Individual-level analyses of the impact of parasite stress on personality: reduced openness only for older individuals

Word Count: 8290

Abstract

The parasite stress hypothesis predicts that individuals living in regions with higher infectious disease rates will show lower openness, agreeableness, and extraversion, but higher conscientiousness. This paper, using data from over 250,000 US Facebook users, reports tests of these predictions at the level of both US states and individuals and evaluates criticisms of previous findings. State-level results for agreeableness and conscientiousness are consistent with previously reported cross-national findings, but others (a significant positive correlation with extraversion, and no correlation with openness) are not. However effects of parasite stress on conscientiousness and agreeableness are not found when analyses account for the data's hierarchical structure and include controls. We find that only openness is robustly related to parasite stress in these analyses, and we also find a significant interaction with age: Older, but not younger, inhabitants of areas of high parasite stress show lower openness. Interpretations of the findings are discussed.

Keywords: Personality, parasite stress, Facebook, Openness, Aging

Various hypotheses about the origins of individual differences in personality have been proposed, making reference for example to genetic and evolutionary factors (e.g., Buss, 2009; Nettle, 2006; Penke, Denissen, & Miller, 2007), and environmental influences (Thornhill & Fincher, 2014). The present paper focusses on the potential role of parasite stress in the environment (Thornhill & Fincher, 2014) and on how the effect of parasite stress on personality may have changed over time. According to the parasite stress hypothesis, personality traits can be understood at least in part as an adaptive response to prevailing levels of non-zoonotic infectious disease in the environment. Non-zoonotic infections are those that are passed through contact and interaction with other humans, and so when the prevalence of such infections is high it is adaptive to reduce interactions with individuals – particularly those from other communities – who could carry dangerous diseases.

The parasite stress approach to the origin of individual differences in personality both contrasts with and complements existing evolutionary/adaptive approaches (Buss, 1991, 2009; Buss & Hawley, 2011; Dingemanse, Kazem, Reale & Wright, 2010; Gangestad, Haselton & Buss, 2006; Nettle, 2006). A key element of many adaptive accounts of individual differences in non-human animals is the idea of tradeoffs, and this idea has more recently been applied to the study of human personality (e.g., Nettle & Penke, 2010). Nettle (2006), for example, argues that individuals' locations along the "Big 5" personality dimensions represent tradeoffs between costs and benefits to fitness. For example, while high conscientiousness is associated with longevity, at least partly due to hygiene maintenance and the avoidance of risky health behaviors (Bogg & Roberts, 2004), fitness-threatening behaviors such as various types of eating disorder are associated with conscientiousness-linked traits such as over-control (Claes et al., 2006) and/or low novelty seeking (Cassin & von Ranson, 2005).

There is good reason to believe that parasite stress effects will significantly impact the evolution or development of population characteristics due to similar tradeoffs. The avoidance of infection is a major evolutionary force, or at least has been so in the past (e.g., Tooby, 1982). For example, until relatively recent times infectious diseases led to the demise before reproduction age of almost 50% of children (Volk & Atkinson, 2013). The immunological defenses that an organism possesses are specialized, being tuned for maximum effectiveness against parasite species that are prevalent in the local environment (Thompson, 2005). Exposure to, and interaction with, members of out-groups may therefore carry a risk of being exposed to infectious diseases that are unfamiliar to the immunological defense system and hence pose a relatively high risk of death or disease (Fincher, Thornhill, Murray, & Schaller, 2008). The specific question addressed here is whether an individual's personality adapts to the level of infection risk in the environment. We also ask a further question, which to our knowledge has not been previously addressed: If personality does adapt, has the effect changed over time, perhaps for example because medical advances have reduced the threat of infectious disease upon survival? Or, does it change during an individual's lifespan, with the effect becoming larger as aging weakens the immune system thus increasing the threat of disease?

A key prediction of the parasite stress hypothesis is that the level of disease threat in the environment will affect individuals' attitudes towards outgroup members and that higher levels of disease threat will lead to greater conformity, xenophobia, and distrust of different others (e.g., Murray, Trudeau, & Schaller, 2011; Neuberg, Kenrick, & Schaller, 2011; Thornhill, Fincher, & Aran, 2009). Negative attitudes towards outgroup members have been shown to correlate with a number of the big 5 personality traits. The strongest relationships have been found with openness and agreeableness, with higher levels of each of these predicting lower outgroup prejudice (Ekehammar & Akrami, 2003, 2007; Flynn, 2005). The relationship with openness to new experience has been argued to be a natural extension of the parasite stress hypothesis. Individuals high in openness will be less constrained by the norms of their culture (many of which will have evolved to reduce infection risk) and, being high in curiosity, may be more likely to explore new environments (which may contain dangerous parasites) and due to their reduced outgroup prejudice will be more likely to engage with unknown outgroup members who may carry novel infections. Thus, although other components of openness are less socially relevant, we follow previous authors in assuming that being more open to new ideas and experiences generally may increase one's chances of being exposed to new pathogens. Moreover, in the case of openness there is a direct trade-off between the threat of exposure to disease and the potential benefits of discovering new ideas, trading partners, and natural resources, or expanding the gene pool of the group (see Brown, Fincher, & Walasek, 2016).

Extraversion is also related to outgroup prejudice: Higher extraversion is associated with lower prejudice, although this association is smaller than those between lower prejudice and agreeableness and openness. Extraversion is linked to risky sexual behaviors, and has been hypothesized to be lower in regions of high parasite stress (e.g., Schaller & Murray, 2008). However it is not clear whether higher extraversion directly relates to more positive outgroup attitudes, or whether extraversion results in a quicker strengthening of intergroup relations only after an initial link has been established (Turner, Dhont, Hewstone, Prestwich, & Vonofakou, 2014).

Predictions regarding the relation between pathogen stress and other personality traits are less straightforward. Agreeableness has been linked to reduced prejudice (e.g., Sibley & Duckitt, 2008) and greater likelihood of initiating intergoup contact (Jackson & Poulsen, 2005), but its effect on prejudice may be redundant on “dark personality” traits such as narcissism and psychopathy (Hodson, Hogg, & MacInnis, 2009). Finally, conscientiousness may not have a large direct role upon social interaction, but it could form a part of a social immune system in other ways as conscientiousness is linked to increased attention to hygiene as well as greater adherence to social norms, such as those involving traditional food preparation (Bogg & Roberts, 2004, Schaller & Park, 2011). Many such traditions help protect against parasites and potentially dangerous foods that were, or are, prevalent in the region where the tradition developed.

Previous research on the relationship between regional parasite stress and personality has broadly confirmed several of the above predictions. In regions with higher levels of environmental parasite stress, the average levels of openness and extraversion are lower (Schaller & Murray, 2008). Furthermore, when the measure of parasite stress is restricted such that it only includes non-zoonotic infections (infections that can be passed from human-to-human) the finding remains robust, but the stress-personality relationship is not present for prevalence of zoonotic infections (those transmitted to humans by livestock and other species) (Thornhill, Fincher, Murray, & Schaller, 2010).

Despite the effects they have found, these previous studies have significant limitations. Many existing findings rely upon analyses performed at the level of the nation state. A potential problem with this is that there is significant variation in the methods and accuracy with which parasite stress is recorded (Hruschka & Hackman, 2014). Moreover, there are potential confounds in the measurement of personality. It is known that there are cultural differences in the way that personality factors are viewed and expressed (Heine, Buchtel, & Norenzayan, 2008) and that personality judgements are often relative, with people judging themselves by comparison to other known individuals and perceived cultural norms (Wood, Brown, Maltby, & Watkinson, 2012).

