THE DISGUSTED MIND:

INVESTIGATING THE EFFECTS OF

PARASITE STRESS ON SOCIAL

BEHAVIOUR AND BELIEFS

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Abstract

The parasite-stress theory of values and sociality offers a compelling evolutionary explanation as to why and how there is such wide variation and diversity of cultures and their underlying value and belief systems. Its authors propose that temporal and geographical variation in parasite stress in the ecological environment imposes causal effects on human behaviour by activating the behavioural immune system and motivating assortative sociality, i.e. philopatry, ethnocentrism, xenophobia, and religiosity. High parasite stress levels motivate strong assortative sociality thereby causing group isolation from which values and beliefs then arise and evolve independently and differently from outside groups, resulting in distinct cultural systems. There is an expanding body of correlational evidence to support this theory but critics argue that we should be cautious about attributing causal mechanisms. The main aim of this thesis was to provide some initial experimental tests of the parasite-stress theory. Four studies were conducted in this endeavour. The first study generated a new cross-culturally validated four-factor disgust image set to be employed in the subsequent studies as visual parasite stress. The next study tested whether variation in parasite stress could generate variation in the value given to physical attractiveness as a phenotypic indicator of genetic quality. The third study tested whether variation in parasite stress could lead individuals to diverge in their preferences for assortative versus prosocial rule systems in the formation of a hypothetical new society. Whereas, the final study tested whether variation in parasite stress could generate variation in the expression of assortative social behaviours. Results were mixed. The third study provided support for the parasite-stress theory, while the second and fourth studies did not. However, as these studies did support the evolutionary theory on which the parasite-stress theory is founded, the findings may be products of design issues. The parasite-stress theory is still valid and ripe for experimental investigation.

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Chapter 1: General Introduction

"I would imagine the most important damage from social behavior to be the spread of communicable disease."

George C. Williams (1966, p.133)

1.1 Introduction

While the number and diversity of cultures throughout history cannot be fully known, the numbers and diversity of contemporary cultures is readily apparent. Cultures are made up of their respective values, i.e. the norms, traditions, attitudes and beliefs of the members of their underlying social groups, the societies. A group's distinct culture is shared and acquired within the group, thus maintaining and facilitating culturally distinct behaviour from outside groups (Boyd & Richerson, 2004; Richerson & Boyd, 2005).

Throughout history, religion has arguably been one of the most important aspects of a group's culture and can be seen as a system of values and moral guidance which help preserve the moral purity of the society and of the individuals within it. Religion, and the religious thoughts and behaviours (i.e. religious concepts, beliefs, practices) that underpin all religion, is a uniquely human behaviour found in all human societies and groups (Boyer, 2003; Peoples, Duda, & Marlowe, 2016). In earlier human societies, and even in many of today's societies, each individual society typically adhered to one over-arching cultural belief system, i.e. the in-group religion, with little to no room for deviation or external influence. The relationship between a culture's values and its religious beliefs forms a self-contained positive feedback loop, in that cultural values affect a society's belief system and beliefs conversely affect a society's value system. They are intrinsically linked. It is estimated by some that there are or have been approximately 10,000 religions in the world and there is vast cultural dynamism among them (Barrett, Kurian, & Johnson, 2001; Lester, 2002; Norenzayan, 2013).

This highlights some important questions. For example: if an early-human group, sharing the same evolved cognitive 'machinery', lived within the same feedback loop of vertically and horizontally acquired and shared values and beliefs, then how did that group originally diverge to become two or more culturally distinct groups with distinctly different beliefs? Why are there so many culturally distinct groups today with

such wide variation between their corresponding values and religions? And why is there such wide within-group variation of these behaviours, including degree of belief and adherence, both temporally and geographically? Moreover, from where did the original values and beliefs derive initially? Traditionally, researchers from various disciplines, including political science, sociology and psychology, have focused on wealth and economic development as the fundamental cause and effect of these cultural variations (see Thornhill & Fincher, 2014b for a review), but these do not take into account the evolutionary pressures imposed on individuals, and thus on their societies and cultures. More recently, however, an evolutionary perspective appears to offer alternative insights.

Evidence suggest that the values and beliefs of individuals and societies are products of evolutionary processes, which means that cultures are also affected by these processes. Thornhill and Fincher (2014b) have put forward one of the most compelling and comprehensive theories to explain the putative effects that the evolutionary processes of host-parasite interactions have on the origins, ontogeny, variance, and evolution in and of human values and beliefs, and the effects these have on social behaviour and culture. They propose through the parasite-stress theory of human values and sociality that parasite stress in the ecological environment imposes causal effects on the ontogeny of individuals, therefore on the origins, ontogeny and trajectory of their values and beliefs, and subsequently of their group's overarching culture. They argue that this may explain the diversification and wide variation of cultures. The main theme of this thesis comprises experimentally investigating various aspects of their theory to ascertain the validity of this claim.

1.2 The Parasite-stress Theory of Human Values and Sociality

Over the past decade, evolutionary researchers Corey Fincher and Randy Thornhill (alphabetically listed unless otherwise cited) have proposed through a growing body of work, a new theory entitled: The Parasite-stress Theory of Human Values and Sociality, to explain a range of social behaviours, including value and belief systems and the subsequent global diversification and variance of cultures. This theory, henceforth referred to as the parasite-stress theory, is founded on our understanding of the evolution and ecology of the host-parasite interaction and its effects on human morbidity and mortality (Fincher & Thornhill, 2008a; 2008b; 2012; Fincher, Thornhill, Murray, & Schaller, 2008; Thornhill & Fincher, 2014a). This section provides an overview of the theory. I will lay out its foundations, as well as

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several underlying hypotheses, and then present evidence for and arguments against the theory, which helped to form the purpose and aims of the following research.

1.2.1 The Evolution of Disgust and the Behavioural Immune System

Animals, including humans, have long lived and evolved in proximity to parasitic infectious microorganisms such as bacteria, viruses, and helminths (Schaller, 2011). Proximity to these parasites (henceforth interchangeable with pathogens and infectious diseases) has imposed considerable selection pressures throughout evolutionary history. This has resulted in an ongoing coevolutionary arms race between host and parasite, whereby parasitic organisms evolve adaptive mechanisms and strategies to increase their chances of survival and transmission, and hosts evolve counter-adaptive mechanisms and strategies which help combat against parasitic infection in order to survive and successfully reproduce (Del Giudice, 2019; Thornhill & Fincher, 2014a; Tooby, 1982; Van Valen, 1973). In humans (and other animals, see Hart, 1990; Oaten, Stevenson, & Case, 2009), this interaction has resulted in the selection of two main adaptive lines of defence – the classical immune system and the behavioural immune system (BIS: Schaller, 2006; Schaller & Duncan, 2007). The classical immune system fights infection physiologically at the biochemical, cellular, and tissue level after infectious agents enter the body; however, the BIS acts as the first line of defence against infection by coordinating behaviour to help prevent potential threats of infection from coming into contact with the body (Lieberman & Patrick, 2014; Schaller, 2006; Schaller & Park, 2011).

The BIS consists of a suite of ancestrally evolved psychological mechanisms which collaborate to process and infer the risks of pathogens and related infection through perceptual cues, then function to activate aversive emotional and cognitive responses, which in turn function to motivate avoidance behaviours to neutralise the perceived pathogen threat (Schaller, 2006; Schaller, 2011). For example, humans and animals have evolved a range of counter-adaptations – behaviours pertaining to infection-avoidance which function to reduce these risks (see Hart, 1990 for review). In humans, a – if not the (see Lieberman & Patrick, 2014) – primary component of the BIS is the disgust emotion, which is experienced as a revulsive sensation accompanied by a feeling of strong and immediate desire to withdraw from the perceived or inferred infectious stimulus (Oaten et al., 2009; Rozin, Haidt, & McCauley, 2000). In other words, disgust functions to distance the self from sources that connote potential threat of contamination.

Other species exhibit similar pathogen detection and avoidance behaviour, i.e. avoiding/removing parasites or pathogens, or avoiding potentially infected conspecifics, contaminants or contaminated areas (Curtis, 2014; Sarabian, Ngoubangoye, & MacIntosh, 2017). In social lobsters (*Panulirus argus*), conspecifics who are virally infected are avoided in denning (Behringer, Butler, & Shields, 2006); in mandrills (*Mandrillus sphinx*), group members who are heavily parasitized are groomed less often than other members (Poirotte et al., 2017); birds remove ectoparasites by preening (Clayton, Koop, Harbison, Moyer, & Bush, 2010); and grazing ungulates engage in selective foraging and selective defecation to avoid parasites (Ezenwa, 2004). Sarabian et al. (2017) found that when food was exposed to biological contaminants such as faeces, blood, and semen, chimpanzees (*Pan troglodytes troglodytes*) delayed eating, distanced themselves from the contaminants, and/or refused to eat. These are but a few examples.

In addition to characteristic cognitions and avoidance behaviours, disgust is characterised by specific physiological changes (see Olatunji, Haidt, McKay, & David, 2008) and a characteristic facial expression (see Ekman, Friesen, & Hager, 2002) found to be universal among humans (Ekman & Friesen, 1975). Disgust is thought to develop in early childhood, approximately age 4-7, during the ontogenetic development of children's ability to understand and detect threats of illness, pathogens and contagion (Boyer & Bergstrom, 2011), reason about their causes (Legare, Wellman, & Gelman, 2009), and recognise the characteristic facial expression of disgust (e.g. Hertenstein & Campos, 2004; but see Rottman, 2014).

Disgust can be triggered by a range of objects, events, and people (Curtis & Biran, 2001; Curtis, Aunger, & Rabie, 2004). Although, there is individual variation in the degree to which people perceive and react to potential sources of infection. The degree of BIS strength is typically measured in terms of disgust sensitivity (e.g. Haidt, McCauley, & Rozin, 1994; Tybur, Lieberman, & Griskevicius, 2009) and perceived vulnerability to disease (Duncan, Schaller, & Park, 2009). Some individual differences are, of course, due to issues involving atypical brain function caused by, for example, issues with disgust-relevant neural structures (e.g. insular cortex, Wicker et al., 2003), brain injury (Calder, Keane, Manes, Antoun, & Young, 2000), genetic diseases (e.g. Huntington's disease, Mitchell, Heims, Neville, & Rickards, 2005; Sprengelmeyer et al., 1996), and other disorders such as depression (Surguladze et al., 2010) and obsessive-compulsive disorder (Shapira et al., 2003; Sprengelmeyer et al., 1997).

However, this thesis concentrates on differences in typically functioning brains– that is, on the variation produced in the BIS response of humans in general by differences in, for example, ontogenetic experience. Evidence suggests that the triggering of the BIS is strongly associated with a wide array of individual, social and cultural behaviours, which will be discussed throughout this thesis.

1.2.2 Host-Parasite Localisation and Interaction

Hosts and parasites coevolve in perpetual antagonistic races in adaptation, counter-adaptation, and counter-counter adaptation, and so on (Thornhill & Fincher, 2014a; Red Queen's race: Van Valen, 1973). However, these perpetual host-parasite races are geographically localised throughout the range of a host species, creating what Thornhill and Fincher (2014, p.258) describe as "a coevolutionary mosaic of genetic and phenotypic differences in host immune adaptation and corresponding parasite counter-adaptation" (also see Thompson, 2005). The result of this localisation is that host defence is adapted to and thus more effective against local parasite species, strains, or genotypes, and less effective against non-local (i.e. novel) forms that co-evolved with host-groups from locations outside the local area (Fincher & Thornhill, 2012; see Thornhill & Fincher, 2014b for a more detailed treatment of the evidence for geographically localized host–parasite coevolution).

Considering this notion of geographical localisation, and the fact that a major potential source of infection for humans is of course other humans, it is expected that the risk of morbidity and mortality from infection would be more severe from out-group individuals (Fincher & Thornhill, 2008a; 2008b). Whereas members of the local group share immunological adaptedness to the local pathogens, individuals from outside the local group pose the risk of carrying novel pathogens to which the locals are not adapted. Moreover, members of the in-group are also more likely to know and adhere to the in-group's developed norms, many of which are, in part, designed to reduce or prevent infection and transmission of local parasites. These norms may include localised, group-specific customs, practices and even laws regarding, for example, food preparation and hygiene-related behaviour (Fincher et al., 2008). In contrast, out-group individuals have their own group-specific norms designed to mitigate the risks of parasites of their own region(s). Out-group individuals are thus likely to be perceived to deviate from the norms of the local group (Terrizzi, Shook, & McDaniel, 2013) and are also more likely to violate local norms about which they may

lack sufficient knowledge or be unaware (Schaller & Murray, 2008; Schaller & Neuberg, 2008).

Based on this understanding, Fincher and Thornhill propose that the threat of infectious diseases throughout evolutionary history has resulted in the evolution of the BIS which helps defend from infection by reducing the risk of coming into contact with novel parasites carried by out-group individuals. They argue that, in addition to other cognitions and behaviours (e.g. sensory processing, the disgust emotion, etc.), the BIS incorporates a system of values and beliefs expressed through "in-group assortative sociality" (Thornhill & Fincher, 2014b, p.237). The theory holds that in-group assortative sociality is evolutionarily 'designed' to bias individuals toward in-group members with shared immunological adaptedness and to discriminate and avoid out-group individuals because of their potential to carry novel parasites. Moreover, there is environmental and geographical variance in parasite stress, both of which can vary temporally. They therefore suggest that degrees of assortative sociality, and associated values and beliefs, fall along a continuum - dependent on and covarying with levels of pathogen stress. In other words, groups living in environments with high pathogen stress will tend to exhibit a stronger degree of assortative sociality on one end of the continuum (i.e. conservative, traditional, collectivistic, etc.) compared with those living in environments of low pathogen stress (i.e. liberal, progressive, individualistic, etc.). This is thought to be because of the trade-off between the benefits and costs associated with them.

