humans (Thornhill et al. 2010). Human-to-human transmitted infectious diseases are of two types, referred to as human-specific and multi-host diseases, respectively. Human-specific diseases are ones that humans are only able to acquire from other humans (e.g., measles, cholera, hookworm), whereas multi-host diseases are those that humans contract from other humans but in which the parasites can use either human or other animals as hosts to carry out their reproductive life (e.g., leishmaniasis, leprosy, dengue fever). These two types of infectious diseases contrast with zoonotic diseases (e.g., lyme disease, rabies, tularemia) that humans are only able to acquire from species other than humans (livestock and wildlife). Using Smith et al.’s (2007) classification of these disease types, we determined the prevalence (number of cases) of human-specific and multi-host infectious diseases per country (called “nonzoonotic”) and of zoonotic diseases, based on data from the GIDEON database (Global Infectious Disease & Epidemiology Network; www.gideononline.com). The earlier cross-national study of cultural variation by Thornhill et al. (2010) used a different measure of these diseases: the number of diseases of each type, not the prevalence (Thornhill et al. 2010). Prevalence measures are likely better assays of the impact of parasitic diseases than the number of such diseases (Dunn et al. 2010). *Nonzoonotic Parasite Prevalence* was correlated positively with *Zoonotic Parasite Prevalence* ($r = .61$, $n = 226$, $p < .0001$). *Nonzoonotic Parasite Prevalence* was correlated positively with *Infectious Disease DALY* ($r = .76$, $n = 192$, $p < .0001$), as was *Zoonotic Parasite Prevalence* ($r = .16$, $n = 192$, $p = .03$). See ES 1.H for further details on the construction of this measure. The *Electronic Supplement 4* (ES 4) which can be viewed at <http://www.journals.cambridge.org/bbs2012004>, contains the list of infectious diseases and their classification. The *Electronic Supplement 2* contains the national values for the nonzoonotic and zoonotic parasite prevalence variables.

4.4.3. Cross-national: Combined Parasite-Stress. Because there is overlap and covariation in our infectious disease measures, we standardized *Infectious Disease DALY*, and *Nonzoonotic Parasite Prevalence*, and then summed these scores for each country to become *Combined Parasite-Stress* (Cronbach’s $\alpha = .76$, $n = 192$). *Zoonotic Parasite Prevalence* was not included because of its minimal relationship with the dependent variables (see sect. 5.1.1). *Combined Parasite-Stress* was the focal variable

used in the cross-national multivariate analyses (see sect. 4.5.1). These scores are in *ES 2*.

4.4.4. United States: Parasite-Stress USA. We obtained the annual *Morbidity and Mortality Weekly Report's* "Summary of Notifiable Diseases, United States" from the Centers for Disease Control (CDC) for the years 1993 to 2007 (available at: www.cdc.gov). For each year, we adjusted the number of cases of all infectious diseases tracked by the CDC for which there was information for all states for that year with the CDC-reported population size for each state (i.e., for some diseases – not all states reported whether cases occurred [termed "non-notifiable" by CDC]; these unreported diseases were not included in the tally). For each state, we determined the average z -score of this population-adjusted disease incidence score for the 15-year time-span. This approach was necessary because the infectious diseases tracked by the CDC can vary between years, though there was often great similarity between years. The standardization allowed us to pinpoint a state's position along a parasite-stress gradient relative to the other states. See *ES 1.1* for validation of this index. The *Electronic Supplement 5* (*ES 5*) which can be viewed at <http://www.journals.cambridge.org/bbs2012005>, contains the list of diseases included in our index for each year and the data are in *ES 3*.

4.5. Potentially confounding influences

As described in the introduction, there are features other than parasite-stress and assortative sociality (e.g., economic development) that have been proposed as explanations of the strength of family ties and religiosity. We next outline our approach used to explore alternative causal conjectures.

4.5.1. Cross-national approach. We examined zero-order correlations between the potentially confounding factors (described below) and the dependent variables. Potentially confounding variables that were significantly correlated ($p \leq .05$) were then entered into multiple regressions with *Combined Parasite-Stress* and the dependent variables to determine whether the associations predicted by the parasite-stress theory remained after removing the effect of the potentially confounding variables. For the cross-national analysis, we examined the effects of national wealth (Gross domestic product per capita in US dollars purchasing power parity averaged over the years 1960–2008 [*GDP per capita*]; raw data obtained from data.worldbank.org) and the equitability of resource distribution within a nation. For the equitability of resource distribution, we used the measure produced by Vanhanen (2003), called resource distribution (and referred to here as *Resource Distribution*), that incorporates GDP per capita, percentages of university students and literates, the degree to which land ownership is widespread, and the degree of decentralization of non-agricultural economic resources. We also examined the effects of human freedom (e.g., the freedoms of expression and belief), using the average of cross-national scores of civil liberties from Freedom House for the years 1972–2008, *Civil Liberty* (www.freedomhouse.org). In our regression analyses, we used two model specifications. The most general model contained *Combined Parasite-*

Stress, *Civil Liberty*, and *Resource Distribution* as the predictor variables of each of the dependent variables. *Resource Distribution* includes *GDP per capita*; however, because of the large amount of research that focuses on GDP per capita we tested a second model that used *GDP per capita* and *Combined Parasite-Stress* as the predictor variables.

While we have identified some potentially confounding factors there are likely others that we have not identified. Because we propose that parasite-stress is an encompassing causal factor, we regressed the average life expectancy at birth (for the year 2008) for both sexes combined (data from data.worldbank.org) on *Nonzoonotic Parasite Prevalence* ($r^2 = .51$, $n = 190$, $p < .0001$). *Infectious Disease DALY* was not included, because its calculation by WHO incorporates life expectancy. The residuals from this regression represent the variation in life span expectancy that cannot be explained by parasite-stress (i.e., potentially, this variation represents other causal factors besides parasite-stress). We then used these residuals in correlations with the strength of family ties and religiosity variables to address the potential of causal factors besides parasite-stress to account for international variation in strength of family ties and religiosity.

4.5.2. United States approach. For addressing potentially confounding variables in the USA analysis, we followed a similar approach as in the cross-national analysis. We examined zero-order correlations among the dependent variables and the potentially confounding factors described below. Variables that were significantly correlated ($p \leq .05$) were then entered into multiple regressions with *Parasite-Stress USA* to examine whether the predicted associations between parasite-stress and the dependent variables remained after controlling the potentially confounding factors. The factors across states that we considered were GDP per capita and the Gini index (a measure of wealth inequality). *GDP per capita* was an average of the values for years 1999 to 2007 obtained from the Bureau of Economic Analysis (data from www.bea.gov). *Gini* was measured at the family level for 1999, the last year available for the variable from the Census Bureau (data from www.census.gov).

As with the cross-national analysis, we regressed average life expectancy at birth for both sexes combined for the year 2000 (obtained from www.census.gov) on *Parasite-Stress USA*. This regression was significant for the larger USA data set ($r^2 = .45$, $n = 50$, $p < .0001$) as well as for the restricted Pew Forum dataset ($r^2 = .46$, $n = 46$, $p < .0001$). The residuals of these regressions represent the variation in life expectancy that is not explained by our measure of parasite-stress. The finding of statistically significant covariation between these residuals and any one of the dependent variables would imply causation other than parasite-stress.

4.6. The problem of nonindependence

Geographically adjacent countries or U.S. states may be similar to each other due to common influences such as experiencing similar levels of infectious disease. Because of this, statistical independence among analytical units in the cross-national and the USA analyses may be questioned. To account for this potential problem, we used

the following approach: We divided the countries into six world regions according to the method devised by Murdock (1949), which is based on geographical proximity and cultural historical contact. Murdock's division of world cultures reduces the interdependence between societies among the six regions. The country assignments to the world regions are indicated in *ES 2*. Then, we conducted correlations using the mean values for each of the variables for each world region. This approach allowed us to characterize a region composed of multiple countries (or states) into a single value (thus deflating sample size). The small sample size makes the p -values suspect, but it does allow us to examine whether the correlations remain in the direction predicted by the parasite-stress theory after reducing the sample size. We also conducted a nested-effect linear regression that accounts for the nested design of our analysis. In the cross-national case, *Combined Parasite-Stress* was nested within each world region as the independent variable and used to predict the different dependent variables. Similarly, for the USA, we divided the states into the nine geographic regions used by the Census Bureau and used both approaches as we did for the cross-national analysis.

5. Results

5.1. Cross-national analyses

5.1.1. Are nonzoonotic infectious diseases more important for explaining assortative sociality than are zoonotics? The answer is, *Yes*. Each of the dependent variables was correlated positively and significantly with *Nonzoonotic Parasite Prevalence* (correlation coefficients ranged from .40 to .65) while *Zoonotic Parasite Prevalence* was insignificantly correlated with all but one of the dependent variables (correlation coefficients ranged from $-.17$ to $.17$) (*ES 6.A*, *The Electronic Supplement 6*, which can be viewed at <http://www.journals.cambridge.org/bbs2012006>, contains tabulations of the results presented throughout sect. 5.) The only significant relationship between a dependent variable, *Proportion of Religionists*, and *Zoonotic Parasite Prevalence* showed a negative sign ($-.17$) and hence was in the direction opposite that seen with nonzoonotics. Zoonotic diseases were not generally predictive of the strength of family ties and religiosity cross-nationally. Therefore, *Zoonotic Parasite Prevalence* was not included in further analyses.

5.1.2. Is the strength of family ties predicted by parasite-stress? Again, the answer is, *Yes*. The *Strength of Family Ties* was correlated positively with the parasite-stress variables measured singly or in combination; correlation coefficients ranged from .57 to .64 (*ES 6.A*).

5.1.3. Is religious affiliation positively correlated with parasite-stress? *Yes*. Each of the infectious-disease-stress variables was correlated positively with each of the two religious affiliation variables, the *Proportion of Religionists* and the *Proportion of Believers*; correlation coefficients ranged from .40 to .64 (*ES 6.A*).

5.1.4. Is religious participation and value positively correlated with parasite-stress? *Yes*. Each of the two variables measuring religious participation and value,

Religious Participation and Value and the *Proportion That Prayed Every Day*, were correlated positively with each of the parasite-stress variables; correlation coefficients ranged from .50 to .73 (*ES 6.A*).

5.1.5. Is in-group assortative sociality predicted by parasite-stress? *Yes*. The synthetic measure, *In-Group Assortativeness*, was correlated positively with the infectious-disease-stress variables; correlation coefficients ranged from .65 to .72 (*ES 6.A*) (see Fig. 1).

5.1.6. Are these findings repeated in world regions? *Yes*. When considering the correlation between the dependent variables and *Combined Parasite-Stress* at the world regional level, all correlations were positive and thus in the direction predicted by the parasite-stress theory (*Strength of Family Ties*: $r = .94$; *Proportion of Religionists*: $r = .70$; *Proportion of Believers*: $r = .82$; *Religious Participation and Value*: $r = .76$; *Proportion That Prayed Every Day*: $r = .46$; *In-group Assortativeness*: $r = .89$; $n = 6$ world regions for all).

When nested within world regions, *Combined Parasite-Stress* predicted significantly the *Strength of Family Ties* ($r^2 = .47$, $n = 69$); the *Proportion of Religionists* ($r^2 = .25$, $n = 191$); the *Proportion of Believers* ($r^2 = .44$, $n = 136$); *Religious Participation and Value* ($r^2 = .55$, $n = 89$); the *Proportion That Prayed Every Day* ($r^2 = .47$, $n = 57$); and, *In-Group Assortativeness* ($r^2 = .57$, $n = 65$). All regressions were significant ($p < .0001$).

5.1.7. Are these findings confounded by variation in other causal variables such as human freedom, resource distribution, or unidentified variables? In this case the answer is, *No*. Amongst the three focal, potentially confounding variables, only *Civil Liberty* scores were non-significantly correlated with the *Proportion of Religionists*; the other two potentially confounding variables had significant zero-order correlations with the *Strength of Family Ties*, the two religious affiliation variables, and the two religious participation and value variables, and *In-Group Assortativeness* (*ES 6.A*). Therefore, each relevant, potentially confounding variable was checked to see if it

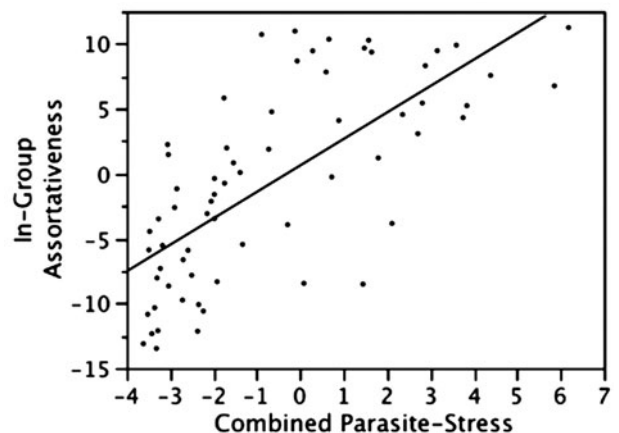


Figure 1. The correlation between *Combined Parasite-Stress* and *In-Group Assortativeness* for the 65 nations with correspondent data for all 11 items that make up the 2 variables ($r = .71$, $p < .0001$). The line is the regression line.

accounted for the correlation between parasite-stress and family ties or religiosity variables. None did (ES 6.B). In a series of multiple regressions, *Combined Parasite-Stress* remained a positive predictor of the *Strength of Family Ties*, the four religion variables, and *In-Group Assortativeness* after controlling the effects of the potential confounders (standardized beta coefficients for parasite-stress ranged from .28 to .59). Thus, the positive association between parasite-stress and family ties or religiosity was robust to the effects of freedom, resource distribution, or economic development, as captured by *Civil Liberty*, *Resource Distribution*, and *GDP per capita*.

The majority of the correlations between the residuals of the regression of life span on *Combined Parasite-Stress* and *Strength of Family Ties*, the religiosity variables, and *In-group Assortativeness* were statistically insignificant (ES 6.C). The *Proportion of Believers* showed a significant correlation, but the effect size was much reduced and in the opposite direction compared to the correlation between *Combined Parasite-Stress* and the same variable ($-.18$ versus $.63$). In general, the relationship between life expectancy independent of parasite-stress and the dependent variables was trivial.

5.2. United States analyses

5.2.1. Is collectivism and family ties predicted positively by parasite-stress? *Yes.* *Parasite-Stress USA* was correlated positively and significantly with *Collectivism* and the *Strength of Family Ties USA* (ES 6.D).

5.2.2. Is religious affiliation positively correlated with parasite-stress? *Yes.* *Parasite-Stress USA* was correlated positively and significantly with each of the two religious affiliation variables, the *Proportion of Religious Adherents* and the *Proportion of Religionists USA* (ES 6.D).

5.2.3. Is religious participation and value positively correlated with parasite-stress? *Yes.* *Parasite-Stress USA* was correlated positively and significantly with *Religious Participation and Value USA* (ES 6.D).

5.2.4. Is in-group assortative sociality predicted positively by parasite-stress? *Yes.* *Parasite-Stress USA* was correlated positively and significantly with the synthetic measure of *In-Group Assortativeness USA* (ES 6.D) (see Fig. 2).

5.2.5. Are these findings repeated in regional analyses? *Yes.* When considering the correlation between the dependent variables and *Parasite-Stress USA* at the regional level, all correlations were in the direction predicted by the parasite-stress theory (*Collectivism*: $r = .83$; *Strength of Family Ties USA*: $r = .51$; *Proportion of Religionists USA*: $r = .60$; *Proportion of Religious Adherents*: $r = .40$; *Religious Participation and Value USA*: $r = .85$; *In-Group Assortativeness USA*: $r = .89$; $n = 9$ for all).

When nested within USA regions, *Parasite-Stress USA* predicted significantly the *Strength of Family Ties USA* ($r^2 = .34$, $n = 50$, $p = .0326$); *Collectivism* ($r^2 = .45$, $n = 50$, $p = .0021$); the *Proportion of Religionists USA* ($r^2 = .61$, $n = 48$, $p < .0001$); the *Proportion of Religious Adherents* ($r^2 = .39$, $n = 50$, $p = .0106$); *Religious*

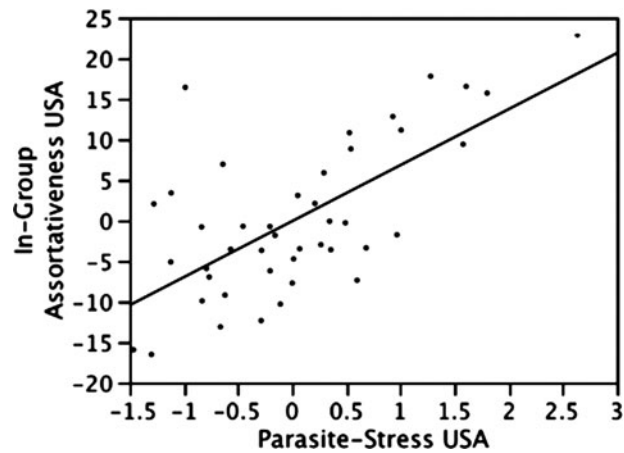


Figure 2. The correlation between *Parasite-Stress USA* and *In-Group Assortativeness USA* for the 43 states/state combinations with correspondent data for all 14 items that make up the 2 variables ($r = .66$, $p < .0001$). The line is the regression line.

Participation and Value USA ($r^2 = .54$, $n = 46$, $p = .0004$); and *In-Group Assortativeness USA* ($r^2 = .66$, $n = 43$, $p < .0001$).

5.2.6. Are these findings confounded by other causal variables such as wealth, wealth disparity, or perhaps unidentified variables? *No.* Of the potentially confounding variables, *Gini* was significantly correlated with *Collectivism*, *Strength of Family Ties USA*, and *In-Group Assortativeness USA* but not with the *Proportion of Religionists USA*, *Proportion of Religious Adherents*, or *Religious Participation and Value USA*; *GDP per capita* was significantly correlated with *Religious Participation and Value USA* and *In-Group Assortativeness USA* (ES 6.D). Given these significant zero-order correlations, *Gini* was entered in a multiple regression with *Parasite-Stress USA* as predictors of *Collectivism* and *Strength of Family Ties USA*. And *GDP per capita* was entered in a multiple regression with *Parasite-Stress USA* as predictors of *Religious Participation and Value USA*. Both *Gini* and *GDP per capita* were included with *Parasite-Stress USA* as predictors of *In-Group Assortativeness USA*. The results of these regressions are shown in ES 6.E. In all cases, *Parasite-Stress USA* remained a significant, positive predictor of the dependent variables. Thus, the correlation between parasite-stress and family ties or religiosity was not confounded with the effects of economic inequality and development as captured by the *Gini* index and *GDP per capita*.

The residuals from regressing state-level life expectancy on *Parasite-Stress USA* were not significantly correlated with *Collectivism* ($r = .11$, $n = 50$, $p = .4367$), *Strength of Family Ties USA* ($r = .22$, $n = 50$, $p = .1330$), the *Proportion of Religionists USA* ($r = -.10$, $n = 48$, $p = .4839$), or the *Proportion of Religious Adherents* ($r = .09$, $n = 50$, $p = .5180$). The residuals were correlated with *Religious Participation and Value USA* ($r = -.38$, $n = 46$, $p = .0083$) and *In-group Assortativeness USA* ($r = -.35$, $n = 43$, $p = .0214$). Therefore, the relationship between life expectancy independent of parasite-stress and collectivism, strength of family ties, and religious affiliation was

trivial, while there was a significant negative relationship between life expectancy independent of parasite-stress and religious participation and value and in-group assortativeness. The significance of the parasite-stress-independent variation may reflect the greater prevalence of non-infectious diseases such as forms of diabetes, heart disease, and cancer in the United States as compared to other countries that have lower income levels (see Lopez et al. 2006).

6. Discussion

Mainly, we show that when comparing countries or states within the United States, in-group assortative sociality, as reflected in strong family ties and heightened religiosity, is positively associated with parasite-stress. These findings were predicted from the parasite-stress theory of sociality. Also, paramount was the finding that the prevalence of nonzoonotic infectious diseases was more important for explaining these patterns, in the cross-national analysis, than were zoonotic infectious diseases. The findings remain when statistically removing the effects of other potential causal factors such as societal wealth and freedom. We presented the hypothesis in section 2.1 that people have psychological adaptations for enculturation that select cultural elements based on local utility in navigation of the social environment pertaining to infectious disease threats. Such adaptation is consistent with our findings on cross-national and interstate variation in values of family ties and religiosity.

6.1. Family ties

Our cross-national analysis showed that the strength of family ties was positively correlated with all measures of parasite-stress. And, as predicted, the strength of family ties was correlated more strongly with nonzoonotic infectious diseases than with zoonotic infectious diseases. Within the United States the strength of family ties and collectivism were both strongly, positively correlated with parasite-stress. Our findings are cross-cultural extensions to the ethnographic work that demonstrated the important role of nepotistic and other in-group altruistic support for surviving parasitic infections (Gurven et al. 2000; Hill & Hurtado 2009; Sugiyama 2004; Sugiyama & Sugiyama 2003).

The findings cross-nationally and across the USA that strong family ties was correlated with parasite-stress complement our earlier work that linked collectivism-individualism with parasite-stress (Fincher et al. 2008; Thornhill et al. 2010). Our finding of the strong positive correlation between Vandello and Cohen's measure of collectivism and parasite-stress within the United States is also an important complement to the cross-national findings of the same relationship reported in Fincher et al. (2008) and Thornhill et al. (2010).

It would be relevant to explore regional analysis within other countries that contain significant parasite gradients. For example, Japan's northern island of Hokkaido rivals the high individualism in the United States (Kitayama et al. 2006). Probably, Hokkaido has a much lower level of parasite-stress than does southern Japan, given the negative covariation of parasite-stress and latitude (e.g., Guernier et al. 2004). Also, in China, historically much

of the innovation originating in China derived from the northern region, which was much lower in parasite-stress than the southern portion, below the Yellow River (McNeill 1998). Innovation – both its generation and the willingness of people to adopt it – corresponds to individualistic values (Thornhill et al. 2009). The regional development of innovation in China and elsewhere could be studied more thoroughly in its relation to historical pathogen stress. In the United States we found significant regional variation in values in spite of generally low parasite-stress relative to many other areas of the world. We expect this pattern to be repeated across the world in nations that have a parasite gradient.

One aspect of human family life that has been studied often is the demographic transition from large families to smaller families. One of the more convincing explanations for this phenomenon comes from Newson et al. (2005). They argue that the demographic transition arose from an increase over time in the ratio of non-kin to kin in individuals' social networks. We agree but offer a reinterpretation of the meaning of the demographic transition. Based on our earlier studies on collectivism (cited already) and the present article on collectivism and family ties, it is reasonable to assume that this increase in the non-kin to kin ratio is related to a decrease in parasite-stress over time and the corresponding increase in individualism. Moreover, the countries in which the demographic transition has occurred are the same ones that have experienced a relative emancipation from infectious disease (Thornhill et al. 2009).

In-group assortative sociality is not restricted to humans; indeed, it appears to be widespread across animal taxa (Fincher & Thornhill 2008a). We hypothesize that parasite-stress was one of the main forces of selection responsible for adaptations that function in family life (see also Lewis [1998] with respect to the evolution of kin altruism as a response to parasite-stress). Hence, we propose that variation in parasite prevalence accounts for the large variation, across animal species, in the degree of extended nepotism exhibited outside the social unit of parent(s) and offspring.

Andersson (1984), Brockmann (1984), and Emlen (1994; 1995; 1997) provide important reviews of family evolution. The study of family life first became based in evolutionary science with Hamilton's (1964) realization that an individual's fitness can be more than the individual's phenotypic design for production of direct descendant relatives – that is, more than the individual's classical or Darwinian fitness. Hence, one's fitness can include nepotistic design for increasing the offspring production of non-descendant kin, such as siblings, cousins, nieces, and nephews. However, this inclusive fitness theory of fitness striving, a major part of the modern theory of social life, does not account for why nepotism is variable across social systems. Why is nepotism limited to the nuclear family in many systems but extended beyond the nuclear family in others? We provide in this article evidence that parasite-stress accounts for this variation across human social systems. The parasite-stress theory of sociality suggests a general theory of family life across animal taxa.

The social organization of animal species varies along a cooperative breeding continuum, or, said differently, a continuum of eusociality (Andersson 1984; Sherman et al. 1995). A mother alone investing in her offspring, or

much less commonly across species, a father alone investing in offspring, are on the highest asociality end of the continuum. Species in which both mother and father nepotistically assist the offspring (so-called biparental species) are more eusocial in degree on the continuum. This is followed by varying degrees of extended nepotism outside the nuclear family. Sterility – shown by adult members of the group who serve as helpers and thereby assist relatives, or in some cases, non-relatives, instead of producing their own offspring – occurs in certain taxa of vertebrates, including the human species, as well as in invertebrates. The sterility ranges from temporary to permanent, depending on the species. The temporary case is that of delayed striving to produce descendant kin while being engaged, instead, in in-group altruism (e.g., certain human groups [Hill & Hurtado 2009] and certain species of wasps, birds, and carnivores). The permanent case is one of life-long, exclusive, extended nepotism (as is characteristic in ants and termites). Both temporary and permanent cases constitute in-group assortative sociality. Also, the relatively eusocial species on the continuum – that is, the more cooperative in terms of group breeding – in general exhibit marked sedentism, delayed or no dispersal from the natal location, and territorial defense by the family group or, in some cases, by a larger in-group (e.g., Arnold & Owens 1998). According to the parasite-stress model, the sedentism and limited dispersal are analogs (similarity by independent evolution by selection, i.e., convergent evolution), or, in some cases, homologs (similarity resulting from common ancestry) of human philopatry. The territoriality is the analog or homolog, depending on the comparison, of human xenophobia.

At a minimum, the parasite-stress theory applied to family evolution is supported by the fact that cooperative breeding in birds and eusocial systems in insects are more common, or, in the case of eusociality, more eusocial, in tropical regions than in temperate regions for many different taxa (e.g., birds [Brown 1987; Ekman 2006; Blumstein & Møller 2008], wasps [Wilson 1971]).