Another, broader, issue is that the analyses are based upon average personality traits within a region and this analytic approach introduces several confounds (see Hackman & Hruschka, 2013; Hruschka et al., 2014; Hruschka & Hackman, 2014; Hruschka & Henrich, 2013; Thornhill & Fincher, 2013). In particular, in such analyses it is not possible to control for, or measure, the effect of individual-level variables such as gender or age. Any correlations between these confounds and either the expressed personality traits, or the measure of parasite stress, would bias any subsequent analysis. This is a particular concern because personality traits vary with age (Roberts, Walton, & Viechtbauer, 2006; Sunning, Stillwell, Michal, & Rust, 2015), and there are significant differences between genders (Weisberg, De Young, & Hirsh, 2011). These relationships can themselves vary greatly between cultures (Costa, Terracciano, & McCrae, 2001). Equally, the age profile of a population may be different in regions with especially high or low levels of infectious disease risk, and it is likely that social policies and the prevalence of particular diseases will impact genders differently.

A further concern is that the parasite stress index used in a number of previous studies is confounded with the racial composition of US states. African Americans have higher STD rates and these STD rates contribute strongly to the parasite stress index used by Fincher and Thornhill (2012) (Hackman & Hruschka, 2014; Koenig, Van Leeuwen & Park, 2017). This is important theoretically because high STD rates may reflect people's adoption of a fast life history strategy (an adaptive response to living in an impoverished or threatening environment which involves having children early and investing in quantity rather than quality) and it is therefore possible that behaviors associated with fast life history strategy may occur with greater frequency in high-stress areas. We address this issue in our analyses below by showing that our key findings remain qualitatively unchanged when we use a mortality-based measure of parasite stress that does not include STDs. We also note (anticipating our results) that there is little evidence for race differences in personality (Tate & McDaniel, 2008), at least for openness which is the only construct on which we find a robust effect in multi-level analyses below, and that the interactions with age that we find are not readily susceptible to alternative explanations in terms of life history strategy.

The availability of individual-level variables allow an analysis to control for potential confounds, but they also make it possible to test specific additional hypotheses. Here, the hypotheses concern the relationship between age and the parasite stress effect. One hypothesis is that older people will, due to decreased immune function, be more at risk from infection and hence may have more reason to avoid infection. This hypothesis predicts that openness and perhaps extraversion will be reduced in older individuals who are living in regions with high parasite stress.

Reduced openness in older adults could also reflect the fact that such individuals were raised in an environment in which infection-related disease and mortality rates were much greater than they are now. An individual's personality is strongly influenced by genes and by early life experience (Asendorpf & van Aken, 2003). Therefore, if an individual spends their early childhood in an environment with high/low infection risk, that environment may shape their personality in a way that will last for the rest of their life. In the first half of the 20th century infectious disease posed a significant risk to survival (e.g., Tooby, 1982; Volk & Atkinson, 2013). However, with the advent of modern medicine and improvements in hygiene, the risk of death by infectious disease in the United States plummeted (Figure 1). This means that of Americans alive today, older individuals spent their early childhoods in an environment where disease and infection posed a significant risk to survival, but younger individuals are likely never to have even known anyone who suffered from – much less died from – diseases such as measles, whooping cough, or polio. Therefore, this hypothesis also predicts that within the US there should be a significant interaction with age: Older individuals should show significant differences in their personality traits depending upon the prevalence of infectious disease, but the effect should be smaller, or extinct, in younger adults. In support of our hypothesis, some recent evidence has suggested that this change over time is present in political ideology: Brown et al. (2015) found direct links between voting patterns and various measures of pathogen stress in US States, with higher levels of Republican voting being associated with higher levels of infection risk in the 1960s and 1970s, but not more recently.

There are thus two reasons for predicting that older adults should show a stronger relationship between personality and parasite stress levels. According to the first (the weakened immune system hypothesis) it might be expected that levels of parasite stress in the state in which an individual currently resides would most strongly relate to their personality, while according to the second (the developmental hypothesis) infection levels in the state in which they grew up would be more relevant. We provide a preliminary test of these alternative possibilities below.

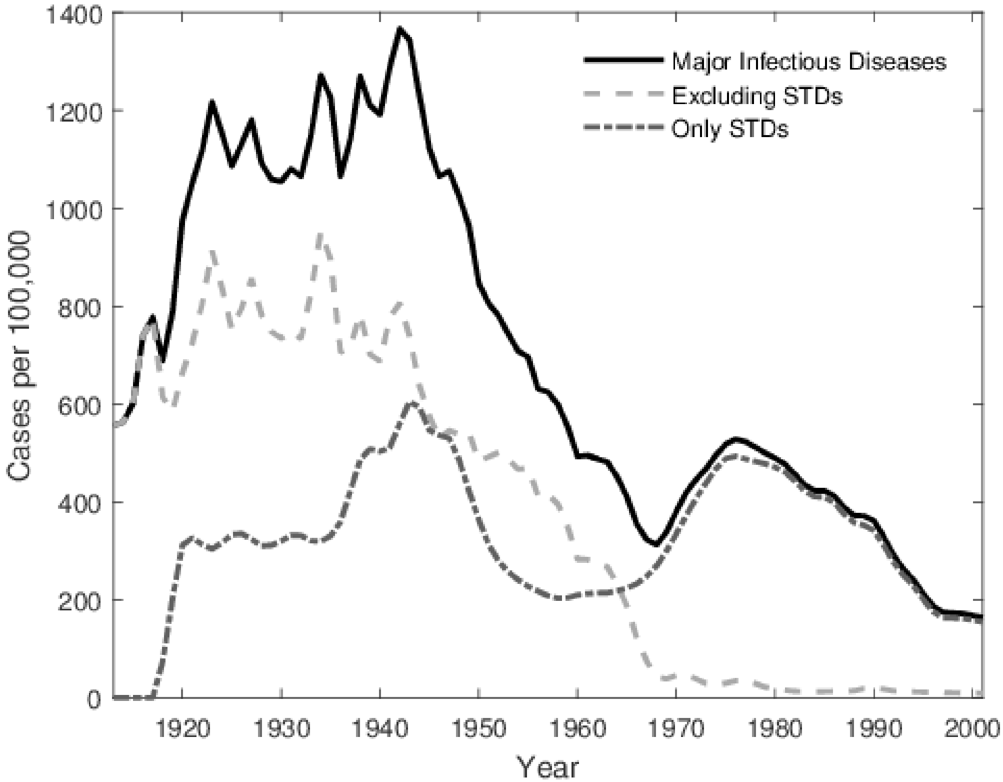

Figure 1. The change in rates of infectious disease over time. The diseases included are tuberculosis, malaria, typhoid, diphtheria, whooping cough, measles, polio, syphilis, gonorrhoea, and AIDS.