1.2.3 Assortative sociality

Assortative sociality refers to the "preferential association between similar individuals who comprise an in-group versus an out-group or dissimilar others" (Thornhill & Fincher, 2014b, p.237). More precisely, it can be described as the alliance with, or preference for, similar individuals in social contact; and these social behaviours can serve for purposes of mating, reciprocity, religious service, various forms of cooperation, and more (Fincher & Thornhill, 2008a). For example, assortative mating (homogamy) is a pattern which can be observed across taxa as a form of sexual selection, whereby individuals with similar phenotypes and genotypes mate together more frequently than a random mating pattern would predict. Similarly, assortative mixing (homophily) is the sociological principle whereby contact between individuals occurs at a higher rate for similar rather than dissimilar people (McPherson, Smith-Lovin, & Cook, 2001). While, endogamy is the practice of allowing marriage only to

individuals within the same ethnic, religious, class, or social group. Indeed, the underpinnings of societies throughout human history include many forms of assortative behaviours, such as racism, classism, tribalism, and nationalism. Religions form arguably one of the most assortative grouping behaviours in the history of human civilisation. Religious groups are assortative by nature and by design, delineated by lines of supernatural beliefs drawn in the sands of real human behaviour.

The underlying theme of these examples of assortative social behaviour is that they promote assortative interactions through selective contact (or contact bias) with specific individuals or groups, which motivate (whether intentional or by default) reduced interaction or out-right avoidance of others, thus delimiting a boundary between in-group and out-group(s) (Fincher & Thornhill, 2008a). These assortative preferences are directly related to features of the BIS. Indeed, the three general social components of in-group assortative sociality (philopatry, ethnocentrism, and xenophobia) likely evolved to help negotiate threats of infectious disease – resulting in what Fincher and Thornhill term as a 'parasite-driven wedge' between in-groups and out-groups (e.g. Fincher & Thornhill, 2008a; 2008b; 2012). These components are defined as:

- *Philopatry* – is, in zoological terms, the tendency for an organism to remain in or habitually return to its birthplace (also known as site fidelity or limited dispersal). It is a strong isolation mechanism which can lead to genetic isolation, divergence and, ultimately, speciation (Stearns, Tilmon, & Wood, 2013). In human social behaviour it is the absence of, or limited, dispersal from one's natal locale, which results in an increase in social interactions among local, similarly immunologically-adapted individuals and a decrease of social interactions and contact with distant individuals of dissimilar immunology and novel parasites.

- *Ethnocentrism* – is in-group favouritism or bias through behaviours such as nepotism and altruism toward family and friends, as well as toward ideologically and immunologically similar members of the in-group (see Raden, 2003 for types of ethnocentrism). Ethnocentric behaviour can help defend against the effects of parasites, such as morbidity and mortality, by creating a reliable, embedded network of in-group members who can provide or reciprocate sources of aid and care in times of infection or debilitating illness.

- *Xenophobia* – is the avoidance of, and even dislike of, out-group individuals. It is expressed through the discouragement of contact or interaction with members of out-groups, and thus the novel parasites they are likely to carry. Therefore, it acts as a disease-avoidance mechanism to avoid contact with distant or unknown populations. Further, *neophobia* – a functional component of xenophobia – motivates the dislike and avoidance of new values, ideas and ways. Perhaps not coincidentally, these are only likely to be introduced by contact with out-groups.

Assortative sociality is therefore an aspect of the BIS, forming a foundational multi-faceted value dimension which functions through associated cognitions and behaviours to motivate intra-group embeddedness, cohesion and protectionism and the avoidance of out-groups as they may contain novel, non-localised parasites to which the (localised) in-group is not immunologically adapted (e.g. Faulkner, Schaller, Park, & Duncan, 2004; Fincher & Thornhill, 2008a; 2008b; 2012; Fincher et al., 2008; Navarrete & Fessler, 2006; Thornhill & Fincher, 2014a).

The proximate mechanisms involved in the assessment by individuals of local parasite stress in the ecological environment are not fully understood. However, it is likely that there are several mechanisms, whether acting singly or in concert, which activate the classical immune system and evoke ontogenetic and contingent expression of the corresponding degree of assortative sociality (Fincher & Thornhill, 2012). These include, for example, frequency of infection, social learning of local diseases and disease risks, and direct observation of pathogen threat (Fincher & Thornhill, 2012; Stevenson, Case, & Oaten, 2009). Fincher and Thornhill propose that the combination of these mechanisms may explain inter-individual and within-individual variation in the values associated with in-group/out-group preferences that underpin assortative sociality. In other words, repeated activation of the classical immune system ontogenetically and conditionally dictates the degree to which values associated with assortative sociality are adopted (Fincher & Thornhill, 2012).

Fincher and Thornhill contend in their theory that parasite stress affects "every aspect of human values and social behavior" (Gurven, 2015). They argue that activation of the BIS motivates in-group assortative sociality in individuals and that these values and associated behaviours encourage more socially and culturally conservative values and beliefs in regions and/or times of high parasite prevalence. In turn, these will lead to group isolation in which the associated norms, traditions,

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customs, and attitudes of groups arise and evolve differently and independently of each other (e.g. directions, times, rates, due to temporal and geographical differences in environmental pressures). This suggests the possibility that geographical and environmental differences in pathogen prevalence may be responsible for the origins and maintenance of the divergence and differences between groups – that is, of cultural diversity and variance (Boyd & Richerson, 2004; Thornhill & Fincher, 2014b).

1.3 Cultural emergence, divergence, and variation

"Culture is a set of guidelines (both explicit and implicit) which individuals inherit as members of a particular society, and which tells them how to view the world, how to experience it emotionally, and how to behave in relation to other people, to supernatural forces or gods, and to the natural environment." (Helman, 2007, p.2)

Culture constitutes a variety of elements, including sets of values, beliefs, practices, attitudes, ideas, skills, artefacts, and inventions that characterise and distinguish groups of people, and there is wide cultural variation along these aspects around the globe and throughout history. For example, some cultures are to varying degrees more conservative, traditional, religious, collectivistic, and autocratic, rendering them more oppressive, restrictive and closed off to the acceptance and influence of new or outside values, ideas and ways. Other cultures are to varying degrees more liberal, progressive, secular, individualistic and democratic, rendering them more permissive and open to the acceptance and influence of new or outside values, ideas and ways. These aspects are associated with a plethora of other cultural elements.

Cultural elements are thought to emerge via two pathways: transmission and evocation (Gangestad, Haselton, & Buss, 2006). Some cultural elements, for example – cumulative knowledge of skills and technology, are considered to be socially acquired and transmitted vertically and horizontally through multiple forms of social learning, such as teaching and imitation (Boyd & Richerson, 2004; Caldwell & Millen, 2008; Richerson & Boyd, 2005). However, Tooby and Cosmides (1992) argue in their *evoked culture* hypothesis that some cultural elements are products of social and ecological evocation. That is, some cultural elements are expressions of behavioural repertoires produced by domain-specific psychological adaptations in response to environmental inputs – they are environmentally contingent (Gangestad et al., 2006). But as environments are not static, therefore, neither are the expressions of the relative behaviours produced in individuals by the corresponding psychological adaptations.

Moreover, individuals vary in their genotype and phenotype, and in their ontogenetic experiences, and therefore in the ability, need, and degree to which they respond to environmental input.

In this view, humans are considered cultural strategists, whereby ancestrally evolved psychological adaptations drive the learning, adoption, retaining/discarding and modifying/not modifying of cultural items that maximise reproductive fitness of the individual (Thornhill & Fincher, 2014b). The evocation pathway is a cornerstone of the parasite-stress theory, particularly regarding values, which include mating, ethical, moral, political, religious, social and aesthetic values which form an individual's sense of, or beliefs about, what is 'good' or 'bad' (e.g. what constitutes as being right or wrong, moral or immoral, beautiful or not, etc.) and which are broadly shared by the members of the society. Values, and the degree to which people and societies believe in and adhere to them, vary widely. It is therefore argued that cultural variation regarding these aspects (and others) is due to proximate causes such as variation in genetic make-up, environment, and ecology (Cohen, 2001; Gangestad et al., 2006; Nettle, 2009; Richerson & Boyd, 2005; Thornhill & Fincher, 2014b).

The parasite-stress theory encompasses each of these, in that it holds that variation in parasite stress across geographical locales is one of the main causes of wide inter-culture variation via genotypic differences in the population and the way individuals subsequently behave and interact in response to the stress and its overarching impositions. For example, there is wide variation in levels of parasite stress geographically (e.g. latitudinal differences), which also varies over time due to environmental changes (e.g. temperature, rainfall); there is individual variation in immune-related genotypic expression, such as in the major histocompatibility complex (MHC, known as human leukocyte antigen, HLA, in humans), and in the corresponding physiological responses to parasite stress; and there is individual variation in BIS strength and in the corresponding behavioural responses to parasite stress. Evidence suggests that these collaboratively (to various degrees) account for individual differences in an array of overlapping personality traits and values that impose effects on social behaviours and beliefs thus producing cross-cultural differences.

To illustrate, individuals, of course, make up a society and its overarching culture. But individuals differ on a number of various personality traits, such as on the Big Five traits of agreeableness, conscientiousness, extraversion, neuroticism, and

openness to experience, as well as on sociosexuality. However, the expression of some traits is not distributed equally across geographic regions of the world (Schmitt, 2005; Schmitt, Allik, Mccrae, Benet-Martinez, & et al., 2007). Variability in some of these differences appears to be geographically clustered, resulting in regional differences expressed in cross-culturally specific variations along some of these traits. For example, Schaller and Murray (2008) found that the level of infectious disease prevalence across geopolitical regions was predictive of negative correlations between unrestricted sociosexuality, extraversion, and openness to experience. It is argued that this is due to a form of cost/benefit analysis. Engaging in these behaviours is potentially costly in that they place an individual at higher risk of contracting infectious diseases; therefore, in regions of higher pathogen prevalence it benefits individuals to be more restricted and cautious in their behaviours, and thus express more conservative personality traits. Conversely, in places of low pathogen prevalence individuals can benefit in a number of ways by being less restricted sociosexually, more extraverted, and more open to new experiences. A recent study (Mullett, Brown, Fincher, Kosinski, & Stillwell, 2019) found similar results regarding the relationship between parasite site stress (regional infectious disease rates) and openness to new experiences in the U.S. Individuals living in regions with higher infectious disease rates showed lower scores in openness to new experiences. However, this relationship was significant in older individuals but not younger.

The relationship between parasites and personality traits is found in non-human animals as well. As in humans, there is heritable variation in animal personality traits (e.g. boldness, exploration, activity, sociability, aggressiveness) which are associated with variation in behaviours, and this variation in behaviour generates differential levels of exposure for individuals to parasites (Barber & Dingemanse, 2010). Moreover, the relationship is bi-directional. Different parasites motivate different responses in different hosts along the various personality traits in ways that aim to facilitate the parasites' life cycle (see Table 1 in Barber & Dingemanse, 2010 for a list of studies that demonstrate this relationship).

In addition to personality traits, evidence suggests that variation in pathogen prevalence is predictive of cross-cultural differences for humans in mating strategies (Low, 1990), parenting strategies (Quinlan, 2007), food preparation techniques (Sherman & Billing, 1999), and religiosity (Fincher & Thornhill, 2008a), as well as differences in political ideology (Aarøe, Petersen, & Arceneaux, 2017; Tybur et al.,

2016) and governmental systems (Thornhill, Fincher, & Aran, 2009). These findings suggest that differences in pathogen prevalence do explain the relative inter-cultural variance. However, it would also account for intra-cultural variance, in that in-group individuals with a stronger BIS response will tend to lean toward more conservative values and beliefs, whereas, the converse would hold for in-group individuals with a weaker BIS response. In-group variation in BIS strength/weakness, whether resulting from genetic differences or differences in ontogenetic experience, may also then explain how a group can polarise and diverge into separate groups, whereby differing values and beliefs can emerge and evolve separately in accordance with their individual sub-group responses to their shared local ecological environment.

Thornhill and Fincher (2014b) treat the effects that parasite stress putatively has on a wider range of behaviours and in much more detail than this thesis which focuses specifically on testing the effects of parasite stress on the values and beliefs that underpin and are inextricably linked to particular social behaviours of interest. The following subsections will treat the relevant hypotheses and evidence that underpin Fincher and Thornhill's parasite-stress theory and which are the focus of this thesis. They will centre specifically on the core components of assortative sociality: mating, philopatry, ethnocentrism, xenophobia, and religiosity; but also on the effects these would potentially subsequently impose on moral and ethical behaviour, judicial and political behaviour, and governmental systems. These behaviours, and their underlying values and associated beliefs, are specifically relevant as they individually and jointly illustrate how culture may be evoked, diverge and vary via contingent responses to variance in parasite stress in the ecological environment.