6.2. Religiosity

As predicted, our cross-national analysis showed that religiosity, as measured by religious affiliation and religious participation and value, was positively correlated with all measures of parasite-stress; and religiosity was correlated more strongly with the prevalence of nonzoonotic infectious diseases than with zoonotic infectious diseases. Within the United States, too, religiosity was also correlated positively with parasite-stress. Our results are consistent with the hypothesis that religiosity functions as an honest signal (see sect. 3.2). Costly signaling theory emphasizes the necessity of high-cost signals in order to reliably communicate information. Religiosity's costs allow honest communication of in-group allegiance, as well as provide a social boundary that protects adherents from out-groups that may possess new infectious agents and different values and norms. As expected from costly-signaling theory, the degree of religiosity – and, thereby, the extent of its costs – covaries positively with parasite-stress across regions. Hence, the parasite-stress theory of sociality in conjunction with costly-signaling theory can potentially explain all forms of religiosity, from the

irreligious to the ultra-religious, as arising from the relative position of cultures along a parasite-stress gradient and corresponding collectivism-individualism gradient.

Although we found that the multiple religiosity variables were correlated with societal wealth variables, as predicted by the conditions-of-living model in Inglehart and Baker (2000), Norris and Inglehart (2004), and McCleary and Barro (2006), the effect of parasite-stress for explaining variation in religiosity was still significant when the effects of societal wealth and resource inequality were removed. Furthermore, parasite-stress was significant after removing the effects of differences in freedoms, as measured by the Freedom House *Civil Liberty* scores. This was as predicted. However, societal wealth, resource inequality, and freedom are hardly separable from parasite-stress. This is because the values that lead to democracies versus autocracies or wealth versus dearth appear to causally arise from different infectious diseases ecologies (Thornhill et al. 2009). The long-standing tradition in economics, historical scholarship, political science, and sociology is to view economic measures, such as GDP as an encompassing causal factor. However, according to the parasite-stress theory of sociality, variation in parasite-stress is a proximate cause of variation in GDP and in resource inequality. Parasite-stress not only strongly and negatively influences human labor capacity (e.g., Price-Smith 2002), but also, the undemocratic values parasite-stress generates cause widespread economic dearth and inequality. High parasite-stress yields philopatry and localized/ethnocentric economic priorities and investment, devaluation and divestment outside the dominant in-group, and limitations of innovation, willingness to adopt new ideas and technologies, and private property rights. Low parasite-stress has the opposite effects. Hence, these effects of parasite-stress level manifest cross-nationally as economic variables (see Thornhill et al. 2009; also Fincher et al. 2008; Schaller & Murray 2008).

Norris and Inglehart (2004) describe patterns of secularization (the declining religiosity in many countries of the world). They note that religiosity has declined most in wealthy nations but very little if any in poor nations. They attribute this to the importance of the lack of wealth (poor living conditions) for promoting heightened religiosity. We note that the poorest nations are also those that have the highest parasite-stress. This is evident in the negative correlation between *GDP per capita* and *Combined Parasite-Stress* ($r = -.77$, $n = 184$, $p < .0001$). We hypothesize that the reason that the poorest nations have maintained similar levels of high religiosity over time is because of the salience placed on tradition, conformity, and other in-group values, which in turn are caused by high parasite-stress. We tested this by cross-national comparison of the religiosity of people born before 1945 versus during or after 1945. This temporal break is very meaningful in terms of the marked reduction in parasite-stress in regions with medical interventions such as widespread antibiotic availability, child vaccination programs, and disease-vector control (Thornhill et al. 2009). We used one question from the World Values Survey that is a component of our cross-national *Religious Participation and Value* measure (rating the importance of God from 1 to 10). We then subtracted the proportion of those born in 1945 and later who rated

their response a 10 from the proportion of those born before 1945 who rated their response a 10 within each country, and then correlated this difference with *Combined Parasite-Stress*. The correlation was significantly negative ($r = -.32$, $n = 91$, $p = .0022$), indicating that in the countries with high pathogen-stress there was very little difference between those born before or after 1945 in how they felt about God's importance; whereas, in countries with low parasite-stress there was a significantly larger difference between people born before 1945 and those born more recently in how they perceived God's importance.

It is clear that religiousness, religious identities, and beliefs form at early ages (Finkel et al. 2009). It is also clear that people develop an awareness of pathogens at relatively early ages (Siegal 1988). Their correspondence suggests an important aspect of the developmental

some support for this hypothesis. When focusing on the world regions, the correlation between *In-Group Assortativeness* and *Combined Parasite-Stress* in Africa was negative ($-.31$), instead of positive as in the other five world regions (full results available from Fincher). This means that the people in the African countries expressed less in-group assortativeness as parasite-stress increased, rather than more in-group assortativeness as did the people in other world regions. We explain this unusual result by the fact that parasite-stress is exceptionally high in Africa – and therefore generally yields extrinsic mortality – as compared to the other world regions. (A post-hoc Tukey HSD means-test showed Africa to be distinctly high in pathogen-stress: Africa, mean *Combined Parasite-Stress* = 3.36, A [world areas not followed by the same letter are significantly different]; South America, $M = .85$, B; East Eurasia, $M = .53$, BC; North America, $M = -.51$, BC; Insular Pacific, $M = -.65$, C; West Eurasia, $M = -2.28$, D.) Therefore, the people in Africa are unable to ameliorate the impact of parasite-stress to their fitness through nepotistic investment, and, instead, evoke a fast life-history strategy. Presumably, the level and nature of the parasite-stress in other world regions is such that individuals are able to mediate it through investment in maintaining strong family-ties and other forms of in-group assortative sociality (it is intrinsic rather than extrinsic mortality).

6.4. Future directions

One limitation of our research reported herein is that the empirical tests of the parasite-stress theory's application to family values and religiosity were at the macro-scale across countries of the world, or on a finer but still large scale within a single polity, the USA. It would be useful to conduct additional tests of this application within more localized regions. One such method of testing the hypotheses is to record people's changes in religiosity and family values after infectious disease levels are reduced locally (e.g. by greater access to modern medicine and safe water) or increased locally (e.g. by the emergence of a new infectious disease). Evidence we have discussed herein indicates that changes in people's values can occur immediately (sect. 2.1.) and may change and stabilize across one or a few generations (see Thornhill et al. 2009). Easily administered, brief, valid questionnaires that could measure the relevant value changes are available (this study; Faulkner et al. 2004; Gelfand et al. 2004; Thornhill & Fincher 2007). At another, micro-scale, we predict that a questionnaire study would find that religious commitment within churches and between churches in a restricted region such as a United States county or city will correlate positively with individual differences in perceived vulnerability to disease, philopatry, involvement with extended family, and collectivism, and will correlate negatively with individuals' recent history of infectious disease and the two factors of personality, openness and extraversion. We predict, too, that disgust and contamination sensitivity will covary positively with religious commitment and its covariates, and that these sensitivities will covary negatively with a recent history of infectious disease.

The parasite-stress theory of sociality seems to offer many other avenues for exploration. For example, we

compiled a cross-national measure we call *Strength of National Ties*. This measure taps into the value placed on an individual for adopting the customs of, being born in, and/or having ancestors from, a particular country in order to make a claim of citizenship (ES 1.J and data are in ES 2). The *Strength of National Ties* was correlated positively with *Combined Parasite-Stress* ($r = .71$, $n = 40$ countries, $p < .0001$). This relationship could be studied more thoroughly to explore the foundations of nationalism and other similar cultural features. Also, xenophobic attitudes cross-nationally seem to be related positively to pathogen-stress (as expected from the parasite-stress theory of sociality). For example, participants in the World Values Survey were asked about different types of people that they would not want as a neighbor. The proportion of those that said they did not want to live next to someone of a different race was positively associated with *Combined Parasite-Stress* ($r = .35$, $n = 88$ countries, $p = .0009$; see also Schaller & Murray 2010). Other similar questions are posed in the World Values Survey with similar relationships to *Combined Parasite-Stress* (e.g., proportion not wanting to live next to someone that speaks a different language: $r = .42$, $n = 44$ countries, $p = .0044$).

Colonialism, imperialism, large-scale intergroup conquest, and related forms of societal expansion have large benefits (primarily reaped by elites) in the acquisition of land and other resources, and the enslavement of conquered people. During such events, expansionists often coercively force their value systems on the original inhabitants of the acquired region. Typically, this involves committed and encompassing efforts by the conquerors, with religious beliefs being central to ideological reformation. This colonialist effort in part, we hypothesize, is to spread and enforce the conquerors' behavioral norms that reduce the cost of the conquest to the imperialists. If the conquered have the same value system as the conquerors, then the cost of the conquest, in terms of contagion risk, is reduced, allowing sustained intergroup contact. Accordingly, the coercive spread of values (notably religious ideology) is a means of reducing the costs of conquest (costs of encountering new infectious diseases) to the point that the benefits of conquest exceed these costs. Additional research could examine our hypothesis' application to conquest events in the historical record.

A related issue is the geographical pattern of large-scale historical conquests by Eurasian imperialism, described by Diamond (1998), whose thesis focused on unique aspects of geography, such as the east-west orientation of the Eurasian continent and the distribution of domesticable animals and plants. We (with Kenneth Letendre) have suggested a complementary, and in part alternative, model for this history (Letendre et al. 2010). First, conservative and collectivist values are correlated positively with severity of infectious disease. Second, such values include parochialism and associated closedness toward innovations. Third, collectivism is concentrated at low latitudes. Fourth, collectivism is related negatively with societal wealth and associated technology. Hence, we have argued that, as humans migrated from Africa to higher latitudes in Eurasia, they moved into climates less hospitable to human infectious diseases, which, in turn, generated relatively individualistic cultures that have an

increased openness to and value of innovation and which place a positive value on long-range dispersal. Thus, the accumulation of wealth and technology, the domestication of plants and animals, and the large population sizes that enabled the imperial domination of otherwise impoverished and less innovative cultures resulted not from aspects of Eurasian geography, but from the relative emancipation from parasites, which allowed and promoted the rise of cultures that were more individualistic than their forebearers'. The technological dominance and individualism of these cultures motivated their expansion to obtain the benefits of conquest of other peoples, and the enforcement of the conquerors' cultural values reduced the contagion-related costs of contact with out-groups.

Vigil (2009) presented a model (the socio-relational framework of expressive behaviors) for the evolution of the expression of emotion. Based on Vigil's model, many aspects of the behaviors we discuss here need also be considered in the light of their evolved function as expressed emotions. For example, in high-parasite-stress regions where maintaining strong family-ties is paramount, perhaps in-group submissive behaviors would be emphasized strategically. Or, maybe, the within-individual variation (e.g., across the life span) in emotional expression of in-group assortative sociality could be explained by changes in capacity-traits across the life span (capacity-traits include features such as the ability to provide material or social resources). Perhaps individuals express in-group biases at points in their life when they are less capable but express more out-group bias during stages when they are more capable. Similarly, this thinking may apply to individual differences in phenotypic and genetic quality. Certainly, Vigil's socio-relational framework offers an avenue for further exploration of in-group assortative sociality on an individual level.

Throughout this target article we have treated ethnocentrism and xenophobia as though they are always positively associated. However, xenophobia and ethnocentrism can arise from separate causes leading to cases where they may be uncorrelated (Brewer 1999; Cashdan 2001b). Cashdan (2001b) demonstrated that ethnocentrism was high in traditional societies that experienced catastrophic food shortage, while xenophobia was high where the threat of intergroup violence was high. Further extension of the parasite-stress model of sociality can provide a basis for making more refined predictions about the patterns of xenophobia and ethnocentrism. For example, in a given area zoonotic diseases may generate high mortality. In this setting, ethnocentrism is predicted to be high but xenophobia low because zoonotic infections are not transmitted between human hosts.

A large literature indicates that the relationships between religiosity and mental health and freedom from coronary disease and certain cancers typically are positive (George et al. 2002; Koenig 1997). Future research could focus on the covariation of religiosity and infectious diseases *per se*. According to the parasite-stress model, religiosity will reduce recent infectious disease problems via its associated ethnocentrism and xenophobia. As George et al. (2002) emphasize, despite a great deal of research, little is known about the mediators of the positive relationship between religiosity and health. Our approach suggests that the relationship between infectious diseases and religion will be mediated by collectivism/conservatism and

related values, and by disgust and contamination sensitivity. Although high disease severity in childhood, according to the parasite-stress model, is expected to produce high in-group assortative sociality and emotionality, once those values are acquired ontogenetically, they will reduce the incidence of recent infectious diseases. Such research would add a new empirical approach to the study of the relationship between health and religiosity.

Lastly, we acknowledge that our treatment of religiosity has ignored many important aspects of religion, such as beliefs in the afterlife and attribution to supernatural causation. We have deliberately focused on features such as religious affiliation and commitment which have been measured comparably across all kinds of people, including the areligious and irreligious. The predictive power of the parasite-stress theory does not end with these features. We predict that certain unique elements of religion may be disentangled with an eye towards the human history of contending with parasites. For example, ancestor worship is a widespread component of many religions but variation in its extent and nature does exist (Rossano 2007). We predict that the strength of family ties of the living, which is caused by the degree of parasite-stress, could provide a foundation for the strength of worship of ancestors.

SUPPLEMENTARY MATERIALS

Electronic Supplement 1:

<http://www.journals.cambridge.org/bbs2012001>

Electronic Supplement 2:

<http://www.journals.cambridge.org/bbs2012002>

Electronic Supplement 3:

<http://www.journals.cambridge.org/bbs2012003>

Electronic Supplement 4:

<http://www.journals.cambridge.org/bbs2012004>

Electronic Supplement 5:

<http://www.journals.cambridge.org/bbs2012005>

Electronic Supplement 6:

<http://www.journals.cambridge.org/bbs2012006>

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NOTES

1. An additional model of religiosity that has received much attention in the literature, called the supply-side model, suggests that religious vitality (typically measured by some aspect of religiosity) is positively associated with religious pluralism because the increased commodity possibilities under high religious pluralism allows for an individual to better find the religion that suits him or her best (see, e.g., Finke & Stark 1988). Because people can find such great fits, they will tend to engage in greater religious behavior, leading to the prediction of a positive association between religiosity and religious pluralism. This model was supported with some empirical patterns but was largely dismissed by Chaves and Gorski (2001) on the grounds that the empirical evidence was overwhelmingly unresponsive of the basic general contention that religious pluralism was positively associated with religious

vitality. For completeness, we correlated each of our three cross-national measures of religiosity described in section 4.2 with the religious pluralism index produced by McCleary and Barro (2006) (*Proportion of Religionists*: $r = -.14$, $n = 67$, $p = .2553$; *Proportion of Believers*: $r = -.02$, $n = 63$, $p = .8959$; *Religious Participation and Value*: $r = .05$, $n = 63$, $p = .6920$). These patterns do not support the supply-side model.

2. Our cross-national analyses were of geopolitical regions that maintain a separate government (e.g., United States, Hong Kong). We refer to them as countries or nations.

3. Our United States analyses did not include the District of Columbia.

Open Peer Commentary

Parasite stress is not so critical to the history of religions or major modern group formations

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Abstract: Fincher & Thornhill's (F&T's) central hypothesis is that strong in-group norms were formed in part to foster parochial social alliances so as to enable cultural groups to adaptively respond to parasite stress. Applied to ancestral hominid environments, the story fits with evolutionary theory and the fragmentary data available on early hominid social formations and their geographical distributions. Applied to modern social formations, however, the arguments and inferences from data are problematic.

Fincher & Thornhill's (F&T's) central hypothesis is that strong in-group norms were formed in part to foster parochial social alliances – including values for bonding families, castes, ethnicities, and religions – so as to enable cultural groups to adaptively respond to parasite stress. Applied to ancestral hominid environments, the story fits with evolutionary theory and the fragmentary data available on early hominid social formations and their geographical distributions. Applied to modern social formations, however, the arguments and inferences from data are problematic. There is also too precipitous a leap from correlation to cause, which is the distance that is the task of science to cover.

Thus, to say that “castes were formed” from differential response to parasite stress is to put the historical cart before the horse. Castes were initially formed to keep conquering Indo-European invaders from diluting power with “inferior” native peoples of South Asia. (The genetic affinity of Indians to Europeans is proportionate to caste rank, the upper castes being most similar to Europeans, whereas lower castes are more like other South Asians; Bamshad et al. 2001). The imposed conditions of substandard health and hygiene (relative to the conquerors) reinforced social separation through fear of contagion, where risk from biological contagion was readily confounded with social and mental contagion. Variations on this type of process, of course, marked the history of European colonialism as well (Stoler 2010).

Although ethnic exclusivity is probably as old as our species (Atran 2001), in modern forms of nationalism it is more a social construction that stems in large part from the failed European political and social revolutions of 1848. These revolutions were

fueled by ideologies preaching the emancipation of peoples and the dismantling of political and social boundaries. The lesson drawn by the victorious ruling elites to forestall future uprisings was that the “lower classes” must be made to feel themselves integral parts of exclusive nationalities steeped in common “blood,” but where rich and poor still had almost inescapably distinct derivations from the common national “essence” (Dowe 2001). These developments, again, reinforced the social and biological isolation of cultural groups and subgroups, including differential susceptibility and response to pathogens and parasite stress.

But it is with respect to the role of religion that the authors' arguments are most problematic. It is certainly plausible that “religious groups adopt their own distinct costly versions of supernatural beliefs in order to heighten costs of participation and distance themselves from out-groups” (target article, sect. 3.2, para. 3). Nevertheless, for at least the past three millennia or so, the most expansive and successful religions aimed to include as many genetic strangers as possible (Atran & Henrich 2010). Consider Christianity, the first truly universal religion, which still today has the largest group following on the planet. Originally attached to Jewish diaspora settlements throughout the Roman empire, it steadily gained a following of a few percentage points of the empire's population each year – especially among women, slaves, and other disadvantaged elements – until gaining a majority shortly before Emperor Constantine's conversion. Before Constantine's militarization of the faith in the fourth century, Christianity progressed mainly through costly, charitable acts of self-sacrifice, most notably in tending strangers with plague and other infectious diseases who were usually abandoned by their own kinfolk (Stark 1997). The first true hospitals to care for the sick, including contagious lepers, were founded by Christians at Constantinople. Islam was militarized from the beginning, but realized its greatest expansion and flowering among non-Arab peoples (Berbers, Jews, Latins, Germans, Persians, Kurds, Turks, and so forth). With initial assistance from Christians, Islamic hospitals were tending those afflicted by infectious diseases by the beginning of the eighth century (Risse 1999). Buddha also taught to tend the sick strangers, of whatever caste, so as to help eliminate all castes (largely a failure in India but very successful elsewhere). Pentacostalists and other Evangelical groups, as well as Muslim missionaries, are still converting millions in Asia, Africa, and the Americas through open-door charitable efforts (see Atran & Henrich 2010).

F&T claim that religiosity involves “an underlying mental mechanism” (sect. 3.2, para. 6) that encourages religious group similarity. This is misleading. There are no set principles or rules specific to religion, nor any adaptive religious complex that seems stable enough to undergo evolution by natural selection (Atran & Norenzayan 2004). Rather, religions involve a host of ordinary cognitive mechanisms (including those which produce fairy tales and supernaturals) whose distributions take on a characteristic religious aspect (in a “family resemblance” sort of way) in trying to deal with certain irresolvable but ineluctable aspects of the human condition (including “existential dilemmas” such as death, deception, catastrophe, and so forth). Moreover, in today's world, religions are as permeable as the transnational ideological *-isms* (actually, secular salvational monotheisms) that began to vie for domination of modern political life with the American and French Revolutions.

The inference that economic development “causes” religious decline and promotes democracy is also somewhat misleading. It is simply that institutionalized religions in the West were traditionally associated with older power structures. These have been largely replaced by secular political ideologies and parties, which continue to have “sacred” and transcendent (if not supernatural) aspects, whether attributed to Providence or Nature (Atran 2010; Atran & Axelrod 2008). The one consistent finding from political science is that the best predictor of

democracy is not economic development per se, but the presence of a large and stable middle class. The initial rise of the American and European middle class was heavily religion-and-community based (de Tocqueville (1835/1984); Weber 1958). "Individualism," which is a phenomenon largely associated with the demise of American community life in the later decades of the twentieth century (Putnam 2001), has become an analytic category chiefly because the country's major social analysts now recognize that much of the rest of world still has community-sharing traditions ("collectivists"). This is not *because* the rest of the world is more prone to parasite stress, and therefore more responsive to religion and less taken with democracy, but because modern forms of health care and hygiene, secular rights, and democratic governance, are all fairly new and still predominantly localized with the former colonial metropolises and their oldest former colonies.

Finally, even if parasite stress is significantly correlated with phenomena such as high religiosity or lack of democracy, that in no way informs us how religious or political systems are actually structured or modified under evolution. But, given the correlation data presented, parasite stress does merit further consideration as a possible selection factor in their persistence or hindrance.

Connecting biological concepts and religious behavior

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Abstract: This commentary proposes experiments to examine connections between the presence of out-group members, neurovisceral reactions, religiosity, and ethnocentrism, to clarify the meaning of the correlational findings presented in the target article. It also suggests different ways of describing religious socialization and of viewing assertions about religion and health or about the human ability to detect pathogens.

Intriguing correlational findings should lead to crucial experiments. Fincher & Thornhill (F&T) quote research showing that the sight of disease symptoms activates the immune system. We need evidence of neurovisceral reactions (Porges 2010), as well as heightened ethnocentrism and religiosity, under (a) visual images (b) imagined encounters, (c) anticipating encounters, and (d) the actual presence of out-group members, in the presence or absence of disease and injury symptoms, compared with identical in-group encounters, and with other stimuli representing biological and psychological risk. A series of experiments following this design will clarify and advance the authors' claims.

References to behavioral research on religion in the target article are inconsistent. The authors state that "Religion is often defined as a value system that is based on supernatural phenomena (Boyer 2001)" (sect. 3.2, para. 3). Boyer (2001) offers no such definition. The closest statement to a definition there states only that "Religion is about the existence and causal powers of non-observable entities and agencies" (p. 8). Boyer (2001) does not use either "value system" or "supernatural phenomena" in his text. The term "supernatural phenomena" assumes that a supernatural realm exists, because a phenomenon is something known through the senses, but Boyer (2001) states that religious claims are about non-observable entities and agencies.

How is a religious identity acquired? The authors state: "It is clear that religiousness, religious identities, and beliefs form at early ages" (sect. 6.2, para. 4), but they also offer a totally

different portrayal earlier in the target article: "To learn the emotionality and associated language of a religion requires a long developmental (ontogenetic) exposure to the belief system" (sect. 3.2, para. 1). F&T argue that "Participation in a religion has certain costs for the participant, which include the time and effort involved in learning a religion and practicing it, the loss of opportunity to engage in other beneficial activities (opportunity costs), and risks such as the avoidance of modern medical care or extended fasting" (sect. 3.2, para. 1).

This description conceives of religious involvement as individual "participation" – that is, taking an active part voluntarily – a matter of personal choice. Embracing a religious identity by choice, or even having alternatives, is rare and historically recent. The process is social rather than individual. Choice ends for most believers in an accident of birth which predicts best their lifetime religious trajectory. Through kinship we acquire, or inherit, not only religious identity, but also ethnicity, political affiliation, sports fanships, and other group attachments. Conversion, although enjoying scholarly attention, is a rarity among the world's billions of believers, as would be predicted from the F&T's own theory of assortative sociality (cf. Beit-Hallahmi, in press; Beit-Hallahmi & Argyle 1997). Religious loyalty is psychologically tied to kinship loyalty. Conversion or religious exogamy are experienced as a betrayal.

Learning a particular religious system, just like learning "language or dialect, word use, dress, music, smell" (sect. 3.2, para. 8), starts – and ends, in most cases – in early childhood, within the family. Religious narratives, by their very nature, are accessible to young children, who absorb them without effort, just as they enjoy religious holidays. Children are a captive audience, and the imposition of religious beliefs by parents can be lethal. The authors mention "the avoidance of modern medical care" (sect. 3.2, para. 2) as one of the costs of "participation" in religion. This cost is usually borne by children who never had a choice, but die or suffer without proper health care (Asser & Swan 1998). These extreme cases illustrate the powerlessness of children in relation to inherited and imposed religious identity.

F&T express surprising optimism when they refer to "an awareness of pathogens" (sect. 6.2, para. 4), and approvingly cite Curtis (2007), who believes that humans have "intuitions" about pathogens around them. F&T state: "It is also clear that people develop an awareness of pathogens at relatively early ages (Siegal 1988)" (sect. 6.2, para. 4), and tie this to the early learning of religion. But the Siegal study was done in the United States and merely shows that young children in the First World remember the lessons they are being taught about hygiene.

Whether humans do indeed have an "awareness" (conscious?) or "intuition" (non-conscious?) of pathogens can be tested easily. Do individuals detect the presence of salmonella or HIV? Why is it that in West Africa those who wash corpses of cholera victims later prepare funeral feasts, which leads to renewed outbreaks of the disease? (See Gunnlaugsson et al. 1998; Sack & Siddique 1998.) If humans possessed such mental mechanisms, the history of human encounters with parasites would have been vastly different. We see no evidence of pathogen detection in numerous risky and lethal practices, and little evidence for any pathogen awareness till fairly recent times (*vide* Ignaz Semmelweis).

While pathogen awareness has been absent, intuitions about disease causation (including recent AIDS outbreaks) lead humankind to imagine angry gods punishing human transgressions or acts of sorcery (Forster 1998; Murdock 1980). This is an important connection between religion, the belief in the spirit world, and health. We must wonder whether such fantasies, sometimes interpreted as expressing an unconscious processing of family tensions (Beit-Hallahmi 1989; 1996; 2010), are adaptive, and in what way.

The religion-biology connection is presented rather cheerfully when F&T state that "A large literature indicates that the

relationships between religiosity and mental health and freedom from coronary disease and certain cancers typically are positive" (sect. 6.4, para. 7). Freedom from coronary disease and certain cancers? Reading Sloan (2008) should serve as an antidote to such claims. How does this reported positive correlation between religion and health square with the authors' own finding of a worldwide positive correlation between religiosity and parasite-stress? Are the more religious people of Afghanistan healthier than the less religious people of Sweden? Ideas about the supernatural causation of illness are indeed found together with high parasite-stress and a reality of poor health.