Laboratory studies examining behavior and personality at the individual-level show more equivocal results than population-level analyses. These lab-based studies address an additional prediction of the parasite stress hypothesis. This is that, as well as being less open and less extroverted, individuals from high parasite stress regions will also be more sensitive to disease cues, as such cues have a greater relevance to their survival. However, results from studies examining links between personality and reactions to disease related stimuli have been mixed. Duncan, Schaller and Park (2009) found small correlations between “Big 5” personality traits and a measure of perceived vulnerability to infection as well as a measure of germ aversion. Tybur et al. (2011), using the Three Domain Disgust Scale which provides separate measures of pathogen, sexual and moral disgust (Tybur, Lieberman, & Griskevicius, 2009) and the extended HEXACO measure of personality, which adds a modesty-humility dimension to the Big 5, found that only openness correlated negatively with pathogen disgust, while Tybur et al. (2009) themselves found that pathogen disgust was correlated only with neuroticism (positively), and not with extraversion or openness. However, Mortensen, Becker, Ackerman, Neuberg, and Kenrick (2010) found that exposure to disease-depicting pictures can result in temporary changes in self - reported personality (reduced extraversion and openness).

Thus, laboratory studies show some lack of agreement. The only trait which shows a significant relationship in more than one study is openness, but even this association is not universally observed. Interestingly for our age-related hypothesis, the vast majority of subjects in these studies were university undergraduates and were therefore young.

This paper uses a powerful large dataset first to provide a new examination of the correlations between regional averages of parasite stress and personality. Our data then allow us to go further, performing multi-level analyses that explicitly control for – and test – the effect of individual-level traits such as age, as well as comparing the impact of parasite stress in the state where individuals spent their childhoods (their home state), to that of the state they currently reside in. We restrict our analyses to individuals living in the US thus minimizing problems around consistent measurement of parasite stress and around cultural relativity issues in personality measures. The large geographical area of the US means that there is still significant variance in the level of parasite stress between different regions.

To foreshadow the results: Our analyses show that effects of parasite stress on agreeableness and conscientiousness are found in simple state-level correlation analyses, but are not found after the hierarchical structure of the data is accounted for and relevant statistical controls are added. For openness, no main effect is found in simple correlation analysis, but after controlling for age, we find a strong interaction effect such that older individuals show a large negative relationship between openness and parasite stress (as predicted), while younger individuals show a smaller positive relationship. This age-related effect is robust across a wide range of analyses and after controlling for numerous variables. The effect appears to be one of parasite stress levels in the state in which people are currently living, rather than levels in their home state.

Methodology and use of Facebook dataset

Data from Facebook users are increasingly widely used in the social sciences (see Gosling, Augustine, Vazire, Holtzman, & Gaddis, 2011, for a review), and personality predicts online social networking behavior (Gosling et al., 2011; Kosinski, Bachrach, Stillwell, Kohli & Graepel, 2013). Moreover, “Likes” data from Facebook can predict personality and other individual differences (Kosinski et al., 2011; Sunning, Kosinski & Stillwell, 2015). Here we make use of data from US Facebook users for whom we have data on (a) age and gender, (b) current state of residence, and (c) personality. This results in a total sample size of 274,685.

Datasets

The data used in this paper were collected using the Facebook application “MyPersonality” (Kosinski et al., 2015). This was a popular application which was launched in 2007. Participants completed the 20 question measure of the International Personality Item Pool (IPIP) thus providing estimates of their scores on the five factor model of personality (Goldberg et al., 2006).

Participants received no payment and completed the survey in order to receive information and feedback regarding their personality which they could then share using Facebook’s social networking tools. After completing the survey, participants were asked if they would consent to their responses and Facebook profile information being used for research purposes. Further information, including how to access the MyPersonality datasets, is available at http://mypersonality.org.

The United States is significantly over-represented within the Facebook population and within the MyPersonality sample. As the US state-level measures of parasite stress are also amongst the most robust and validated, we focused our analyses upon this subsample. We selected individuals from the MyPersonality dataset who had completed the “Current State” / “Current Town” information on their profiles and indicated a location within the US. Those living in Washington DC were excluded as there is no reliable parasite stress measure available. We also restricted our analysis to individuals who were over 16.

The demographics of this sample were representative of the Facebook population, with a gender bias of 62% female and a mean age of 27. The distribution of ages also showed a significant positive skew (Figure 2). Note that although the proportion of older individuals appears comparatively small, the absolute numbers are still very large, meaning the dataset provides excellent statistical power.

The scale reliabilities (α values) were .72 (extraversion), .65 (neuroticism), .58 (agreeableness), .68 (conscientiousness) and .53 (openness). These are a little lower than the values reported by Donnellan, Oswald, Baird, and Lucas (2006) in development of the mini-IPIP scale (.82, .70, .75, .75, and .70 respectively), probably reflecting the less controlled testing conditions in our dataset.

We used a number of measures of parasite stress. Our primary measure was taken from Fincher and Thornhill (2012). This measure is created by taking incidence rates of diseases for the years 1993 – 2007, as reported by the US Centre for Disease Control. These incidence rates are normalized by state populations and transformed into a Z-score. Two additional scores are taken from Fincher and Thornhill (2012): zoonotic and non-zoonotic. Zoonotic parasite stress describes all diseases that are only transmitted to humans by contact with animals and livestock (as defined by the GIDEON database; Global Infectious Disease & Epidemiology Network: www.gideononline.com). Non-zoonotic diseases include any which can be transferred from human to human. This provides an important robustness check, as the parasite stress hypothesis predicts that only non-zoonotic stress should result in social behavior change, as it is only for these diseases that avoiding social interactions with other individuals is beneficial to health.

As a further robustness check another measure was calculated using mortality figures obtained from the CDC Wonder Online database (wonder.cdc.gov/DataSets.html). The measure took the state-wise median infection-related mortality rates for the years 1979 – 1998. This time period was chosen because the methodology used to estimate mortality changes periodically and this represents the longest period of time where one methodology (code IDC-8) was used continuously. Insufficient data were available to allow use of a time-varying measure.

This additional dataset allowed us to create a measure with all STDs removed, thus adding a control for the effect of sexual life history.