1.3.1 Mating Psychology: preferences, practices, and systems

The value placed on the qualities of potential mates, i.e. beliefs about what is considered attractive in potential mates, is expressed through mate preferences, practices, and mating systems (e.g. Gangestad & Scheyd, 2005; Little, Jones, & DeBruine, 2011; Roberts et al., 2011; Scheyd, Garver-Apgar, & Gangestad, 2008; Thornhill & Gangestad, 1993). But these vary across cultures (DeBruine, Jones, Crawford, Welling, & Little, 2010; Gangestad & Buss, 1993; Gangestad et al., 2006; Low, 1990; Marlowe, 2003; Schaller & Murray, 2008). The parasite-stress model suggests that this variation is likely due to differences in pathogen prevalence of the corresponding ecologies – it is a result of environmentally contingent responses to the local ecology. The notion that parasite prevalence may predict various aspects of

cultural variability related to mating is founded on the parasite-stress theory of sexual selection, which includes the indicator traits hypothesis and several other related hypotheses: the Hamilton-Zuk hypothesis (1982), the Zahavi handicap principle (Zahavi, 1975), the immunocompetence handicap hypothesis (Folstad & Karter, 1992), and the good genes hypothesis. To briefly summarise, these add up to the overarching proposal that female mate choice is influenced by the trade-offs in costs and benefits provided by potential partners, particularly related to current health (e.g. parasite load) and indicators of genetic quality that signal strong parasite resistance (Gangestad & Simpson, 2000). Mate choice should therefore be strongly affected by parasite stress.

Considering this foundation, it is expected that mating values and associated beliefs and behaviours (e.g. preferences for attractiveness, monogamy, parental investment) will differ in areas and environments of high pathogen stress compared to those of low pathogen stress. Indeed, mate preferences should be evolutionarily designed to discriminate between potential mates based on cues of health because mate choosers are less likely to become infected by healthy mates, healthy mates are more likely to be capable of investment in offspring, and their offspring will likely incur enhanced viability and heritable fitness (Gangestad & Simpson, 2000; Gangestad et al., 2006; Hamilton & Zuk, 1982; Trivers, 1972). Three main indicators of health and genetic quality in males are sexually dimorphic, average, and symmetrical physical characteristics, for example, facial masculinity, facial averageness, and facial symmetry (Gangestad & Scheyd, 2005; Scheyd et al., 2008; Thornhill & Gangestad, 1993). These features offer some indication of the level of developmental stability of an individual's morphology against the environmental pressures as well as genetic diversity related to parasite resistance, i.e. MHC genes (Gangestad & Thornhill, 1997; Little et al., 2011; Thornhill & Gangestad, 1993; Thornhill & Gangestad, 1994). It is thought that these characteristics, as well as olfactory characteristics of body odour, are related to genotypic expression of MHC-heterozygosity which may be indicative of immune-specific genetic diversity and quality, and thus potential benefits, regarding parasite resistance in potential progeny (see Havlíček & Roberts, 2009; Thornhill & Gangestad, 1993 for review). Given this background, there may be a relationship between geographical variance in parasite prevalence and mate preferences for MHC-heterozygosity.

There is a considerable amount of evidence to suggest that geographical variation in parasite prevalence may account for cultural variation in health-related mating

psychology. For example, Gangestad and Buss (1993) analysed the cross-cultural data (29 out of the 37 countries: 7,139 individuals) from Buss (1989) and found a positive correlation between parasite prevalence and the importance of physical attractiveness in mates at a cultural level. Similar to this, DeBruine et al. (2010) analysed data from 30 countries and found that women's preferences for facial masculinity in males increased as the health index of the countries decreased. The relationship held even after controlling for differences in wealth or women's mating strategies across the cultures. But also, as mentioned in section 1.3, mating attitude and behaviour measured in sociosexuality has been found to be negatively correlated to pathogen prevalence across geopolitical regions (Schaller & Murray, 2008). People, particularly women, express more conservative sociosexuality in regions of higher pathogen prevalence.

Additionally, by analysing the data from 186 indigenous societies in the Standard Cross-Cultural Sample (SCCS: Murdock & White, 1969), Low (1990) found that groups living in ecological environments with higher pathogen prevalence expressed higher levels of polygyny. She reasoned in her parasite-stress hypothesis of human polygyny that the investment capabilities of a portion of the men in the population may be compromised by parasites, and the corresponding reduction in viable mates makes being the second mate of a man who will/can invest more desirable than being the only mate of an attractive available man who will/can not invest (Gangestad et al., 2006). In further support of Low, Marlowe (2003) analysed only the data for the foragers or hunter-gatherer sub-groups from the SCCS and found similar findings.

Thornhill and Fincher (2014b) have proposed a further related connection between polygyny and parasite-driven conservative values and behaviour. They hypothesise that parasite adversity evokes collectivism, i.e. a collectivist value system, which then imposes proximate causation on polygyny. They predict that across the societies within the SCCS, the degree of collectivism and the degree of polygyny will positively correlate. There is some support for this hypothesis. For example, studies have revealed a connection between various measures of collectivist and conservative values and approval of polygynous sexual relationships (see Thornhill & Fincher, 2014b for a brief review).

Examples such as these provide clear evidence of the relationship between pathogen stress and the corresponding adaptive responses produced and expressed in mating psychology, as well as how this relates to other conservative values and behaviour. But more specific to this thesis, the evidence provides support for the

argument that pathogen stress likely imposes causal effects on cultural variability in mate values. An aspect of this argument, particularly as it relates to parasite-driven preferences for MHC-heterozygosity, will be experimentally tested in Chapter 3.

1.3.2 Philopatry, Ethnocentrism, and Xenophobia

As noted in section 1.2.3, philopatry, ethnocentrism, and xenophobia make up the three general components of in-group assortative sociality, which itself is considered to be the expressed dimensional values of the BIS. Again, the parasite-stress theory maintains that cultural differences in assortative behaviours are likely due to differences in pathogen prevalence of the corresponding ecologies. That is, in regions of high pathogen prevalence natural selection has favoured the cultural adoption of these more conservative and collectivistic behaviours, causing individuals and their corresponding cultures to express the associated value dimensions more strongly than individuals and corresponding cultures in regions of lower pathogen prevalence (Fincher et al., 2008; Fincher & Thornhill, 2008a; Fincher & Thornhill, 2012; Thornhill & Fincher, 2014b)[1]. The argument is that the costs to inclusive fitness associated with high parasite stress will evoke collectivistic values as a defence against infectious disease; whereas, individualistic values will offer more benefits to fitness when parasite stress is low or negligible. Again, there is a considerable body of correlational evidence to support this aspect of the theory.

Fincher et al. (2008), for example, analysed epidemiological data alongside worldwide cross-national survey findings, particularly regarding the cultural unidimensional value of individualism/collectivism. They indexed this unidimensional value with measures of 'in-group collectivism practices' and found that these cultural indicators of collectivism shared a strong positive correlation with regional pathogen prevalence while indicators of individualism shared a strong negative correlation. Their findings suggest that collectivism is strongly related to pathogen stress and the associated epidemiological pressures.

In a similar vein, Morand & Walther (2018) tested the hypothesis that collectivistic countries should then have fewer infectious disease outbreaks than individualistic countries by analysing the historical pathogen burden, recent number of infectious disease outbreaks and zoonotic disease outbreaks, and emerging infectious

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[1] It is important to note that there is a plethora of evidence to show that collectivism is strongly correlated with conservatism and individualism is strongly correlated with liberalism – suggesting that "high collectivism is high conservatism and high individualism is high liberalism" (see Thornhill & Fincher, 2014b, p.85 for review).

disease events for 66 countries. They found a negative correlation between countries expressing individualistic values and historical pathogen burden and a positive correlation between countries expressing collectivistic values and the number of infectious disease outbreaks and zoonotic disease outbreaks. Although no correlation was found for emerging infectious disease events, the findings interestingly suggest that individualistic societies may incur a cost of being more susceptible to disease outbreaks.

Behavioural manifestations of collectivism include, for example, high value in in-group traditions and conformity (and less tolerance for norm deviation), high in-group embeddedness, greater distinction between in- versus out-group, limited dispersal, and strong family ties and embeddedness, among many others; whereas the converse of these are manifestations of individualism (see Table 4.1 in Thornhill & Fincher, 2014b for list of examples and relevant research). These collectivistic behavioural manifestations comprise the in-group assortative social behaviours of philopatry, ethnocentrism, and xenophobia, values and behaviours of which show a strong correlation with regional pathogen prevalence. Values and behaviours associated with religiosity are also included, such as high religious participation, commitment, devotion and dogmatism; however, these will be discussed in subsection 1.3.3 and Chapter 5.

Cashdan & Steele (2013) also found some support for the relationship between collectivistic cultural values and pathogen prevalence. They analysed the ethnographic data of the 186 societies in the SCCS using two indices of pathogen prevalence (eight coded pathogens specific to local conditions) and coded value measures of collectivism and individualism, including intergroup mobility (adult dispersal), intergroup contact, and group bias (in-group loyalty and xenophobia). They found that in cultures in high pathogen regions children were more likely to be inculcated toward collectivist values of obedience rather than individualistic values of self-reliance. They also found a significant negative correlation between high pathogen prevalence and adult dispersal. That is, philopatric behaviour was positively associated with pathogen prevalence. The relationship held even after controlling for latitude and population density, although they found no relationship between their measures of intergroup contact or group bias.

Other support for the hypothesised relationship between pathogen stress and dispersal behaviour is evidenced by Fincher and Thornhill (2008a). They analysed data from previous studies regarding range size and mobility and pathogen prevalence in

traditional societies. Their findings show a negative correlation between societal range size in traditional societies and pathogen prevalence, suggesting a significant reduction in range size in areas with higher pathogen prevalence. They also analysed the data considering two types of mobility patterns: number of moves annually and distance of moves annually. The former positively correlated with pathogen prevalence while the latter correlated negatively. This suggests that in regions of high pathogen prevalence people in traditional societies move more often but disperse over shorter distances; whereas, the converse holds in regions of lower pathogen prevalence. Similarly, Fincher and Thornhill (2012) also found a correlation between strong family ties and parasite stress across nations as well as states within the USA, which particularly relates to the findings regarding dispersal behaviour, as philopatry is associated with an increase in family associations and embeddedness (see Alesina & Giuliano, 2010; also observed in animals: Clutton-Brock & Lukas, 2012; Lee, Lee, & Hatchwell, 2010; Loehle, 1995).

Other studies have provided evidence for the parasite-stress theory regarding ethnocentrism and xenophobia. Navarrete and Fessler (2006) conducted two studies on disease-avoidance and ethnocentrism. The first study included a sample of American participants, and found that measures of ethnocentrism positively correlated with perceived vulnerability to disease; whereas the second study found that measures of in-group attraction, a characteristic of ethnocentrism, increased with disgust sensitivity and also increased as a result of disgust priming. Additionally, Wu and Chang (2012) conducted a set of studies on university and high school students from southern China and found that perceived vulnerability to disease correlated with measures of conformity, which is an ethnocentric behaviour and collectivist value, and that participants primed with disgust salience conformed more than participants in the control group. Similarly, Faulkner et al. (2004) conducted multiple studies within a Canadian sample and found that xenophobia measured via negative attitudes towards out-group members and immigration policies correlated with participants' chronic disease worries, with this too increasing as a result of disgust priming.

The examples laid out above provide further support for the parasite-stress theory. More specifically, they illustrate the relationship that pathogen stress has between conservatism/collectivism and the three components of assortative sociality – philopatry, ethnocentrism, and xenophobia. This relationship will be experimentally explored in Chapter 5.

1.3.3 Religiosity

Religion is an aspect, arguably one of the most important aspects, of a group's culture and can be viewed as a system of values and moral guidance which help preserve the moral purity of the society and of the individuals within the society. In fact, religions throughout history are steeped in traditions of physical and symbolic spiritual cleansing designed to wash away sin (e.g. moral and purity violations) and protect individuals from threat of soul contamination (Ricoeur, 1967; Ritter & Preston, 2011; Terrizzi, Shook, & Ventis, 2012). Within the parasite-stress theory of sociality, Fincher and Thornhill present the parasite-stress hypothesis of religiosity, specifically regarding the effects of parasite stress on religion and religious behaviour (Thornhill & Fincher, 2014b). The hypothesis is formed on the foundations of the evolutionary costly signalling theory, through which religiosity is seen as a signal to others of in-group allegiance via costly efforts of participation and commitment (Alcorta & Sosis, 2005; Sosis & Alcorta, 2003; Sosis, Kress, & Boster, 2007). Participation in and commitment to religion and the religious in-group incurs expensive associated costs. These include loss of opportunities to engage in other more beneficial/productive activities (e.g. working, hunting/foraging, securing resources, family time), loss of resources (e.g. tithes and offerings, cognitive demand of learning religious practices), risks associated with certain rituals (e.g. extended fasting, avoidance of modern medicine, scarring/circumcision), and more (see Alcorta & Sosis, 2005; Sosis & Alcorta, 2003; Sosis et al., 2007). According to Fincher and Thornhill, the practice and signalling of religious allegiance to others aids in the formation and maintenance of in-group assortative sociality and provides two benefits:

> "… (a) the protective barrier provided by isolation from out-group individuals who may harbour novel infectious diseases as well as perform non-normative behaviour with associated contagion risks, and (b) in-group embeddedness and its associated reliable social network that reduce morbidity and mortality caused when infectious disease invades the in-group." (Thornhill & Fincher, 2014b, p.239)

The parasite-stress model holds that, with regard to religious affiliation, individuals/groups will adhere to local religious systems to a stronger degree in regions of higher parasite stress than individuals/groups in regions with low parasite stress, due to the notion that values in low parasite stress regions would allow for people to be more flexible in their degree of religious adherence (Thornhill & Fincher, 2014b). Therefore, the parasite-stress hypothesis of religiosity reasons that variation in

pathogen stress across regions should be predictive of the magnitude of the costs associated with religiosity, as well as of the degree to which people in a region find religion important, and therefore of their willingness to engage and incur the associated costs (Thornhill & Fincher, 2014b). In other words, the hypothesis predicts that the importance of in-group assortative sociality – in this case religious participation and commitment (i.e. religiosity), should be positively related across regions to respective levels of parasite stress (Fincher & Thornhill, 2012; Thornhill & Fincher, 2014b). Fincher and Thornhill present several lines of evidence that meet the predictions and support the theory.