Condition-dependent adaptive phenotypic plasticity and interspecific gene-culture coevolution

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Abstract: Evolutionary socioecological theory and research proposing linking parasites with human social organization is uncommon and therefore welcome. However, more generally, condition-dependent adaptive phenotypic plasticity requires environmental uncertainty on a small scale, accompanied by reliable cues. In addition, genes in parasites may select among biologically adaptive cultural alternatives directly without necessarily going through human genetic predispositions, resulting in inter-specific gene-culture coevolution.

Human evolutionary ecological theory and research pertaining to antagonists (parasites and predators) is less extensively developed than that pertaining to resources such as food. Moreover, evolutionary socioecology linking parasites in particular to specific kinds of social organization is even less so. On these two grounds alone the target article by Fincher & Thornhill (F&T), reviewing the theory and evidence that high parasite-stress is associated with positively assortative sociality in humans and extending it to include strong family ties and heightened religiosity, is welcome. I will not comment one way or another on that specific theory or the evidence for it but confine my comments instead to the more general theory placed between these two aspects, because it is less precise than is required in one respect, and perhaps more circuitous than is required in another.

The more general theory attributes an association between parasite stress and assortative sociality to ancestrally adaptive genetic evolution of condition-dependent phenotypic plasticity, including, but not restricted to, the case in which culture mediates the selection pressure from parasites. On the first point, condition-dependent adaptive phenotypic plasticity is attributed to local variation, change, and complexity. However, variation and change on a scale between individuals/generations would simply result in the direction of selection varying and changing. It is environmental *uncertainty*, and on a scale within individuals/generations, that is necessary for adaptive plasticity. Even that is not sufficient for condition-dependent adaptive plasticity, because simple environmental uncertainty favors plasticity of the probability-matching type in which behaviors are emitted at random, but with a probability matching that of the environmental conditions to which they are adapted. Specifically, condition-dependent adaptive phenotypic plasticity requires (i) environmental uncertainty; (ii) such uncertainty on the correct small scale; and (iii) that the uncertainty nevertheless be accompanied by reliable cues (Roff 2002, Ch. 6).

On the possible role of culture, that people choose their values is far from the "traditional sociological view," or the anthropological one for that matter (and note that the Jost et al. [2009] review cited by F&T [sect. 2.1, para. 11] is from the psychological literature on the social psychology of political ideology). F&T share a common misconception that the books by Cavalli-Sforza and Feldman (1981), Lumsden and Wilson (1981), and Boyd and Richerson (1985) were about coevolution between culture and genes. The Cavalli-Sforza and Feldman book was about purely cultural, not genetic evolution at all. Although referring to coevolution, the Lumsden and Wilson book was about how genes create rules which bias the cultural alternatives preferred by individuals (along the lines favored in this article minus the emphasis on adaptive plasticity). Boyd and Richerson (1985) called their theory a dual inheritance, not a dual evolutionary one. Although they included sociocultural selection under the label of "biased transmission" (direct, indirect, and positively frequency-dependent), biological and sociocultural adaptedness were commonly implicitly equated and the authors were very concerned with the biological evolution of human capacities for individual learning, cultural transmission, and cultural selection. In none of these books were genes and culture really understood as both varying, being transmitted, being selected and hence evolving, and to be doing so in interaction with each other (for reviews and summaries of the originals, see Blute 1987). The first extensive treatment of coevolution in this full sense was Durham (1991) who, in the context of a series of anthropological case studies, described genes selecting among cultural alternatives as "genetic mediation" and cultural alternatives selecting among genes as "cultural mediation" – both of which were once, and mostly still are, called gene-culture coevolution, but what some today, including the authors of the present target article, distinguish as gene-culture and culture-gene coevolution, respectively. To bring the latter up to date, Laland et al. (2010) recently reviewed more than a hundred human genes organized into eight functional groups whose evolution can plausibly be attributed to cultural selection pressures.

The version of culture-gene coevolution presented in F&T's article is one in which parasites select for human cultural practices, which in turn select for human genes affecting psychological states, which in turn promote those cultural practices. The insertion of human genetic differences in the middle in this way is logically wholly unnecessary to a possible coevolutionary interpretation. Because culture is not only transmitted but can also vary, be selected, and therefore literally evolve (e.g., Blute 2010), and because the bulk of the cultural practices involved are transmitted roughly vertically, making them generally biologically adaptive (Blute 2006), alternative genes in parasites can select for alternative biologically adaptive anti-parasitic cultural practices in humans directly. Human genetic differences might conceivably mediate this process in some cases. That depends on whether or not there is (or was) additive genetic variance in humans for most of the psychological states/behavioral traits in question. Given that most of the heritability of complex diseases even is "missing" in genome-wide association studies (Manolio et al. 2009), most social scientists remain skeptical. But the truth is that for the vast majority of cases, nobody really knows either way.

On the simpler direct coevolutionary interpretation, a parasite stress theory of assortative sociality would still remain a particularly interesting case. That is because, on the one hand, like the original biological concept of purely genetic coevolution between species, it would be interspecific. On the other hand, like the original concept of gene-culture coevolution in humans, it would be between genes and culture. So it would be unique in either coevolution literatures, because it would be one of *interspecific gene-culture coevolution* – that is, of genes in one or more species evolving in interaction with cultural elements in another. On these grounds, too, I very much appreciate the authors having presented this theory.

In-group loyalty or out-group avoidance? Isolating the links between pathogens and in-group assortative sociality

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Abstract: The target article gives two explanations for the correlation between pathogens, family ties, and religiosity: one highlights the benefits of xenophobic attitudes for reducing pathogen exposure, the other highlights the benefits of ethnic loyalty for mitigating the costs when a person falls ill. Preliminary data from traditional societies provide some support for the former explanation but not the latter.

It is not unusual in hunter-gatherer populations for a quarter or more of those born to die before their first birthday and for only half of the population to make it to adulthood. Infectious disease is a major cause of this mortality, but it has not received its due as an important selective force shaping human psychology and behavior. I welcome Fincher & Thornhill's (F&T's) contribution, which adds family ties and religiosity to the other aspects of "in-group assortative sociality" associated with pathogen stress.

Two hypotheses, not one. The authors cite three core features of in-group assortative sociality: philopatry (reduced mobility outside the natal group), xenophobia, and ethnocentrism. The rationale given for the association of pathogens with philopatry and xenophobia is the avoidance of exposure to novel strains of pathogens to which the individual has poor resistance. A different argument is given for ethnocentrism: Close relationships with other group members help people to survive infectious diseases. In the target article, pathogens are hypothesized to lead to greater religiosity through both mechanisms, whereas close family ties would seem to be most directly related to in-group loyalty.

These are very different arguments, with different implications. The former explanation (reducing exposure through reduced contact with outsiders) is highly specific to pathogens, especially non-zoonotic pathogens, which adds to its power. The latter explanation (the benefits of social support) is weaker, since social support would be valuable in coping with many sources of stress in addition to infectious disease. It is helpful to keep these two lines of argument separate because, as the authors note in their conclusion, they can lead to different predictions.

An anthropological perspective (and preliminary results). Data supporting the relationship between pathogens and in-group assortative sociality have come almost exclusively from modern state-level societies, but if the behaviors are part of our evolved psychology they were presumably shaped in contexts closer to those found in traditional anthropological populations. In these societies, mortality from pathogens is a greater threat, and there are fewer non-social means of buffering risks of all sorts. The need for social mechanisms to cope with the threat of infectious disease, therefore, should be especially important in these societies.

In a recent preliminary analysis using the Standard Cross-Cultural Sample of traditional societies, Cashdan and Steele (2010) found support for the argument that individuals will reduce exposure to novel pathogens through reduced mobility and xenophobia. Mobility among communities (a more direct measure than range size) was inversely correlated with pathogen load, and the relationship held when controlling for latitude (no relationship was found with inter-group contact). There was also some evidence, albeit weaker, for a relationship between overall pathogen risk and xenophobia (also controlling for latitude). Both of these support the argument that behaviors and attitudes that

reduce contact with members of other groups will be more prevalent where pathogen risk is greater.

Does pathogen risk also foster ethnocentrism? In this preliminary study (Cashdan & Steele 2010), no relationship existed between pathogen stress and ethnocentrism (ethnic loyalty) at either the local or regional level. Since ethnocentrism and xenophobia were uncorrelated in the Standard Cross-Cultural Sample (Cashdan 2001b), the data permit the isolation of the two lines of argument highlighted above. They suggest that the relationship between pathogens and in-group assortative sociality (including religiosity) is likely to be driven primarily by the way the latter reduces exposure to other groups, and that other related variables may be correlated with pathogens because they are correlated with traits that reduce this exposure.

Pathogens promote matrilineal family ties and the copying of foreign religions

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Abstract: Within the same pathogen-stress framework as proposed by Fincher & Thornhill (F&T), we argue further that pathogen stress promotes matrilineal rather than patrilineal family ties which, in turn, slow down the process of modernity; and that pathogen stress promotes social learning or copying, including the adoption of foreign religions.

Fincher & Thornhill (F&T) have presented cross-national and American data to support the hypothesis that pathogen stress is positively associated with family ties and religious affiliation constituting in-group sociality. Their evolutionary argument that pathogen stress is an ultimate cause of family and religious sociality is well grounded both in theory and in data. However, their broad-stroke analyses and explanations leave out two seemingly counterintuitive conclusions which we try to address by attending to more detailed analyses within the same pathogen-stress framework.

First, with respect to the hypothesis about pathogen-driven family ties, existing research based on the Standard Cross Culture Sample (Murdock & White 1969) shows a positive association between pathogen stress and polygyny (Katz & Konner 1981; Low 1988; 1990; Marlowe 2000; 2003). In harsh (high latitude, cold climate) environments with low pathogen levels and low population density, polygynously and monogamously married women especially rely on male provision for raising their young. The kind of polygyny found in temperate climates with a high pathogen load is mainly gene-based rather than resource-based, and it involves little paternal provisioning or parenting (Low 1990). Because bi-parenting is essential for the evolution of human family sociality, it is seemingly difficult to argue for stronger family ties associated with gene-based polygyny with little paternal involvement compared to monogamy or resource-based polygyny with paternal provision.

However, a more detailed analysis would show an association between pathogen load and post-marital residence mode. High pathogen regions historically tend to have practiced matrilocality more than low pathogen regions. According to the *Ethnographic Atlas* (Murdock 1967), the matrilineal-to-patrilineal ratio (MPR) is .17 in Circum-Mediterranean (an area which includes today's Europe but also northern Africa). Today's Europe has a low historical pathogen load (HPL = -0.62) and a low current pathogen

load (CPL = -2.88). The matrilineal-to-patrilineal ratio is much higher for high pathogen areas such as South and Central America (MPR = 1.37; HPL = 0.26; CPL = 1.42), Insular Pacific (MPR = 0.57; HPL = -0.24; CPL = -0.65), and sub-Saharan Africa (MPR = 0.20; HPL = 2.08; CPL = 3.79). Similarly, matrilineal residence accounts for half of the historical societies in the Pacific islands (Jordan et al. 2009). Societies based on matrilineal rather than patrilineal residence should develop stronger and larger kinship networks due to reduced paternity uncertainty. Thus, pathogen stress may have a direct effect on post-marital residence, which in turn affects family ties and kinship relations. Close family ties and kinship interactions especially among maternal relatives promote a culture that favors reproduction and kinship association over non-reproductive and individualistic behaviors and attitudes constituting modernity (Newson & Richerson 2009; Newson et al. 2005). Modernity versus traditionalism also accounts for much of the variance in in-group sociality.

Second, relevant to the religiosity hypothesis, it should be noted that the vast majority of the world's population (55% of the global population) practice Christianity and Islam (*The World Factbook*, Central Intelligence Agency 2010). Few societies practice polytheistic beliefs today. Most of the data reported in the target article concern these two religions. Some of the most pathogen stressed regions include Africa (HPL = 2.08; CPL = 3.79), South and Central America (HPL = 0.26; CPL = 1.42), and a part of Asia represented by Indonesia (HPL = 0.61; CPL = 3.60) and the Philippines (HPL = 0.50; CPL = 1.64), all of whose populations mainly practice one of these two religions. These two religions originated from low pathogen areas, that is, today's Middle East countries (average HPL = 0.14; average CPL = -0.90), and were brought to high-pathogen areas, not the other way around. The fact that populations under high rather than low pathogenic stress could be converted from their local beliefs and persuaded to embrace foreign religions seemingly contradicts the argument for a pathogen-driven in-group religious sociality including ethnocentrism and xenophobia. One explanation could be that these religions were brought to the peoples of these regions together with medicine and technology which helped to reduce the local normative pathogenic level at the time. Colonial brutality and failed local resistance could be another explanation.

We offer an alternative explanation that is framed within the cultural evolution theory (Boyd & Richerson 2005). There are two broad adaptive strategies: social learning, or copying existing solutions; and individual learning, or innovating new ones (Boyd & Richerson 2005). Adaptation toward one of these two strategic directions is normally conditioned by the extent to which new and old situations are similar enough to benefit existing solutions. When the local environment is relatively stable, social learning prevails; whereas adaptive strategies tend to favor individual learning when a rapidly changing environment offsets the cost of trial and error. Pathogens affect environmental variability and human adaptive response in two ways. First, they add to environmental stability. The pathogenic level of a humanly habitable environment must not exceed the human physical immune threshold. A higher versus a lower pathogen load suggests that the mean pathogenic level is chronically closer to or farther away from the human immune threshold, which sets the upper limit on the pathogenic distribution to result in a smaller (with a higher pathogen mean closer to threshold) versus larger (with a lower mean farther away from threshold) variability of the distribution. In accordance with this logic, a high pathogen load is associated with low environmental variability, which should elicit copying and social learning as a behavioral response. Second, the life threatening situation of infectious diseases raises the cost-benefit ratio of trial and error or individual learning. Copying or social learning, including its psychological facilitators, conformity and compliance, has been found to correlate with high pathogen stress both at the societal (Chang et al.

2011; Murray et al. 2011) and the individual level (Wu & Chang, under review). Copying existing solutions and conforming to local norms prove to be more adaptive than trial and error when dealing with infectious diseases (Murray et al. 2011). This pathogen specific adaptation spreads to other domains of life to result in high copying and high social conformity and compliance among people living under high pathogen conditions (Chang et al. 2011; Murray et al. 2011). Thus, so far in human history, new religions, technologies, and fashions have tended to be developed in low pathogen regions and brought to and copied by high pathogen regions, not the other way around.

Analyses do not support the parasite-stress theory of human sociality

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Abstract: Re-analysis of the data provided in the target article reveals a lack of evidence for a strong, universal relationship between parasite stress and the variables relating to sociality. Furthermore, even if associations between these variables do exist, the analyses presented here do not provide evidence for Fincher & Thornhill's (F&T's) proposed causal mechanism.

There are many problems with the arguments that Fincher & Thornhill (F&T) make, given the data and analyses they present in the target article (and elsewhere). We will limit our criticisms to three main points:

1. The units of analysis are not independent.
2. Correlations may result from association with other variables.
3. There is no evidence of the proposed cognitive mechanism from these analyses.

Because of their historical relationships, countries (F&T's unit of analysis) cannot be considered as independent for the purposes of statistical analysis. Although F&T do acknowledge this, their handling of the issue is flawed. While there is not necessarily a single correct grouping variable, as multiple historical processes may lead to non-independence, the grouping used in their cross-national analyses is problematic. Murdock's (1949) classification of world regions was designed with the analysis of traditional societies in mind. For example, Australia and New Zealand, whose populations are now predominantly of European descent (culturally and biologically), are included in an "Insular Pacific" region along with Indonesia and the Philippines.

We examined the data provided by F&T and reclassified countries into "Europe," "North Africa and Middle East," "Sub-Saharan Africa," "East Eurasia," and "New World" (the Americas, Australia, and New Zealand), reflecting more recent regional historical relationships (see Table 1). A more in-depth analysis would undoubtedly involve some kind of hierarchical linear model (Raudenbush & Bryk 2002), or a phylogenetic comparative method within regions (Currie et al. 2010). However, F&T's argument is for a universal human response to pathogen stress, so if the relationship between the variables is strong, correlations should hold within these groups. As the target article focuses on religiosity, here we examine the variable "Religious participation and value" (although our arguments apply to other aspects of sociality discussed by F&T).

Table 1 (Currie & Mace). World region classification, absolute latitude, and lnGDP for countries for which Religiosity data were available (NAfrME = North Africa and the Middle East)

Country	World region	Absolute latitude	ln GDP
Albania	Europe	41	8.91
Algeria	NAfrME	28	8.91
Andorra	Europe	42.5	10.71
Argentina	New World	34	9.6
Armenia	Europe	40	8.67
Australia	New World	27	10.63
Austria	Europe	47.33	10.6
Azerbaijan	Europe	40.5	9.31
Bangladesh	East Eurasia	24	7.44
Belarus	Europe	53	9.5
Belgium	Europe	50.83	10.54
Bosnia and Herzegovina	Europe	44	8.79
Brazil	New World	10	9.3
Bulgaria	Europe	43	9.46
Burkina Faso	Africa	13	7.09
Canada	New World	60	10.59
Chile	New World	30	9.65
China	East Eurasia	35	8.91
Colombia	New World	4	9.19
Croatia	Europe	45.17	9.77
Cyprus	Europe	35	9.95
Czech Republic	Europe	49.75	10.15
Denmark	Europe	56	10.51
Dominican Republic	New World	19	9.06
Egypt	NAfrME	27	8.73
El Salvador	New World	13.83	8.9
Estonia	Europe	59	9.85
Ethiopia	Africa	8	6.91
Finland	Europe	64	10.47
France	Europe	46	10.41
Georgia	Europe	42	8.48
Germany	Europe	51	10.49
Ghana	Africa	8	7.38
Greece	Europe	39	10.32
Hong Kong	East Eurasia	22.25	10.73
Hungary	Europe	47	9.85
Iceland	Europe	65	10.51
India	East Eurasia	20	8.13
Indonesia	East Eurasia	5	8.37
Iran	NAfrME	32	9.32
Iraq	NAfrME	33	8.19
Ireland	Europe	53	10.53
Italy	Europe	42.83	10.33
Japan	East Eurasia	36	10.44
Jordan	NAfrME	31	8.58
Kyrgyzstan	East Eurasia	41	7.7
Latvia	Europe	57	9.57
Lithuania	Europe	56	9.67
Luxembourg	Europe	49.75	11.31
Macedonia	Europe	41.83	9.15
Mali	Africa	17	7.09
Malta	Europe	35.83	10.13
Mexico	New World	23	9.53

(continues)

Table 1 (Currie & Mace). (Continued)

Country	World region	Absolute latitude	ln GDP
Moldova	Europe	47	7.82
Montenegro	Europe	42	9.2
Morocco	NAfrME	32	8.5
Netherlands	Europe	52.5	10.61
New Zealand	New World	41	10.24
Nigeria	Africa	10	7.78
Norway	Europe	62	10.99
Pakistan	East Eurasia	30	7.78
Peru	New World	10	9.13
Philippines	East Eurasia	13	8.16
Poland	Europe	52	9.84
Portugal	Europe	39.5	10.04
Puerto Rico	New World	18.25	9.7
Republic of Korea (South)	East Eurasia	37	10.32
Romania	Europe	46	9.35
Russia	Europe	60	9.67
Rwanda	Africa	2	7
Saudi Arabia	NAfrME	25	10.09
Serbia	Europe	44	9.31
Singapore	East Eurasia	1.37	10.95
Slovakia	Europe	48.67	10.01
Slovenia	Europe	46	10.25
South Africa	Africa	29	9.28
Spain	Europe	40	10.29
Sweden	Europe	62	10.57
Switzerland	Europe	47	10.67
Taiwan	East Eurasia	23.5	10.49
Tanzania	Africa	6	7.31
Thailand	East Eurasia	15	9.07
Trinidad and Tobago	New World	11	10
Turkey	NAfrME	39	9.42
Uganda	Africa	1	7.09
Ukraine	Europe	49	8.81
United Kingdom	Europe	54	10.47
United States	New World	38	10.77
Uruguay	New World	33	9.57
Venezuela	New World	8	9.44
Vietnam	East Eurasia	16	8.04
Zambia	Africa	15	7.31
Zimbabwe	Africa	20	5.99

Plotting out the relationship between combined parasite stress and religious participation reveals a number of interesting patterns (see our Fig. 1). Europe, for example, exhibits relatively little variation in parasite stress but relatively substantial variation in religious participation. Furthermore, while taking all regions together a positive relationship between the two variables can be seen, the correlation within these regions is not consistent (Pearson correlation coefficients, sub-script represents *n*: Africa, $r_{11} = 0.39, p = 0.24$; East Eurasia, $r_{12} = 0.34, p = 0.28$, Europe, $r_{43} = -0.02, p = 0.92$, North Africa, $r_8 = 0.05, p = 0.90$, New World, $r_{15} = 0.69, p = 0.005$). Although these are admittedly small sample sizes within all regions except Europe (where there is practically no relationship in any case), the only region in which there is a substantial relationship between parasite stress and religious participation is the "New World." However, even within this region further inspection

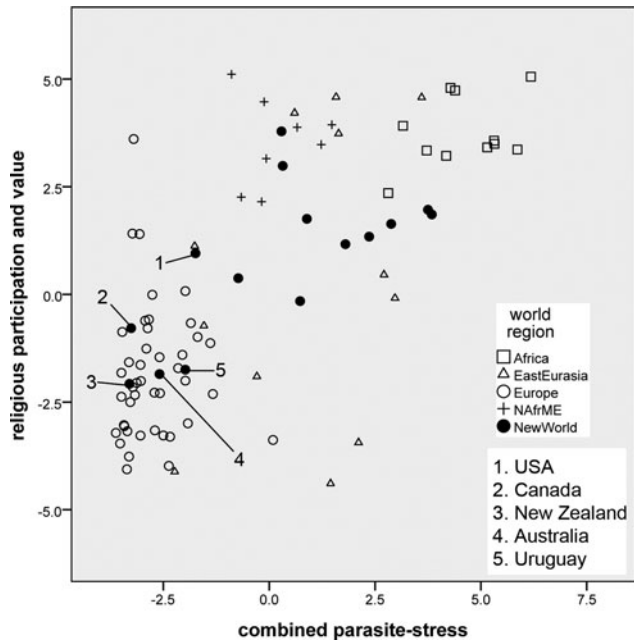


Figure 1 (Currie et al.). Relationship between the variables *religious participation and value* and *combined parasite-stress* with countries grouped according to world region. Although overall there is a negative relationship between the two variables, a strong negative relationship exists only within the “New World” region (see text for details).

reveals that this correlation is being driven by the four English-speaking countries that were settled predominantly by northern Europeans (Canada, USA, Australia, New Zealand). The relationship in the “New World” is no longer statistically significant if these four countries are removed ($r_{11} = 0.43$, $p = 0.18$). Additionally, the remaining positive relationship appears entirely due to the presence of Uruguay (the correlation coefficient in the remaining ten countries is 0.05 , $p = 0.90$). The apparent overall strong relationship between religious participation (and other sociality variables) and parasite stress therefore appears at least partly a result of not adequately identifying and controlling for sources of non-independence in the data.

Even if a relationship does remain between the dependent variables and parasite stress after properly controlling for the problem of non-independence, this does not necessarily indicate a causal relationship. As we have pointed out before (Currie & Mace 2009; in press; Mace & Jordan 2011), many ecological variables (including parasite stress) co-vary with latitude. Furthermore, religious participation and parasite stress also co-vary with economic indicators of development such as gross domestic product (GDP). Therefore, the positive association between religious participation and parasite stress may be due to their common co-variation with other factors. Although F&T claim to have controlled for a number of potential confounds, this does not appear to have been conducted in a systematic manner. Indeed, if we enter $\ln\text{GDP}$, *absolute latitude*, and *combined parasite stress* into a multiple regression model with *religious participation* as the dependent variable then both $\ln\text{GDP}$ ($\beta = -0.26$, $p = 0.02$) and *absolute latitude* ($\beta = -0.53$, $p < 0.001$) are statistically significant predictors, while *combined parasite stress* is not ($\beta = 0.06$, $p = 0.73$). Teasing apart causal relationships from spurious associations is not easy; however, future work should at least assess alternative models more thoroughly to see whether they do at least as well, if not better, than F&T’s favoured hypothesis. We feel it is likely that some other ecological factor or factors that co-vary with latitude (and therefore parasite stress) and affect such

things as subsistence strategies and population densities, may ultimately underlie the relationships reported by F&T here and elsewhere.

Finally, even if a robust relationship were to be shown between parasites and the various measures of sociality, using cross-national data, it does not demonstrate that the causal mechanism is the same as that proposed by F&T. They argue for a cognitive mechanism that is sensitive to parasite stress and causes people to exhibit more in-group favouritism accordingly. Yet, there is no direct evidence for such a cognitive mechanism from these analyses. An alternative explanation could be that it is purely cultural evolution, with groups that have a social organization or cultural practices that expose them to greater parasite stress, leaving behind fewer representatives in subsequent generations. These issues will not be addressed by yet more cross-national studies attempting to show that parasite stress is correlated with everything imaginable.

In short, while parasites and diseases have undoubtedly played an important role in shaping human history (Diamond 1997), the analyses presented here do not demonstrate that parasite stress is the strong, universal shaper of human psychology and social behaviour in the manner proposed by F&T.

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Are the pathogens of out-groups really more dangerous?

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Abstract: We question the plausibility of Fincher & Thornhill’s (F&T’s) argument that localised pathogen-host coevolution leads to out-groups having pathogens more damaging than those infecting one’s own family or religious group.

In this and related articles, Fincher & Thornhill (F&T) present an innovative and bold analysis of cross-cultural differences in psychology and behaviour. It is clear that parasitism – like predation – has acted as a powerful selection pressure on animal cognition and behaviour. However, a critical assumption of F&T’s thesis is that pathogens carried by out-groups (neighbouring families or communities) will be more dangerous than those of one’s own family and community. Empirical support for this proposition is tenuous.