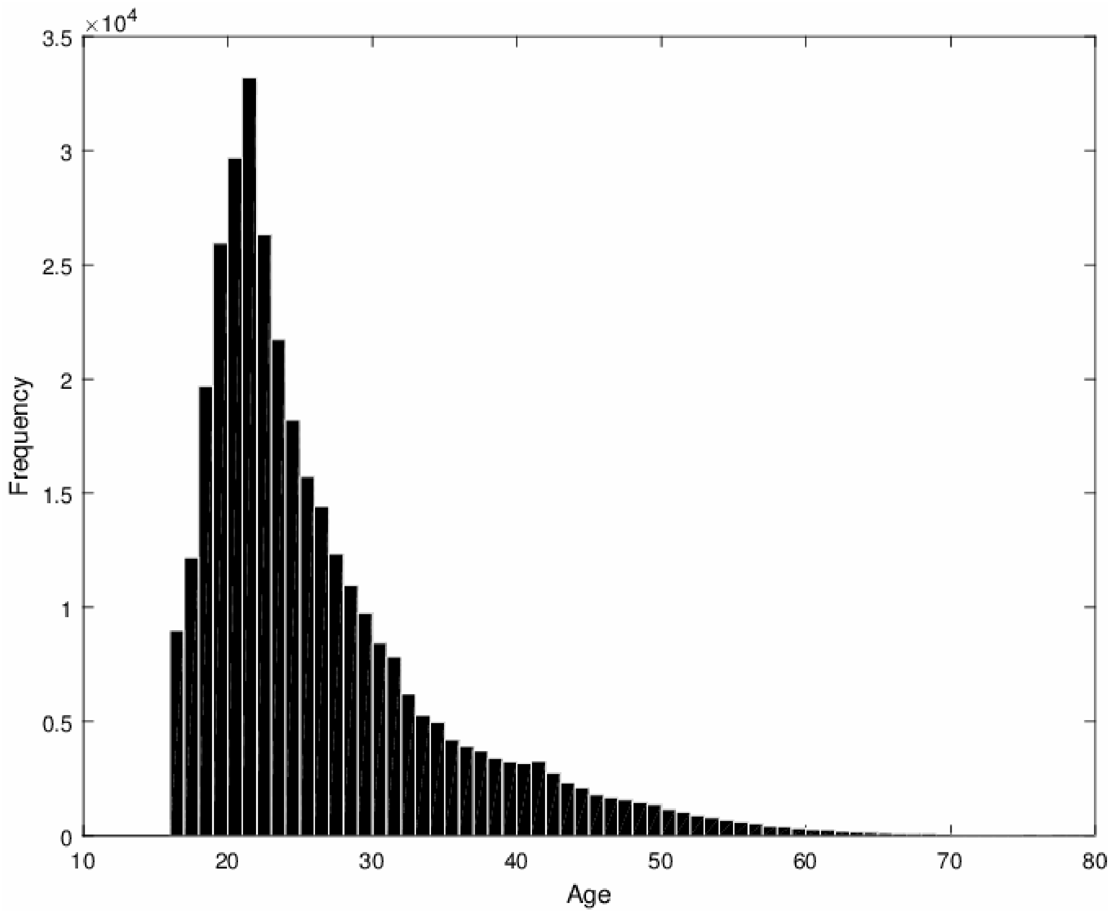

Figure 2. The distribution of participants' ages.

Results

We first report state-level correlation analyses analogous to those applied in previous nation-level investigations. After this we make use of individual-level controls, including individual and state-level data in multi-level analyses. In the first stage, the average personality measures were calculated for each state and correlated with state-level measures of parasite stress. As expected on the basis of prior results and the parasite stress hypothesis, there was a significant negative correlation between parasite stress and agreeableness (r = -.31, p = .027) and a positive correlation with conscientiousness (r = .38, p = .007). However, counter to predictions, there was a significant positive correlation between parasite stress and extraversion (r = .61, *p*<0.001), and no significant correlation with openness (r = .23, *p* = .102), or with neuroticism (r = -.16, *p* = 0.282).

To provide a measure of the effect of age within these simple correlation analyses the sample was split by age into 15 bins with equal numbers of observations. The mean personality was calculated for each state in each age bin. This was then correlated with the state-wise parasite stress measure. Figure 3 shows how the strength of correlation changes across age. The only dimension which shows any obvious change by age is openness. This also reveals why there was no relationship between openness and parasite stress in the overall correlation analysis: Whilst older individuals show the negative relationship predicted by the parasite stress hypothesis, those in younger age bins actually show a slight positive relationship, meaning the overall average is close to zero.

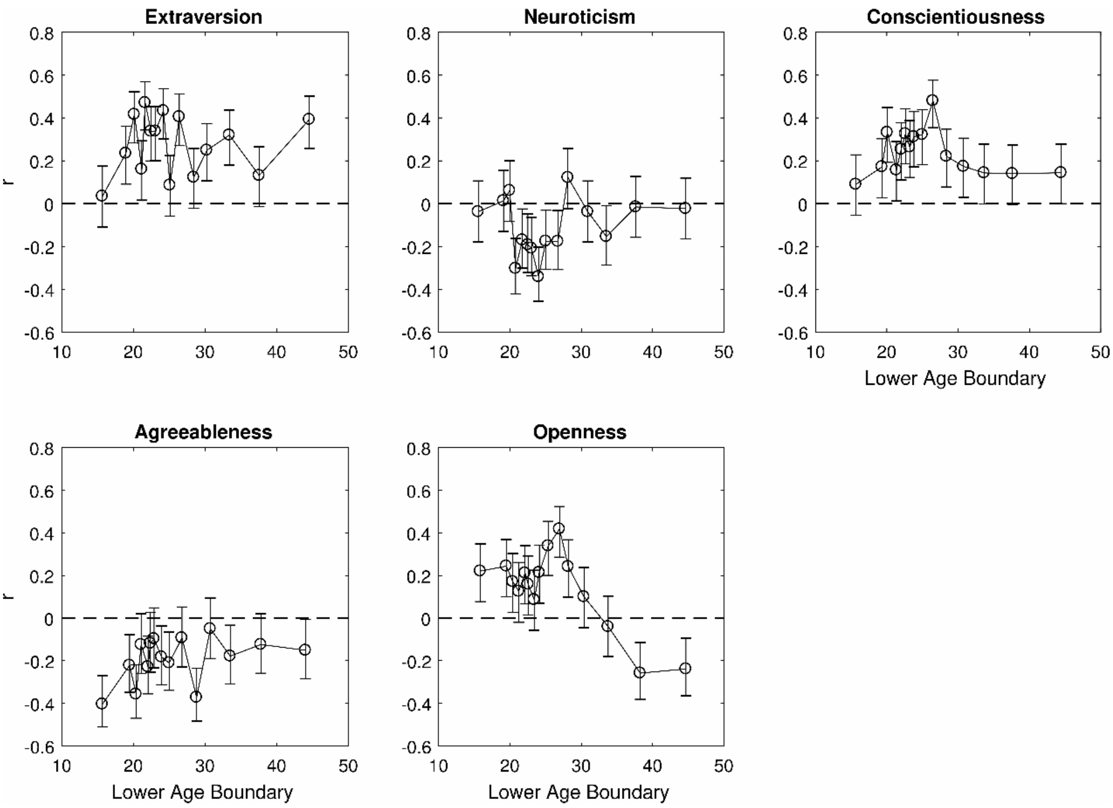

Figure 3. The strength of correlation between state-level average personality traits and parasite stress when separated into 15 age bins with equal numbers of subjects.

The next step was to perform analyses that account for the hierarchical structure of the data, and which include relevant controls. The predictors of interest were parasite stress and the interaction between parasite stress and age. Control variables were included to account for individual-level demographics and potentially relevant state-level socioeconomic measures. These were age, gender, GINI measure of inequality (U.S. Census Bureau, 2012a), percent of population in urbanized regions (U.S. Census Bureau, 2010), and log transformed median income of state residents (U.S. Census Bureau, 2012b). Income, but no other variable, was transformed on the grounds that utility (and subjective well-being) are typically assumed to be logarithmic, or similar, functions of income (e.g. Layard, Nickell, & Mayraz, 2008). The specific controls were chosen as it seemed plausible that each of these factors could be responsible for individual differences (e.g., income inequality is associated with more concern for status-relevant positional goods: Walasek & Brown, 2015; higher population densities are associated with slower life history strategies: Sng, Neuberg, Varnum & Kenrick, 2017)[1].

As parasite stress and socio-economic data are only available at the state-level (i.e., individual-level measures of infection-sensitivity and economic circumstance were unavailable), it was necessary to use mixed modeling. Both fixed and random effects were estimated for the individual-level predictors, with state as the grouping variable. An intercept was also estimated for state. The model was fitted using maximum likelihood estimation.