In one of their seminal studies, Fincher and Thornhill (2008a) tested their prediction that religion diversity would positively correlate to infectious disease stress across the globe. They constructed measures of *Religion Richness* – the total number of religions within 219 countries or territories, *Pathogen Richness* – total number of all listed global infections, and *Pathogen Prevalence* – a value based on disease levels of seven groups of parasites in each country. Their results revealed that disease richness and pathogen prevalence were positively correlated with religion richness as a whole. Moreover, religion richness positively correlated with both disease richness and pathogen prevalence across all six regions of the world. There was also a significant negative correlation between absolute latitude and religion richness, which fits the hypothesis that pathogens are more prevalent in lower latitudes therefore religions should be as well. These findings support the parasite-stress theory of religion diversity in that religion diversity appears to be highest in regions of highest disease diversity, and vice versa with lowest diversities (Fincher & Thornhill, 2008a)

In another study, Fincher & Thornhill also tested their prediction that there would be a positive association, both cross-nationally and between the states across the US, between religiosity and parasite stress, by indexing religiosity with (1) religious affiliation, and (2) religious participation and value (Fincher & Thornhill, 2012). They included cross-national *Proportion of Religionists* and *Proportion of Believers* and the *Proportion of Religionists* and *Proportion of Religious Adherents* in US states as variables of religious affiliation. And they included the cross-national variable *Proportion that Prayed Every Day* and the variable *Religious Participation and Value USA* for the inter-state measure of religious participation and value. In-group variables, as measures of in-group assortative sociality, were constructed into a cross-national *In-group Assortativeness* variable and an *In-group Assortativeness USA* inter-state

variable. For parasite-stress measures, Fincher & Thornhill included the variable *Infectious Disease DALY* (Disability Adjusted Life Years) – a cross-national measure of mortality and morbidity used by the World Health Organization (WHO), a variable of cross-national zoonotic versus non-zoonotic parasite prevalence, a variable of cross-national combined parasite stress (summed from the two previous variables), and a *Parasite-stress USA* variable for inter-state measures related to morbidity and mortality (for full description of how these variables were constructed, see Fincher & Thornhill, 2012).

Cross-national analyses showed that both religiosity measures – religious affiliation and religious participation and value – were positively correlated with each of the parasite-stress variables, when measured both singly and combined. The In-group measure of in-group assortative sociality was also positively correlated with the variables of infectious-disease-stress. The statistics show that these dependent variables also positively correlate with the *Combined Parasite-stress* variable across world regions. Analyses of the USA data showed that both affiliation variables, *Proportion of Religious Adherents* and the *Proportion of Religionists*, positively and significantly correlated with the *Parasite-stress USA* variable. The variables of *Religious Participation and Value USA* positively correlated with the *Parasite-stress USA* variable. And, the measure of *In-group Assortative Sociality USA* was positively and significantly correlated with *Parasite-stress USA*. These correlations are also observed in regional analyses as well. Comparing both countries and states in the US, these correlational findings showed that measures of in-group assortative sociality and religiosity are associated positively with parasite stress, thus providing evidence to support the parasite-stress theory, and the proposal that religiosity may function to both signal in-group allegiance and to help delimit social boundaries for protection against out-group infections, values and norms (Fincher & Thornhill, 2012).

A main assumption of the parasite-stress hypothesis is that religiosity and in-group assortative sociality – i.e. in-group preference and out-group dislike – are positively related (Thornhill & Fincher, 2014b). Thornhill and Fincher cite evidence from several studies conducted prior to the formulation of their theory as support for this assumption. For example, they cite one study (Jackson & Hunsberger, 1999) conducted on the relationship between religiosity and prejudicial attitudes towards others – religious and non-religious, which found that the attitudes of religious participants toward religious others were significantly positive, whereas their attitudes

toward non-religious others were negative. Furthermore, the level of religiosity, or degree of religious fundamentalism, corresponded to the level or degree of their prejudice. Another study they cited (Bulbulia & Mahoney, 2008) found altruism was stronger for New Zealand Christians toward Canadian Christians than by New Zealand citizens toward New Zealand compatriots. A further study found that participants with strong Christian beliefs judged others to be more kind and moral if they were displaying a Christian religious symbol (e.g. a cross) than those who were not displaying a Christian symbol (Widman, Corcoran, & Nagy, 2009). Similar evidence regarding the positive associations between religiosity and in-group assortative sociality comes from Terrizzi et al. (2012), who reported that prejudice against sexual minorities (e.g. homosexuals) was positively predicted by the degree of an individual's religiosity.

However, there are other connections as well. Assortative interactions are known to be heavily linked to the origins and facilitation of several traits – e.g. language, ethnic markers (Fincher & Thornhill, 2008a). Perhaps not coincidentally, studies (e.g. Nettle et al., 2007) show that religious diversity and language globally covary. Evidence has also emerged from other related lines of research. For example, using a repeated taste-test paradigm, Ritter and Preston (2011) asked Christian participants to rate a lemon drink for disgust before and after hand-copying passages from the Bible, the Qur'an, from atheist Richard Dawkins' The God Delusion, and a control text from the dictionary. They found that disgust was elicited when participants copied text from The God Delusion and the Qur'an, but was not elicited by copying biblical text or the control. In other words, disgust was elicited in religious participants simply by contact with an out-group's religious beliefs (termed as a rejected religious belief). This illustrates how disgust, and therefore the BIS, can easily be enlisted to motivate in-group allegiance and out-group avoidance. Interestingly, if participants were allowed to wash their hands after copying the passage disgust was reduced and even eliminated. The BIS seems to treat out-group beliefs as if they are pathogenic – a threat of infection on an individual's belief system and soul. This is an example of the component of xenophobia known as neophobia. This also sheds some light on the historical evolutionary relationship between religiosity and disease.

As in previous sections, these examples illustrate the relationship between parasite stress and assortative social behaviour, in this case – religiosity; and, in conjunction with the previous sections, the evidence provides more support for the

parasite-stress theory. But beyond this, as the theory contends, the value placed on these assortative behaviours would also likely affect the moral and ethical values and beliefs of a society, which would ultimately affect the political and judicial values and beliefs of a society as well as the overarching governmental systems – for example, conservative versus liberal, collectivist versus individualist, religious versus secular, autocratic versus democratic.

1.4 Thesis aims and outline

Fincher & Thornhill contend that, similar to biological philopatry leading to genetic isolation, divergence and subsequent speciation, parasite stress activates assortative social behaviours and leads to cultural isolation and divergence, and thus to a form of cultural 'speciation'. Criticisms of the theory will be discussed briefly in Chapter 6, but it is important to remember that this thesis is not aimed at countering criticisms, *per se*. It is merely aimed at testing the plausibility of the potential for pathogen stress to produce divergence in the values and beliefs associated with these specific assortative behaviours, which would suggest that variance in pathogen stress can indeed generate variation in these behaviours which could then lead to cultural isolation and divergence. However, as illustrated in the introduction of this thesis, and as Fincher and Thornhill and others (e.g. see peer commentary in Fincher & Thornhill, 2012) aptly note, there are two notable points of consideration regarding much of the evidence supporting their parasite stress model. Aside from some select studies that implement experimental manipulation or focus on individual-level analysis, (1) the supporting body of evidence is mostly correlational, from which causal conclusions cannot be conclusively drawn, and (2) the primary unit of analysis is geopolitical regions, i.e. countries, nations, territories, or states within the USA (Thornhill & Fincher, 2014b). These two points are related.

Directly investigating causation requires experimental manipulation and obviously the necessary experiments would be difficult if not impossible to conduct on a culture or cultures. However, given that cultures are made up of the individuals within them, the effects on cultures by parasite stress should be observable in individual differences of BIS responses to the stress. This is not to suggest that the correlational evidence is less convincing than evidence revealed by experimentation, or that experiment is the only true theoretical test (Thornhill & Fincher, 2014b). The goal of experimentation is to control for confounding variables that are near impossible to account for in correlational studies, particularly in large group-level analysis.

Considering these points, the central aim of this thesis is to experimentally manipulate and analyse the BIS responses of individuals in order to contribute empirical findings to the theoretical argument regarding aspects of the parasite-stress theory. I focused specifically on the assortative social behaviours, i.e. the values, of MHC-related mate selection, philopatry, ethnocentrism, xenophobia, and religiosity, and the putative causal link between parasite stress and cultural isolation and diversification, with individuals as the primary unit of analysis. If the results of the studies suggest that parasite stress has direct causal effects on these values in individuals then this would provide empirical evidence to corroborate the correlational evidence through which Fincher and Thornhill predict a causal relationship, thus further supporting their parasite-stress theory. It would confirm that variation in pathogen stress can indeed produce individual differences in values and the associated beliefs, which would suggest that the cultural variance of these values and beliefs globally are, at least in part, caused by environmental and geographical variance in pathogen stress. It would lend empirical weight to the idea that pathogens may, at least in part, be responsible for the isolation, divergence and variation of cultures and their underlying value and belief systems, including religiosity.

One crucial question arose at the outset – how could the disgust emotion be effectively triggered, thus activating the BIS of individuals in order to observe and analyse any subsequent relevant behavioural output? One of the most, if not the most, important forms of sensory input in avoidance of potential threats in the environment is vision. Coincidentally, the easiest way to recruit and collect a large number of participants and data is online, which is, necessarily, a visual medium. Therefore, I decided to employ the use of disgust images to experimentally manipulate participants' BIS. This raised a further issue – there was a lack of suitable visual stimuli that were specifically designed and validated to cross-culturally activate the BIS for use in this context. This in itself was problematic, not only for this thesis, but for BIS-related research in general. For this reason, I first set out to devise a new instrument designed specifically to visually evoke disgust and activate the BIS not only for my subsequent studies, but also for the broader related disciplines and fields.

As a whole, this thesis includes four empirical chapters, three of which consist of studies designed to experimentally test some of the aforementioned aspects of the parasite-stress theory. The first empirical chapter (Chapter 2), describes a multi-stage study conducted to devise a new cross-culturally validated set of images to be

employed in each of the three empirical chapters that follow it (3, 4, and 5). In Chapter 3, I tested the extent to which visual pathogen stress (or threat), i.e. BIS-activation, influences mate selection via its effects on an individual's mate-related MHC preferences. Chapter 4 consists of a study I conducted to test the potential for visual BIS-activation to influence cultural isolation and divergence via a social rule-building task and a hypothetical premise. In the fourth and final empirical chapter (Chapter 5), I tested the effects of visual BIS-activation on various measurements of assortative sociality, which includes philopatry, ethnocentrism, xenophobia, and religiosity. My aim is that this thesis will shed new and welcomed experimental light on the parasite-stress theory and contribute to the current understanding of various aspects of related human behaviour.

Chapter 2: Visually activating pathogen disgust

This chapter is based on the following publication[2]:

Culpepper, P., Havlíček, J., Leongómez, J.D., & Roberts, S.C. (2018). Visually activating pathogen disgust: Developing a new tool for studying the behavioural immune system, *Frontiers in Psychology*, *9*:1397.

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[2] This chapter is written and presented in 1st person plural as this is how it has already been published.

2.1 Introduction

The emotion disgust is commonly characterized as a negatively valenced affective state consisting of a set of interlinked cognitive, behavioural, and physiological processes (Rozin, Lowery, & Ebert, 1994). It has been proposed that these processes represent a putative adaptation to avoid disease, principally functioning to minimise direct contact with threats of infectious microorganisms, i.e. pathogens (Curtis et al., 2004; Oaten et al., 2009). Earlier literature suggests the role of disgust to be primarily concerned with avoidance of oral ingestion of noxious stimuli (e.g. Rozin et al., 2000), but, based on the understanding that bacterial and viral infections can be transmitted through bodily excretions and secretions, Curtis and colleagues extended this idea to describe it as an adaptation that evolved to "…prevent the acquisition of infectious diseases" in general (Curtis et al., 2004, p.132), rather than simply via oral ingestion. While research suggests that disgust may also cross into sexual and moral domains (see Tybur et al., 2009), the pathogen disgust domain is likely the adaptation's foundational domain.

More recently, disgust has been cast as a key component in the concept of the behavioural immune system (BIS), an evolved set of disease-avoidance processes which serves as a psychological first line of defence against pathogen threats in the environment (Lieberman & Patrick, 2014; Schaller, 2006). The BIS is defined as behaviourally analogous to the classic immune system, consisting of a collaborative suite of evolved psychological mechanisms responsible for (1) processing and inferring potential risks of infection through perceptual cues, (2) activating aversive emotional and cognitive responses, which (3) motivate avoidance behaviours in order to neutralise the perceived threat (Fincher & Thornhill, 2012; Schaller, 2006; Schaller, 2011). The similarities and overlap between pathogen disgust and the BIS are overtly apparent. In fact, researchers argue that they are functionally the same, declaring the distinction as no longer necessary or useful (Lieberman & Patrick, 2014). Whether this is the case or not, the initial step in activating the BIS is to prime the corresponding processing and inferential mechanisms with perceptual cues that 'trigger' pathogen disgust.

2.1.1 Visual cues to disgust

Several studies have demonstrated that experimentally priming people with pathogen-relevant cues can activate the BIS and alter their subsequent behaviour (Tybur, Pollet, & Frankenhuis, 2014). Such primes can be introduced through different

sensory modalities, including olfactory, tactile and visual cues (Tybur et al., 2014). For example, after experimental exposure to odour evocative of faeces, participants reported increased intention to use condoms compared to participants in a control condition (Tybur, Bryan, Magnan, & Hooper, 2011).