Like footballers, pathogens tend to play better at home. In the ecological literature, this pattern is termed *local adaptation* and is defined as a situation where a pathogen has greater fitness within its local host population than within a non-local group. Local adaptation is not universal – F&T cite an example where fungi were better able to infect “out-group” plants (Kaltz et al. 1999) – but a recent meta-analysis concludes it is the general pattern (Hoeksema & Forde 2008). Selection on pathogens favours traits that enable them to spread within their *current host population*, not those that help them in neighbouring families or groups. Hence, when pathogens spread from their usual host population to another, they often have a reduced capacity to overcome host immune defences or spread from person to person. F&T present no clear evidence that the diseases used to

compute their *Parasite Stress Index* exhibit local maladaptation in humans across relevant spatial scales – that is, neighbouring kin or religious groups.

What F&T do emphasize is that pathogen genomes show considerable geographic variation (Rougeron et al. 2009). However, this variation may be due to a range of factors, including adaptation to ecology, secondary host biology, behaviour of host(s), or processes besides natural selection. Pathogen genetic variation in and of itself does not imply higher virulence or transmissibility in neighbouring groups. Likewise, examples of *host immune specialisation* cited by F&T may simply reflect hosts with generally better immune systems (e.g., more major histocompatibility complex diversity offering protection from a broad array of pathogens; Corby-Harris & Promislow 2008) or host groups whose immune systems differ because of founder effects (Miller et al. 2007). While the authors refer to cases where inter-group contact has resulted in catastrophic epidemics, these rare occurrences are due to the evolution of highly virulent “crowd diseases” in large and completely isolated populations, and are not relevant to coevolutionary processes in neighbouring kin or religious groups.

Our point is not to claim that human groups are *never* more susceptible to the pathogens of neighbours due to coevolution, only that this is not the general pattern, and often the opposite will be true. Pathogen avoidance strategies involve critical compromises: out-groups may have valuable mates, allies, tools, resources, or good ideas. All of these can be fitness enhancing, and we are unconvinced that pathogen-host coevolution results in a world where forgoing these benefits generally makes adaptive sense.

If coevolution doesn't result in out-groups with more dangerous pathogens, how are F&T's results explained? One possibility is that assortative sociality is more beneficial in high-pathogen stress areas because of how it influences the shape of people's social network. Assortative sociality means people are clustered in groups such that people are well connected with each other, and poorly connected with other clusters. When a population is organised in this fashion the capacity of epidemics to spread is reduced (Keeling 1999; Salathé & Jones 2010). Hence, assortative sociality may be increasingly beneficial where pathogens are more common, independent of host/parasite coevolution. Another possibility is that ontogenetic changes in the immune system leave people more vulnerable to out-group pathogens. Illness in childhood, for example, often results in memory B-cells that respond quickly and effectively to subsequent exposure to the same pathogen. Adults may therefore be somewhat more vulnerable to pathogens of other groups, again independent of any coevolutionary processes. No doubt other factors – some unrelated to pathogens – also affect the payoffs of different social systems. Given the complexity and diversity of possible causal relationships between social relationships and disease transmission, we would encourage more formal modelling of how inter-group behaviour is optimized under different conditions of pathogen prevalence.

Extending parasite-stress theory to variation in human mate preferences

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Abstract: In this commentary we suggest that Fincher & Thornhill's (F&T's) parasite-stress theory of social behaviors and attitudes can be

extended to mating behaviors and preferences. We discuss evidence from prior correlational and experimental studies that support this claim. We also reanalyze data from two of those studies using F&T's new parasite stress measures.

Parasites, and the arms races between parasites and other organisms, have long been associated with theories of sexual selection because organisms benefit from choosing parasite-free and parasite-resistant mates (e.g., Hamilton & Zuk 1982). With rising parasite load, organisms should channel their energies away from display to fight parasites and so may be less able to invest in attractive traits (Folstad & Karter 1992). Because parasites are generally detrimental to health and survival, high parasite load increases the importance of selection of mates who possess traits indicating resistance to parasites; and so we can predict that relative parasite stress will affect human preferences for traits associated with health and disease resistance.

Several previous studies in humans have reported positive correlations between various measures of parasite stress and preferences for putative cues of long-term health, suggesting that individuals place greater emphasis on potential mates' health cues in regions where pathogens impose a greater selection pressure (Gangestad & Buss 1993; Low 1990). For example, in a study of 29 cultures, Gangestad et al. (2006) observed positive correlations between a measure of pathogen prevalence and the importance placed on potential mates' physical attractiveness, health, and intelligence.

Human faces contain several potential cues to parasite resistance and have been the focus of much research in attractiveness (e.g., Thornhill & Gangestad 1999). A recent study of 30 Westernized countries showed that regional differences in women's preferences for masculine traits in men's faces, a cue of men's long-term health (Rhodes et al. 2003; Thornhill & Gangestad 2006), were correlated with a potential proxy measure for parasite stress: a composite health measure derived from various World Health Organization statistics on mortality and life expectancy (std $\beta = -0.515$, $t = -3.18$, $p = 0.004$; DeBruine et al. 2010). The relationship between women's masculinity preferences and this health measure remained even after controlling for regional variation in wealth and mating strategies (DeBruine et al. 2010) or controlling for homicide rates (DeBruine et al. 2011), a potential indicator of intrasexual competition (Brooks et al. 2011). A similar correlation (std $\beta = -0.478$, $t = -3.77$, $p < 0.001$) was also observed in a U.S. sample using a composite health measure derived from the United States Centers for Disease Control statistics on mortality due to illness and disease across 50 states, even after controlling for regional variation in wealth, income inequality, fertility, and homicide rates (DeBruine et al. 2011). These data indicate that women in regions with lower health exhibit stronger preferences for secondary sexual traits associated with long-term health in male faces.

Here, we have re-analyzed both samples of data using Fincher & Thornhill's (F&T's) measures of parasite stress. Linear regression using the weighted least squares (WLS) method to control for number of participants per country showed that, across countries, there was a significant positive relationship between parasite stress and women's preferences for masculine men (std $\beta = 0.654$, $t = 4.58$, $p < 0.001$). Using the same analysis, across the states of the United States, a significant positive relationship was also observed between these variables (std $\beta = 0.443$, $t = 3.43$, $p = 0.001$). These re-analyses show that F&T's parasite stress measures generate the same results as our previously used composite health measures; parasite stress predicted regional variation in women's preference for male facial masculinity in a nearly identical way to the health measures. Indeed, our health measures and these parasite stress measures were highly correlated in both samples of 30 Westernized countries ($r = -0.880$, $p < 0.001$) and 50 US states ($r = -0.668$, $p < 0.001$).

Although many studies have implicated pathogen stress in regional variation in behavior, the correlational nature of these studies and the large number of covarying ecological factors mean that it is not possible to draw firm conclusions about the effects of pathogen stress on behavior (Brooks et al. 2011; DeBruine et al. 2011; Lee & Zeisch 2011; Little et al. 2011). F&T address this limitation of correlational studies by noting experimental research in which viewing cues to disease salience affected behavior in ways predicted by their parasite-stress theory of social behavior, whereas viewing control images did not (e.g., Mortensen et al. 2010). Similarly, we have also found that viewing cues to disease salience increased preferences for facial cues of long-term health in potential mates, but not same-sex individuals (Little et al. 2011). Similarly, after women are primed with questions about pathogen prevalence, their preferences for traits indicating genetic quality (e.g., intelligence and muscularity) increase in relation to preferences for traits indicating parental quality (e.g., kindness and nurturing; Lee & Zeisch in press).

Collectively, these correlational and experimental findings, together with our new analyses, suggest that F&T's parasite-stress theory of social behaviors and attitudes can be usefully extended to understand regional variation in mating behaviors and preferences, further underlining the importance of pathogens in shaping human behavior.

Parasite stress, ethnocentrism, and life history strategy

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Abstract: Fincher & Thornhill (F&T) present a compelling argument that parasite stress underlies certain cultural practices promoting assortative sociality. However, we suggest that the theoretical framework proposed is limited in several ways, and that life history theory provides a more explanatory and inclusive framework, making more specific predictions about the trade-offs faced by organisms in the allocation of bioenergetic and material resources.

Fincher & Thornhill (F&T) present correlational cross-national data as evidence that parasite stress underlies certain cultural practices, such as religiosity and family coherence. They argue that the ancestrally evolved adaptive feelings of *philopatry*, *ethnocentrism*, and *xenophobia* limit the introduction of novel parasites to local populations.

Ethnocentrism was originally defined as “a view of things in which a group other than one’s own is the center of everything, and all others, including one’s own group, are scaled and rated with reference to it” (Sumner 1906, p. 13). Subsequently, this construct has been subdivided into *positive* ethnocentrism, denoting in-group attraction, affiliation, or “love,” and *negative* ethnocentrism, denoting out-group repulsion, aversion, or “hate” (Figueredo et al. 2011a). In spite of this distinction, F&T conflate *philopatry*, *ethnocentrism*, and *xenophobia* as common “elements of in-group assortative sociality” (sect. 2.1, para. 6). Nevertheless, in a survey done of 30 ethnic groups in East Africa, Brewer and Campbell (1976) found that positive in-

group biases were overall completely unrelated to social distance toward out-groups. Allport (1954) and Brewer (1999) had previously observed that in-group love may be correlated with out-group hate: (1) positively, (2) negatively, or (3) zero. In addition, F&T cite several sources that indicate that a number of variables commonly used in cross-cultural psychology are correlated, such as conservatism-liberalism and collectivism-individualism. However, F&T do not report the *magnitudes* of these correlations. Qualitative expressions like “overlap considerably” or “are similar to” are insufficient to relate these sociocultural constructs psychometrically. Because these terms are afterwards used interchangeably, it would be useful to know exactly how correlated they are, empirically and quantitatively rather than merely theoretically.

This theoretical argument would appear to fit easily within a life history framework, but the way that synthesis might be accomplished remains unclear. F&T acknowledge that parental effort and nepotistic effort are key life history variables (e.g., Figueredo et al. 2007). Religiosity and moral attitudes are also correlates of slow life history strategy (e.g., Figueredo et al. 2007; Gladden et al. 2009). Furthermore, F&T also note that slow life history strategy has been empirically linked to higher degrees of assortative pairing of both social and romantic partners in a recent cross-cultural study (Figueredo & Wolf 2009). A complicating factor, however, is that another recent cross-cultural study (Andrzejczak et al. 2007; Figueredo et al. 2011a; Jones et al., submitted) found that slow life history is positively predictive of positive ethnocentrism but negatively predictive of negative ethnocentrism. This latter finding does not appear to fit the pattern.

F&T acknowledge that local parasite prevalence is a major force in life history evolution. Indeed, the balance between intrinsic and extrinsic mortality is an important feature in an organism’s ecology that, according to life history theory, leads to very specific predictions about behavioral adaptations (see Ellis et al. 2009). *Intrinsic* morbidity-mortality denotes a threat over which the organism has some control by means of evolvable adaptive responses, such as reallocating resources to buffer or eliminate the threat. Characteristics that may serve in this strategic response include “age, health, size, competitive abilities, metabolism, immune functioning, and related competencies” (Ellis et al. 2009, p. 14). *Extrinsic* morbidity-mortality denotes a threat that cannot be averted by the organism’s attempted countermeasures: An organism may implement behavioral tactics directed towards escaping the threat, but the source of morbidity-mortality is insensitive to these responses. This failure is not due to suboptimal decision-making on the part of the organism. *Extrinsic* threat is simply unavoidable.

One of the predictions that F&T derive from these life history considerations is that there should be a curvilinear, rather than rectilinear, relationship between parasite prevalence and extrinsic mortality, and hence (indirectly) with assortative sociality. Curiously, though, they only address these with some *post hoc* comparisons at the end, rather than formally testing the proper curvilinear regression models, which could be readily accomplished with the existing data. Either way, we remain skeptical that mere parasite *prevalence* is sufficient to select a fast life history strategy (Ellis et al. 2009). Rather, two other factors are paramount: (1) the schedule of *age-specific* morbidity-mortality, and (2) the *temporal stability* of these schedules. When systematic variance in juvenile morbidity-mortality is high, it becomes possible to engage in counteracting behaviors, such as investing in competitive ability, to *buffer* the threats of morbidity-mortality. When threats vary unpredictably across juveniles within a single generation, a strategy that diversifies offspring to *partially evade* these threats is instead selected. When adults are at greater risk, a strategy of *earlier reproduction* is selected.

Eppig et al. (2010) recently argued that general cognitive ability is reduced developmentally by parasite stress as a result of a trade-off between investing in two bioenergetically

demanding domains: general cognitive functioning and immune functioning. If infectious disease stress can disrupt general cognitive ability developmentally, it may also disrupt executive control, or inhibition of prepotent responses. Some evidence suggests that executive control may inhibit xenophobia (and related features, including disgust sensitivity and in-group preference) (e.g., Gladden 2010; MacDonald et al. 2007). The finding that infectious disease stress disrupts general cognitive functioning also suggests the alternative hypothesis that disease stress may increase ethnocentrism and xenophobia by disrupting executive control as a *side effect* of a developmental trade-off with investing immune functioning, rather than as an adaptive tactic to guard against pathogenic transmission. Because executive functioning is implicated in general criminality (Gottfredson & Hirschi 1990) and interpersonal aggression (Figueredo et al. 2011b), this alternative mediating mechanism might explain the reported correlation between infectious disease stress and violent aggression across the United States (Thornhill 2010).

Finally, high disease stress could result in another proposed feature of assortative sociality: philopatry itself. Disease stress could render unhealthy individuals unable to migrate sufficiently long distances to leave their natal group. This alternative hypothesis suggests that the pattern of correlations offered in support of the parasite stress theory of sociality may result as a non-adaptive *by-product* of infectious disease stress rather than as an adaptive strategy to avoid disease. This alternative side-effect hypothesis needs to be addressed to strengthen the proposed interpretation.

The evolution and development of human social systems requires more than parasite-stress avoidance explanation

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Abstract: Fincher & Thornhill (F&T) present a model of in-group assortative sociality resulting from differing levels of parasite-stress in differing geographical locations in the United States and the world. Their model, while compelling, overlooks some important issues, such as mutualistic associations with parasites that are beneficial to humans and how some religious practices increase parasite risk.

Fincher & Thornhill (F&T) present a compelling model of in-group assortative sociality and religiosity as adaptations to high levels of parasite-stress in local environments. Humans have acquired approximately 300 species of parasitic worms and 70 species of protozoan parasites that they have interacted and coevolved with over the last million years or so (Cox 2002). It would seem to make evolutionary sense that humans would have developed psychological as well as biological adaptations to counter parasitic threat. F&T attempt to incorporate parasite-stress into evolutionary models of sociality. However, although they present a strong case, there are four major issues I have with their arguments.

The first issue is that their model does not address the evolutionary benefits from mutualistic associations – that is, associations between two individuals of the same or different species that confers a fitness benefit to both. Humans have received mutualistic fitness benefits from parasitic microorganisms, phylogenetically and ontogenetically. For example, it is believed that the evolutionary precursor of mitochondria, the primary energy producing organelle in our cells, originated as an invasive, parasitic bacterium (Searcy 2003). The microflora that inhabit our intestines are essential to many aspects of healthy

human functioning, including preventing growth of pathogenic bacteria, and are transmitted horizontally from the mother to infant during the first birth year (Dethlefsen et al. 2007; Goodacre 2007). If humans possessed adaptations for parasite stress, it would seem that they would be only for the parasites that were potentially lethal or immediately hazardous. For a parasite-stress adaptation to be considered an evolutionary success it would have to accurately identify legitimate threats from potentially beneficial microorganisms and non-communicable diseases. Additionally, false positives could occur from individual differences due to biological development, injury, or age. Without the ability to correctly sort out legitimate parasite threats from harmless non-communicable symptoms, we run the risk of avoiding anyone who does not fit an idealized healthy appearance.

The second issue stems from the first and it involves the level of analysis. The primary function of F&T's study is to examine sociological measures of large geographic areas such as states and countries comprising large populations or groups; however, it is difficult to draw conclusions about individual behavior from such domains. What I am most curious about is how the in-group pressure, or assortative sociality, would work at an individual level. F&T postulate that in-group assortative sociality results, in part, from the avoidance of out-group parasitic threats; however, individuals may also be exposed to parasites from in-group members. This issue is mentioned in section 6.3.1 in terms of a "life-history theory" in regions of high parasite-stress. Yet F&T have not addressed how collective attitudes can override the social exclusion of those group members who may be differentially likely to carry disease in areas of less-than-extreme levels of parasite-stress: At what point does an individual participating in a religious event come to regard a nearby person with a sign of parasite infection as no longer a member of the in-group? Considering that, historically, individuals with infections or illness were seen to be suffering from something they did to themselves or resulting from divine wrath (de Avila-Pires 1998), the drive towards collectivism seems to be a unique human trait compared to other primates; and, although this was not the primary focus of F&T's study, it nonetheless begs the question.

The third issue is regarding F&T's argument about the causal effects of parasite stress on the formation of human sociality: specifically, that parasite stress was one of the primary driving forces that shaped social, religious, and family life. The proposition that parasite stress is directly responsible for the development of animal social structure is rather overreaching for a correlational human social study. The development of any trait, including parasite avoidance, involves a complex mixture of many elements and often follows a nonlinear path. For example, the development of any disease is the direct result of the history of and interaction between biology (i.e., genetic predispositions, timing of exposure), ecology (i.e., local flora and fauna, nutritional sources, latitude), and social factors (i.e., population density, access to quality health care, group size), as opposed to a single identifiable outside threat. The concept that maintaining in-group allegiances serves to protect "co-adapted gene complexes" (target article, sect. 2.1., para. 4) from outside parasitic threat does not hold up to medical evidence. For example, genetic research is finding that genes are secondary causes of health disparities in the United States, compared with social and environmental factors (i.e., racial discrimination, poverty) (Dressler et al. 2005; Sankar et al. 2004). I believe that the patterns found on a large scale in the F&T's study will break down on an individual psychological level.

The last issue I would like to address is F&T's argument that religiosity and religious practices are derived from parasite-stress. If parasite-stress drives the development of religious beliefs and practices, this suggests that those beliefs and practices would reflect some kind of avoidance or prevention measures for parasite-stress – and in many cases this does seem to be the case, such as avoiding pork in the Jewish tradition. However, there are also many cases where religious and/or cultural practices have

actually increased the spread of disease: for example, the well-known spread of the CJD-like disease among the Fore tribe in Papua New Guinea due to cannibalistic rituals. The rapid spread of HIV in Africa is connected to cultural practices that increase the risk of transmission, such as circumcision, medicinal bloodletting, and blood rituals, as well as sharing instruments during ritual sacrificing, tattooing, and piercing (Hrdy 1987).

F&T present a solid model for parasite-stress factors shaping large-scale patterns of human family, cultural, and religious systems. I believe, however, that they cast a net too large to reveal the causal relationships between parasite threat and specific human behavior. Immune responses to parasite threat as well as human social systems are amazingly complex and dynamic, involving many interactions over time. F&T address the legitimate threat that parasites have posed, but the precise manner in which parasite-stress and human psychological, cultural, and religious beliefs and practices have coevolved is somewhat overlooked in their current model.

Coping with germs and people: Investigating the link between pathogen threat and human social cognition

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Abstract: Group assortative biases are stronger in regions where pathogen stress has been historically prevalent. Pushing the logic of this approach, extensions should include investigations of how cultural norms related to prosociality and relational striving may also covary with regional pathogen stress. Likewise, the pan-specific observation that diseased animals show decreased motor activity to facilitate recovery suggests that norms relevant to sickness behaviors may also vary as a function of regional parasite stress.

Fincher & Thornhill (F&T) extend both theory and evidence for a *behavioral immune system* theory of cognition and behavior to the level of cultural norms regarding family and religion. The theory posits the existence of an evolved psychological system that generates prophylactic, pathogen-avoidant response strategies to pathogen threat in the environment, which may consist of beliefs, attitudes, and psychological orientations that serve as the psychological substrates for avoiding potential disease vectors. Unlike the somatic immune system, which typically responds to pathogen attacks via the activity of pro-inflammatory cytokines, the behavioral immune system responds to perceptual threats – before infections occurs – which may include assortative biases for one's own group versus others as a defense against vectors of novel parasites.

In a bold extension of this framework, F&T hypothesize that the behavioral immune system may extend to beliefs and customs transmitted at the cultural or societal level, where norms regarding the tightness of family ties and religiosity (“assortative sociality”) are expected to be stronger in environments where pathogen loads have been historically prevalent. In an inter-regional and cross-national analysis, F&T demonstrate that such assortative sociality is indeed predicted by historical parasite stress in the region. These findings hold even when controlling for factors expected to covary with disease threat, such as economic development. There are many potential alternative explanations for why parasite threat might covary with assortative biases (such as more general existential fears). However, F&T find that their effects are strongest in environments where human-specific transferred diseases were most prevalent, relative to those transferred through other means.

I don't think the importance of this last point about the disease specificity of this phenomenon can be underemphasized, because it is so compelling as to all but preclude the plausibility of any competing theory in explaining these findings. F&T have made a solid advance in the scientific understanding of some of the most fundamental domains of the human condition – families, groups, and religion – by extrapolating from a major theme in biology: disease, an adaptive problem for all life forms.

The arguments and findings of F&T are compelling in their conceptual clarity and theoretical integration, and are sweeping in their explanatory power. The authors have clarified and built on the ruminations of others (e.g., Curtis & Biran 2001; Fessler 2002; Navarrete & Fessler 2006; Schaller 2006; Wronska 1990) to develop an enterprise that is maturing much faster and more convincingly than anyone would have imagined possible just a few years ago.

Given their success, I am tempted to push them even further. As F&T are aware, but do not emphasize, the behavioral immune system need not be relegated solely to a psychological system whose functions are only prophylactic. F&T rightly paraphrase Navarrete and Fessler (2006) in noting that assortative sociality not only serves protective functions, but can also function as an “insurance policy” to facilitate the healing process after the fact. If this is indeed the case, might F&T be able to find evidence for greater prosociality relevant to helping the sick and weak within families and religious groups in response to disease threat cross-culturally? I'm not sure how readily testable this notion is compared with what the authors have already heroically demonstrated, but the challenge is put.

Along similar lines, one might push the notion even further that the behavioral immune system should generate not only behavioral prophylaxis, but should also include psychological mechanisms underlying behavioral responses to infection that allow the organism to heal and recover, should prophylaxis fail (*sensu* Hart 1988). The action of pro-inflammatory cytokines not only serves to neutralize pathogens in the body, but also may play a role in neurological changes that increase the likelihood of sickness behaviors, which cause an organism to not over-exert itself while it is still vulnerable and on the mend. Research describes a syndrome associated with cytokine activity where diseased animals will show decreased motor activity and food intake, reduced foraging, less exploratory behavior, increased sleep, and decreased grooming behavior (Kelley et al. 2003).

Previously believed to be mere artifacts of exogenous cytokines, these changes in behavior are now widely believed to be an import-526.1(it)3295f iTc[(295f)-52.5d295fberly(be)-416.1(iroc(furth)-il)-s

and it would be no more potentially sensitive than is F&T's bold and impressive work at hand.

High illness loads (physical and social) do not always force high levels of mass religiosity

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Abstract: The hypothesis that high levels of religiosity are partly caused by high disease loads is in accord with studies showing that societal dysfunction promotes mass supernaturalism. However, some cultures suffering from high rates of disease and other socioeconomic dysfunction exhibit low levels of popular religiosity. At this point, it appears that religion is hard pressed to thrive in healthy societies, but poor conditions do not always make religion popular, either.

The hypothesis by Fincher & Thornhill (F&T) in the target article (see also Fincher & Thornhill 2008) that high levels of popular religiosity are correlated with and perhaps, in part, caused by high disease loads, is a subhypothesis within the larger socioeconomic dysfunctionality hypothesis that proposes that religious supernaturalism tends to suffer serious losses in popularity as general living conditions improve. This uncertainty hypothesis is being supported by a rapidly expanding set of studies, and, as such, strongly contradicts the thesis that supernaturalistic religiosity is the innate, universal human condition (Barber 2011); Delamontagne 2010; Gill & Lundsgaarde 2004; Norris & Inglehart 2004; Paul 2009; 2010a; 2010b; in press; Rees 2009; Ruiters & Tubergen 2009; Verweij et al. 1997; Zuckerman 2009).

However, there are certain under-appreciated factors that impact the subject. It has commonly been assumed that levels of supernaturalism are persistently high among "primitive" populations that live under harsh conditions. This appears to not be the case. African Hadza hunter-gatherers are currently living lives not dramatically different than they did in the late Pleistocene. Yet they exhibit minimal religiosity (Barber, in press; Marlowe 2002; 2010; Paul 2010a; in press). Although the Hadza fear death, they do not believe in an after-life. In Hadza cosmology the sun is a supernatural entity, but they do not actively worship it or try to influence its actions in their favor. Pre- and post-hunting rituals are absent, and other rituals are limited in scope. Shamans are absent, and the tribe has proved highly resistant to Christian recruitment. Similarly, the Amazonian Piraha are also theistically unconvertible; Everett (2008) found the Piraha to be markedly less religious than devout Christians, especially in their absence of god figures that provide moral guidance.

Preindustrial civilizations have also exhibited strong variations in mass religiosity. The Chinese majority has never developed or adopted major god figures (Yao & Zhao 2010), and the relatively philosophical civilization appears to have been markedly less pious than neighboring India or pre-Renaissance Europe.

It appears that the high parasite loads and other forms of dysfunction that are continuing to afflict peoples living in undeveloped societies have not consistently forced the development of high levels of religiosity in the population. For example, it is unlikely that the infection, symptom, and mortality rates of the Hadza (Marlowe 2004) are markedly lower than those of other recent hunter-gatherers with much higher levels of supernaturalism. On the other hand, all First-world democracies with historically low levels of socioeconomic dysfunction exhibit historically low levels of

religiosity. These patterns suggest that although an inadequate habitat commonly encourages mass religiosity, the effect is not consistent, but that the highest levels of economic and physical security are reliably antithetical to mass religious faith. These hypotheses warrant further research and analysis in a field of human behavior that has not received the full scientific attention it needs.

