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 Shiwiar, 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 pro-sociality 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. For example, we make predictions based on the fact that out-group conspecifics that carry novel infectious diseases can be potentially dangerous to an individual's reproductive success. This leads to predictions about the evolution of human psychology and its manifestations in values or ideology that are not generated from the models presented by Inglehart and Baker (2000), Norris and Inglehart (2004) or McCleary and Barro (2006). Furthermore, the conditions-of-living model, as currently formulated, assumes that individuals will turn to an in-group under conditions of stress. However, this assumption isn't framed to consider the costs and benefits of seeking support from an out-group under ecological stress. Contact with an out-group can provide benefits unattainable from an in-group. We attempt to erect this framework by providing a fundamental explanation for the relative costs of interacting with in-groups versus out-groups under different ecological settings of parasite-stress.

4. Methods for establishing an empirical link between family ties, religiosity, and parasite-stress

4.1. Strength of family ties

We propose that individuals who value strong family ties will be found predominantly in areas with greater parasite-stress because of the benefits of in-group assortativeness promoted by family embeddedness. We predict,

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-national[2]: 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 States[3]: 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.I* 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
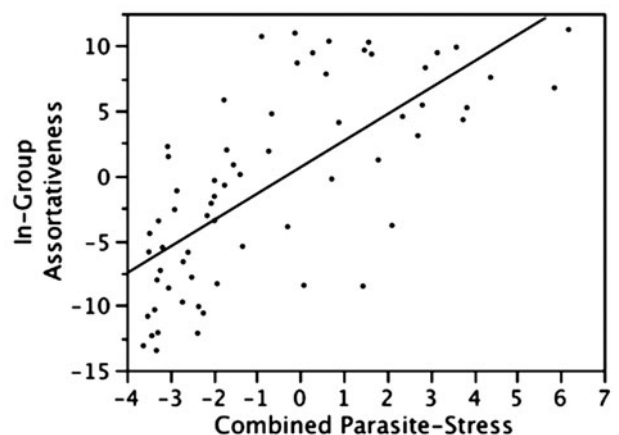

Figure 1. The correlation between *Combined Parasite-Stress* and *In-Group Assortativeness* for the 65 nations with correspondent data for all 11 items that make up the 2 variables ($r = .71$, $p < .0001$). The line is the regression line.

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*
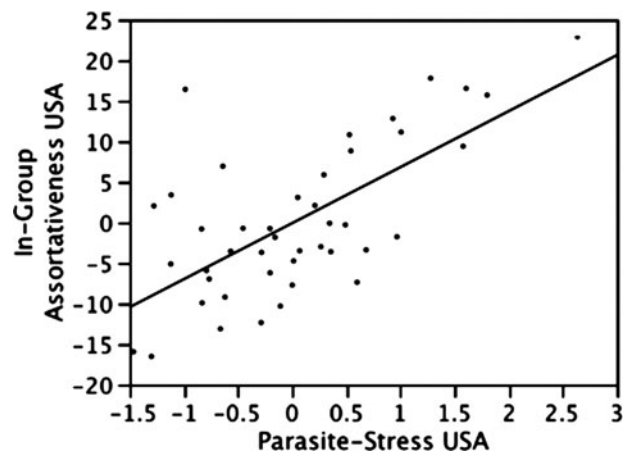

Figure 2. The correlation between *Parasite-Stress USA* and *In-Group Assortativeness USA* for the 43 states/state combinations with correspondent data for all 14 items that make up the 2 variables ($r = .66$, $p < .0001$). The line is the regression line.

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 ecology of values and ideology. It is unknown at this point what cues are relevant, but they may include infection frequency experienced by individuals (Stevenson et al. 2009). We discussed various potential ontogenetic causes of values earlier in the article (see sect. 2.1).

6.3. In-group assortative sociality

Taken together, the findings for strong family ties and heightened religiosity in the face of parasite threat provide further support for the parasite-stress theory of sociality. We argue that in-group assortative sociality represents an adaptive response to heightened parasite-stress. Furthermore, we can add variation in the strength of family ties and religiosity to the list of features of human sociality requiring an explanation couched in the parasite-stress model of sociality. The predictability and apparent universality of this adaptive response suggests that the adaptive response of in-group assortative sociality in the face of parasite-stress is an ancient feature in *Homo sapiens*. Furthermore, the indications that similar types of adaptive responses are found in other animals (Freeland 1976; Loehle 1995) suggest that parasites had important impacts upon social life in deep-time evolutionary history.