However, most studies conducted to date have employed the use of visual cues to pathogens (e.g. Faulkner et al., 2004, studies 5 and 6; Wu & Chang, 2012, studies 2 and 3), but these often have methodological or experimental limitations. For example, Faulkner and colleagues exposed participants to an 11-picture "Disease slide show", noted as appropriate for teaching health education, that depicted "various ways that diseases are transmitted in daily life" (2004, p.345). There were some limitations to these images: one showed a woman in a kitchen attempting to kill cartoon germs, while another depicted a microscopic view of a hair with bacteria surrounding it, with the label 'Hair Bacteria'. The process by which these images were chosen or validated as effective BIS triggers was not explained, and the use of descriptive text labels arguably defeats the purpose of visually cueing the BIS. Furthermore, the control condition consisted not of images that were similar but lacking in disease relevance, but was rather an "Accidents slide show" showing a series of potential safety threats (e.g. 'School Bus Hazards', 'Electricity and Water Don't mix'). In Wu and Chang's (2012) study, participants were exposed to a 10-image slide show depicting maggots and gory wounds, which is arguably more ecologically valid than those used by Faulkner et al., but the process of image selection and validation was also not described (and they similarly employed an 'accident' slide show as the control condition). Moreover, neither of these studies asked their participants to rate the images for disgust, which would have provided evidence as to the effectiveness of the images in eliciting disgust. Several other image sets have been devised and validated to study affective responses generally, including disgust, such as the International Affective Picture System (IAPS: Lang, Bradley, & Cuthbert, 2008), the Nencki Affective Picture System (NAPS: Marchewka, Zurawski, Jednoróg, & Grabowska, 2014), the Geneva Affective Picture Database (GAPED: Dan-Glauser & Scherer, 2011), and the Emotional Picture System (EmoPicS: Wessa et al., 2010), however, none of these were specifically designed as instruments to be used in the study of disgust.

For over a decade, the main set of photo stimuli produced specifically for the purposes of studying disgust was the set by Curtis, Aunger, & Rabie (2004). Devised from an evolutionary perspective, this set depicts 7 images of disease-salient stimuli

(bowl of bodily fluid, feverish face, a crowded train carriage, red-green secretion on a towel, open wound, intestinal parasites, a louse) and a control set of 7 images that contextually matched each individual disease photo but lacked its corresponding disease relevance. Participants from across the world rated the disease-salient photos as more disgusting than their disease-free counterpart, providing support for the tested hypothesis that disgust evolved to motivate pathogen-avoidance (Curtis et al., 2004), and exposure to these disease-salient images has been shown to influence behaviour (e.g. strategic mate preferences, Little, DeBruine, & Jones, 2011). Despite these advantages, the image set is relatively small and the range of disgust elicitors is thus limited. Furthermore, although they demonstrably elicit the emotion of disgust, the choice of images likely does not include the kinds of stimuli that elicit the most disgust; for example, there is no representation of faecal stimuli that appears to be one of the most evocative triggers of disgust around the world (e.g. Curtis & Biran, 2001).

More recently, as the current study neared completion, Haberkamp et al. (2017) developed their own validated set of images: the DIsgust-RelaTed-Images (DIRTI) picture set. The DIRTI was designed from a clinical perspective through a top-down approach, targeting six preselected disgust categories considered to play a role in psychiatric disorders: food, animals, body products, injuries/infections, death, and hygiene. It consists of 300 images, each category containing 40 related disgust images and 10 matched neutral images, and importantly each are copyright-free and accessible for re-use. We therefore think this set is extremely useful; however, one potential objection is that the categories were selected in top-down fashion by the researchers (similar to the image selection by Curtis et al.), rather than being driven by a bottom-up quantitative approach to category and item selection and with cross-cultural input.

2.1.2 Study rationale

Against this background, we set out to develop a cross-culturally validated set of reliable visually priming stimuli for use in the study of disgust. To do this, we employed a multi-stage, bottom-up item-generation process modelled after methods used to generate other widely used instruments, such as the Three Domain Disgust Scale (Tybur et al., 2009), the original Disgust Scale (Haidt et al., 1994) and the Liverpool and Singaporean odour perception scales (Ferdenzi et al., 2011), and followed guidance on scale construction from Spector (1992). Each stage was necessary to increase the chances of generating images built from the most comprehensive list of possible universal disgust triggers.

In Stage 1 we asked a large cross-cultural sample of people about the five most disgusting items that came to mind. The intent was to assemble the widest possible, most diverse range of items that individuals consider to be disgusting. We then filtered the item set (e.g. removing duplicates) while retaining the range, scope, and novelty of the original set (Stage 2) and had an independent set of raters score these items for disgust, providing a hierarchical ranking of the retained items and revealing those which were most commonly and consistently associated with disgust (Stage 3). We then extracted items that were determined to fall within the pathogen domain of disgust (Stage 4), used factor analysis to understand underlying structure of the remaining items (Stage 5), and adopted a set of decision rules to guide the selection and generation of 20 image-items and their controls (Stage 6; the final set of 20 paired images are hereafter referred to as the Culpepper Disgust Image Set, C-DIS). Finally, in Stage 7 we collected ratings of disgust elicited by these new disgust and control images and compared these responses with those obtained for the most commonly used images in previous disgust research (those by Curtis et al. 2004).

We reasoned that, to be considered an improvement, the C-DIS must meet specific criteria: it must elicit (1) a significantly larger overall mean disgust score for the pathogen-salient images compared to the pathogen-salient images in the Curtis set, (2) no significant increase (or some reduction) in the overall mean disgust score for the pathogen-free images compared to the disgust score for the pathogen-free images in the Curtis set, and therefore (3) a significantly larger difference in disgust scores given to the pathogen-salient and pathogen-free images compared to that of the Curtis set. Meeting these criteria would provide evidence to suggest that the C-DIS will more effectively trigger pathogen disgust, thus enabling more reliable manipulation of disgust and the behavioural immune system in future studies and across cultures.

2.2 Method

Ethics statement

This study received ethical approval from the General University Ethics Panel at the University of Stirling and adhered to the ethical guidelines of the British Psychological Society and the American Psychological Association. All participants provided prior informed consent. No reward was offered for participation in any stage.

2.2.1 Stage 1: The disgust item survey

Survey distribution

An online survey was generated which asked participants their age and gender, and then asked them to freely and in no particular order list 5 items (i.e. objects, scenarios, etc.) that they considered to be the most disgusting that came to mind. The survey was translated from English into two other languages (Czech, Spanish) by two bilingual researchers. The link to the English version was distributed across social media (e.g. Facebook, Twitter), which included mostly individuals from North America, the UK, and other English-speakers from other parts of the world, as well as to psychology students and staff at the University of Stirling in Scotland. The link for the Czech version was distributed to participants using a Facebook-based snowball method (Flegr & Kuba, 2016). The link to the Spanish version was distributed to staff and students at El Bosque University and the University of La Sabana in Colombia, several of whom also posted it on social media.

Participants

The surveys collectively garnered 865 total respondents: English version ($N =$ 212), Czech version ($N = 434$), Spanish version ($N = 219$). The responses from the Spanish and English version surveys were filtered by removing all respondents that listed less than 3 of the requested 5 disgust items (Spanish: $N = 179$; English: $N = 134$). Due to the larger number of Czech respondents, the translator selected only the respondents that listed all of the 5 disgust items, leaving 225 cases. She then removed every third respondent and translated the remaining 150 cases. Three of those were under age 18 and therefore removed ($N = 147$). To check for participants who responded to the survey more than once we assessed the IP addresses for duplicates. One duplicate IP address was discovered in the Colombian data; however, this is likely because the responders were students or staff at the same university. This resulted in a final total of 460 participants, including 114 men (24.8%), 344 women (74.8%), and 2 transgenders (0.4%), with an overall mean age 31.84 ± SD 12.22 (range 18-69). Each survey version was responded to by individuals from a range of different global regions. More detailed descriptive statistics of participants for each individual survey version and the list of the countries are provided in ESM 1 and ESM2, respectively.

2.2.2 Stage 2: Disgust item reduction
Decision rules for disgust item reduction

Responses from the Czech and Colombian surveys were translated into English by the same two bilingual speakers. Responses from all three surveys were collated, providing a total of 2,287 disgust item responses (see ESM 2). A set of decision rules was followed to facilitate item-reduction.

First, we removed verbatim duplicate responses and responses that describe the same item through similar words, e.g. we assumed, for example, "cruelty to animals" and "the smell of fish" to be equivalent to "animal cruelty" and "fish smell", respectively. Items were retained if they appeared to describe something conceptually or contextually different, e.g. we retained both "touching spiders" and "spiders". The second rule served to generalise the responses where appropriate, e.g. "Czech politics" was altered to simply "politics". A third rule served to remove responses that were either too specific or not specific enough. For example, "Minister of Finance" was removed as not all governments have this position and because it implies a specific person who holds that position in that specific participant's country/government. Other items referring to specific individuals such as "my ex-husband" were also removed.

A further step was performed to help make the responses more comprehensible in subsequent stages by including brief descriptions to clarify some items for raters who may not know the meaning of, or have experience with, the regional vernacular regarding some items. For example, "touching the holding tubes in the public transport" was changed to "touching the holding tubes (hand-rails, etc.) in the public transport" and "the smell of the bathrooms in tube" was amended to "the smell of the bathrooms in tube (underground train)". Responses such as "none" were also removed.

2.2.3 Stage 3: Disgust item rating task
Task objectives

The remaining 773 disgust items were then each rated for levels of disgust. A separate group of 20 participants (10 men, mean age $\pm$ SD = 38.7 $\pm$ 8.3, range 23-47; 10 women, age 34.2 $\pm$ 12.9, range 19-53) from the UK were recruited via email for this task. Participants rated each individual item for disgust on an 11-point scale (0 = *not at all disgusting,* 10 = *extremely disgusting*). The item-ratings were then standardised to *z*-scores for each of the 773 items. There was high concordance among raters across these items (Cronbach's α = .925). Ratings were then summed across raters to provide a mean score for each item, which were then ranked in descending order. Of these

ranked disgust items, only the items within the upper quartile of disgust ranking were retained (N = 193) for use in Stage 4 (see ESM 3 for the item list).

2.2.4 Stage 4: Item categorisation
Task objectives

In this stage, the remaining 193 items were categorised into major disgust domains – 'pathogen', 'sexual', or 'moral' (see Tybur et al., 2009); or as 'other' if the item did not fall into one of Tybur et al.'s three domains. Three raters (2 men and 1 woman), each familiar with Tybur et al.'s domain categorisation, indicated to which domain they would assign each individual item. A Cronbach's *alpha* reliability test performed on their ratings indicated high inter-rater reliability (for all 3 raters α = .934).

Since the aim of this study was to select items related to the pathogen domain, items were retained if at least one researcher rated the item as relating to pathogen risk. Other items that were unanimously rated as belonging to the 'moral' (e.g. "cruelty to animals", "abuse to spouse", "senseless murder", "racism") or 'other' (e.g. "the sound of breaking bones") were removed. No items were unanimously rated as 'sexual' domain items. Although several items were labelled as 'sexual' by two raters (e.g. "incest", "animal intercourse (bestiality/zoophilia)"), these were retained because the third rater categorised these in the pathogen risk category. This step resulted in 131 remaining pathogen items (listed in ESM 4).

Finally, it was then necessary to perform a further reduction and unification procedure on the remaining items as it would not be possible to effectively, ethically, or unambiguously represent some items in an image. For instance, due to the difficulty of effectively depicting scenarios that describe auditory and tactile stimuli, such items were removed, e.g. "the crunch it makes when biting into a cartilage or tendon", "burping in someone's face", "eating something alive and feeling its movement in my mouth". Items which could not be accurately assessed in an image were removed (e.g. "sperm other than from my partner and especially from a homeless person", "bad or unpleasant odours"). Several items were related to "unwashed genitals" which could not ethically be represented and were removed. Several more were extremely similar and were unified into one item (e.g. "human entrails" and "gutted human bodies" were combined into "human entrails"; similarly, "cat vomit", "children's vomit" and "vomit" were combined into "vomit"). Following this, 64 items (Tables 2.1 and 2.2) were retained.

Table 2.1 The 64 pathogen disgust items listed in ranked order of disgust rating from Stage 5.