An ethical and prudential argument for prioritizing the reduction of parasite-stress in the allocation of health care resources

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Abstract: The link between parasite-stress and complex psychological dispositions implies that the social, political, and economic benefits likely to flow from public health interventions that reduce rates of non-zoonotic infectious disease are far greater than have traditionally been thought. We sketch a prudential and ethical argument for increasing public health resources globally and redistributing these to focus on the alleviation of parasite-stress in human populations.

If Fincher & Thornhill's (F&T's) thesis is correct, there should be significant changes to the priorities of global health institutions, as well as a substantial increase in the overall global investment in health care. The link between parasite-stress and complex social psychological dispositions implies that the ethical, social, economic, and political benefits that are likely to flow from public health interventions that reduce rates of non-zoonotic/multi-host infectious disease are far greater than have traditionally been thought. These include not only immediate health benefits to afflicted individuals and averted medical costs due to reduced rates of infection, but also the ontogenetic production of personality configurations that promote democratic values and could lead to a significant reduction of intergroup conflicts and human rights violations worldwide within a short time frame. Here, we sketch a prudential and ethical argument for increasing public health resources globally and redistributing these to focus research and development efforts on the alleviation of parasite-stress in human populations.

The dominant approach to the evaluation of health care policy is cost-effectiveness analysis, which compares the cost of biomedical interventions with their medical efficacy (Beauchamp & Childress 2001). This narrow focus on illness, averted medical costs, and other health-related impacts has caused policy makers to underestimate the expected utility of many public health interventions. A growing body of research indicates that the well-established causal pathway from higher income to better health also runs in the opposite direction, with health underwriting economic development through its effects on labor productivity, fertility rates, education, and cognitive development (Bloom & Canning 2000). The impact of public health on economic growth has been demonstrated for the use of antibiotics, antimicrobials, vaccination, sanitation measures, and vector reduction (Bloom et al. 2005; Hotez et al. 2006).

However, if F&T's thesis is correct, then infectious disease-related interventions are likely to have more far-reaching social, economic, and political implications. It is well known that societal choices can affect susceptibilities to infectious disease, but few have imagined a proximate causal pathway through which infectious disease can shape sociopolitical choices. The authors have identified such a pathway, one mediated by adaptively plastic social psychological mechanisms that are contingent on environmental cues of parasite-stress. These cues trigger mechanisms of in-group assortative sociality that lead to the ontogenetic production of personality configurations associated with a particular range of political psychologies and organizations. Dispositions toward ethnocentrism, xenophobia, distrust, derogation, intolerance, and hostility towards out-group members act to buttress authoritarian political institutions and reinforce gender inequalities and racial hierarchies. Such non-egalitarian attitudes impede the development of liberal democratic institutions and breed antagonistic intergroup relations that can spawn large-scale human rights violations (Hewstone et al. 2002), with consequent political and economic instability. The rhetoric of dehumanization that often accompanies bouts of ethnic cleansing and genocide strategically plays on the disgust-modulated operation of the behavioral immune system, with out-group members frequently compared to rats, cockroaches, lice, or other disease vectors (Navarrete & Fessler 2006).

All major conceptions of morality and justice view impartiality as a core moral ideal (Hauser 2006). Moral progress since the Enlightenment is characterized by an expanding circle of moral concern encompassing not just members of one's ethnic, political, or religious group, but also wider humanity and even some nonhuman animals (Singer 1981). The principle of equality that drives this moral expansion underpins the liberal political institutions that characterize modern constitutional democracy and the rule of law. It requires that individuals be treated equally and be afforded the same basic rights, privileges, and access to social resources. Perhaps the greatest challenge to implementing the impartial moral standpoint comes from strong biopsychological dispositions toward in-group partiality and out-group apathy or antagonism, which create a social-psychological climate in which it is difficult for democratic values and institutions to take root. Moreover, solving the most pressing problems of the 21st century, including global poverty, climate change, and terrorism, will require enhanced levels of intergroup cooperation that historically have been hampered by the restricted altruism and negative intergroup dispositions that characterize strong assortative sociality. We therefore have weighty moral, prudential, and economic reasons for altering ecological conditions that are conducive to the acquisition and perpetuation of such biases, and for assigning these interventions a high priority in the allocation of scarce resources.

The question of how to distribute limited medical resources is a question of distributive justice, of which there are various theories. According to utilitarianism, resources should be distributed so as to maximize utility, where utility is measured in terms of happiness, preference satisfaction, or some objective measure of well-being (Bykvist 2010). From a utilitarian standpoint, the moral imperative to dedicate more resources to alleviating parasite-stress is straightforward, given that the expected utility of such interventions clearly outweighs their cost even on narrow views of the benefits (Hotez et al. 2006; Lee et al. 2011). Another dominant theory, liberal egalitarianism, prioritizes individuals in greatest need of the resources being distributed (Rawls 1971). This philosophical tradition widely regards basic health-care as a fundamental human need, the moral force of which is amplified by the impact of health on economic growth, social justice, and the development of liberal political institutions. Even if one thinks that physicians should focus exclusively on the medical interests of their patients for professional reasons, it is appropriate that governments, international health

organizations and funding bodies take these non-health-related impact factors into consideration and reform the narrowly defined methods by which they evaluate proposed health care interventions.

The fact that the postulated psychological mechanism is phenotypically plastic and sensitive to specific environmental cues implies that it is highly amenable to intervention. Reducing rates of non-zoonotic infectious disease will result in a corresponding reduction of in-group assortative sociality and its consequent sociopolitical benefits within a reasonably short timeframe. Altering the ecological conditions that seed social injustice and intergroup conflict is of the foremost ethical concern. If in-group assortative sociality is, like fever or inflammation, an adaptive strategic defense against infection, then rather than merely treating the symptom we have strong moral reasons to eliminate its root cause.

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Mechanisms by which parasites influence cultures, and why they matter

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Abstract: At least four conceptually distinct mechanisms may mediate relations between parasite-stress and cultural outcomes: genetic evolution, developmental plasticity, neurocognitive flexibility, and cultural transmission. These mechanisms may operate independently or in conjunction with one another. Rigorous research on specific mediating mechanisms is required to more completely articulate implications of parasite stress on human psychology and human culture.

Fincher & Thornhill (F&T) contribute important new evidence to a growing literature linking the prevalence of disease-causing parasites to cultural outcomes. Increasingly, the question is not whether parasite prevalence has cultural consequences, but *how*: Exactly what mediating mechanisms account for relations between the parasite load in the local ecology and the traits, values, and social norms observed within the human population occupying that ecology?

As currently articulated, the parasite-stress model predicts outcomes observed at a societal level (e.g., religiosity, strong family ties, collectivistic values, authoritarian governments), but it does not specify the exact mechanisms through which those outcomes emerge. Societal outcomes don't just happen. They are emergent products of individuals' actions and interactions, which are, in turn, products of individuals' cognitions, emotions, and behavioral dispositions. These, in turn, are products of the developmental process through which genetic material builds bodies. Multiple levels of analysis are implicated, along with multiple conceptually distinct mechanisms that may be influenced by parasite-stress. One mechanism is *genetic evolution*: Heritable traits that reduce contact with parasites (and the alleles associated with those traits) may become more common in populations occupying ecologies characterized by high levels of parasite-stress. A second mechanism is *developmental plasticity*: The phenotypic consequences of genetic information depend on whether and how the genes are expressed during development; genes for traits that reduce contact with parasites may be expressed more readily in ecologies characterized by high levels of

parasite-stress. A third mechanism is *neurocognitive flexibility*: Human nervous systems are adaptively designed to detect threat-connoting cues in the immediate perceptual context, and to respond flexibly depending on the presence of these cues; responses that reduce contact with parasites may occur more frequently, and more strongly, when perceptual processes register a greater prevalence of cues connoting infection. A fourth mechanism is *cultural transmission*: Societal outcomes depend in part upon the exact nature of the interpersonal influence that occurs when individuals interact and communicate with one another; behavioral tendencies that limit contact with parasites may be transmitted more readily when people perceive greater threat of infection.

There is evidence that implicates each of these mechanisms as a plausible route through which parasite-stress may lead to cultural differences (Schaller & Murray 2011). And, although conceptually independent, these mechanisms may also influence each other. (Neurocognitive flexibility has implications for cultural transmission; cultural transmission reshapes the social ecology and so has implications for genetic evolution; and so forth.) But just because they have potential implications for one another, this does not mean they are all equally implicated as mediating mechanisms in the causal link between parasite-stress and cultural outcomes. Nor is it logically necessary for each cultural outcome to result equally from each of the plausible mediating mechanisms. Highly heritable individual-level traits (such as religiosity; Waller et al. 1990) may be more strongly influenced by genetic mechanisms, whereas societal outcomes such as democratization and the strength of family ties may be more strongly influenced by cultural transmission. Each specific mechanism must be considered, and tested, as a possible mechanistic explanation for each specific cultural outcome predicted by the parasite-stress model. By doing so we can address additional questions about the effects of parasites on human culture.

One question pertains to the time lag between ecological and cultural change. Parasite ecologies can change quickly, especially when people apply technological interventions (e.g., vaccination programs) toward the purpose of eliminating infectious diseases. Research linking parasite-stress to cultural outcomes offers the intriguing implication that these interventions may also have unintended consequences on a broad range of cultural outcomes (secularization, democratization, the reduction of xenophobia, the disintegration of family ties, etc.). If so, how quickly might this happen? To the extent that an effect is mediated by population-level changes in gene frequencies, it may take a very long time indeed. To the extent it is mediated by developmental plasticity, it may take just a single generation. To the extent it is mediated by neurocognitive flexibility, it may take virtually no time at all. And to the extent it is mediated by cultural transmission, the implications for cultural change are more complicated. Interpersonal communication processes allow for rapid diffusion of novel behavioral norms. However, the psychology of interpersonal influence often emphasizes conformity and resistance to change instead; these conformity pressures tend to be especially strong under conditions of high parasite-stress (Murray et al. 2011).

A second question pertains to a broader set of possible psychological and societal outcomes. Any single mediating mechanism may not only produce outcomes that are predicted by the parasite-stress model, but also additional outcomes that aren't. Genes that promote individual-level traits linked to the reduction of infection (e.g., religiosity, xenophobia) probably do so because of their phenotypic expression within specific neurotransmitter systems (e.g., the serotonin transmitter system; Chao & Blizinsky 2010). Each neurotransmitter system has wide-ranging implications for additional traits too, many of which have no obvious bearing on infection-reduction at all. These consequences cannot be predicted by the parasite-stress model alone; meaningful explanation of these additional consequences requires explicit

inquiry into the specific mediating mechanism. Analogously, religious practices that reduce infection risk are neither practiced nor preached in isolation from other practices. For example, in many societies, Islamic law requires that women wear veils and heavy clothing, which reduces incidence of mosquito-borne infections (Russell 1952); but this particular practice is bundled into a broader set of religious rituals, many of which are infection-irrelevant. Cultural transmission mechanisms tend to operate on these bundles, rather than on single practices, with the result that many infection-irrelevant norms may also be linked to parasite-stress. Again, any real understanding of these cultural outcomes requires careful articulation of the specific mechanisms that produces them.

The bottom line is this: It is only by considering mediating mechanisms more explicitly that we can more completely predict, explain, and appreciate the implications of parasite-stress on people, and on the cultures that people create.

Form and function in religious signaling under pathogen stress

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Abstract: The evolution of religious traditions may be partially explained by out-group avoidance due to pathogen stress. However, many religious rituals may increase rather than decrease performers' susceptibility to infection. Moreover, religions often spread through proselytizing, which requires out-group interaction; and in other cases, the benefits of economic exchange increase religious pluralism and social interactions with out-groups.

Fincher & Thornhill (F&T) present a strong argument for the primacy of host-parasite coevolutionary races as causal drivers of the geographic distribution of religiosity and family ties. As evolutionary anthropologists interested in both how and why religion does what it does, we applaud this work as a truly biosocial approach to religion. The claim that socially learned and cultural behavior is geared toward dealing with parasite invasions connects proximate- and ultimate-level explanations for religion and can potentially inform neuroscientific, cognitive, and behavioral studies. We focus our comments on costly signaling, warfare, and economic interrelationships.

F&T argue that parasite sociality and evolutionary signaling models complement each other. In areas of high parasite stress, individuals who signal religious commitment reap the benefits from an enhanced barrier that screens out-group members, and from increased support and care in the case of infection. Evolutionary signaling models of religion propose that religious groups achieve efficiency in cooperation through the deterrence of free-riders who would reduce it (Bulbulia 2004; Irons 2001; Sosis 2003; Sosis & Alcorta 2003). What stops potential free-riders from exploiting membership in these groups? F&T's framework provides an answer for both out-group individuals and potential free-riders within the group. Out-group members can be prevented from joining religious groups by being subjected to the contempt and disgust that violations of local norms and the risk of infection generate in existing members. This may be one area where the supernatural content of religious beliefs provides a unique ability to achieve this ostracism by casting out-group individuals as animalistic, demonic, or evil subhuman beings (Hansen & Norenzayan 2006).

On the other hand, even when the costs of religious participation are the same across individuals, within-group differences in immunocompetence may produce a situation where the benefits for signaling are greater for individuals who are more susceptible to disease. Indeed, we regularly find that religion figures prominently in conceptions of illness and healing practices (Reynolds & Tanner 1995, pp. 237–66). Receivers of these signals would benefit from knowing who is the least likely to interact with out-group members who may transmit novel pathogens. Individuals who are better able to balance the risk of infection with the benefits of interaction with out-group members would be expected to signal religious participation at lower levels. In this way, the extent of intergroup interaction may depend on the level of heterogeneity in immunocompetence within groups. This would be an intriguing avenue for empirical study, especially in traditional societies.

However, there may be a tension between the need to avoid pathogens and religious signaling practices. The most effective signals – the ones that are least likely to be faked by low-commitment individuals – may in fact involve opening the body in order to sacrifice blood or body parts, ingesting toxic substances, engaging in extreme physical exertion, or otherwise potentially compromising one's immune system. There is some evidence that scarification and its placement are related to pathogen stress (Singh & Bronstad 1997). It would be interesting to investigate how signaling takes different forms in the areas of highest and lowest parasite prevalence to determine how this tradeoff is managed.

A potentially important piece of this argument is how warfare interacts with in-group assortative sociality and parasite stress. For example, signaling behaviors are utilized cross-culturally in solving collective action problems related to intra- and intergroup warfare (Sosis et al. 2007). War requires a degree of xenophobia to rationalize hostility to out-groups, and competing developmental models include pathogen stress and risk of resource failure in order to explain socialization into violence (see Ember & Ember 1992; 2007). It may be possible to make predictions about culturally mediated behaviors toward out-groups based on the interaction between parasite stress and temporally varying resource stress. Cashdan's (2001) results suggest that xenophobia and ethnocentrism are independent phenomena correlated with violence (both within and across groups) and resource stress, respectively. Where parasite stress is high and neighboring groups have a history of conflict, resource stress would be unlikely to relax these tensions and motivate intergroup trade. Even between groups with a history of relative peace, F&T's argument predicts that during times of famine the group with relative plenty should only risk infection to exchange with stressed groups if they have a large probability of experiencing a future catastrophic shortfall of their own, or if they can greatly exploit the other group in the process. Exactly how contagion risk trades off against economic benefit is an issue that deserves empirical study.

While religion does indeed circumscribe social relations and often limits social contact with other groups, religions are diverse, and some traditions may increase rather than limit exposure to individuals from other geographic locations due to economic reasons. Proselytizing, for example, likely increases exposure to strangers. Thus, a further test of the parasite-stress theory of sociality would assess whether parasite stress and the degree of proselytizing within a religion are negatively related. Aside from proselytizing, religious groups often fill important economic niches by establishing trade relations with coreligionists in distant lands, thereby increasing exposure between individuals who have presumably adapted to different disease environments. It has been argued, for example, that the spread of certain religions, such as Islam throughout Africa, is partially a result of the benefits that shared religious identity has among traders who have little reputational information on each other because of their

geographic separation (Ensminger 1997; Sosis 2005). Then again, in some contexts, economic relations maintain religious pluralism. The religiously pluralistic Silk Road in Eurasia, for instance, consisted of remarkably expansive trade networks of regularly interacting individuals of many religious traditions from various ethnic groups, including Buddhists, Manicheans, Muslims, Zoroastrians, shamanists, and animists (Beckwith 2009; Foltz 1999). Presumably, pathogen stress was significantly higher at this time than at present. To further evaluate the parasite-stress theory of sociality, future work should examine the differences across religions in their social and economic interactions with outsiders.

Rethinking innovative designs to further test parasite-stress theory

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Abstract: Fincher & Thornhill's (F&T's) parasite-stress theory of sociality is supported largely by correlational evidence; its persuasiveness would increase significantly via lab and natural experiments and demonstrations of its mediating role. How the theory is linked to other approaches to group differences in psychological differences and to production and dissemination of cultural ideas and practices, need further clarification. So does the theory's view on the possible reduction of negative group interactions.

The target article by Fincher & Thornhill (F&T) describes a parasite-stress theory of sociality stating that social life in humans (and other animals) is shaped by the demands of ecological adversity and infectious-disease stress. A discussion of the variables forming in-group assortative sociality in terms of parasite-stress – philopatry, ethnocentrism, and xenophobia – is at the center of the article. Through the use of large-scale data sets, the article provides compelling evidence from around the world of the relationship between parasite-stress and strength of family ties and religiosity. It proposes an account of human history (e.g. why people migrated from Africa to Eurasia) that is an alternative to other accounts such as those suggested by Diamond (1998) and Inglehart (e.g., Inglehart & Baker 2000).

F&T's ambitious theoretical account is tested primarily by the use of existing data sets on the hypothesized relationship between parasite-stress and in-group assortative sociality. This approach has both advantages and disadvantages. The advantages include large sample sizes, access to data collected in various parts of the world, thereby permitting comparisons between geographic locations (e.g., Africa, where parasite-stress is exceptionally high, versus other world regions, where it is not), and the ability to generalize the findings across many cases. Disadvantages include a reliance on the operational definitions of social variables of interest adopted by existing surveys, making it difficult to take into account cultural differences in survey responses and question comprehension, and the exclusion of experimental research.

The heavy reliance on surveys restricts the article to drawing on correlational empirical evidence. Exceptions are studies by Schaller et al. (2010) and Mortensen et al. (2010) which note a change in immediate immune response and behavioral actions following visual cues pertinent to the risk of parasitic infection. Given the nature of the data and the hypotheses tested (e.g., the impossibility to induce infectious diseases to

examine resulting psychological consequences!), one might claim that correlational designs are most appropriate. However, F&T at times claim that the evidence is causal and should be interpreted as such. More experimental work is needed to be able to refer to the role of parasite-stress as a causal factor in certain aspects of human social life. The need of more causal evidence in this area of work should not be seen as limited to labu(r)5.3xexoul7(A27.2(540..287)-43.1(43.5(-404.1uth)-5321(540..287)ri(i)2Tc[lper)6(y404.1(a)]TJ0-1.115TD0.0146c esu2.8(638Tc)5.6(c)-7.2(li)2Tc[y98269129i440265en eessi63-571(epeatTc[(s)5.(li263)5(h)24.9(ve)2.571(o)-398.ii),804.1(a)]TJ0-1.115T50. value10.07ts p38.7a927.997.8(paras(s)e)24.13

(Van de Vliert 2011a; Van de Vliert & Tol 2011). Both societal collectivism and political autocracy are strongest in lower-income countries with more demanding cold or hot climates, moderate in countries with temperate climates irrespective of income per head, and weakest in higher-income countries with more demanding cold or hot climates.

In sum, there are conceptual and empirical reasons to view parasitic stress and climato-economic livability as competing explanations of national culture. We combined databases from the target article and the public sources mentioned below, in order to test the hypothesis that climato-economic livability is a stronger predictor than parasitic stress of cross-national differences in societal collectivism and political autocracy. After introducing how we measured parasitic stress, climato-economic livability, and collectivistic and autocratic culture, we present and briefly discuss the results.

The prevalences of nonzoonotic and zoonotic diseases were taken from the target article's *Electronic Supplement 2*. Nonzoonotic and zoonotic disease burdens, and their interaction, were included as predictors. As is usual in our novel line of climato-economic research, livability was represented by climatic demands, income resources, and their interaction. Climatic demands were measured across each country's major cities as average absolute deviations from 22°C in the coldest and hottest months, respectively (source: Van de Vliert 2009). Data on income resources, measured as the natural logarithm of the purchasing power product per capita in 2002, were available for 174 nations (source: United Nations Development Programme 2004). For societal collectivism, we used an internally consistent and externally valid 121-nation index of familism, nepotism, and compatriotism (source: Van de Vliert 2011b). Finally, for political autocracy, Pemstein et al.'s (2010) integrated index of ten measures of regime type was chosen over other indices because the breadth of its domain did in no way undermine its internal reliability. The modest overlap between societal collectivism and political autocracy ($r = .55, n = 121, p < .001$) made separate analyses meaningful.

As shown in Table 1, hierarchical regression analysis with standardized predictors estimating societal collectivism in 121 nations, and political autocracy in 174 nations, yielded three results. First, reconfirming and refining F&T's interesting finding that nonzoonotic rather than zoonotic infectious diseases

explain in-group assortive sociality (target article, sect. 5.1.1), zoonotic disease stress has no significant main or interactive effects on societal collectivism and political autocracy. Second, when parasitic stress is first controlled for, climato-economic livability still accounts for the largest part of the variation in societal collectivism ($\Delta R^2 = .31$; total $R^2 = .47$) and political autocracy ($\Delta R^2 = .21$; total $R^2 = .35$). Third, when climato-economic livability is first controlled for, parasitic stress cannot additionally account for any variation in societal collectivism ($\Delta R^2 = .00$; total $R^2 = .47$) and political autocracy ($\Delta R^2 = .00$; total $R^2 = .35$).

It is important to emphasize that the parasite-stress model has been successfully applied to a spectrum of components of culture, so these disconfirmatory results do not invalidate the model. It is clearly the case that parasitic stressors may influence cultural values and practices. Yet, it is also likely that the evolution of culture in humans, just like evolution in animals and plants, has climatic underpinnings. In comparison with latent concerns over parasites, it would appear that climato-economic livability is the more powerful predictor of cultural orientations towards collectivism and autocracy.

Parasite-stress, cultures of honor, and the emergence of gender bias in purity norms

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Abstract: Of the many far-reaching implications of Fincher & Thornhill's (F&T's) theory, we focus on the consequences of parasite stress for mating strategies, marriage, and the differing roles and restrictions for men and women. In particular, we explain how examination of cultures of honor can provide a theoretical bridge between effects of parasite stress and disproportionate emphasis on female purity.

Table 1 (Van de Vliert & Postmes). Results of hierarchical regression analyses predicting societal collectivism and political autocracy.

Coefficients	Societal Collectivism			Political Autocracy		
	ΔR^2	ΔR^2	B	ΔR^2	ΔR^2	B
Parasitic Stress						
Nonzoonotic (NO)	.13***			.12***		
Zoonotic (ZO)	.00			.02		
NO * ZO	.03			.00		
Climato-Economic Livability						
Climatic Demands (CD)	.00	.04*	.01	.00	.06**	-.02
Income Resources (IR)	.22***	.33***	-.36***	.13***	.22***	-.36***
CD * IR	.09***	.10***	-.31***	.08***	.07***	-.26***
Parasitic Stress						
Nonzoonotic (NO)		.00	.05		.00	.05
Zoonotic (ZO)		.00	.00		.00	.00
NO * ZO		.00	-.06		.00	-.05
R ² (F)		.47 (17.21)***			.35 (14.78)***	

*** $p < .001$, ** $p < .01$, * $p < .05$ ($n = 121$ for societal collectivism; $n = 174$ for political autocracy). Unstandardized beta weights shown in the B columns are from the final step in both prediction models. There was no multicollinearity ($VIFs < 5.22$), and there were no outliers (Cook's $Ds < .23$).

The last couple of decades have seen a rise in prominence of both cultural and evolutionary approaches in psychology. At times, they have been unfairly and mistakenly seen as at odds with each other, with one approach emphasizing enormous human variability and the other emphasizing underlying human universals. Fincher & Thornhill (F&T) remind us that human evolution occurs within a social context that is responsive to changing local environments. Humans coevolve with other organisms in their environment – including various parasites. F&T offer an impressive theory that represents an able synthesis of evolutionary and cultural approaches, with far-ranging implications for a number of social-psychological phenomena.

One of the most exciting implications of the theory is its provision of a framework linking ecology to culture and social behavior (see Berry 1979; Triandis 1994). We believe that the parasite-stress theory may help illuminate cultural differences in relationships between men and women. While F&T point out (sect. 2.2, para. 4) the link between greater parasite stress, assortative sociality, and less freedom for women, they (understandably) do not theorize about why this is the case. We propose that the problem of mate selection, particularly within cultures of honor, can provide some explanation.

Perhaps one of the most fundamental dilemmas humans must confront is the optimal choice of a mate. The choice poses two competing risks. On one hand, as articulated by F&T, out-group members may introduce dangerous infectious diseases from novel foreign parasites. This may motivate the avoidance of coupling beyond the in-group. On the other hand, exclusive inbreeding runs the risk of congenital birth defects, and virtually every society has incest taboos to guard against this possibility (Brown 1991). One solution is to be very selective about choosing partners outside of the immediate in-group, paying particular attention to cues that signal “purity.” Many societies have developed strict regulations regarding purity, along with great concern for purity as a central domain of morality (Rozin et al. 1999; Shweder et al. 1997).

Behavioral rituals and attitudes that signal one’s commitment to moral purity should be highly valued, particularly in environments of high parasite stress. These signals of moral purity should be doubly important in traditional cultures in which economic prosperity is highly linked to social reputation and forged with family alliances, as is the case in cultures of honor (Peristiany 1965). In many such stratified societies, families can move up the social ladder through marriage alliances. It is almost always the case that with hypergamy (up-status marriage), it is women who marry into higher status families, and subsequently those women’s families who stand to benefit (Ortner 1978). In this sense, purity (spiritual, moral, and sexual) is a woman’s value. As the anthropologist Jane Schneider (1971) noted when discussing honor cultures of the Mediterranean, women are a “contested resource” and their comportment defines the honor of their social groups.