When considering how to center and normalize the predictors, an additional issue must be considered. One of our hypotheses relates to parasite stress, which is a state-level (or level 2) variable, and the other relates to the interaction between parasite stress and age, with age being an individual-level (or level 1) variable. Tests of these two hypotheses require different approaches when preparing the data for hierarchical analysis (Enders & Tofighi, 2007). When the variable of interest is the main effect of a level 2 variable, level 1 predictors should be grand mean centered so that the level 2 variable represents the partial coefficient of the state-level predictor. When the variable of interest is a level 1 main effect, or an interaction term between level 1 and level 2 predictors (such as age by parasite stress), level 1 variables should be centered within a cluster (a state). Given that full understanding of the parasite stress effects requires estimates of both, we report two sets of analyses, and signpost

[1] Full results with and without controls are presented in the supplementary materials.

throughout which analyses are most appropriate for the interpretation of each effect/hypothesis.

The first analysis centered all predictors by the grand mean prior to standardizing them. This is designed to best examine the main effect of parasite stress. The results in Table 1 show that there is a significant positive association between parasite stress and openness. There is also a smaller positive association with extraversion, and a negative association with neuroticism. Contrary to the state-level correlations, there is no effect of agreeableness and no effect of conscientiousness.

The second analysis centered level 1 predictors within clusters (i.e., for each state) before being standardized by the grand standard deviation. This is designed to best examine the interaction effect between parasite stress and age. Note that standardizing by the overall variance after centering does not affect the overall results (see supplementary information for non-standardized analyses). Only openness shows a significant interaction between parasite stress and age, with older people in higher parasite stress states showing lower openness (Table 2).

Interestingly, these cluster-centered analyses indicate the presence of a significant positive effect of parasite stress on conscientiousness. This demonstrates the importance of seemingly minor decisions about analysis strategy, as the effect is not present in the previous (grand mean centered) analysis, which is specifically designed to test main effects.

Table 1. Full model results for all 5 traits when predicted using the aggregate parasite stress measure and using grand mean centering.

Personality Trait	Openness	Extraversion	Neuroticism	Agreeableness	Conscientiousness
Intercept	0.068***	0.000	0.036***	-0.003	-0.004
	[0.050, 0.087]	[-0.016, 0.017]	[0.016, 0.056]	[-0.024, 0.019]	[-0.022, 0.014]
Current Parasite	0.034**	0.020*	-0.023*	-0.015	0.002
	[0.015, 0.053]	[0.003, 0.036]	[-0.041, -0.005]	[-0.037, 0.008]	[-0.015, 0.020]
Current Parasite * Age	-0.034***	-0.002	0.004	0.010	0.014
	[-0.049, -0.019]	[-0.017, 0.013]	[-0.010, 0.018]	[-0.037, 0.008]	[-0.003, 0.031]
Age	-1.305***	-0.405	0.143	-0.013	-0.350
	[-1.781, -0.830]	[-0.876, 0.065]	[-0.269, 0.555]	[-0.519, 0.494]	[-0.901, 0.201]

Gender	-0.042***	0.027***	0.180***	0.032***	0.034***
	[-0.047, -0.037]	[0.023, 0.031]	[0.174, 0.185]	[0.027, 0.037]	[0.029, 0.038]
GINI	-0.002	-0.011	0.031**	-0.047**	-0.017
	[-0.024, 0.021]	[-0.030, 0.008]	[0.010, 0.052]	[-0.074, -0.020]	[-0.038, 0.004]
Perc urban	0.040**	-0.002	-0.021	0.034*	0.038**
	[0.017, 0.064]	[-0.021, 0.018]	[-0.042, 0.000]	[0.007, 0.061]	[0.016, 0.059]
Median Income	-0.043**	-0.014	0.028*	-0.031*	-0.045***
	[-0.066, -0.019]	[-0.034, 0.005]	[0.006, 0.049]	[-0.059, -0.003]	[-0.067, -0.024]
GINI * Age	0.156*	0.116	0.032	0.087	0.031
	[0.004, 0.307]	[-0.034, 0.266]	[-0.101, 0.165]	[-0.006, 0.026]	[-0.143, 0.206]
Urban * Age	-0.043	0.045*	-0.033	-0.029	-0.062*
	[-0.087, 0.001]	[0.001, 0.089]	[-0.072, 0.006]	[-0.075, 0.017]	[-0.112, -0.012]
Income*age	1.160***	0.220	-0.178	-0.009	0.534*
	[0.706, 1.614]	[-0.230, 0.670]	[-0.575, 0.218]	[-0.490, 0.473]	[0.012, 1.057]
-2 Log Likelihood	777034	783610	778479	780803	771745
BIC	777260	783835	778704	781028	771970

* p<0.05; ** p<0.01; ***p<0.001. Confidence intervals are presented in the row below each coefficient.

Table 2. Full model results for all 5 traits when predicted using the aggregate parasite stress measure and using state mean centering.

Personality Trait	Openness	Extraversion	Neuroticism	Agreeableness	Conscientiousness
Intercept	-0.003	-0.002	0.007	-0.004	0.003
	[-0.015, 0.010]	[-0.011, 0.007]	[-0.008, 0.023]	[-0.019, 0.012]	[-0.008, 0.014]
Current Parasite	0.002	0.018***	-0.018*	-0.006	0.015**
	[-0.009, 0.012]	[0.010, 0.026]	[-0.030, -0.005]	[-0.019, 0.007]	[0.005, 0.024]
Current Parasite * Age	-0.011***	-0.001	0.001	0.003	0.005
	[-0.016, -0.006]	[-0.006, 0.004]	[-0.003, 0.006]	[-0.003, 0.009]	[-0.001, 0.011]
Age	-0.035***	-0.030***	-0.034***	0.041***	0.165***
	[-0.040, -0.030]	[-0.035, -0.026]	[-0.038, -0.030]	[0.036, 0.046]	[0.160, 0.171]
Gender	-0.043***	0.028***	0.182***	0.033***	0.035***
	[-0.048, -0.038]	[0.024, 0.032]	[0.176, 0.187]	[0.028, 0.038]	[0.030, 0.039]
GINI	0.015*	0.001	0.032***	-0.037***	-0.016**

	[0.002, 0.028]	[-0.009, 0.011	[0.017, 0.048]	[-0.053, -0.021]	[-0.028, -0.005]
Perc urban	0.024**	0.016**	-0.034***	0.023**	0.016**
	[0.011, 0.037]	[0.006, 0.026]	[-0.049, -0.019]	[0.007, 0.039]	[0.004, 0.027]
Median Income	0.001	-0.006	0.017*	-0.033***	-0.033***
	[-0.012, 0.015]	[-0.016, 0.004]	[0.001, 0.033]	[-0.050, -0.017]	[-0.045, -0.021]
GINI * Age	0.006	0.004	0.001	0.003	0.001
	[-0.000, 0.011]	[-0.001, 0.010]	[-0.004, 0.006]	[-0.003, 0.009]	[-0.006, 0.008]
Urban * Age	-0.006	0.006*	-0.005	-0.004	-0.008*
	[-0.012, 0.000]	[0.000, 0.012]	[-0.010, 0.001]	[-0.011, 0.002]	[-0.015, -0.001]
Income*age	0.015***	0.003	-0.002	-0.000	0.007
	[0.009, 0.021]	[-0.003, 0.009]	[-0.007, 0.003]	[-0.006, 0.006]	[0.000, 0.014]
-2 Log Likelihood	777812	778804	769772	777909	770702
BIC	778038	779030	769997	778135	770928

* p<0.05; ** p<0.01; ***p<0.001. Confidence intervals are presented in the row below each coefficient.