Overall Rating	Disgust Items	Overall Rating	Disgust Items
5.21	Ingesting faecal matter	3.48	Stepping in dog faeces
4.9	Eating uncooked rotting masses (any)	3.47	A baby diaper/nappy full of diarrhoea
4.82	Rotting flesh crawling with worms	3.46	Bloody phlegm
4.66	Worms in the food (where don't belong)	3.34	Animal entrails
4.54	Maggots in wound of a living human	3.33	Bad body odour
4.37	Decomposing human carcass	3.28	Phlegm on sidewalks
4.31	Eating a cockroach	3.23	Halitosis (bad breath)
4.26	Parasites/worms that grow in humans	3.18	The smell of garbage
4.17	Flesh-eating disease (parasites/bacteria)	3.12	Mucus, phlegm, snot
4.04	Gaping infected wounds oozing pus	3.07	Exposed brains
3.97	Body parasites	3.05	Crawling swarms of insects
3.92	Really dirty, fungus-infected toenails	3.04	Cockroaches
3.89	Sewage	3	Skin infections/diseases
3.87	Decomposing animal carcass	2.99	Ball of hair in communal showers
3.87	Intestinal parasites	2.91	Putrid or stagnant water
3.86	Dead, disfigured body	2.90	A gob of spit in the street
3.82	Vomit	2.89	Sour milk
3.81	Rotting meat	2.84	The bad odour of feet
3.79	Kissing someone with disgusting lips	2.83	Hair in your food
3.75	Dirty sanitary items	2.78	When people chew with mouth open
3.69	Dirty or unflushed toilets	2.77	Long and dirty finger nails
3.68	Maggots	2.75	Eating animal organs - brain, liver, etc.
3.64	Bugs, flies in food	2.72	Sloppy eaters
3.63	Exposed intestines	2.72	Severe acne (whiteheads, pus, etc.)
3.62	When people eat their snot/bogeys	2.68	Close-up of a mouth while eating
3.58	Liquid that comes out of the rubbish	2.64	Mouldy food
3.57	A dog eating faeces	2.64	Dirty scalp
3.56	Human entrails	2.63	Fat slobs who look filthy
3.55	Human faeces	2.61	Severe injuries (fractures, wounds)
3.54	Rotting garbage	2.60	Dog shit
3.54	Open animal carcass	2.55	Open wounds
3.48	Bad dental hygiene, black teeth, decay	2.30	Tumours

2.2.5 Stage 5: Factor analysis of pathogen items

Rating task objectives

The remaining 64 pathogen items were rated by another group of 111 participants (36 men, mean age $\pm$ *SD* = 36.9 $\pm$ 10.2, range 21-55; 75 women, age 35.7 $\pm$ 12.9, range 20-70) via an online survey. The survey was in English but country of origin was not collected. The survey asked participants two demographic questions – gender and age, and then to rate the 64 items, delivered in a randomised order for each participant, for disgust on a 7-point scale (0=*not at all disgusting, 6=extremely disgusting*). These ratings provided a ranked order of the remaining items, as shown in Table 2.1.

Factor extraction

We conducted exploratory factor analysis in order to investigate underlying structure of the data and to aid in further item reduction. We based our choice of factor analysis method and rotation on two main assumptions, (1) the 64 items likely correlate to some degree on disgust in general, and (2) the analysis will result in distinct, easily interpretable, uncorrelated components of disgust. Based on recommendations for these assumptions (Field, 2013), we conducted a principal components analysis (PCA) with orthogonal rotation (Varimax with Kaiser normalisation). The Kaiser-Meyer-Olkin measure of adequacy (KMO = .84) and Bartlett's test of sphericity ($p < .001$) both indicated a sufficient shared amount of common variance between the individual items to support this analysis. In order to determine which factors to extract from the data, two main criteria were used: (1) a visual scree plot (Cattell, 1966), to visualise the inflexion in the slope along the mapped eigenvalues, and (2) a comparison between the initial eigenvalues > 1 and the inflexion shown in the scree plot. The scree plot showed that the inflexion would justify retaining four factors. These four factors are also the only factors with eigenvalues > 2. Twelve factors had eigenvalues > 1, however, the first largest jump in eigenvalue rested between factors 4 (2.587) and 5 (1.964), thus justifying the extraction of four factors. These four factors cumulatively accounted for 58.91% of the variance.

For due diligence, two more tests to justify four-factor extraction were included. We re-ran the analysis using the four-factor extraction specification, which then provided post-extraction communality scores as well as the percentage of non-redundant residuals with absolute values greater than 0.05. The overall average of the communalities was 0.59, and fit closely to Kaiser's recommended criterion for accuracy in determining the number of factors to extract (as cited in Field, 2013; and Stevens, 2002). Second, Field (2013) notes that the percentage of non-redundant residuals with absolute values > 0.05 is indicative of how well the data fits the model, where the smaller the percentage (no more than 50%) the better the model fit. In this dataset, only 684 non-redundant residuals had absolute values > 0.05 (33%), suggesting an acceptable model fit. Table 2.2 shows the loadings for these four factors after rotation. The items clustered into four components labelled as: Hygiene Issues (Factor 1), Parasite/Infection (Factor 2), Food/Environmental (Factor 3), and Injury/Viscera (Factor 4). Ten of the items failed to load above .512, the minimum loading value recommended by Stevens (2002) for sample sizes of 100. Four items cross-loaded onto

more than one factor and were subsequently removed from further analyses: 'a dog eating faeces', 'sewage', 'open animal carcass' and 'decomposing human carcass'. The lower part of Table 2.2 is ordered the same way as the upper part but shows the loadings that fall below the threshold only, i.e. it illustrates the trend of the items' loadings onto the factors.

Cronbach's *alpha* (α = .978) indicated high internal consistency across the ratings of the 64 text items, and could not be increased by deleting any of the 64 items. Cronbach's *alpha* scores across each of individual factors also indicated internal consistency for each factor (Factor 1: α = 957; Factor 2: α = .926; Factor 3: α = .938; and Factor 4: α = .947; α could not be increased in any of the factors by deleting any of the items within them). The four retained factors were then used in Stage 6 for the generation of the final image set.

2.2.6 Stage 6: Image-item selection and image generation
Decision rules for image-item selection

We chose to represent five items from each of the four factors, resulting in a total of 20 images. These items were selected by following a set of decision rules designed to reduce subjectivity in item selection, taking into account the disgust ratings of the 64 items and their respective factor loadings. First, we focused on items that loaded above the threshold (.512) in only one factor; items that loaded above the threshold in more than one factor were excluded from subsequent decisions in order to draw a distinct boundary between factors. Within these remaining items, we selected the 4 items which had the highest overall disgust rating among items loading onto each factor, according to the ranked order shown in Table 2.1. For example, the item that loaded (above the threshold) onto the 'Hygiene Issues' factor with the highest overall disgust rating is 'dirty sanitary items' (loading = .634, rating = 3.75), therefore this item was selected. However, because some of the items in each factor are somewhat similar, we applied a third rule to avoid selection of similar items: only items that were considered to be distinct from the previous selected item(s) were selected. For example, based on the disgust rankings "maggots in the wound of a living human" should be the third selected item from the 'Parasite/Infection' factor. However, because it is more similar to the first two selections ("rotting flesh crawling with worms" and "worms in food...") than the remaining items on this factor, we skipped this item, as well as "parasites that grow in humans", but selected the next highest-ranking item that loaded on this factor, "flesh-eating disease". These rules were applied across the factors, generating 16 items.

Table 2.2 PCA factor loadings of the 64 pathogen items for the four-factor model. The upper section shows the items loading > .512 (bold) onto the corresponding 4 factors: Hygiene Issues, Parasite/Infection, Food/Environmental, and Injury/Viscera. The lower section shows the trends for items loading < .512 (bold). Items listed with bracketed numbers are those selected as representative of the numbered factor.

	Four Factors			
Disgust Item	**Hygiene Issues**	**Parasite / Infection**	**Food/Envi ronment**	**Injury / Viscera**
Factor loadings > .512				
Halitosis (bad breath)	**.720**	.228	.237	.119
Dirty or unflushed toilets (1)	**.626**	.266	.311	.169
Bad body odour	**.736**	.206	.277	.067
Close-up of a mouth while eating	**.694**	.003	.089	.085
Dirty sanitary items (1)	**.634**	.252	.369	.176
Human faeces	**.578**	.182	.320	.268
Hair in your food	**.598**	.286	.187	.167
Ball of hair in communal showers (e.g. the dorms)	**.671**	.275	.227	.184
When people eat their snot/bogeys (boogers) (1)	**.590**	.280	.311	.276
Bloody phlegm	**.544**	.479	.000	.284
Mucus, phlegm, snot	**.696**	.350	.182	.205
Long and dirty finger nails	**.640**	.462	.054	.179
Fat slobs who look filthy	**.541**	.358	.185	.025
When people chew with their mouth open	**.753**	-.144	.155	.111
Sloppy eaters	**.676**	-.003	.252	.147
Dirty scalp	**.601**	.500	.155	.128
Bad dental hygiene, black teeth, tooth decay (1)	**.654**	.443	.058	.144
The bad odour of feet	**.742**	.247	.247	.117
A gob of spit in the street	**.697**	.045	.342	.087
Phlegm on sidewalks	**.699**	.101	.283	.216
Flesh-eating disease (parasites, bacteria) (2)	-.023	**.617**	.169	.316
Body parasites	-.043	**.654**	.371	.329
Eating a cockroach	.268	**.575**	.227	.213
Cockroaches	.241	**.554**	.271	.081
Parasites/worms that grow in humans	.131	**.797**	.186	.170
Intestinal parasites	.131	**.794**	.139	.180
Maggots	.218	**.576**	.327	.287
Maggots in the wound of a living human	.123	**.725**	.268	.289
Really dirty, fungus-infected toenails (2)	.474	**.652**	.037	.086
Worms in the food (where they don't belong) (2)	.261	**.573**	.367	.182
Rotting flesh crawling with worms (2)	.096	**.644**	.425	.253
Skin infections/diseases	.220	**.555**	.097	.150
Decomposing animal carcass (3)	.202	.192	**.542**	.423
Stepping in dog faeces (3)	.394	.273	**.580**	.202
Mouldy food	.370	.286	**.569**	.094
Putrid or stagnant water	.421	.356	**.529**	.121
Rotting garbage	.374	.238	**.674**	.175
Rotting meat (3)	.257	.305	**.518**	.203
Liquid that comes out of the rubbish (3)	.374	.290	**.651**	.116
The smell of garbage	.503	.191	**.683**	.115
Sour milk	.263	.137	**.644**	.191
A dog eating faeces	.520*	.115	**.527**	.172
Sewage	.527*	.337	**.608**	.101
Open animal carcass	.089	.240	**.587**	.517*
Decomposing human carcass	.101	.187	540*	**.591**
Dead, disfigured body (4)	.107	.176	.334	**.724**
Tumours	.306	.220	.159	**.616**
Animal entrails	.298	.199	.325	**.570**
Exposed intestines (4)	-.012	.252	.259	**.788**

Exposed brains (4)	.076	.127	.195	**.750**
Human entrails	.181	.105	.291	**.737**
Gaping infected wounds oozing pus (4)	.162	.453	.149	**.557**
Open wounds	.329	.273	-.089	**.751**
Severe injuries (fractures, open wounds)	.285	.241	-.231	**.726**

Factor loading trends < .512

Ingesting faecal matter (1)	**.439**	.155	.397	.310
A baby diaper (nappy) full of diarrhoea	**.398**	.272	.205	.355
Kissing someone w/disgusting lips (e.g. smell/morphologic)	**.474**	.450	.253	.115
Crawling swarms of insects (2)	.362	**.472**	.245	.118
Severe acne (when there are big whiteheads, pus, etc.)	.438	**.496**	.076	.155
Dog shit	.466	.152	**.476**	.291
Eating of uncooked rotting masses (of any kind) (3)	.188	.334	**.480**	.192
Bugs, flies in food	.306	.401	**.502**	.150
Eating animal organs - brains, liver, tail, etc.	.210	.344	.180	**.363**
Vomit (4)	.349	.337	.213	**.387**

Table 2.3 The 20 pathogen-salient items selected for depiction in final image set.

	Hygiene Issues	Parasite/Infection	Food/Environmental	Injury/Viscera
Item 1	Dirty sanitary items	Rotting flesh crawling with worms	Decomposing animal carcass	Dead, disfigured body
Item 2	Dirty/unflushed toilets	Worms in the food	Rotting meat	Gaping, infected wounds oozing pus
Item 3	Bad dental hygiene	Really dirty, fungus-infected toenails	Liquid that comes out of the rubbish	Exposed intestines
Item 4	When people eat their snot/bogeys	Flesh-eating disease	Stepping in dog faeces	Exposed brains
Item 5	Ingesting faecal matter	Crawling swarm of insects	Eating uncooked rotting masses	Vomit

Some text is abbreviated

Finally, we further selected one item per factor from the factors' trend loadings (items loading below .512), because these items included the two highest-ranking disgust scores in Table 2.1 ('ingesting faecal matter' and 'eating uncooked rotting masses'). Thus, within this group of items, we selected the item with the highest disgust score. Following this procedure resulted in the final total of 20 items to be depicted in the final image set, with 5 items from each of the 4 factors. Table 2.3 contains the final list.

Generating the images

Images were generated to represent, as closely as possible, the final 20 items. To gather some generalised ideas of what the public considers to be illustrative of the text of each item, we conducted an internet search (Google.com) using the exact item-wording of the individual items. Scenes were then prepared to closely, but uniquely,

represent a generalised version of the collective group of item-images retrieved. We prepared the scenes for 19 of these images, in 8 of which we enlisted the help of professional special effects artists; for the remaining item ('decomposing animal carcass'), a photograph was taken of a real dead squirrel. Full colour photographs were taken of each prepared scene. Furthermore, following Curtis et al. (2004), we also generated a matching image which lacked pathogen relevance but was otherwise similar. For example, for the disgust image depicting 'dirty/unflushed toilet', the matching image was of a clean/flushed toilet. We thus created 20 paired images – 20 pathogen-salient images, each with a matching pathogen-free counterpart image (Figure 1). Each of the 40 images were created to provide as similar degree of focus, depth, and clarity as possible. They are uniformly sized – some images at 400x600 pixels in portrait and some at 600x400 pixels in landscape orientation (where both images of each individual image-pair are formatted in the same orientation).

Figure 2.1 The Culpepper Disgust Image Set. Twenty pathogen-salient images (left) with their matching pathogen-free counterparts (right). F1 – F4 represent the four disgust factors, F1: Hygiene Issues, F2: Parasite/Infection, F3: Food/ Environmental, and F4: Injury/Viscera. (The orientation for images 1 and 4 in F2, and image 1 in F3 has been adjusted from landscape to portrait for the purpose of this collage.)