This established phenomenon takes on new meaning in light of F&T’s theory, because in each of these marriage alliances, the male partner’s family takes a risk in bringing a new member into their unit, and would not be inclined to do so without assurance of the conformity of the woman with all applicable norms. Therefore, women, who bear the responsibility of serving as ambassadors from their native unit, must be especially zealous in signaling their moral and physical purity.

Our recent work (Vandello et al. 2011) provides evidence that norms for moral purity are stronger for females than males in virtually all nations globally, though there is also great variation in the extent to which female purity norms hold sway. As part of this research, we have developed an index measuring the extent to which cultures emphasize female purity (over and above emphasis on male purity), using cross-national data on things like sexual practices, preferences for virgins, and smoking and drinking rates of women relative to men. As an initial test of whether there might be a connection between

F&T’s notion of high parasite-stress environments and cultural concerns with female purity, we correlated our purity index with F&T’s national ratings of non-zoonotic infectious disease prevalence. The association is quite strong, $r = 0.60$, $n = 146$, $p < 0.001$, suggesting that in places where parasite stress is heightened, cultures emphasize female purity, perhaps as a way of ensuring women’s “marketability” in a risky mating pool.

Also relevant is Schmitt’s (2005) cross-cultural data on sociosexual mating orientations (monogamous versus promiscuous). Using his data on the extent to which male and female sociosexuality is restricted or unrestricted, non-zoonotic disease prevalence is associated with a more restricted female sociosexuality, $r = 0.38$, $n = 45$, $p < 0.01$, but is not associated with male sociosexuality, $r = 0.11$, $n = 45$, $p = 0.46$, again suggesting stringent female purity norms may especially co-occur with environments of high parasite stress. While this may seem of questionable relevance for modern, progressive societies, we have gathered evidence that purity norms remain stronger for females than males among contemporary American college students (Hettinger & Vandello 2011), and women are policed more strictly than men to ensure against purity violations.

We acknowledge that this link between pathogen prevalence and female purity is quite speculative and awaits further testing, but we use it as an example of what we feel is a strength of F&T’s theory – the possibility of linking ecological features to cultural norms and socio-psychological traits. More generally, F&T’s theory may prove valuable in understanding the origins of cultures of honor, which are typically characterized by high degrees of suspicion, competition, and conflict between rival families and small clans who compete for strategic resources. It may be that in such cultures, where there is often very little sense of community beyond the family, and reciprocal hostility among groups is quite common (fostering in-group assortative sociality), pathogens are widespread.

Intra-regional assortative sociality may be better explained by social network dynamics rather than pathogen risk avoidance

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Abstract: Fincher & Thornhill’s (F&T’s) model is not entirely supported by common patterns of affect behaviors among people who live under varying climatic conditions and among people who endorse varying levels of (Western) religiosity and conservative political ideals. The authors’ model is also unable to account for intra-regional heterogeneity in assortative sociality, which, we argue, can be better explained by a framework that emphasizes the differential expression of fundamental social cues for maintaining distinct social network structures.

Fincher & Thornhill’s (F&T’s) model predicts that individuals who live under heightened parasitic loads should be motivated to form fewer, more restrictive, and less fluid social relationships, and express higher levels of affect and related gestural behaviors that function to attract and maintain smaller, more intimate social networks. This thesis is contradicted by cross-cultural studies showing that people who live closer to the equator and in warmer climates – conditions that favor parasitic diversity – report higher levels of happiness and confidence, whereas people who live in darker and colder climates report more

sadness and worrying behaviors (Agumadu et al. 2004; de Graaf et al. 2005; Van de Vliert et al. 2004; Kovalenko et al. 2000; Okawa et al. 1996; Rehdanz & Maddison 2005). Indeed, expressed happiness is rated among the most preferred characteristics in a potential new friend, and is thus effective for attracting novel/risky relationship partners (Chang 2004; Farmer et al. 2003; Vigil 2007; Xu & Zhang 2007), thereby increasing the size of one's social network and risk of exposure to foreign pathogens. On the other hand, sadness and worrying behaviors are more effective for inducing solicitous responses from reliable/existing relationship partners (e.g., Kaniasty & Norris 1995; Terwogt 2002; Vigil 2008). Related incongruities are findings of higher levels of happiness and of confidence, and the formation of larger social networks among more religious and more conservative-leaning people in Western samples (e.g., Keyes & Reitzes 2007; Napier & Jost 2008; Vigil 2010). Other research has failed altogether to find a correlation between sensitivity to pathogen disgust and conservatism (Tybur et al. 2010).

An alternative "socio-relational" model for explaining the above findings suggests that people are primed to behaviorally advertise differing fundamental components of their *reciprocity potential*, or value as a prospective social partner, depending on the opportunity and the effectiveness at using such traits for regulating different types of social networks (Vigil 2009). Some affect behaviors, such as expressed joy and confidence, are functional for demonstrating personal empowerment or one's *capacity* to reciprocate, whereas other behaviors, such as sadness and worrying, are more effective at conveying the impression of appeasement and vulnerability (i.e., non-threat) and general *trustworthiness* attributes. Capacity cues (e.g., physical attributes) are more immediately discernable through limited interactions as compared to trustworthiness cues (e.g., interpersonal attributes), which instead require repeated interactions to accurately verify in others. Humans may have therefore relied on the former to regulate larger, more fluid, peer networks that limit the amount of time that can be invested in individual relationships' and relied on the latter to regulate smaller, more intimate social networks that facilitate the opportunity to advertise time-consuming investment behaviors (Vigil 2009). Thus, from a socio-relational perspective, it makes sense that people would be primed to heuristically express more network-aggrandizing capacity cues (e.g., felt happiness) under climatic conditions that facilitate the ability to interact with a greater number of affiliates (warmer climates), and to express network-consolidating trustworthiness cues (e.g., felt sadness) under climatic and topographical conditions that physically limit the ability to interact with others (colder climates; Vigil 2009). Similarly, patterns among conservatives (e.g., higher income, more joy and aggression, and, important here, more peer relationships; Vigil 2010) can be understood from the socio-relational thesis that experiential prosperity precipitates the behavioral advertisement of personal empowerment cues that are effective at regulating larger, riskier social networks (Vigil 2009; 2010).

However, perhaps the greatest limitation of F&T's model is that it cannot currently account for *intra-regional* variability in assortative sociality, such as the phenomenon of developmental changes and sex differences in many of the phenotypes that the authors describe. For instance, females show higher levels of religiosity, liberal-political ideals, in-group helping (compassion) behaviors, and out-group stigmatization; and they form smaller, more intimate and exclusive social networks as compared with males (Eagly & Crowley 1986; Ekehammar et al. 2003; Geary et al. 2003; Norrander & Wilcox 2008; Rose & Rudolph 2006; Stark 2002; Walter & Davie 1998; Vigil 2009). Though not addressed by the authors, many of these sex differences can be explained by an evolutionary history of male-male coalitional competition and male-biased philopatry, whereby males tended to remain in closer proximity to their male-kin, while females emigrated into the social networks of their husbands, essentially heightening their risk of parasitic infection (Geary 2002; Geary

2010; Geary & Flinn 2002; Wrangham & Peterson 1996). Females have more active immune systems than do males (Bouman et al. 2005; Klein 2000; Zuk & McKean 1996). Thus, some sex differences in assortative sociality and immune functioning are consistent with the parasitic-threat hypothesis that sex differences in societal behaviors and in social networks may be due to ancestral females having been exposed to higher levels of parasitic threat in their ecology.

Still, sex differences in emotional functioning are well established, with males reporting higher levels of empowerment gestures (e.g., inflated confidence), and females reporting higher levels of vulnerability gestures (e.g., sadness, worrying, and pain behaviors; see Vigil 2009). These dimorphisms are accountable by the socio-relational model which predicts that male-biased philopatry increased the benefit for females to form smaller and more protective social networks, to develop higher cognitive thresholds for trusting peers, and to signal higher levels of trustworthiness (e.g., vulnerability) cues to attract and maintain more continuous and reliable relationship partners in the absence of strong (inclusive-fitness) familial bonds. Males, in contrast, having evolved within kin-based communities, would have experienced a reduced benefit to form intimate, time-consuming relationships and a greater cost for advertising trust cues in favor of capacity gestures, which may be more efficient for regulating a greater number of relationships, and thus larger and more functional coalitions (Vigil 2009). Hence, many of the instances of *intra-regional* assortative sociality that covary with sex can be accounted by a socio-relational model which capitalizes on the differential expression of fundamental social cues for maintaining distinct social networks. It is therefore likely that the selection pressures that each model emphasizes complement each other in their ability to account for both inter- and intra-regional assortative social cognitive/behavioral strategies.

Immigration, parasitic infection, and United States religiosity

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Abstract: Fincher & Thornhill (F&T) present a powerful case for the relationship between parasite-stress and religiosity. We argue, however, that the United States may be more religious than can be accounted for by parasite-stress. This greater religiosity might be attributable to greater sensitivity to immigration, which may hyperactivate evolved mechanisms that motivate avoidance of potential carriers of novel parasites.

Fincher & Thornhill (F&T) document a large and predicted correlation between parasite-stress and religiosity cross-nationally and within the United States. F&T also present a powerful theoretical and empirical case for the effects of parasite-stress on the promotion of boundaries between in-group and out-groups, including the generation and maintenance of ethnocentrism and xenophobia. We argue, however, that the United States may be more religious than can be accounted for by parasite-stress. This greater religiosity (relative to cultures with similar parasite-stress levels) might be attributable to greater sensitivity to immigration, which may hyperactivate evolved mechanisms that motivate avoidance of potential carriers of novel parasites.

Historically, the United States has been a Mecca for immigration and for concerns about immigration: from the first settlers on Native American soil, to the enormous influx of Europeans in the early 1900s, to today's perpetual dialogue on the fear or protection of Hispanic and Middle Eastern immigrants. Recent research indicates that the United States is less favorably disposed toward immigrants than are most European countries (who, in turn, are less religious; e.g., Isernia et al. 2010). This apparent hypersensitivity to immigration in the United States could be the product of several factors. First, since the inception of the country, immigration of one group or another has been cause for concern among native citizens. The Irish, the Polish, the Japanese, and the Russians are each groups that have been the focus of concern coinciding with their mass immigration to the United States. This intense and typically negative concern about immigrants and immigration might reflect hypersensitivity to the changes and threats they bring. Out-groups, including immigrants, may be (or are perceived to be) "lacking knowledge of and therefore violating local customs or norms, many of which, like hygiene and methods of food preparation, may prevent infection from local parasites" (target article, sect. 2.1, para. 3). These violations are registered as threats by our "behavioral immune system," which F&T explain is "comprised of ancestrally adaptive feelings, attitudes, and values about and behaviors toward out-group and in-group members, caution about unwillingness to interact with out-group people, and prejudice against people perceived as unhealthy, contaminated, or unclean" (sect. 2.1, para. 1). To many Americans, immigrants are seen as just that: "unhealthy, contaminated, or unclean." But why is this? Perhaps the American media and other interest groups are priming individuals for fear of parasitic infection with certain "keywords" in connection to immigrants.

It is not uncommon to hear remarks from conservative personalities, politicians, and news sources comparing immigrants to subhuman species. The use of terms that compare immigrants to particular nonhuman species seems to justify the treatment of them as such (see Livingstone Smith 2011). Representative Curry Todd (2010), a republican from Tennessee, commented during a Joint Fiscal Review Committee meeting on a medical program that covers Tennessee children, including immigrant children: "We can go out there like rats, and multiply then, I guess," in reference to the pregnant women that come into America. Michael Savage (2006), a conservative talk-show host, referred to Mexican immigrants as "vermin" and Rush Limbaugh (2005), a conservative radio host, referred to immigrants as an invasive species: "So invasive species like mollusks and spermatozoa are not good, and we've got a federal judge say, 'You can't bring it in here,' but invasive species in the form of illegal immigration is fine and dandy - bring 'em on, as many as possible." F&T summarize the results of recent research on diverse Western samples which indicate:

that scores among individuals on scales that measure the degree of xenophobia and ethnocentrism correspond to chronic individual differences in perceived vulnerability to infectious disease; those who perceive high disease risk are more xenophobic and ethnocentric than those who perceive low disease risk. Importantly, this research also shows that xenophobia and ethnocentrism within individuals increases under experimental primes of greater disease salience in the current environment. (sect. 2.1, para. 13)

The relationship of hypersensitivity to immigrants and increased religiosity might be attributable, in part, to the select terms and vitriol often used to describe immigrants by the religious conservative media. Likening immigrants to "vermin" and "rats" may prime disease salience and, therefore, motivate greater assortative sociality (see also Livingstone Smith 2011).

A second possible explanation for the apparent US hypersensitivity to immigration is the relative isolation of the United States from other countries. The mainland is bordered by just two

countries. Latin American immigrants tend to be treated more poorly than are Canadian immigrants, certainly by the conservative religious media and other interest groups. This might be attributable to the perceived potential threat posed by immigrants from countries with higher parasite-stress, such as Mexico and other Latin American countries. This difference in treatment of immigrants might be exacerbated by the fact that Mexicans and other Latin Americans comprise a much larger proportion of immigrants than do Canadians. The more striking cultural differences and associated perceived threats between Americans and Latin Americans might therefore be doubly threatening, given the much larger immigrant population. In addition, because the US mainland shares its borders with just two countries, its citizens may be less accustomed to cross-national travel. In Europe, in contrast, one can traverse through multiple countries within a day's time. Individuals in the United States therefore may be more aware of immigrants entering the country, simply because immigration is more apparent when it occurs.

We speculate that, in combination with parasite-stress, increased sensitivity to immigration into the United States (with immigrants perceived as potential carriers of novel parasites) hyperactivates evolved mechanisms that motivate assortative sociality. The current levels of parasite-stress in combination with the sensitivity to immigration might explain the collectivistic and especially religious nature of the United States, relative to other countries with similar parasite-stress levels. Furthermore, as immigrants enter the United States, native individuals within areas of high parasite-stress may be more likely to enforce the dividing line between in-group and out-group, promoting and maintaining ethnocentric and xenophobic behaviors and in-group connectivity with religious activities. The elevated parasite-stress in combination with hypersensitivity to immigration might form a perfect storm for increased religiosity as protection against novel infectious diseases.

Time allocation, religious observance, and illness in Mayan horticulturalists

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Abstract: Analysis of individual differences in religious observance in a Belizean community showed that the most religious (pastors and church workers) reported more illnesses, and that there was no tendency for the religiously observant to restrict their interactions to family or extended family. Instead, the most religiously observant tended to have community roles that widened their social contact: religion did not aid isolation – thus violating a key assumption of the parasite-stress theory of sociality.

If humans evolved adaptive flexibility in religiosity and family focus depending on pathogen prevalence in their local geographic area, time allocation studies should show that religious individuals choose isolation from outsiders, and as a consequence experience fewer communicable illnesses than less-religious individuals in the same location. The group or regional differences found by Fincher & Thornhill (F&T) must represent aggregated differences in individuals' behaviour.

As tests of whether reduced contact with outsiders is an aspect of religiosity, and whether religious individuals experience fewer illnesses as a result, I analyzed interview-based data from

anthropological fieldwork carried out in 1997 in Cayo, Western Belize, on 56 men in two Mayan villages in which many individuals had in the past decade converted to one of two evangelical faiths (Pentecostalism and a Baptist church), usually from Catholicism. In addition, a significant minority of villagers had lapsed in religious observance, and a few stated that they were agnostic. Information on reported illness in the year prior to interview was used to construct a variable consisting of the number of illnesses experienced in the past year that completely stopped the man from doing his normal daily activity for one or more days. This included acute illness (most commonly flu-like illness, but sometimes dengue fever or malaria), and chronic conditions that periodically became acute (for example, one man had a chronic ear infection that flared up regularly to the point of incapacitating pain). It was not possible to separate zoonotic versus non-zoonotic diseases, as no definitive medical diagnosis was made in almost all cases. Analysis of these self-reported illness data on the religiously observant versus non-observant did not yield a significant difference between the two groups (t -test: $t = 0.7$, $p = 0.25$). However, eight of the men in the sample were religious officials, including ministers, elders, and assistants. These eight men reported significantly more illness than either observant or non-observant/agnostic individuals (see Fig. 1).

Time-use data on the men's weekend time allocation (consisting of a total of 1,344 hourly blocks for the sample of 56 men: for detailed methods, see Waynforth 1999), showed that increased religious observance (categorized as in Fig. 1 above) was associated with less time spent with immediate family (Analysis of Variance [ANOVA]: $F = 18.9$, $p < 0.01$, $n = 56$). The reasons why this was the case are not obvious: Religiously observant men appeared to spend their time across a wider range of activities rather than engaging in any single activity, more than non-observant men. Religiosity was not significantly associated with increased time spent with biological relatives other than immediate family (ANOVA: $F = 1.28$, $p < 0.25$, $n = 56$). Instead, being family-focused in this Mayan community may be related to resource acquisition rather than pathogen avoidance: The Maya often practice a family-based approach to farming in which the entire family, including young children, contribute to the family's economic output (e.g., see Kramer 2005). In support of this alternative explanation, time spent with family was strongly positively associated with being a farmer (for farmers vs. non-farming families, t -test:

$t = -3.45$, $p < 0.001$): Those who worked paid jobs, for example in the logging or tourist industries, spent much less weekend time with their nuclear family. This raises the prospect that family-oriented time allocation may increase fitness through resource acquisition efficiency for farming families in this population, rather than being a parasite-avoidance strategy.

Church roles for the Christian officials/organizers in the sample included direct contact with parishioners both at church services and in the community, movement outside of their village, and regular contact with sick individuals. For this reason, F&T's argument may not hold for Christianity in developing nations: Rather than forming small self-contained sects that would reduce the chances of contracting parasitic infections from the wider population, evangelical Christian ministers and church officials may often have *increased* social contact and exposure to parasitic disease, and may spread infection to parishioners during epidemics. In the relatively pathogen-prevalent Mayan village context, this cost of religion may be offset by advantages, both in terms of political influence for church officials, and in terms of the benefits of out-group innovation and trade opportunities. Second, the Mayan communities in Belize have experienced repeated influxes of newcomers over the past 150 years or more, from whom it was and is presently not possible to maintain total separation. Globally, many isolated societies cannot repel outsiders, and therefore cannot avoid contact with their pathogens: no degree of religiously-induced xenophobia will stop powerful colonial invaders. Third, other aspects of the behavioural immune system may prevent parasitic disease without carrying costs of cultural isolation: Disgust at disease symptoms results in stigmatization and avoidance of diseased individuals (see Kurzban & Leary 2001). This mechanism would afford less costly protection from communicable diseases, except in cases where asymptomatic individuals are vectors, and for zoonotic infections.

In sum, key questions about the parasite-stress theory of sociality remain unanswered: Does it work? And if it does, how important is it for understanding human sociality? The Belizean Mayan data analyzed here did not suggest that religious individuals have time-allocation or activity patterns that reduce contact with the outside world. If religious individuals do not have significantly less contact with the outside world, then the measures of religiosity at a regional or national level analysed by F&T do not reliably indicate degree of out-group contact. Assuming that religiosity does reduce out-group contact, other evolutionary pressures must simultaneously contribute to selection for religion; for example, via costly signalling-based cooperative benefits (e.g., Sosis 2003). Similarly, placing high value on close family ties may be an adaptive flexible response to the benefits of cooperative breeding in a particular environment. The relative importance of lowered parasite-stress compared with other advantages of in-group favoritism needs to be addressed.

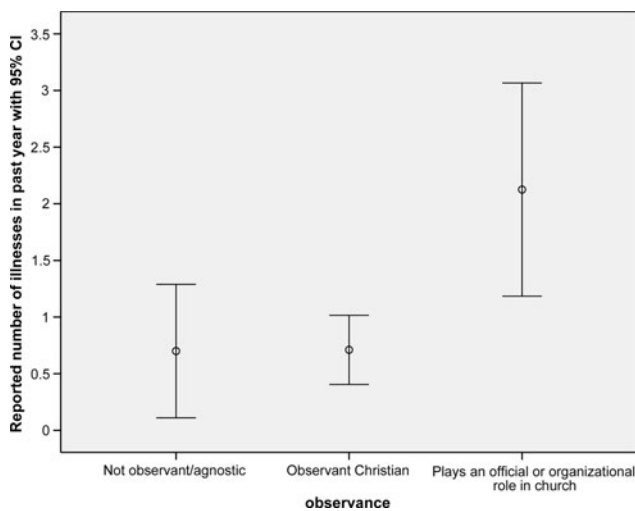


Figure 1 (Waynforth). Taking an active role in the church was associated with more reported illnesses in the past year. In an ANOVA analysis, the difference between groups was statistically significant at $p < 0.01$. This difference may be because church officials and staff have very active roles in the community, and are likely to come into direct contact with very sick individuals via their pastoral activities.

Authors' Response

The parasite-stress theory may be a general theory of culture and sociality

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Abstract: In the target article, we presented the hypothesis that parasite-stress variation was a causal factor in the variation of in-group assortative sociality, cross-nationally and across the United States, which we indexed with variables that measured different aspects of the strength of family ties and religiosity. We presented evidence supportive of our hypothesis in the form of analyses that controlled for variation in freedom, wealth resources, and wealth inequality across nations and the states of the USA. Here, we respond to criticisms from commentators and attempt to clarify and expand the parasite-stress theory of sociality used to fuel our research presented in the target article.

R1. Introduction

We greatly appreciate the collegial interest, time, and effort that all the commentators directed toward improving the research we reported in our target article (T.A.). The commentaries were wide-ranging; we try to address in this response article the major themes of the commentaries. Some commentators identified areas of the T.A. in need of clarification. Others disagreed with our ideas, proposed alternatives, or proposed new applications of the parasite-stress theory of sociality/values. We provide suggestions for further testing of the parasite-stress theory.

R2. The evolution of condition-dependence and culture-gene coevolution

Blute commented on our treatment of (1) condition-dependent enculturation resulting from psychological adaptation designed for culture-acquisition to meet local ecological problems, particularly variation in parasite-stress, and (2) a possible role for culture-gene coevolution. With regard to (1), she points out that we did not discuss one of the conditions necessary for Darwinian selection to favor conditional phenotypic expression: that change or uncertainty in an ecological condition affecting relevant variation in reproductive success of individuals must happen within the lifetime of individuals. We certainly had this in mind, as it is required for favorable selection of the plasticity. Our attention to this requirement is seen in our emphasis that psychological adaptation for culture is the ultimate product of selection at the individual level for inclusive fitness maximization. Also, we mentioned in the target article that parasite adversity faced by people could quickly change as a result of changing host-parasite contact. This applies on the short time-scale of an individual's life. The number of kinds and virulence of parasites and the number of infectious-disease vectors can change over a short time-frame.

Hence, collectively, the conditions necessary for the evolution by Darwinian selection of adaptive phenotypic plasticity are as **Blute** succinctly puts it: environmental uncertainty on the right small time-scale within a generation, accompanied by cues that reliably allow individuals to adjust to a better local adaptive optimum. These conditions are required for the evolution of any condition-dependent adaptation, including human cultural capacity, the set of psychological adaptations by which humans obtain and use their cultural behaviors.

With regard to (2), **Blute** criticizes our claim that certain earlier ideas (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981; Lumsden & Wilson 1981) have

overlap with our hypothesis for the coevolution of culture and parasites. Certainly, in the details of the comparison, her criticism is warranted, because in large part, the early ideas mentioned are different than our own, as she discusses in her commentary. We agree too that our perspective on culture-gene coevolution comes closer to certain ideas provided by Durham (1991) than to those in the studies we cite in the target article.

In hope of making our views on enculturation and culture-gene coevolution clear, we summarize them. In regard to enculturation, we propose that people have psychological adaptations that are functionally designed for choosing cultural items that reflect features that would have maximized inclusive fitness in human evolutionary history. Consider the adoption of a new religious belief – for example, drinking strychnine as a good way to properly worship God, a practice of a contemporary fundamentalist Christian group in the southern United States (Hood & Lanza 2000).

individuals even if they possess region-specific genetic adaptation to the cultural ecology.

R3. Out-group and in-group parasites are important

Commentators **de Barra & Curtis** question an assumption that they perceive is part of the parasite-stress theory of sociality: “A critical assumption of F&T’s thesis is that pathogens carried by out-groups (neighbouring families or communities) will be more dangerous than those of one’s own family and community.” Actually, we do not make this assumption. In the T.A., we discussed that behavioral immunity has two design features as a result of direct Darwinian selection for them: (1) protection against novel parasites harbored in out-groups to which individuals in the in-group are not adapted, and (2) managing the negative effects of parasites within the in-group. Accordingly, xenophobia and limited dispersal are the adaptations for out-group contagion avoidance. In-group embeddedness, including family ties and religiosity, functions for managing present parasites within groups. If out-group contagion were “more dangerous” than in-group contagion, one would expect out-group psychological and behavioral defenses to be better or only designed for defense than in-group defenses. This is not an empirically apparent pattern as seen in the T.A. For example, in the case of religiosity, our results in the target article suggest that it is functional for in-group embeddedness and out-group boundary formation. Both in-group and out-group parasites can present the host with novelty to which it is not immune. In-group parasites do so during the co-evolutionary races with a host – new features arise in the parasite that circumvent evolved host defense. Out-group parasites can be as dangerous as in-group parasites because the spatially localized host-parasite races may not equip the host with immunity to new out-group parasites.

In their commentary, **de Barra and Curtis** discuss some examples of parasites that have more success in out-groups of hosts than in in-groups. This is an interesting scenario because when a parasite can achieve high reproductive success by invading individuals across a cultural boundary, selection is strong on the parasite to invade the adjacent group. This in turn will promote the adoption of cultural behaviors of xenophobia and more restricted dispersal in the culture being invaded by the parasite.

Grotuss mentions that the research so far inspired by the parasite-stress theory has not addressed the matter of psychological and behavioral components to reduce contact with parasites present within the in-group. We agree with Freeland (1976) and Kurzban and Leary (2001) in predicting that stigmatization and prejudice resulting in marginalization and isolation, or ostracism and periods of quarantining, are adaptations for this purpose. If this is true, these adaptations are components of the behavioral immune system.