To further examine the significant interaction effect for openness, we performed a regions of significance analysis and a simple slopes analyses. This approach allows us to identify the age ranges at which the overall effect of the interaction results in a predicted effect that is significantly different from zero, and then estimate the effect size at representative ages. The grand mean model was used to attain an estimate of the ages at which the slope becomes significant. The slopes became significant when age was at least 0.096 SD below the mean, or at least 1.16 SD above it. This means that parasite stress has a significant negative relationship with openness for ages above 38.5, and a positive relationship for ages below 17.9. This is similar to the results of the simple correlational analyses as illustrated in figure 2.

To examine the predicted size of the effect at representative ages, we used a simple slopes analysis. We examined the effect at the age of 16, the lowest age permitted for inclusion in our dataset; at the age of 45, the lowest age boundary for the oldest age group in figure 2; and at the age of 65 as it is a common retirement age. The results show that at 16 there is a positive slope of 0.015 ($p = 0.027$) meaning that, at that age, a 1 SD increase in parasite stress results in an increase of 0.015 SD in openness. For

45, the effect is reversed: -0.019 ($p = 0.005$), and for 65, the effect is much larger: -0.042 ($p<0.001$).

The above analyses used the measure of overall parasite stress developed by Fincher and Thornhill (2012), which includes both zoonotic infections (those which are passed only by animals) and non-zoonotic infections (passed through human contact). However, Fincher and Thornhill also make available separate measures of non-zoonotic stress and zoonotic stress. If the effects we see from the aggregate measure are due to social adaptation in response to potential infection from other people, then the results should replicate for the measure of non-zoonotic stress but not for the zoonotic measure. Furthermore, to test for the effect with an independent measure, and to examine whether the results can be explained by sexual life history, analyses were also replicated using the mortality measure we developed from CDC data, and the mortality measure excluding STDs. The full results for these measures are provided in supplementary materials, but Table 3 provides a summary of the findings. This table shows the beta estimates and levels of statistical significance for the effect of parasite stress (as estimated by a model using grand mean centering) and for its interaction with age (as estimated by a model using within cluster centering).

The results show that the effect of openness and its interaction with age are robust, and a significant effect is found with all measures except for zoonotic stress (where no relationship is predicted). For other traits, no parasite stress measure shows a significant interaction with age. Extraversion is positively predicted by both mortality measures, and for zoonotic, but not non-zoonotic, parasite stress. This is curious, suggesting that the potential for human-to-human infection may not be the ultimate cause. Neuroticism shows a significant negative relationship with all parasite measures except for zoonotic and the mortality measure, though the relationship is present for the mortality measure that does not include STDs.

Table 3. Results from the final stage of the mixed modeling when performed using alternative measures of parasite stress. Full results for separate measures and confidence intervals are provided in supplementary materials.

		Aggregate	Non-Zoonotic	Zoonotic	Mortality Measure	Mortality NoSTD	State Correlations
Openness	Parasite	0.034**	0.034**	0.004	0.043***	0.030**	.22
	Parasite x Age	-0.011***	-0.010**	-0.004	-0.011***	-0.007**	

Extraversion	Parasite	0.020*	0.013	0.018*	0.024**	0.002	.59***
	Parasite x Age	-0.001	0.002	-0.004	-0.003	0.001	
Neuroticism	Parasite	-0.023*	-0.026**	-0.018	-0.012	-0.030**	-.16
	Parasite x Age	0.001	-0.001	0.004	0.003	0.004	
Agreeableness	Parasite	-0.015	-0.002	-0.004	-0.042**	-0.006	-.32*
	Parasite x Age	0.003	0.002	0.001	0.006	0.002	
Conscientiousness	Parasite	0.002	0.001	-0.000	-0.000	0.003	.38**
	Parasite x Age	0.005	0.005	0.002	0.005	0.003	

* p<0.05; ** p<0.01; ***p<0.001

The analyses reported above have all used, as the key predictor, levels of parasite stress in the US state where participants currently live. However, many participants also provided their “home” state. In order to gain some traction on the issue of the underlying cause of age interactions (i.e., whether parasite stress effects reflect early childhood environment or adaptive responses to current environment) we conducted additional analyses to examine the role of home state.

Within our sample, 78% of individuals completed the home state information and identified a US state. Of these, 26.5% had moved from their home state. Ideally, we would directly compare the predictive power of parasite stress or controls in the current state with that of the home state. However, the hierarchical nature of the data and analyses makes this difficult, as individuals are simultaneously members of two different clustering hierarchies. Hence we employ two complementary approaches which both support the same conclusions. In the first, we use the grand mean centered analysis outlined above, but also include home state control variables and parasite stress measures as predictors. This analysis confirms the association between openness and parasite stress, and an interaction with age is only found for the current state measure of parasite stress.

Table 4. Effects of parasite stress on personality traits comparing parasite stress in an individual’s current state and their home state.

	Openness	Extraversion	Neuroticism	Agreeable-ness	Conscientio-usness
Intercept	-0.009	0.004	0.011	0.001	0.013**

	[-0.023, 0.004]	[-0.006, 0.015]	[-0.005, 0.028]	[-0.014, 0.017]	[0.004, 0.022]
Current Parasite	-0.007	0.010	-0.013	-0.011	0.020***
	[-0.020, 0.006]	[-0.001, 0020]	[-0.028, 0.001]	[-0.025, 0.004]	[0.009, 0.030]
Homestate Parasite	0.009*	0.013**	-0.010*	0.005	-0.004
	[0.001, 0.017]	[0.005, 0.021]	[-0.018, -0.002]	[-0.003, 0.013]	[-0.012, 0.004]
Current Parasite * Age	-0.012**	0.001	-0.004	0.006	0.008*
	[-0.019, -0.004]	[-0.007, 0.008]	[-0.011, 0.003]	[-0.002, 0.014]	[0.000, 0.016]
Homestate Parasite * Age	0.000	-0.002	0.011**	-0.005	-0.008*
	[-0.007, 0.008]	[-0.010, 0.005]	[0.003, 0.018]	[-0.012, 0.003]	[-0.016, -0.001]
Age	-0.040***	-0.029***	-0.035***	0.042***	0.168***
	[-0.045, -0.035]	[-0.034, -0.025]	[-0.039, -0.031]	[0.036, 0.047]	[0.162, 0.173]
Gender	-0.046***	0.027***	0.186***	0.029***	0.035***
	[-0.052, -0.040]	[0.023, 0.032]	[-0.180, 0.193]	[0.025, 0.034]	[0.030, 0.039]
Current GINI	0.013	-0.005	0.032***	-0.018*	-0.009
	[-0.002, 0.028]	[-0.018, 0.007]	[0.015, 0.049]	[-0.035, -0.001]	[-0.021, 0.002]
Home GINI	0.007	0.008	0.008	-0.025***	-0.007
	[-0.002, 0.015]	[-0.000, 0.017]	[-0.000, 0.016]	[-0.033, -0.016]	[-0.015, 0.002]
Current Perc urban	0.018*	0.013*	-0.022*	0.023*	0.016**
	[0.002, 0.033]	[0.000, 0.026]	[-0.039, -0.005]	[0.005, 0.040]	[0.004, 0.029]
Home Perc urban	0.008	-0.000	-0.014**	0.001	-0.003
	[-0.001, 0.018]	[-0.010, 0.009]	[-0.023, -0.005]	[-0.008, 0.011]	[-0.012, 0.006]
Current Median Income	0.003	-0.006	0.018*	-0.025**	-0.020**
	[-0.013, 0.019]	[-0.019, 0.007]	[0.000, 0.036]	[-0.043, -0.007]	[-0.032, -0.008]
Home Median Income	-0.001	0.005	0.001	-0.007	-0.006
	[-0.010, 0.008]	[-0.004, 0.014]	[-0.008, 0.009]	[-0.016, 0.001]	[-0.014, 0.003]
Current GINI * Age	0.008	-0.001	0.001	-0.001	-0.001
	[-0.001, 0.016]	[-0.009, 0.007]	[-0.007, 0.009]	[-0.009, 0.008]	[-0.010, 0.008]
Home GINI * Age	-0.004	0.005	0.001	0.004	0.004
	[-0.012, 0.004]	[-0.003, 0.012]	[-0.007, 0.008]	[-0.004, 0.012]	[-0.004, 0.012]
Current Urban * Age	-0.005	0.007	-0.004	-0.004	-0.008