2.2.7 Stage 7: Validation of the image set
Survey objectives

The aims of this final stage were two-fold. First, we aimed to compare differences in ratings between the pathogen-salient and pathogen-free images in the new image set, with the clear expectation that the pathogen salient images should elicit higher mean disgust scores than their pathogen-free counterparts; if so, then the new set (the C-DIS) can be considered effective as an instrument for eliciting disgust (by simply exposing people to the pathogen-salient images) or for measuring disgust sensitivity (comparing the difference between an individual's scores for the pathogen-salient and pathogen-free images). Second, we aimed to compare these scores with those elicited by the Curtis et al. (2004) image set. As noted earlier, to be considered an improvement over that set the C-DIS must elicit (1) a significantly larger overall mean disgust score for the pathogen-salient images compared to the pathogen-salient images in the Curtis set, (2) no significant increase (or some reduction) in the overall mean disgust score for the pathogen-free images compared to the disgust score for the pathogen-free image in the Curtis set, and therefore (3) a significantly larger difference in overall disgust ratio between the pathogen-salient and pathogen-free images compared to that of the Curtis set.

Participants and procedure

To meet these objectives, we constructed an online survey which included 54 images – the 40 new images (20 pathogen-free, 20 pathogen-salient) and Curtis' 14 images (7 pathogen-free, 7 pathogen-salient). The images were resized to 350x500 and 500x350 pixels (corresponding to orientation) to better fit the survey pages. A link to the survey (on the Qualtrics.com platform) was shared through social media.

A total of 135 people responded to the survey link. Only participants over 18 years were recruited. For ethical reasons, the survey did not enforce responses to items and some participants did not provide ratings for every image; we therefore excluded eight participants who missed out more than two C-DIS pairs or one of the Curtis image pairs. The remaining 127 participants (mean age = 33.18 years, SD = 12.99, range = 18-66) included 46 men (36%), 79 women (62%), and 2 transgenders (.01%). The native country for these participants were, in order of percentage: Colombia = 25 (20%), USA = 25 (20%), UK = 23 (18%), the Czech Republic = 17 (13%), Lebanon = 8 (6%), Germany = 7 (5%). Seventeen other countries were represented by 2 or less individuals, ordered alphabetically: Australia, Canada, Egypt, Ireland, Italy, Norway,

Pakistan, Slovakia, Spain, Syria, Sweden, The Netherlands, and Turkey. Of these, participants' ethnic background included White ($n = 103$; 81%), Black/African descent ($n = 4$; 3%), and 'Other' ($n = 20$; 16%), which included descriptions such as Native American/Alaskan, Asian, Latin American, Mestiza, Mexican, Middle Eastern, and Arab.

Participants were presented with the 54 images sequentially and in a fully randomised order that was unique to each participant. For each image, they were asked to rate it for disgust on a 7-point scale (0 = *not disgusting at all*, 6 = *extremely disgusting*).

Analyses

For each participant, we computed mean ratings for the pathogen-salient images and the pathogen-free images in each image set. Mean difference ratios were also calculated, by dividing the pathogen-salient image scores by the pathogen-free image scores for each image pair (a high ratio thus indicates that the pathogen-salient images were judged to be particularly disgusting compared to their controls). These same scores were also calculated for each of the four factors in the C-DIS: (1) Hygiene Issues, (2) Parasite/Infection, (3) Food/Environmental, and (4) Injury/Viscera.

The distribution of the data was explored for normality through visual inspection of the Normal Q-Q plot of the mean difference scores (pathogen-free subtracted from pathogen-salient mean scores) for each corresponding analysis rather than via Shapiro-Wilk test outputs, which are not recommended for sample-sizes >50 (Elliott & Woodward, 2007). The data met the assumptions of parametric tests.

Furthermore, in order to verify adequate statistical power, an *a priori* power and sample size analysis was performed using the Statistics Calculators Website (Soper, 2017) and the guidance of Cohen (1992). We calculated the anticipated effect size $d = .80$ at the statistical power level of .80, with a type I error rate of $\alpha = .01$, and found that a minimum total sample size of $N = 78$ is required. Based on our sample size of $N = 127$, sufficient power to detect even a moderate difference was expected.

Internal consistency of image sets, intra-image sets, and factors

Internal consistency was assessed as an estimate of reliability by calculating Cronbach's *alpha* scores on each of the two image sets, on the pathogen-salient and pathogen-free sets within each full image set, and within each of the factors of the C-DIS.

C-DIS: The results indicate high internal consistency for the C-DIS as a whole (α = .946). Internal consistency was high for both the pathogen-salient (α = .944; item variance .527) and pathogen-free images (α = .932; item variance .177). There was also high internal consistency for individual factors in both the pathogen-salient set (Hygiene Issues, α = .810; Parasite/Infection, .787; Food/Environmental, .846; Injury/Viscera, .848) and the pathogen-free set (Hygiene Issues, α = .807; Parasite/Infection, .731; Food/Environmental, .712; Injury/Viscera, .765).

Curtis Image Set: The results indicate high internal consistency for the Curtis image set as a whole (α = .870), as well as for the pathogen-salient (α = .789; item variance .643) and pathogen-free sets (α = .766; item variance 1).

We also calculated Cronbach's *alpha* on the full C-DIS and Curtis sets individually to assess the internal consistency of each set within the four largest subsets of raters split by country of origin: Colombia, USA, UK, and the Czech Republic. There was high internal consistency for C-DIS within each country of origin: Colombia (α = .957), USA (α = .960), UK (α = .945), and the Czech Republic (α = .966). There was also high internal consistency for the Curtis set within each country of origin: Colombia (α = .896), USA (α = .874), UK (α = .884), and the Czech Republic (α = .922).

Overall, the individual images within each analysed set showed similar degree of internal consistently to their corresponding set image cohorts. *Alpha* scores after item (image) deletion indicated that the internal consistency of each set could not be increased by removing any of the images within their corresponding set. Further, none of the images scored under α = .610, and the majority of the scores were above α = .750. The images, the intra sets, and the full image sets showed strong internal consistency as measured across a varied cross-cultural sample of individuals, which lends reliability, accuracy and, therefore, strength to the subsequent findings.

2.3 Results

2.3.1 The C-DIS analysis

Image-set correlations

We first correlated the mean scores for disgust given by participants to the C-DIS pathogen-salient images and the Curtis pathogen-salient images. A strong positive correlation was found between the two measures, Pearson $r(127) = 0.774$, $p < .001$,

showing that the C-DIS and Curtis sets affected raters similarly and suggesting that they measure responses along the same construct. We then proceeded to compare the image sets in more detail.

Disgust ratings

Table 2.4 shows the mean disgust ratings for each of the pathogen-salient and pathogen-free images in the C-DIS and Curtis image sets. Among the C-DIS, pathogen-salient images were judged to be significantly more disgusting than their paired pathogen-free version (paired-samples t tests, $p < .001$ in every case). Paired-samples t-tests were also conducted to compare the mean disgust scores between pathogen-salient and pathogen-free images representing each of the four factors (Table 2.5; here, grand means were calculated for each factor by averaging their 5 constituent item means). Again, grand means for pathogen-salient disgust ratings were significantly larger, for each factor, than the pathogen-free scores.

Table 2.4 also shows the equivalent scores for the Curtis images as determined by our raters, as well as (for purpose of comparison) the scores provided by the original raters in Curtis et al.'s (2004) study. As would be expected, our raters awarded significantly higher disgust scores to pathogen-salient images than the pathogen-free control images, which provides justification for a more direct comparison of the two image sets using the ratings we collected.

2.3.2 Comparing C-DIS and the Curtis image set
Interaction and main effects

To compare the two image sets directly, we used a two-way repeated measures ANOVA with both image set (C-DIS, Curtis) and image type (pathogen-salient, pathogen-free) as within-participants factors. In addition to the expected main effect of image type, with higher disgust scores for pathogen-salient images, $F(1, 126) = 1219.81$, $p < .001$, $\eta_p^2 = .906$, there was a main effect of image set, $F(1, 126) = 344.25$, $p < .001$, $\eta_p^2 = .732$, with higher disgust scores in the C-DIS, due to particularly high ratings in the pathogen-salient condition (Figure 2). More importantly, we found a significant interaction between image set and image-salience, $F(1, 126) = 667.46$, $p < .001$, $\eta_p^2 = .841$. Pairwise *post-hoc* tests confirmed that the pathogen-salient disgust scores were significantly higher for the C-DIS than the Curtis set, $t(126) = 27.22$, $d = 2.5$, while the pathogen-free versions were awarded lower disgust scores in the C-DIS compared with the Curtis set, $t(126) = -9.59$, $d = 0.45$ (both $p < .001$).

Difference ratios

We correlated difference ratios between pathogen-salient and pathogen-free scores of the C-DIS and the Curtis set. A significant, nearly moderate, positive correlation was found between the two measures, Pearson $r(127) = 0.283$, $p < .001$, showing that disgust sensitivity of individual raters was affected and assessed in a similar way by each set.

Table 2.4 Mean disgust scores for pathogen-salient and pathogen-free images, the difference ratio of how much more disgusting the salient images are compared to their pathogen-free counterparts, and the descriptive statistics from paired-sample t-tests for each image pair. Top: C-DIS; Bottom: Curtis image set, original Curtis et al. (2004) study shown in brackets.

Images	Pathogen		Difference		
	Salient	**Free**	**ratio**	**t**	**p**
C-DIS					
Dirty sanitary items	3.90	1.49	2.61	15.46	<.001
Dirty/unflushed toilets	6.14	1.78	3.43	31.54	<.001
Bad dental hygiene	5.79	1.68	3.43	28.69	<.001
Eating snot/bogeys	5.23	1.63	3.19	24.04	<.001
Ingesting faecal matter	6.22	1.43	4.34	34.41	<.001
Rotting flesh crawling w/worms	6.31	1.32	4.76	40.70	<.001
Worms in the food	5.20	1.75	2.96	20.72	<.001
Dirty, fungus-infected toenails	6.17	1.93	3.18	29.82	<.001
Flesh-eating disease	6.07	1.41	4.28	33.94	<.001
Crawling swarm of insects	3.57	1.89	1.88	9.80	<.001
Decomposing animal carcass	3.91	1.18	3.30	16.33	<.001
Rotting meat	4.49	1.76	2.54	16.13	<.001
Liquid coming out of rubbish	3.52	1.63	2.15	13.04	<.001
Stepping in dog faeces	5.25	1.74	3.02	23.35	<.001
Eating uncooked rotting masses	5.16	1.45	3.54	22.41	<.001
Dead, disfigured body	4.14	1.17	3.52	16.94	<.001
Infected wound oozing pus	5.56	1.69	3.29	25.41	<.001
Exposed intestines	5.26	1.48	3.53	24.47	<.001
Exposed brains	4.10	1.53	2.67	14.48	<.001
Vomit	5.05	1.64	3.07	23.93	<.001
Mean	5.05	1.58	3.23	23.28	
Curtis image set (original study)					
Plate of bodily fluid	3.14 (2.6)	1.71 (1.6)	1.83 (1.62)	10.70	<.001
Person looking ill	2.25 (3.1)	1.38 (1.5)	1.62 (2.06)	8.26	<.001
Crowded train carriage	1.70 (2.0)	1.38 (1.2)	1.22 (1.66)	3.78	<.001
Towel stained/bodily secretions	3.75 (3.9)	1.55 (1.6)	2.41 (2.43)	15.03	<.001
Skin lesion/pus-inflammation	5.34 (4.6)	3.07 (3.6)	1.73 (1.27)	16.76	<.001
Gastro-intestinal worm	3.55 (3.8)	3.16 (3.7)	1.12 (1.02)	2.22	.029
Louse	2.62 (3.5)	1.94 (2.8)	1.35 (1.25)	5.16	<.001
Mean	3.19 (3.4)	2.03 (2.3)	1.61 (1.62)	8.84	

As suggested by the significant image set x image type interaction, the mean difference ratio for the C-DIS images was significantly larger than for the Curtis set. On average, the pathogen-salient images in the C-DIS were judged by our raters to be 3.23 times more disgusting than the pathogen-free images (range = 1.88 - 4.76), compared with 1.61 (range = 1.12 – 2.41) times for the Curtis set (and 1.62 times as scored by the original raters in that study). With respect to individual image pairs, the difference ratios were larger for C-DIS image pairs than those for the Curtis images in every case except two: 'crawling swarm of insects' and 'liquid coming from the rubbish' (see Table 2.4). In addition, we observed that the overall mean difference ratios between pathogen-salient and pathogen-free images for each C-DIS factor (shown in Table 2.5) was larger than the Curtis set as a whole.

Table 2.5 Mean disgust scores for pathogen-salient (PS) and pathogen-free (PF) images, and the mean (and standard error) difference ratio (PS/PF), for each of the four factors identified by exploratory factor analysis of disgust items.