R4. The components of in-group assortativeness

Commentators **Figueredo, Gladden, & Black** [Figueredo et al.] question the combination of philopatry, ethnocentrism, and xenophobia into the variable we refer

to as in-group assortative sociality. They point out that ethnocentrism and xenophobia in some research studies show a range of positive, negative, or no correlations, depending upon the society or sample investigated. We recognized this in the T.A. and proposed circumstances under which xenophobia and ethnocentrism would not be positively correlated, and by extension might even show negative or no correlation in a region (sect. 6.4, para. 6).

Cashdan questions our combination of values as well. Cashdan’s commentary presents a summary of unpublished results found by her and M. Steele based on data from the Standard Cross-Cultural Sample of traditional human societies (Cashdan & Steele 2010). They found that parasite-stress significantly predicts negatively the peoples’ “mobility among communities,” a measure of restriction of movement and related philopatry, and positively predicts degree of xenophobia. Cashdan concludes that these two findings support the parasite-stress theory’s prediction that philopatry and xenophobia are features of assortative sociality that reduce contact with other groups and their habitats in high parasite stress situations. Cashdan and Steele (2010), however, found no evidence that “ethnic loyalty” across the societies corresponded to infectious disease stress. Cashdan suggests that ethnic loyalty may defend against ecological stresses in addition to parasite stress.

An empirical question then is whether people have adaptation that functions to promote in-group ties and support under the threat or presence of infectious agents *per se*. The parasite-stress theory implies that people will have such adaptation, and to both nonzoonotic and zoonotic disease cues, because the adversity of either category of diseases can make local in-group embeddedness adaptive. The experimental paradigm of Mortensen et al. (2010) involving presentation of parasite-salient cues to research participants could test this and simultaneously include cues of ecological stressors other than parasite stress.

Figueredo et al. question our interpretation of our findings about human philopatry (limited dispersal away from the natal region). We argue that philopatry is part of the behavioral immune system/assortative sociality and functions to reduce contact with out-groups and their habitats. We reported for traditional human societies that the societies in high parasite regions have smaller range sizes (lower dispersal) than societies in low parasite regions (Fincher & Thornhill 2008b). Figueredo et al. argue that this reduced movement is the result of debilitation by parasites rather than a functional defense against parasites. Their alternative is refuted by our published work as described in the T.A. (sect. 2.2, para. 2).

Vigil & Coulombe mention that disgust sensitivity to pathogens is not higher in conservatives than in liberals, citing Tybur et al. (2010). Results are mixed on this, actually; Inbar et al. (2009) found that conservatives have greater disgust. When the Inbar et al. study is combined with the general literature on the functional design of disgust for pathogen avoidance (Curtis et al. 2011; Oaten et al. 2009), the hypothesis that disgust will be greater in conservatives (collectivists) than in liberals (individualists) remains viable.

R5. A role for mutualistic microbes

Grotuss raises the salient issue of the role of mutualistic microbes of humans in shaping assortative sociality. We

treated this topic in our earlier paper on parasite-stress in relation to the large variation in number of religions across countries of the world (Fincher & Thornhill 2008b). In that paper we proposed that assortative interactions and philopatry increase inclusive fitness in two ways: (a) avoiding and managing parasites, and (b) acquisition and maintenance of an individual host's mutualistic (and commensalistic) microbial community.

Humans begin acquiring their microbial community at birth, but the development and maintenance of this community occurs over the lifetime. Benefits provided by symbionts include provision of metabolic by-products that can be used as fuels (e.g., butyrate), with such microbes acting as a defense system through competition with pathogens preventing the pathogen's colonization and infectivity (reviewed in Dethlefsen et al. 2007). Owing to the localized coevolutionary races between hosts and parasites, and because in high parasite regions these races occur in smaller areas within relatively behaviorally isolated populations, it is probable that humans living in high parasite areas will experience greater specificity and local adaptation in their mutualistic communities. Interacting with out-group members has the potential to disrupt these communities as well as lead to the acquisition of novel pathogens. Hence, we hypothesized that both parasitic and mutualistic interactions may be driving the assortative social life and limited dispersal that operate in the variation in human social behavior (Fincher & Thornhill 2008b). Beneficial symbionts may similarly play a major role in creating the sociality of species other than humans.

Grotuss points out the elegant design of the behavioral immune system implied by the combination of findings reported in the target article that nonzoonotic human parasites impact human values and behavior more than zoonotics and the separate findings on the important role of mutualistic and commensalistic microbes in human health and fitness. The most general implications are that the human psychological adaptations proposed by the parasite-stress theory are not only responsible for a person's ontogenetic acquisition of values, based on experiences with infectious-disease cues; they are also functionally designed to identify and differentially respond to parasite-presence versus parasite-absence in one's environment and/or self, the nature of a present parasite (nonzoonotic vs. zoonotic), and the presence of local beneficial microbes in one's social environment and/or self. This implies, too, that the classical immune system is more sophisticated than traditionally thought. Recognizing self versus non-self is not enough, as many immunologists now recognize. Non-self can include beneficial microbes, which should not be destroyed. Similarly, regarding the behavioral immune system, the beneficial microbes should not be avoided. The parasite-stress theory of sociality and the recent discovery of a very broad range of psychological features and behaviors that may function in dealing with parasites (and beneficial microbes) should greatly enrich immunology, and serve to unify classical immunology with the study of sociality. This suggests also that there should be consideration of an "enrichment system" in addition to the immune system that focuses on the acquisition and management/maintenance of beneficial microbes.

R6. Bidirectional causation

Grotuss raises the question of how parasite-stress may impact social structure indirectly, a topic we did not discuss in the T.A. In an earlier paper on parasite-stress and governmental systems, however, we proposed that there is a bidirectional, proximate causal feedback between parasite stress, economic factors, and liberalization of values (Thornhill et al. 2009). As parasite-stress declines in a region and peoples' values shift to affect widespread economic and other well-being in the region, the changes will further reduce parasite-stress through increases in widespread nutrition, sanitation and improved general living conditions, and access to medical care and educational information. These humanitarian advances cycle back to reduce mortality and morbidity from parasites. Thus, as parasite-stress declines, democratization factors increase, which, in turn, further reduce parasitic disease. The opposite also holds: As parasite-stress increases or maintains high levels, the values of prejudice, inequality and authoritarianism that arise further magnify the morbidity and mortality from infectious disease. Hence, a society's general level of ethnic discrimination and poverty arise from parasite-stress and then feed back and affect parasite-stress.

R7. Proselytizing and related costly commitment devices

Grotuss as well as Swartwout, Purzycki, & Sosis (Swartwout et al.) point out that some religious and other cultural practices such as scarification and proselytizing increase the spread of disease or likelihood of infection. The T.A. argues that religiosity functions to create (a) a cultural boundary between in-group and out-group that reduces contact with novel out-group parasites, and (b) a reliable, embedded social network that defends against parasites within the group. Hence, religious practices that increase exposure to contagion are interesting cases. As Swartwout et al. emphasize, the most honest signals of commitment and embeddedness – those that cannot be faked by low-commitment individuals – sometimes involve compromising the signaler's immune system. They mention scarification and other bloody rituals, extreme physical exertion, and ingesting poisons. We hypothesize that proselytizing may be another example of this and serves as an unfakable signal of commitment to in-group values, given its high costs in terms of contagion risk. We agree with Swartwout et al. that such extreme displays of commitment are best framed in the context of trade-offs, where benefits from social embeddedness exceed high costs from contagion and other personal risks.

We stress that proselytizing is a potentially important area for future research into the validity of the parasite-stress theory of sociality applied to religiosity. We understand honest-signal theory to imply that there will be competition among signalers to use those signals that most honestly define the communicated information (in-group commitment and boundary, in the case of religiosity). Optimal signals of in-group commitment in high parasite-stress regions sometimes may be those that confront the most feared ecological feature – infectious disease.

In regard to the proselytizing hypothesis just mentioned, Swartwout et al. hypothesize that phenotypic and genetic

quality pertaining to immunocompetence will influence the degree of signaling of in-group commitment and willingness to interact with out-groups and thereby achieve the benefits of accessing out-group resources. We briefly touched on this in the target article (sect. 6.4, para. 5) when we suggested that age and individual quality may affect the costs and benefits of out-group contact. We agree with these commentators that this is an intriguing avenue for future empirical and theoretical study.

In a comment related to proselytizing, Atran states that “the most expansive and successful religions aimed to include as many genetic strangers as possible,” as a counter-argument to our claim that religious groups use their unique supernatural belief systems in order to heighten costs of participation and distance themselves from out-groups. This is considered a “most problematic” feature of our arguments regarding religion. It may be that the most successful religions that Atran is referring to (presumably, measured by the number of adherents) are also the most expansive, and that they may be both successful and expansive because of their origin in regions with moderate parasite-stress. These so-called successful, expansive religions are infrequent. There are thousands of other religions. Perhaps there are many smaller religions (judged by number of adherents) that could be considered successful by other measures such as longevity or isolation ability. For those religions in high parasite-stress regions a long period without introduction of an infectious disease epidemic could be a resounding success. By this reckoning, the presence of large, expansive religions is not contrary to our hypothesis regarding parasite-stress and religiosity. In fact, the parasite-stress model could be used to explore why some religions are expansive and others are not. The assumption that all religions should be expansive and, therefore, that a religion’s success should be measured through historical expansion is inaccurate.

R8. Parasites and network size

Vigil & Coulombe see an inconsistency with the parasite-stress model from literature indicating that, in Western samples, people of high religiosity and conservatism have larger social networks than less religious, more liberal people. Certainly, the evidence is mixed on this pattern, as Gelfand et al. (2004) conclude the opposite, at least with regard to collectivists versus individualists: Collectivists have smaller groups and more intimate and durable relations with members than individualists. The pattern may be sample-dependent.

However, the prediction from the parasite-stress theory is more about the nature of social relations between the two types of ideologues rather than social network size. The hypothesis that collectivism compared to individualism is characterized by tight social networks, more cohesive and cooperative friendship groups, in- versus out-group distinctiveness, more permanence of group membership, and more intensity or intimacy of social interactions is supported by a range of studies reviewed and discussed by Gelfand et al. (2004). Hence, it does appear that individualists have more superficial and less durable relationships and with a wider variety of people than collectivists. This pattern is as predicted by the parasite-stress theory of values in light of the established

positive covariation between collectivism and parasite-stress (Fincher et al. 2008; Thornhill et al. 2010).

R9. Sex differences

Vigil & Coulombe raise the interesting issue of sex differences in values. There is some evidence that females may allocate more effort to classical immune function than males (see references in Vigil & Coulombe’s commentary). Also, there is considerable evidence that women are more disgust sensitive than men (see review in Curtis et al. 2011). We returned to the data in the target article for the cross-national variables *Strength of Family Ties* and *Religious Participation and Value* and computed sex-specific values. The Cronbach’s α for the *Strength of Family Ties* for males was .87 and .83 for females; the Cronbach’s α for *Religious Participation and Value* for males was .95 and .91 for females. For both variables, the correlation between the sex-specific value score and *Combined Parasite-Stress* was identical: *Strength of Family Ties*: male $r = .63$, female $r = .63$; $n = 69$ for both correlations; *Religious Participation and Value*: male $r = .70$, female $r = .70$; $n = 89$ for both correlations. Thus, we found no sex differences in the relationship between these values’ dimensions and parasite-stress.

Furthermore, Vigil & Coulombe suggest that known sex differences in values can be explained by an evolutionary history of, among other factors, male-biased philopatry, and conversely, female-biased dispersal from the natal locale. We explored this in contemporary countries by focusing on the question of whether a respondent lived at home with his or her parents (a component of the variable *Strength of Family Ties*). For this one question, we found a significant male-bias in philopatry. A greater proportion of males reported living at home with parents (male $M = .32$; female $M = .25$; $t_{93} = -10.5$, $p < .0001$). However, the positive association between the proportion of those that lived at home with their parents and *Combined Parasite-Stress* for both sexes was not significantly different (male $r = .46$; female $r = .52$; $n = 90$ for both; $z = -.52$, $p = .6031$). Thus, while there is a significant male-biased philopatry, it does not necessarily lead to a sex-difference in the relationships between parasite-stress and values such as *Strength of Family Ties* or *Religious Participation and Value*.

R10. Methodology

Uskul mentions several strengths of the cross-regional (countries and US states) data we use for testing hypotheses. An additional strength of the majority of the data we analyzed was that they are blind to the parasite-stress theory and hence could not be affected by any data-collection biases in favor of the theory.

We agree with Uskul, and point out in the T.A. that additional experimental testing of the parasite-stress theory is important. We also suggest some experiments that would complement the recent experimental research done by Schaller et al. (2010) and Mortensen et al. (2010) that used infectious-disease salient stimuli. The experimental suggestions we make in the target article are field experiments, which have the advantage of more

inherent ecological validity compared to lab experiments. A combination of lab and field experiments and naturalistic observations can potentially best address the specific nature of mediating psychological processes of enculturation that result in the relationship between parasite-stress and cultural patterns. We emphasize though that such research is only one test-ground for the parasite theory of sociality; comparative research is equally important.

Regarding **Uskul's** comment about causation, given that a hypothesis is by definition a statement about possible or presumed causation, evidence supporting a hypothesis simultaneously supports the cause(s) on which the hypothesis is based. This is the case regardless of testing method. Our conclusions in the target article were meant to reflect this only and do not preclude the need for additional research to establish causation, a need we emphasize in the T.A.

Currie & Mace state their view that countries are not statistically independent because of shared cultural history. They fail to mention, however, the alternative view that countries and other regions, and cultures themselves, are independent, even in the case of recently shared cultural history. We discuss in the target article our view of enculturation, which implies cultural independence: Humans are designed by a history of evolution by selection to acquire contingently the cultural items that provide solutions to local ecological, including social, problems. Also, we cite various researchers who view enculturation in ways similar to our view, based on various findings. To claim cultural non-independence (Mace & Pagel 1994) is inconsistent with the evolution of human cultural capacity – the set of psychological adaptations that are functionally designed for adaptive (ancestrally) enculturation of individuals. This capacity was favored by selection because it promoted inclusive fitness of individuals by discriminative adoption of cultural items; arbitrarily or maladaptively learning cultural elements was always selected against. Hence, the values that people adopt during ontogeny in one region are independent of the values adopted in another region, even adjacent regions (cultures), and regardless of the degree of cultural item flow between the regions or the historical connections between cultures involved.

Our analyses in the target article within world area regions and United States census regions, in fact, are not for dealing with issues on non-independence of countries or US states. We do mention that the independence of countries or US states “may be questioned” (see sect. 4.6, para. 1). We, however, are not among the questioners. Our use of subregions is an exercise that can identify whether any particular subregion does not fit the general global analysis. The value of this was found with family ties and parasite-stress in Africa. The relationship of these two variables was negative in Africa, whereas it was positive in other world regions. This supported our hypothesis that high extrinsic mortality, as from the high parasite stress in Africa, leads to reduced collectivism, as predicted by life history theory (see sects. 6.3.1, para. 4 in the T.A. and R12 here.).

Currie & Mace, then, do their own regional subdivision of the globe. The world regions identified by Murdock (1949) and used by us reflect a legacy of research validating the subdivision. At least Currie & Mace should validate their novel subdivision. In the absence of such validation it is difficult to interpret their regional analyses.

R11. Alternative models

A number of commentators have offered alternative models to explain our findings which we address here.

Van de Vliert & Postmes argue that climatic stress is a causal feature for the development of cultural differences, especially when accounting for the wealth of a country. Van de Vliert's earlier work (2009) presented a model showing that climatic stress is met by a compensating cultural response tempered by the average wealth of citizens within a country (i.e., under harsh climatic conditions, citizens from wealthy countries have different options than those from poor countries). Van de Vliert (2009) presented a measure of climatic harshness that indexes the sum of absolute temperature deviations from 22°C for the average lowest and highest temperatures in the hottest and coldest months for a country (called the *Total Index*). The *Total Index* is used in the analyses that Van de Vliert & Postmes present in their commentary. They suggest that harsh climates are more demanding of resources and that people in richer or poorer countries will meet the demands differently: People from poor countries will rely on their in-group affiliates, while people from rich countries will see the demands as challenges and this will enhance individualism. We examined the association between Van de Vliert & Postmes' measure of climatic stress (data collected from Van de Vliert 2009) and two life history measures that reflect reproductive success and found their measure to be lacking in ecological validity. We correlated their *Total Index* of climate harshness with *Under 5 Mortality* (variable was logged; variable represents average for data from the years 1990, 1995, 2000, and 2005 collected from data.worldbank.org) and found the correlation was $-.40$ ($n = 188$ countries, $p < .0001$). We correlated their *Total Index* with the *Life Expectancy* at birth for both sexes (variable was logged; variable represents average for data from the years 1960 to 2008 collected from data.worldbank.org) and found the correlation was $.39$ ($n = 186$, $p < .0001$). Thus, Van de Vliert & Postmes' measure of climatic harshness actually corresponds to increased life span and reduced mortality of young children, just the opposite of what is expected if their index measures ecological harshness. In contrast, one of the focal measures of parasite-stress used in our target article, *Nonzoonotic Parasite Prevalence*, correlated $.75$ ($n = 191$, $p < .0001$) with *Under 5 Mortality* and $-.76$ with *Life Expectancy* ($n = 198$, $p < .0001$). Given these findings, we consider Van de Vliert & Postmes' analyses involving the *Total Index* and our analyses involving measures of parasite-stress, as incomparable.

In their commentary, **Van de Vliert & Postmes** use climate-stress and average wealth to predict a measure of in-group favoritism, *Societal Collectivism*, developed by Van de Vliert (2011b). In their analysis, they show that parasite-stress dropped out of the analysis as a significant factor. Given the problem with their measure of climate harshness, we used the same approach as in the target article for exploring non-parasite-stress causation. We used the residuals from regressing life span expectancy on *Nonzoonotic Parasite Prevalence* as we did in the target article (sect. 4.5.1, para. 2; and sect. 5.1.7, para. 2) and correlated these residuals with Van de Vliert's measure of *Societal Collectivism*. We found a non-significant negative

correlation ($r = -.13$, $n = 119$, $p = .1754$) suggesting the variation in life span independent of the effects of parasite-stress was not associated reliably with *Societal Collectivism*.

Van de Vliert & Postmes' model is also weakened because they don't explain why a person seeks the assistance of in-group members versus out-group members under times of stress. Why is it that when poor and under stress, an individual turns to in-group members instead of to out-group ones who may offer assistance not attainable within the in-group? The parasite-stress theory offers an explanation for this. As stressed in the T.A., out-group interactions can provide many benefits to individuals but such benefits do not exceed costs of infectious-disease encounters under high parasite stress.

Van de Vliert & Postmes consider wealth variation as a given aspect of the ecological setting, but they do not attempt to explain wealth variation itself. Wealth variation arises through the different actions of humans. The parasite-stress model has an inherent economic theory. Accordingly, wealth variation arises in large part due to parasite stress. Economic productivity is impacted negatively through parasite-mediated reductions in intelligence (Eppig et al. 2010; 2011) and in health (Price-Smith 2002; Sachs & Malaney 2002). Moreover, the various values that differ along the collectivism-individualism dimension affect economic productivity. Collectivism retards economic development because it is associated with parochial economic activity – sometimes even restricted to the extended family – and with objection to new technologies and other innovations. Individualism, in contrast, has positive effects on economic productivity by increasing democracy and thereby reducing wealth and educational disparity and enhancing economic opportunity and networking across a region (Thornhill et al. 2009).

Van de Vliert & Postmes discuss some research of ours on governmental systems not presented in the target article. We have argued that cross-national variation in democracy versus autocracy arises from parasite-stress-mediated variation in value systems. We presented in separate papers evidence to support this, based on several measures of democratization (Thornhill et al. 2009; 2010) (see also Murray & Schaller 2010). Taking the cross-national Unified Democracy Scores (Pemstein et al. 2010) for 2008 discussed and analyzed by Van de Vliert & Postmes, we found, as predicted by the parasite-stress theory, that these scores were correlated $-.49$ ($n = 189$, $p < .0001$) with *Combined Parasite-Stress*. Van de Vliert & Postmes analyzed the ability of their climatic-harshness measure, average wealth, and their interaction to predict democracy versus autocracy. In comparison to our measures of parasite-stress, *Nonzoonotic Parasite Prevalence*, *Zoonotic Parasite Prevalence*, and their interaction. Using a hierarchical regression in which they entered climatic harshness and average wealth prior to parasite-stress, Van de Vliert & Postmes reported that parasite-stress was relatively inconsequential for the explanation of cross-national democracy variation. We repeated the analysis they present in their commentary using our primary pathogen measure, *Combined Parasite-Stress*. We also used multiple regression, rather than hierarchical regression, and found that parasite-stress was the largest contributor in terms of standardized beta to the cross-national variation in democracy. The regression results are reported in *Electronic*

Supplement 7.A. (ES 7.A., which can be viewed at <http://www.journals.cambridge.org>)

negative correlation between religiosity and wealth on the premise that, as conditions become more benign, then people need the benefits of religion less and thus religiosity declines (atheism increases, for example). We discussed this model in the T.A., calling it the “conditions-of-living” model (sect. 3.2.1). The hypothesis is reasonable and supported by the data (including Paul’s research: Paul 2009). However, the “conditions-of-living” model (also called “the socioeconomic dysfunctionality model” [Paul 2009], the “uncertainty hypothesis” [e.g., Barber 2011], and the deprivation theory [Solt et al. 2011]) is incomplete because it doesn’t offer explanation for why people don’t turn to out-groups under severe settings. The parasite-stress theory explains this in the following way: Under poor conditions (which are those where parasite-stress is high) the cost of out-group contact (because of the potential for contacting new infectious diseases) can be relatively high, meaning the benefits of wide-spread out-group contact may not outweigh the costs of such contact. The outcome is functional avoidance of out-group members under high parasite-stress conditions. Nevertheless, the empirical reality is that we and the researchers who favor the “conditions-of-living” model can use the same correlations to support our respective models. Herein lies one of the merits of determining the proximate mechanisms whereby parasite-stress is evoked into values (see also the commentary by Schaller & Murray). Describing the design features of these proximate mechanisms can inform researchers of the selection responsible and thus the ecological setting that created the mechanisms ultimately.

We were aware of the intense interest that many researchers maintain in the effects of wealth dynamics for the explanation of all-things-cultural. Therefore, in the analyses included in the target article, we demonstrated that all of the dependent variables for both the cross-national and inter-state comparisons were explained by parasite-stress significantly and positively even when removing the effects of wealth resources and resource inequality (reported in sect. 5.1.7, para. 1; and sect. 5.2.6, para. 1 and in *ES 6*, which can be viewed at <http://www.journals.cambridge.org/bbs2012006>). In many cases, parasite-stress was the only significant predictor; in others, parasite-stress had the largest effect. In 4 of 16 regressions, wealth had a larger effect size than parasite-stress, but not by much (e.g., $-.41$ vs. $.34$). And in these cases, parasite-stress was still a significant causal factor in the predicted direction. Nevertheless, we report here different analyses of wealth resources and the independent effects of parasite-stress for a representative selection of our dependent variables.

For these new analyses, we compared the relative effects of wealth inequality (measured with the Gini index in net household income from the Standardized World Income Inequality Database [SWIID]; Solt 2009; higher values indicate greater inequality) and *Combined Parasite-Stress* for explaining our dependent variables through multiple-regression analysis. Our prediction is that parasite-stress will have a unique predictive effect in spite of any predictive effects attributable to wealth inequality. We tested two models: one that considered wealth inequality (Gini index) and parasite-stress (*Combined Parasite-Stress*) as independent predictors (Model 1) and a second model that included additionally the

interaction between these two variables (Model 2). The results of the analyses are presented in *ES 7.C*. For all dependent variables, using Model 1 parasite-stress was a significant, positive predictor, whereas wealth inequality was a significant predictor in only one case, the *Proportion of Believers*. Using Model 2, parasite-stress was a significant positive predictor for all dependent variables. Wealth inequality was a positive predictor for the *Proportion of Believers* and *Strength of Family Ties*. The interaction between wealth inequality and parasite-stress was a significant predictor for three of the four dependent variables, *In-Group Assortativeness*, *Proportion of Believers*, and *Strength of Family Ties*. In all regressions, whether Model 1 or 2, parasite-stress had the largest effect size. Taken together, this suggests that although wealth inequality is a significant contributor to the variation in religious affiliation and strength of family ties, parasite-stress is a more general contributor to the variation in religiosity and strength of family ties.

Barber (2011) published an analysis of religiosity testing the uncertainty hypothesis, using a different measure of Gini, a measure of parasite prevalence from one of our previous reports (Fincher & Thornhill 2008b) that didn’t separate nonzoonotic from zoonotic parasites, and a few other factors, such as living in a Communist society, as predictors of the variable we called *Proportion of Believers*. Barber’s conclusion was support for the uncertainty hypothesis. However, as we have stated in the T.A. and in this response article, the uncertainty hypothesis (also known as the “conditions-of-living model”, deprivation theory, and socioeconomic dysfunctionality hypothesis) is incomplete because of the lack of consideration of non-contact with out-groups under poor, uncertain conditions. Both Rees (2009) and Solt et al. (2011) have also recently examined the influence of wealth inequality for explaining different aspects of religiosity. We suggest that the best model will include wealth inequality variation itself arising from the causal effects of parasite-stress variation.

Currie & Mace also claim we need to think more about additional alternative hypotheses for religiosity. They seem to favor Gross Domestic Product or latitude, but do not state a hypothesis. Economic indicators and latitude are not variables that are independent of parasite stress and hence any analysis that includes these two variables and parasite-stress will be difficult to interpret. We discuss why economic indicators and climate variables are part of the parasite-stress theory, not alternatives to it, in section 6.2, para. 2, Fincher & Thornhill (2008a), Thornhill et al. (2009), and Thornhill et al. (2010). A theory determines what variables to control and what variables are simply effects of a theory’s causal variable(s). Currie & Mace fail to provide a theory for why their suggested alternatives are actually alternatives to the parasite-stress theory. Admittedly, we control for some variables in our analyses that are not independent of the parasite-stress variables. We do, however, qualify our relevant control analyses by emphasizing that results should be viewed in light of the causal covariation between parasite-stress, economics, and climatic factors.