	[-0.013, 0.004]	[-0.002, 0.015]	[-0.013, 0.004]	[-0.013, 0.005]	[-0.018, 0.001]
Home Urban * Age	-0.003	-0.002	-0.003	0.003	0.002
	[-0.012, 0.006]	[-0.011, 0.007]	[-0.011, 0.006]	[-0.006, 0.011]	[-0.007, 0.011]
Current Income*age	0.016***	0.001	-0.004	0.000	0.005
	[0.008, 0.024]	[-0.008, 0.009]	[-0.012, 0.004]	[-0.008, 0.009]	[-0.004, 0.014]
Home Income*age	-0.003	0.001	0.004	-0.002	0.002
	[-0.012, 0.005]	[-0.007, 0.009]	[-0.004, 0.012]	[-0.010, 0.006]	[-0.006, 0.010]
-2 Log Likelihood	607136	608527	601389	606061	601297
BIC	607455	608846	601708	606380	601617

* p<0.05; ** p<0.01; ***p<0.001. Confidence intervals are presented in the row below each coefficient.

These analyses were again performed using all measures of parasite stress. The results (summarized in table 5, with full results in supplementary information) show that some of the effects change once the home state predictors are included. Openness is predicted by home state parasite stress, as is extraversion. The interaction between current state parasite stress and age remains for openness. The interaction between home state parasite stress and age predicts neuroticism for three of the parasite stress measures. Both home state and current state mortality-based parasite stress measures predict agreeableness, as do their interactions with age. However, these results are not robust across other parasite stress measures. Most striking are the effects of parasite stress on conscientiousness. When the home state predictors are included, all measures of current state parasite stress, except for zoonotic, predict conscientiousness. The interaction between home state parasite stress and age has a small negative effect upon conscientiousness for the aggregate, non-zoonotic and no-STD mortality measures.

Table 5. Results from the final stage of the mixed modeling when performed using alternative measures of parasite stress. Full results for separate measures, and confidence intervals are provided in the supplementary materials.

		Aggregate	Non-Zoonotic	Zoonotic	Mortality Measure	Mortality NoSTD

Openness	Current parasite	-0.009	-0.008	-0.008	0.003	0.001
	Home parasite	0.012***	0.015***	0.003	0.012**	0.012**
	Current x Age	-0.011**	-0.011**	-0.002	-0.010**	-0.008*
	Home x Age	-0.000	0.001	-0.002	-0.002	0.002
Extraversion	Current parasite	0.008	0.011	0.002	0.007	0.002
	Home parasite	0.015***	0.013***	0.004	0.014***	0.006
	Current x Age	-0.001	0.000	-0.003	0.000	0.001
	Home x Age	-0.000	0.002	-0.001	-0.003	0.000
Neuroticism	Current parasite	-0.016	-0.022**	-0.014	-0.006	-0.023**
	Home parasite	-0.006	-0.010**	0.004	0.004	0.005
	Current x Age	-0.003	-0.004	-0.002	-0.002	0.002
	Home x Age	0.009**	0.006	0.010**	0.009**	0.005
Agreeableness	Current parasite	-0.004	0.004	0.001	-0.018*	-0.004
	Home parasite	-0.004	-0.004	-0.010**	-0.009**	0.001
	Current x Age	0.005	0.004	0.004	0.014**	0.004
	Home x Age	-0.003	-0.001	-0.002	-0.008*	-0.004
Conscientiousness	Current parasite	0.021***	0.026***	0.011	0.013*	0.014**
	Home parasite	-0.005	-0.011	-0.005	0.000	-0.003
	Current x Age	0.007	0.007	-0.000	0.006	0.006
	Home x Age	-0.007*	-0.007*	0.004	-0.003	-0.008*

* $p<0.05$; ** $p<0.01$; ***$p<0.001$

The above results should be interpreted with caution, for two reasons. One is that there is no logical way of performing a state-centered analysis when there are two simultaneous ways of defining the individual’s state. The second is that the analysis is clustered by (i.e. random effects are estimated according to) the individual’s current state, which means the analysis did not account for the hierarchical structure of home state effects. We therefore undertook separate current state and home state analyses and compared the fits of the resulting models. The same relevant controls and predictors are used in both, but the values for all are defined in terms of either the individual's current state or their home state. These analyses only include individuals who provided both types of state information, meaning that the analyses are predicting the same outcomes, using the same number of predictors and the same number of free parameters. This allows for direct comparison of goodness of fit statistics. The results in table 6 show that the current state model provides a better fit (with lower error, as shown by the log likelihood) across all parasite stress measures and all personality dimensions except for agreeableness. This is true regardless of the centering approach taken. It is also true in analyses that include all controls for both current and home state. This excludes the possibility that a control could be predictive only for the current state. If this were the case, it would reduce the predictive power of the home state analysis for reasons unrelated to parasite stress measure (see supplementary information for full analysis results).

Table 6. -2Loglikelihood values for models predicting personality for current and home state analyses. Smaller numbers indicate less error in the model predictions.

			Aggregate	Non-Zoonotic	Zoonotic	Mortality Measure	Mortality NoSTD
Openness	Grand centered	Current state	607164	607168	607177	607163	607171
		Home state	607290	607300	607297	607285	607294
	State centered	Current state	607162	607165	607174	607158	607168
		Home state	607292	607301	607297	607285	607288
Extraversion	Grand centered	Current state	608557	608557	608571	608563	608571
		Home state	608580	608580	608594	608584	608592
	State centered	Current state	608557	608558	608571	608580	608572
		Home state	608581	608583	608595	608586	608594
Neuroticism	Grand centered	Current state	601414	601409	601420	601422	601414
		Home state	601551	601547	601563	601564	601558

	State centered	Current state	601413	601409	601419	601421	601413
		Home state	601550	601546	601561	601562	601558
Agreeableness	Grand centered	Current state	606115	606116	606115	606102	606116
		Home state	606099	606100	606099	606092	606100
	State centered	Current state	606116	606117	606116	606119	606117
		Home state	606099	606100	606099	606092	606100
Conscientiousness	Grand centered	Current state	601319	601320	601331	601327	601327
		Home state	601418	601420	601421	601415	601421
	State centered	Current state	601333	601333	601343	601337	601337
		Home state	601418	601421	601424	601416	601418

Discussion

This paper uses a large dataset to address several weaknesses of the sampling approaches and statistical analyses used in previous studies of the relationship between personality and parasite stress (Hackman & Hruschka, 2013; Hruschka et al., 2014; Hruschka & Hackman, 2014; Hruschka & Henrich, 2013; Thornhill & Fincher, 2013). A series of hierarchical statistical analyses were performed, each specialized to answer different questions and examine different effects. One finding, namely the interaction effect of age by parasite stress on openness, was consistent across all relevant analyses. However, findings for other measures of personality were far less consistent, meaning these tests, with this dataset, call such relationships into question.