The social isolation of groups under high parasite-stress is not without costs to individuals in the groups. For example, under conditions of social isolation significant inbreeding can take place, possibly generating inbreeding depression. However, adaptive inbreeding is possible (Shields 1982; Kokko & Ots 2006). This seems especially likely under the ecology of high infectious disease stress, as mentioned in section 2.1 regarding the effects of malaria (Denic & Nicholls 2007; Denic et al. 2008a; 2008b), and perhaps infectious disease stress considered more broadly (Hoben et al. 2010). Social isolation can also limit access to trade with out-groups, innovations generated by out-groups, and out-group social alliances. Out-group interaction and affiliation, as we have explained, is a benefit of individualism/liberalism but one that is only widely optimal under relatively low parasite-stress.

Our findings that infectious disease stress promotes in-group assortative sociality can potentially inform the study of epidemiology or spread of infectious diseases. For example, it is the case that the prevalence of many types of parasites is greater in large, or more dense, populations (Altizer et al. 2003; Guégan & Constantin de Magny 2007). At the same time, under conditions of high parasite-stress,

groups are comparatively more isolated (via in-group assortative sociality) than groups in conditions of low parasite-stress. This suggests that an important consideration for understanding parasite transmission is to recognize the difference between out-group versus in-group contact. Contact rates between individuals may be high within a group that is socially isolated from other groups. This is indeed an implication from the research presented here. Thus, high rates of contact in low pathogen areas are different from high contact rates in high pathogen areas. Based on our research, in low pathogen areas (individualistic locales), a high contact rate implies high rates of contact between genetically different, and differently infected individuals, whereas high contact rates in high pathogen areas (collectivistic locales) occur between individuals that are genetically close and likely carry similar infectious diseases.

6.3.1. In-group assortative sociality and life-history. Gladden et al. (2009) explored the interactions of religiosity, moral intuitions, and life-history patterns. They showed that both the strength of moral intuitions (automatic emotional reactions brought on by norm and other rule violations) and religiosity result from a slow life-history strategy. That is, both are signs of a life-history strategy focused on somatic investment or investment in survival, in contrast to a focus on reproductive effort. Gladden et al. suggested their findings were consistent with the fact that pathogen-stress and collectivism were positively related (Fincher et al. 2008), presumably because much of moral intuitions taps into cognition about pathogens (Oaten et al. 2009). In other work, Figueredo and Wolf (2009) showed that slow life-history people assortatively pair, sexually and socially, more strongly than fast life-history strategists.

Both sets of findings are consistent with what we have presented here, that in-group assortative sociality is strongly and positively associated with pathogen stress.

Nevertheless, whenever parasite-stress is extremely high, collectivistic, nepotistic investment may not be optimal because the extreme parasite-stress yields extrinsic mortality (see Quinlan 2007 and references therein). Because extrinsic mortality, by definition, cannot be reduced by nepotistic investment, comparatively low investment per offspring is predicted from life-history theory when extrinsic mortality is high. Therefore, we hypothesize that there will be reduced nepotistic investment in offspring and other kin in the face of extremely high parasite-stress because of the inability of nepotistic investment to reduce the morbidity and mortality associated with this high level of ecological stress. In this situation, early reproduction with minimum nepotistic investment per family member (e.g., offspring) is optimal according to life-history theory (Charnov 1993; Kaplan & Gangestad 2005) and predicts a curvilinear relationship between parasite-stress and nepotistic investment. Consistent with this, Quinlan (2007) found when he examined a sample of traditional societies, that maternal investment in the form of nursing duration increased along with pathogen stress but then began to decrease after pathogen stress became extreme (i.e., he found a curvilinear relationship).

We hypothesize that the same pattern will be seen in human value systems as well. The current study provides

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.

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 unsupportive 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 sub-groups, 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 transcendental (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