Vigil & Coulombe argue that within-region assortative social behavior is best explained by Vigil’s (2009) socio-relational model than by the parasite-stress theory of sociality. Vigil’s model addresses variation in people’s emotional expression of cues of social interest/disinterest

for functioning in different kinds of social networks. These commentators, however, emphasize also the complementarity of the two theories for certain well-established research areas. We focus our response on the commentators' perceived contradictions with the parasite-stress model. First, the socio-relational model, it is claimed, is consistent with the finding that happiness is higher at low latitudes (high parasite-stress) than at high latitudes. But this, Vigil & Coulombe argue, is the opposite of prediction from the parasite-stress theory because happiness solicits new social partners and therefore carries risk of out-group contact and associated contagion. Sadness, on the other hand, they argue is for obtaining in-group support, and hence should be, according to the parasite-stress model, greatest at low latitudes, not high latitudes. We suggest the following approach to better study variation in happiness or worry across regions and among individuals within regions. The psychometric procedures should be modified to ask about what makes one happy or not worry. The parasite-stress theory predicts that collectivists will reply that the harmony of their connections with extended family and other long-term in-group members will be paramount – the more in-group harmony, the more happiness and less worry. And, the theory predicts that individualists will respond positively based on harmony and success in a network of people who are outside the extended family and ideologically close in-group members. Similarly, it is expected that collectivists will tie self-esteem less to personal success and more to in-group success than will individualists; Gelfand et al. (2004) provide evidence from research that supports this prediction.

Atran suggests that our view that religiosity involves “an underlying mental mechanism” is misleading if it implies there is psychological adaptation for religion itself. Our view does not imply this. There is “an underlying mental mechanism” for typing or doing arithmetic. We are agnostic about whether religiosity reflects special-purpose adaptation for religiosity or is a by-product of adaptations for other purposes. We do propose in the target article the existence of species-typical psychological adaptation that is functionally designed for the adoption and use of values – which include religious values – that solve problems in the local ecology. We believe the research we present can be informative for the question of whether there is a special-purpose adaptation for religiosity, but answering that question was not a goal of our investigation.

In light of the various bodies of evidence – comparative, experimental, observational, and across traditional societies – we are puzzled somewhat by the position taken by Currie & Mace. They claim that the evidence we discuss in the target article, as well as in our other articles on the parasite-stress theory, is problematic or even fundamentally flawed. The background literature they refer to, much of which is summarized briefly in the target article, has been produced by a multitude of research labs, not just ours, and using a variety of methods.

Atran claims that the history of values and social structures accounts best for the secularism and democracy in the West. History is never an alternative to ecological and ultimate causal frameworks. Separately, based on the parasite-stress theory, we have proposed a hypothesis for the earliest democracies as well as the related liberal value system encompassed in the Enlightenment

(Thornhill et al. 2009). The explanatory potential of this hypothesis is its consistency with a range of evidence supporting the parasite-stress theory.

Atran points out that political scientists have documented that democratization reliably corresponds to an expansion of the middle class. Certainly this is the case. This is a definition or description of democratization, not an explanation. Our research with colleagues has attempted to explain the proximate and ultimate causal bases of democratic and autocratic values (Thornhill et al. 2009; 2010).

Figueredo et al. suggest that xenophobia and ethnocentrism may be by-products of adaptation but are not adaptations that function in defense against parasites, as

6.3.1. of the T.A. is quite preliminary but does suggest support of the predicted curvilinear pattern.

We add here the additional test that **Figueredo et al.** requested. The cross-national relationship between *Strength of Family Ties* and *Combined Parasite-Stress* is improved by the quadratic model with an r^2 of .40 for the linear ($\beta = .63$; $t = 6.68$, $p < .0001$) and .47 for the quadratic ($\beta_1 = .87$; $t = 7.37$, $p < .0001$; $\beta_2 = -.36$; $t = -3.07$, $p = .0031$; $n = 69$ countries). Thus, the improved model fit is supportive of the hypothesis that high levels of parasite-stress can become an extrinsic mortality factor and reduce nepotistic and other in-group social investment.

R13. Collectivism and conservatism: similarity

Figueredo et al. ask about the magnitude of the correlation between collectivism and conservatism and individualism and liberalism. We emphasized in the T.A. that these pairs of values overlap considerably. This is supported by a long history of research. Political and cultural psychologists identify several categories of values that differ between conservatives and liberals – conservatives are high on each of the following and liberals are low: conformity, uncertainty avoidance, maintenance of status quo, order and tradition, closedness about new ideas and ways, inequality of people (both social inequality and economic inequality), authoritarianism, dogmatism and rigidity in moral judgment, stereotyping, prejudice, intolerance, hostility toward out-groups, and in-group embeddedness (see reviews by Jost et al. 2009; Schwartz 1992; 2004). Both collectivism-individualism and conservatism-liberalism are unidimensional variables (Gelfand et al. 2004; Jost et al. 2009). All the above-mentioned differences between conservatives and liberals are mirrored in the differences of collectivists and individualists (Gelfand et al. 2004). Correlations *per se* for those values that can be matched closely between the dimensions range from 0.45 to 0.80. (See Gelfand et al.'s [2004] correlation results between Schwartz's conservatism components and Gelfand et al.'s "in-group collectivism practices," and Gelfand et al.'s results on the high correlations between in-group collectivism and various other measures of collectivism [and hence individualism].) Researchers also often add gender inequality-equality as a core value difference between conservatives and liberals (see Archer 2006; Thornhill et al. 2009). Gender inequality, too, shows robust positive correlation with collectivism (negative with individualism) (Gelfand et al. 2004; Thornhill et al. 2009; 2010). Hence, conservatism and liberalism correspond with collectivism and individualism, respectively.

R14. Proximate mechanisms

The "how" **Schaller & Murray** refer to in their commentary is in regard to the proximate mechanisms involved in the acquisition of culture which cause the range of values from high collectivism to high individualism across individuals and regions. **Beit-Hallahmi** and other commentators also mention the need for more research on these proximate mechanisms. We agree completely but emphasize that this aspect of the parasite-stress theory's

foundation is not a total black box. In the target article, we briefly summarized a range of research studies that confirm predictions from the parasite-stress theory about perceptual, affective, cognitive, and behavioral processes that defend against the negative fitness effects of infectious diseases (see sect. 2.1. in the T.A.).

Currie & Mace criticize the target article because its analyses do not provide evidence for "a cognitive mechanism that is sensitive to parasite stress and causes people to exhibit more in-group favouritism" Certainly they are correct. Our analyses assumed such mechanisms (and other mechanisms focused on perception, affect, and motivation). This assumption is reasonable, given the research on such mechanisms discussed in the T.A. (and mentioned above). Also, the cross-regional patterns we document in the target article are consistent with such mechanisms in people's heads. These patterns must arise from information processing and deduction by individuals' brains, as **Schaller & Murray** point out.

R15. Application to other established research areas

Uskul asks how the parasite-stress theory might apply to certain well-established social and behavior science research programs other than the focal areas treated in the target article (collectivism-individualism, family life, and religiosity). Uskul mentions, in particular, the rugged individualism that underlies the "frontier spirit," residential mobility patterns, the creation and diffusion of innovations, cognitive or reasoning styles, and the nature of units of economic productivity.

The frontier spirit, so important in the immigration history of the United States and Hokkaido, Japan, we suggest is caused by various psychological traits enculturated by low parasite-stress and characterizing individualism: independent self, self-efficacy, dispersal proneness, openness to new experiences and associated willingness to engage the adventure of the frontier. Hence, the frontier spirit is the antithesis of high philopatry or remaining in or near the natal region throughout life.

The connection that **Oishi's** (2010) research has found between residential movement patterns of people in modern societies and the people's values of self-identity (independent vs. interdependent) and group affiliation, we hypothesize arises from variation in valuing philopatry versus dispersal. Dispersal patterns in turn, we argue, arise from different ontogenetic experiences with infectious disease and from associated evoked values of collectivism or individualism. As we argue in the T.A., dispersal has benefits, but also costs in terms of exposure to novel parasites, and is expected therefore to be characteristic of individualistic people. To test our hypothesis for the residential movement behavior of people, one might measure perceived vulnerability to disease in relation to history of movement and distance moved. We predict that people who have a high perceived vulnerability to disease will be more philopatric than those scoring low. The component of the parasite-stress theory pertaining to the psychology and behavior of dispersal could be examined experimentally by giving people parasite-salient pictures and measuring their value changes pertaining to dispersal.

The two cognitive styles, holistic and analytical reasoning, have been tied to collectivism-individualism by prior researchers (e.g., Nisbett et al. 2001; Uskul et al. 2008). Holistic reasoning is the interdependent thinking that prioritizes the in-group's well-being, harmony, and goals. According to the parasite-stress theory, holistic reasoning is part of in-group embeddedness, and hence is predicted to be characteristic of relatively high parasite-stress regions and individual ontogenies. In contrast, analytical cognition is the personal intellectual autonomy that prioritizes personal achievement rather than the achievement of in-group goals. Analytical reasoning is described also as a thinking mode that dissects the whole into causal parts that then give a comprehensive explanatory picture of the whole. According to the parasite-stress theory, analytical cognition is optimal when parasite stress is reduced and therefore there is less need to construct and maintain strong and permanent in-group affiliations that function to offset the negative reproductive consequences from parasites. We propose that the experimental exposure of individuals to parasite-salient cues will shift their cognition to more holistic styles of reasoning. Also, we predict that individuals with high perceived vulnerability to diseases or conservatism will exhibit more holistic reasoning.

Uskul et al. (2008) proposed that certain subsistence ecologies such as farming promote interdependent cognitive styles. We suggest that the parasite adversity associated with different subsistence ecologies will explain the cognitive styles involved.

Some economists are interested in why the unit of economic productivity varies across the world. Regions vary in the degree to which economic units are in-groups – in extreme, just the extended family, versus large social networks or markets. Alesina and Giuliano (2007) have provided evidence that collectivism correlates positively (individualism negatively) with the degree to which economic productivity derives from in-group production. According to the parasite-stress theory, this variation arises from variable parasite-stress across regions as well as the values that are known to covary with it. Hence, Uskul et al.'s (2008) proposal, and the evidence they present for it across subsistence types, may be part of the more general patterns of parasite-influenced economic patterns.

Regarding the question raised by Uskul of the origin and dissemination of innovations, we have proposed the following connection with variable parasite-stress and corresponding evoked values: Individualistic values promote and reward intellectual independence, and therefore novel thinking and doing, as well as openness to new ideas and experiences. Collectivist values promote and reward adherence to traditional norms and ways of thinking, as well as closedness to the new and different. Thornhill et al. (2009) emphasize that these value differences are proximately caused by differences in parasite threat (also see Murray et al. [2011] on conformity adherence and parasite stress). We have initiated research in this area by looking at the diffusion of cultural innovations in the states of the USA (Thornhill & Fincher, in preparation). Here we present one representative analysis.

The adoption and use of evidence-based medical technologies varies greatly across US states, which is a major concern among health care workers (Berwick 2003; Jencks et al. 2003). Based on large samples of Medicare beneficiaries involving 22 evidence-based medical treatments (e.g.,

for breast cancer, stroke, diabetes), Jencks et al. (2003) provide a rank for each of the 50 states (highest rank is lowest use of the 22 treatments). The relationship between Vandello and Cohen's collectivism measure (Vandello & Cohen 1999) and state ranks is $r = .44$ ($p = .002$, $n = 50$ states). Hence, the more collectivist the state, the less medical practitioners know about and/or value the medical interventions. The relationship of the ranks with parasite-stress across states is even stronger, $r = .66$. Thus, we find that the greater the parasite-stress in a state, the lower the use of modern medical technology, despite the higher level of morbidity and mortality from infectious diseases in the state. The pattern of collectivism's negative association and parasite stress's negative association with the diffusion of innovation is also seen in agricultural products and thus is not limited to medical innovations (Thornhill & Fincher, in preparation). In addition, a study underway of international trade relations and exchange, pertaining to culture items (music, books, etc.) as well as economic trade in general, indicates that parasite-stress and collectivism predict (negatively) international trade (Fincher 2011).

Navarrete suggests some interesting extensions of the parasite-stress theory of sociality. He notes that the T.A. emphasizes a theoretically important role for assortative sociality in reducing morbidity and mortality of in-group members afflicted with parasites. From this, he hypothesizes that there will be more norms and values specifically focused on in-group health care (extended family and local religious in-group) in high parasite regions than in low parasite regions. This might be tested using data from traditional as well as contemporary societies. Navarrete also proposes that the behavioral immune system may contain psychological adaptation that functions to promote healing behaviors during infection and while mending the bodily damage caused by parasites. Related to this, he also suggests that individual variation in perceived vulnerability to infectious disease might show a link by functional design to cognition that attends to and strengthens in-group relations. An interesting study would be to determine whether people overall, but especially high scorers on perceived vulnerability to disease, when confronted with cues of parasite salience, shift toward greater attractivity and allegiance to extended family and like-minded people in general. The experimental paradigm that Mortensen et al. (2010) have used would be adaptable for such a study.

R16. Religiosity

Chang, Lu, & Wu (Chang et al.) point out that Christianity and Islam are the most popular religions in terms of number of adherents, and that these religions, after arising in the Middle East, spread throughout many high parasite regions. They offer various hypotheses for the successful spread of these religions, such as coercion by colonial powers and the introduction of new medical treatments that reduced parasite-stress. Also, they hypothesize that the spread of these religions was promoted by the high conformity to local norms that has been documented as characteristic of high parasite-stress regions (on this pattern, see their cited references). In our view, the problem with this hypothesis is that conformity involves going along with the majority and with tradition,

which retards the likelihood of adoption of new ideas and ways (see our response earlier about diffusion of innovations). Hence, the colonial-coercion hypothesis seems necessary as a first step to get the new religion at a high enough frequency so that conformity could play a significant role in further spreading the religion. If imperialists can force a majority, or just the leaders, of a conquered group to adopt a new ideology, then conformity should come into play to enhance spread. In the case of the adoption by the socially influential members of a conquered people, the authoritarianism of people in high parasite-stress regions is also expected to play a role in widespread adoption across the populace.

Chang et al. suggest that Islam and Christianity did not arise in extremely high parasite-stress areas. This is true, and it deserves more research because of the strong positive relationship that we have documented between parasite-stress and number of religions across the countries of the world. We have argued that the high in-group assortative sociality, specifically its components of ethnocentrism, xenophobia, and philopatry, in high parasite-stress areas fractionate an original culture's range and thereby give rise to new religions. This is supported not only by the positive relationship between parasite-stress and number of religions across countries, but also by the cross-national positive relationship between parasite-stress and number of languages (Fincher & Thornhill 2008a; 2008b). Cashdan's (2001a) finding that parasite-stress predicts positively the number of ethnic groups, is also supportive of the parasite-stress theory's application to causes of ethnogenesis. Perhaps, the fact that Islam and Christianity arose in areas that are moderate in parasite-stress contributed to their spread through the ability to amass resources (also see our comments on expansive religions in sect. R7, para. 4) and with members more apt to disperse than members of religions that arose from high parasite-stress regions.

Waynforth presents the results of an analysis of 56 Mayan men in Belize, for which he obtained data on serious acute and chronic illnesses in the past year. He found that the eight officials in the local religious communities had significantly more illnesses than a group of men who observed a local religion but were not officials and a group of men who did not observe the religion. He suggests that the pattern arises because religious officials are more likely to contract contagion via their increased activity in the community. In a follow-up study, it would be important to actually measure social contacts or network size, because there are many factors other than being a church official that affect social contact. It would also be useful to measure religiosity, rather than assuming church officials are the most religious. Waynforth also reports in his commentary that the religiously observant men versus the religiously non-observant men showed an insignificant difference in time spent with "biological relatives other than immediate family." Clarification of these categories of relatives is needed. Waynforth proposes that his finding may mean that religiosity in these Mayans does not promote isolation of people or promote family ties. We are skeptical, given our comments.

R17. The USA as a special case

Wall & Shackelford propose that the USA is more religious than can be accounted for by measures of infectious

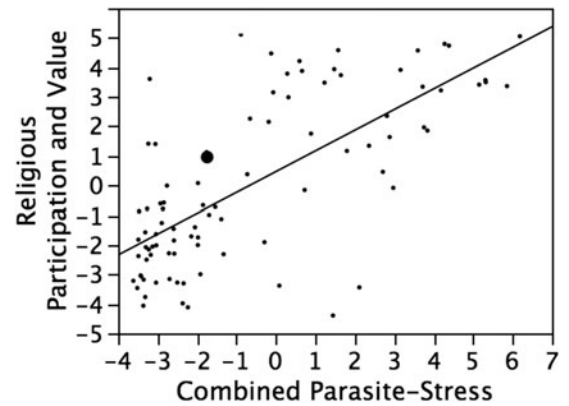


Figure R1. *Religious Participation and Value* regressed on *Combined Parasite-Stress*. The big dot is the USA datum.

diseases. This, they suggest, is the result of high immigration rates that create a hyperactivation of assortative sociality, including religiosity, to the point that the extraordinarily high assortative sociality mismatches the actual parasite-stress.

Evidence does not support the claim that the USA is an outlier in the relationship between religiosity and parasite-stress across nations. Figure R1 is a cross-national plot of *Religious Participation and Value* regressed on *Combined Parasite-Stress*. The USA datum is a positive residual but not as great as Malta and Jordan, which are the two largest positive residuals. Figure R2 shows the *Proportion of Believers* regressed on *Combined Parasite-Stress*. Both linear and quadratic relationships are shown. The USA datum is nearly on the line in this case.

Paul (2009) suggested in his study of religiosity and dysfunctional societies that the best cross-national sample for examining religiosity is the "prosperous democracies" because it avoids confounding factors like "former communist country" or poor data quality for less-developed countries. We explored further the question of the uniqueness of USA's religiosity by focusing on the 17 prosperous democracies included in Paul's sample. They are primarily Western (e.g., Norway, Spain) but also include Japan. *ES 7.D.* shows a plot of *Religious Participation and Value* regressed on *Combined Parasite-Stress*. The USA is a positive residual but Ireland is even further from the line. And,

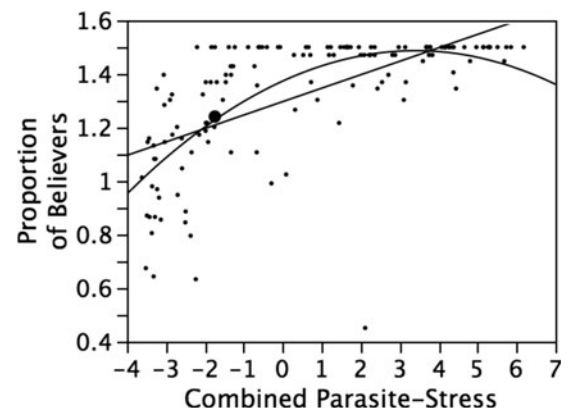


Figure R2. *Proportion of Believers* regressed on *Combined Parasite-Stress*. The big dot is the USA datum.

lastly we plotted the *Proportion of Believers on Combined Parasite-Stress* for the 17 prosperous democracies (ES 7.E.). In this case, the USA datum is on the line. The USA does appear to stand out amongst the prosperous democracies. The evidence we provide indicates that this is because of its high level of parasite-stress in comparison to the other prosperous democracies, not because of its religiosity.

There is much evidence for the hyperactivity feature that **Wall & Shackelford** emphasize. It is likely that hypervigilant parasite detection and avoidance is an adaptation. The penalty for error in detecting parasite presence can be literally grave. Selection has therefore favored the hypersensitivity of this detection and deduction of threat. Said differently, humans are designed to adaptively accept many false positives when it comes to cues of potential infectious disease presence in the environment. Hyperactivity in activation of xenophobia is apparently responsible for human prejudice against people who deviate from the typical range of phenotypes in weight (i.e., over- or underweight) or behavior (e.g., the physically or mentally challenged); this may also explain prejudice against the elderly. Most of these prejudices have been tied empirically to the parasite-stress theory by showing their positive relationship to perceived vulnerability to disease and their increased activation by parasite-relevant cues (Duncan & Schaller 2009; Park et al. 2003; 2007; Schaller & Park 2011).

R18. Mate preferences and mating systems

DeBruine, Little, & Jones (DeBruine et al.) discuss published studies showing that higher value is placed on physical attractiveness and associated health in long-term mate choice by men and women in countries of high parasite-stress than in countries of low parasite-stress (Gangestad & Buss 1993; Gangestad et al. 2006a). This research was inspired by the parasite-stress theory of sexual selection provided by Hamilton and Zuk (1982). This theory of sexual selection argues that sexually selected ornamentation (e.g., bright feathers and elaborate courtship displays) functions as an honest signal of high genetic quality pertaining to immunity and this is why mate choosers assess them and prefer their exaggerated expressions – to place immunity-based alleles in offspring. Low (1988; 1990) examined this theory as it pertains to marriage systems in traditional human societies and found that, as she predicted, harem polygyny is associated with high parasite-stress and monogamy with low parasite-stress. Low reasoned that this was expected because high parasite adversity creates the variation in phenotypic and genetic quality of men that makes it adaptive for women to marry a man of high quality who already has a wife (wives).

DeBruine et al. (with J. R. Crawford and L. L. M. Welling) have recently extended these earlier studies by examining regional differences in women's preferences for masculine features in men's faces. Men's facial masculinity appears to be sexually selected ornamentation that honestly signals genetic and phenotypic quality, in part related to immunocompetence (Thornhill & Gangestad 2006; 2008). Both across countries and across US states, evidence indicates that women in regions of low overall

health exhibit stronger sexual attractiveness preferences for male facial masculinity than do women in regions of greater composite health (DeBruine et al. 2010; 2011). DeBruine et al. extend this work in their commentary by using the data on parasite-stress we provided in the T.A., and hence conduct a more direct test of the parasite-stress theory as applied to mate preference than those based on overall composite health in a region. Their earlier research based on the health composite is repeated with actual parasite-stress, and across both countries and US states. Linking these findings to the individual level and to experimental manipulation of parasite-stress *per se*, Little et al. (2011) have reported that viewing pictures of high parasite salience evokes increased mate preferences for facial markers of health (both facial hormone markers and symmetry).

Chang et al. argue that in traditional societies, matrilineal residence, compared to patrilineal residence, provides strong family ties and extended family support; and hence, according to the parasite-stress theory of sociality, matrilineal residence is expected to be more typical in high parasite-stress regions than in low parasite-stress regions. Also, the reduction of male parental involvement under high parasite-stress, as a result of the associated harem polygyny based on good genes mate choice, provides in part, according to these commentators, the context for the adaptive value of the cultural pattern of matrilineal residence. Consistent with these ideas, Chang et al. provide evidence that matrilineal residence is more frequent in world regions of high than low parasite-stress, using data from the Ethnographic Atlas. They also suggest that the cultural practice of matrilineality disfavors individualism and modernity in general. The interplay between parasite-stress, residence pattern, and collectivism-individualism is a likely fruitful direction for further research.

Vandello & Hettinger provide a novel perspective on the connection between the parasite-stress theory of sociality and an aspect of the culture of honor, specifically the role of female purity (religious, sexual, moral, and hygienic) as a female marriage

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evidence for this pattern as well as new findings are presented in the commentary by **DeBruine et al.** Good looks are signals of phenotypic and genetic quality (Thornhill & Gangestad 2008). Because many women may marry men who provide non-genetic material benefits but who lack high genetic quality, female extra-pair mating may occur. The threat of extra-pair copulation to male paternity may be greater in high parasite regions because of the value women put on good-genes (good looks) in such areas. Accordingly, female purity may be a competitive female signal of her probable faithfulness to a particular partner and is especially valued by desirable long-term male partners in high parasite regions.

Vandello & Hettinger suggest that the parasite-stress theory may be useful for understanding additional features of the culture of honor, such as the ideological importance of family embeddedness and reputation and interfamily boundaries and conflict. Indicating a broad relevance of the parasite-stress theory to the ideology of honor, our findings across the US states show strong positive relationships between parasite-stress and each of the two variables, honor-related homicides and collectivism (Thornhill & Fincher 2011).

R19. Humanitarian implications

Uskul briefly mentions the implication of the parasite-stress theory for a reduction of the negative consequences of ethnocentrism and xenophobia (e.g., holocausts and civil conflict). Commentators **Powell, Clarke, & Savulescu (Powell et al.)** have addressed in some detail humanitarian implications as well as economic benefits of the theory. Powell et al. point out that if the parasite-stress theory continues to receive empirical support, it could be the basis of policies to reduce civil wars and other civil conflicts and social and economic inequality and promote politically stable, democratic governments. We and coauthors have discussed these topics also in recent papers, pointing to the increasing evidence that widespread reduction in parasite-stress through sanitation and healthcare improvements will not only offset morbidity and mortality, but will also evoke widespread liberal or egalitarian values. Hence, parasite-stress reduction may promote all aspects of democracy in a region, ranging from improved sanitation and health care, to civil rights and liberties, social and educational opportunities, private property rights, and gender equality (Letendre et al. 2010; in press; Thornhill et al. 2009; 2010).

The evidence that the parasite-stress theory has generated does not in itself identify liberalism as morally superior to conservatism – the view that scientific evidence identifies moral correctness is the well-known *naturalistic fallacy*. Hence, the evidence can only serve as a tool for achieving moral goals of people and not for identifying the goals. We assume that the majority of people would agree that a reduction of civil conflicts and failed governments would create a better world. We assume too that most would agree, on moral grounds, that adult-on-adult interpersonal violence and child maltreatment are behaviors that should be reduced. There is evidence that these behaviors are caused by high parasite-stress, and in the case of adult-on-adult interpersonal violence, by collectivism (Thornhill & Fincher 2011). Hence, the

breadth of implications from the parasite-stress theory for increasing humanitarianism around the world is huge.

Certainly, as **Schaller & Murray** point out, more research is needed, especially for understanding the causes acting during the ontogeny of values and associated enculturation processes of humans. But we agree with Schaller & Murray when they say that, “Increasingly, the question is not *whether* parasite prevalence has cultural consequences, but *how*: exactly what mediating mechanisms. . .” account for this.

SUPPLEMENTARY MATERIALS

Electronic Supplement 7:

<http://www.journals.cambridge.org/bbs2012007>

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[The letters “a” and “r” before author’s initials stand for target article and response references, respectively]

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