

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

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

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

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

Extending parasite-stress theory to variation in human mate preferences

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Lisa M. DeBruine,^a Anthony C. Little,^b and Benedict C. Jones^a

^aSchool of Psychology, University of Aberdeen, Aberdeen, AB25 3FX, Scotland, United Kingdom; ^bSchool of Natural Sciences, University of Stirling, Stirling, FK9 4LA Scotland, United Kingdom.

l.debruine@abdn.ac.uk anthony.little@stir.ac.uk
ben.jones@abdn.ac.uk <http://facelab.org/debruine>
<http://alittlelab.com> <http://facelab.org/bcjones>

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

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

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

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

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

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

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

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

Parasite stress, ethnocentrism, and life history strategy

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Aurelio José Figueredo,^a Paul Robert Gladden,^b and Candace Jasmine Black^a

^aDepartment of Psychology, University of Arizona, and School of Mind, Brain, and Behavior, College of Science, University of Arizona, Tucson, AZ 85721-0068; ^bDepartment of Psychology and Sociology, Macon State College, Macon, GA 31206.

ajf@u.arizona.edu paul.gladden@maconstate.edu

cjblack@email.arizona.edu http://www.u.arizona.edu/~ajf

http://vista.maconstate.edu/directory/detailsprint.aspx?id = 612

http://www.u.arizona.edu/~cjblack

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

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

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

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

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

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

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

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