Our initial state-level analyses found some results consistent with theoretical expectations and the findings of previous cross-national studies (a negative correlation between parasite stress and agreeableness and a positive correlation between parasite stress and conscientiousness) but others that were not consistent (a significant positive correlation with extraversion, and no correlation with openness). However, our series of multi-level analyses (which enabled us to include individual-level variables) found a robust effect only of openness. The negative effect of parasite stress on openness was larger for older adults, and indeed was reversed in sign for younger people. The fact that we found robust effects only on openness seems unlikely to reflect differential reliability of the five trait measures, as the reliability of the openness measure (at .53) was in fact the lowest of all five measure reliabilities. These results therefore confirm the importance of accounting for participant-level variables and suggest that some of the earlier claims concerning the relationship between parasite stress and personality may not be generalizable.

We interpret our results as reflecting an adaptive response to the threat of infection. Following earlier authors, we hypothesized that reduced openness will be associated with behaviors that are less curious and exploratory and more in line with prevailing cultural norms, and these behaviors in turn reflect the greater need to avoid infection when parasite stress is high. More specifically, we assume that there is a tradeoff between the positive and negative effects of behaviors associated with openness, and that the optimal point on this tradeoff shifts in the direction of less openness when the risk of infection is increased. Brown, Fincher and Walasek (2016) report a simple agent-based computational model of social group formation, and found that mutually-cooperating groups that formed in a social network had more local connections (with fewer long-distance cooperative relationships) when simulated infection risk was higher. It is therefore possible that less open behavior is a way of reducing contact with outgroups who may harbor infections to which immunity has not been developed, although we note that the idea that infection threat can be reduced by avoiding outgroup members has been challenged (e.g., Aarøe, Osmundsen, & Petersen, 2016; de Barra & Curtis, 2012).

We also note that the measure of openness used in the Facebook dataset here primarily measures imagination and abstract thinking rather than assessing novelty-seeking behavior directly, and indeed is often referred to as “intellect/imagination”. It is therefore rather indirectly linked to exploratory or novelty-seeking behavior. We make two observations in this context. First, as noted in the Introduction, openness is strongly linked to outgroup prejudice. More specifically, Ekehammar and Akrami, (2007), using a translated version of the Revised NEO Personality Inventory, found that generalized prejudice was correlated with five of the six facets of openness (Fantasy, Aesthetics, Feelings, Actions, and Values, but not Ideas). It is therefore possible that prejudice against outgroups is at least partly involved in the relationship between openness and infection avoidance, and it is also plausible that specific characteristics that might increase infection risk, such as novelty-seeking and openness to experience is associated with the construct of openness as assessed in the present data even though those facets were not assessed directly. Second, we took advanatge of the fact that when considering the entire Facebook sample 7765 participants completed the full 336-item IPIP proxy. On this sample of 7765 we correlated adventurousness and liberalism with overall openness, as these are the facets of openness that one might expect to be most highly associated with infection risk. We found correlations of .518 and .468 respectively, providing some reassurance that the IPIP measure of openness does reflect novelty-seeking. Note that this sample is from all individuals who complated the BIG5 measure. After restricting the sample to only those who could also be identified as living in a particular US state, and had no missing data in fields required for the analysis, only 1136 remained. Furthermore, a small number of states represented a disproportionately large number of these individuals and many states had very few individuals: 3 each from NH, ND & WY, 1 from SD, and 0 from DE. Because of the small size, and substantial skew of this sample, it was not possible to apply the full analysis to look at specific facets.

For the trait of openness, the interaction between parasite stress and age is strong and statistically significant in every relevant analysis in which it was expected. Why is the association between parasite stress and reduced openness only found in older individuals? In the introduction we noted two possible reasons for such a finding. One possibility is that the behavior of older people is more responsive to levels of parasite stress in their local environment due to age-related reductions in immune function; the other is that effects of infection risk on the development of personality have become smaller or disappeared as health advances have reduced the impact of infection during the 20th century. According to this second explanation older individuals, who were born into environments where infection was still a significant selection pressure, exhibit lower openness in response to parasite stress. Conversely, younger individuals, who were born into environments where the risk from infection was lower, do not show this pattern.

Our data do not enable us to distinguish between these two causal models with complete certainty, but some of our analyses favor the explanation in terms of greater sensitivity to parasite stress in older people due to reduced immune function. Specifically, we found that the parasite stress of an individual's current state of residence, rather than their home state, was the strongest predictor of their openness. This is suggestive of individuals responding adaptively to their present environment and their age.[2] Irrespective of the causal processes underlying our findings, it is clear that future research on the relation between individual differences and infectious diseases will need to take account of participant age as a factor.

We also found a positive relationship between parasite stress and openness in younger individuals. This was not predicted, and there was no *a priori* hypothesis regarding such a relationship. Ex-post, one possible explanation is that due to the relativity of personality judgements (Wood et al., 2012) young people living in high parasite states will be comparing themselves to older peers who are less open, making these young people perceive themselves as more open by comparison. An alternative possibility, suggested to us by a referee, is a desire (amongst people of child-bearing age) to increase the genetic diversity of their offspring when parasite stress is high: Hill, Prokosch and DelPriore (2015) found that women with a history of vulnerability to illness expressed a greater desire for variety in their sexual partners after being exposed to primes that indicated growing levels of disease threat. However, these are only two of a number of possible explanations and we believe the finding will require further investigation.

Another unexpected result was the positive correlation between parasite stress and extraversion. Prior research suggests there should be a negative relationship, or no relationship (Turner, Dhont, Hewstone, Prestwich, & Vonofakou, 2014). It is noteworthy that the effect greatly diminishes after statistical controls are added, and it is not found in all of the analyses, but its presence – such as it is – should certainly be noted. We do not believe existing theory or data shed light on this effect.

To conclude, we demonstrate that when using a large, real world sample of individuals from a single country, and using carefully designed and controlled statistical tests, many prior findings on the relationship between parasite stress and personality cannot be substantiated. However, we also show that when age effects are taken into account the effects of parasite stress on openness remain robust across a

[2] An alternative possibility is that individuals high in openness have failed to survive in areas of high parasite stress and hence are selectively absent from our sample. However, given the age profile of our participants and the relatively low levels of infection-related mortality in present-day USA, we regard this explanation as unlikely.

wide range of analyses. Thus, future investigations of the effect of parasite stress upon individual behavior should explicitly control for age.

Declaration of Conflicting Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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