Factors	Mean PS	Mean PF	Difference Ratio	S.E.	t	df	p
1 Hygiene Issues	5.44	1.61	3.38	0.10	39.23	126	<.001
2 Parasite/Infection	5.47	1.66	3.30	0.10	38.41	126	<.001
3 Food/Environment	4.47	1.55	2.88	0.11	25.69	126	<.001
4 Injury/Viscera	4.83	1.50	3.22	0.12	27.62	126	<.001

To obtain a direct comparison between image sets, we conducted a one-way ANOVA to compare the mean difference ratios for the individual image pairs across the C-DIS ($N = 20$), our current ratings of the Curtis set ($N = 7$) and those from the original study ($N = 7$). Mean difference ratios were significantly different between image sets, $F(2, 31) = 27.94$, $p < .001$, $\eta_p^2 = .643$. Tukey *post hoc* tests revealed that the mean difference ratio for C-DIS (3.23) was significantly larger than for both the current (1.61, 95% CI [0.94-2.29], $p < .001$) and original (1.62, 95% CI [0.95-2.29], $p < .001$) ratings of the Curtis set. Importantly, there was no difference between the ratios generated by our current ratings of the Curtis set and those in the original Curtis study ($p = .999$), reinforcing the earlier finding that our raters assessed those images in the same way and that other differences between the image sets cannot be attributed to unusual ratings in our study.
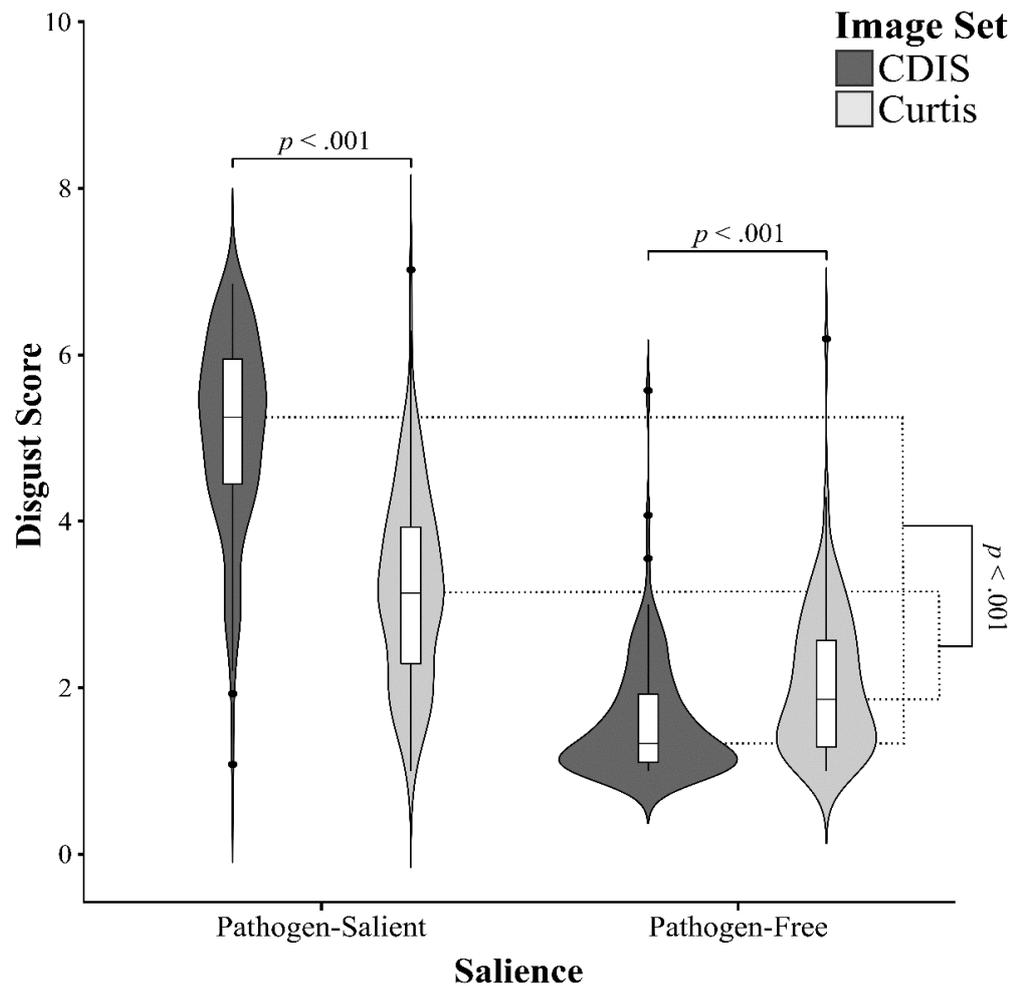
Figure 2.2 Kernel probability density (violin) plots with boxplots for disgust scores, split by image salience (pathogen-salient, pathogen-free) and image set (dark grey: C-DIS; light grey: Curtis). See text for statistical comparisons.

2.4 Discussion

We have reported a 7-stage, bottom-up process culminating in a new image set (the Culpepper Disgust Image Set, C-DIS) which contains 20 pathogen-salient and 20 paired pathogen-free images. The multi-stage process was critical in order to generate a comprehensive overview of what people find disgusting, across different parts of the world, and how these triggers of disgust are inter-related. Importantly, the fact that the images were generated by the researchers, rather than being gleaned from the internet (for example), has two key advantages: it is possible to ensure that in every case the pathogen-free 'control' images are appropriately matched to their pathogen-salient counterparts, and furthermore, from a practical point of view, the images are available to be used freely by researchers without copyright or ethical concerns.

We anticipate that the C-DIS can be used in two ways: (i) to activate pathogen disgust in participants in a treatment condition (i.e., through exposure to the pathogen-salient set) compared with a control group (i.e. participants who see the pathogen-free set), or (ii) as a tool to assess individual participants' pathogen disgust sensitivity (i.e. asking them to score both pathogen-salient and pathogen-free images and subsequently calculating difference scores).

2.4.1 Effectiveness and improvement

There was a strong positive correlation between scores given by individual participants to the pathogen-salient images in both image sets. This indicates convergent validity in ability to elicit the emotion of disgust across the two image sets: if the Curtis pathogen-salient images are judged to trigger disgust, then the C-DIS pathogen-salient images appear to have a similar effect. Furthermore, the significant positive correlation between pathogen-salient: pathogen-free difference ratios in the two image sets also demonstrates convergent validity in the potential for assessing disgust sensitivity. In other words, individual participants who were especially (relative to other participants) disgusted by the Curtis pathogen-salient images compared with the pathogen-free images, and could therefore be said to have high disgust sensitivity, would also be found to have high disgust sensitivity based on responses to the C-DIS images.

Notwithstanding these between-set correlations, we conducted several analyses to determine the effectiveness of the C-DIS as a trigger of disgust and to compare its effectiveness against the images in the Curtis et al. (2004) image set. The analyses indicate that the bottom-up approach has resulted in an image set that is both effective as an experimental instrument and as an improvement to the Curtis set.

Considering the effectiveness of the C-DIS, the disgust scores for the pathogen-salient images were significantly larger than those for the pathogen-free images. The significant difference between these two scores suggests that the pathogen-salient images did elicit the desired effect – disgust – while the pathogen-free images served as effective 'non-disgusting' controls to their salient-image counterparts. This is further supported by the difference ratio calculations between the C-DIS intra-sets representing each of the four identified underlying factors.

The comparisons between the two image sets indicate that each of our three improvement criteria were met. The mean disgust scores for our pathogen-salient

images were significantly larger than for the pathogen-salient images in the Curtis set, suggesting that the C-DIS images activate the disgust response more strongly (*criterion 1*). Furthermore, the mean disgust scores for our pathogen-free images were significantly lower than the pathogen-free images from the Curtis set (*criterion 2*). This reduces the chance, in future experimental studies, for disgust to be unintentionally elicited in participants in the control condition. As a result of these properties, the difference ratios between pathogen-salient and pathogen-free images for the C-DIS were significantly larger than the difference ratios in the Curtis set (*criterion 3*). Larger difference ratios increase the efficacy of any manipulation of disgust, if either pathogen-salient or pathogen-free images are seen by treatment and control groups, respectively. They should also increase the ability to discriminate between different levels of disgust sensitivity, if individual participants are asked to judge both kinds of image.

There are two further advantages worth noting. One relates to the number of images: 20 pathogen-salient (and matched pathogen-free) images in the C-DIS set, whereas the Curtis set consists of only 7. In addition to the average potency of each individual image in eliciting disgust, the C-DIS should therefore also ensure a comparatively prolonged exposure to a more diverse set of pathogen threats when shown to participants in future research, providing an increased likelihood of more effectively activating the behavioural immune system. A second is the underlying structure of the C-DIS, differentiating between four different factors that contribute to pathogen-disgust. Our analyses showed that the disgust scores for pathogen-salient images were significantly larger than for the pathogen-free images in all four factors. This suggests that the four factors are, for the most part, equally supportive of the image set as a whole. As illustrated in Table 2.5, the mean pathogen-free scores for each individual factor in the C-DIS is smaller than the overall mean pathogen-free score for the Curtis set (whether the latter is determined using raters in our study or those in the original Curtis et al. study; see Table 2.4). Similarly, the overall mean pathogen-salient score is larger for each C-DIS factor than both Curtis measurements (current and original), as are the overall mean difference ratios.

2.4.2 The C-DIS and the DIRTI

The coincidental timing of the development of both the C-DIS and the DIRTI (Haberkamp et al., 2017) demonstrates recognition of the need for high-quality and validated image sets for the study of disgust. Both instruments importantly address

methodological issues of the previously developed image sets, specifically target the disgust emotion, and elicit disgust along multiple factors. However, as the two image sets use different perspectives and have different aims, they thus have advantages that correspond to each individual approach. The C-DIS was designed from an evolutionary perspective to investigate the effects of BIS activation on human behaviour, whereas the DIRTI was designed from a clinical perspective to be used for therapeutic and experimental purposes involving psychiatric disorders. There is considerable overlap from both perspectives in that psychiatric disorders such as phobias are considered to have evolutionary origins (Marks & Nesse, 1994; Nesse, 2005; Öhman & Mineka, 2001); therefore, the two sets do not discount each other, and in fact are likely to be complementary. However, compared with the six DIRTI categories (food, animals, body products, injuries/infection, death, hygiene), our analytical categorisation suggests four underlying components to pathogen disgust and items are assigned to categories based on functional considerations rather than the clinical approach focusing on phobias. Thus, for example, the C-DIS treats injuries and infection as two distinct triggers of disgust, while the DIRTI combines them.

2.4.3 Limitations

Despite the above, we acknowledge several limitations of this study. The first limitation is regarding the nature of the sample. Participants for each stage of the study were recruited via online surveys distributed throughout various social media outlets and through universities. For example, in Stage 1 there were 460 participants of various ages and gender. While the study was cross-cultural to the extent that we solicited items that trigger disgust from participants across four countries, and had the final images similarly rated, our method of recruitment suggests that most of the participants were of reasonably WEIRD backgrounds (Westernised, Educated, Industrialised, Rich, and Democratic: see Henrich, Heine, & Norenzayan, 2010). For example, each participant had to have access to a computer with global internet service; they had to be somewhat educated in order to use a computer and read somewhat complex instructions; and they had to have, or at least have access to (e.g. via parent(s), the financial means that allow for such access to computers and education. Many of the participants were students or staff recruited via universities and university. This may have biased the kinds of items suggested by the participants in Stage 1. Future studies, including future attempts to devise a new image set or to improve upon the new set of images devised here, would do well to include non-WEIRD participants from an even wider geographical spread, if possible.

Demographic data was not collected regarding participant work experience or education, or of the topic of study by students and staff for any of the stages. This may have biased results in that, for example, participants working or studying in the medical field may be exposed to these types of disgust items more regularly than others. Repeated exposure to disgust items may reduce disgust sensitivity, which would have affected the overall disgust scores. Level of hunger was not recorded either, which could be important when attempting to measure disgust sensitivity. Hunger can induce disgust suppression for pathogenic foods (Al-Shawaf, Conroy-Beam, Asao, & Buss, 2014), which can have an effect on the disgust ratings for the pathogenic food images in future studies. Furthermore, as with all online studies, it is impossible to control whether participants are under the influence of stimulants (e.g. coffee, cigarettes) and other intoxicants or medication (e.g. alcohol, anti-anxiety) that can affect perception and dull senses (noted in Culpepper, 2014). For accuracy and validity, further studies should consider this variation in rater experience. Having said this, such issues should not have affected the specific comparisons we made between image sets.

In Stage 4, it was necessary to make some judgments regarding item distinctiveness. For example, we conflated the individual items "cat vomit", "children's vomit" and "vomit" into an umbrella category "vomit". It is possible that some of the items lost in this process might have been rated more disgusting than the resulting umbrella term. However, the decision could be justified in that it was likely to be conservative in effect, and it is unlikely that the basic items would be visually distinguished from images in any case. It is therefore unlikely that these rare unification instances jeopardised the integrity of the process.

Finally, although the results of Stage 6 and 7 suggest that the images accomplished the goal they were devised to accomplish, the decisions of how to depict these items and scenarios in their respective images were somewhat subjective. However, we attempted to reduce this through the initial internet search on specific item wordings, selecting a scene that best represented the images generated by the search.

2.4.4 Conclusion

Overall, the current study set out to create a new set of disgust images that can be used in future experimental work on the behavioural immune system. We employed a bottom-up approach to attempt to devise a larger, more comprehensive, and arguably more representative set of images, constructed of items, scenes, and scenarios that

trigger pathogen disgust, which is thought to be the most evolutionarily ancient domain of the emotion (Schaller, 2006; Schaller & Duncan, 2007; Tybur et al., 2009). This is particularly important when considering research into this adaptation at a cross-cultural level. This methodological process resulted in a set of 20 cross-culturally determined and validated disgust images specifically designed to trigger pathogen disgust and activate the behavioural immune system. One of the main validation steps for this new set was to compare it against a set already available in the literature and used by other researchers, the Curtis et al. (2004) image set. The new set needed to (i) elicit pathogen disgust; to do so reliably (ii) in individuals, and (iii) in cross-cultural samples; (iv) to elicit disgust more strongly than Curtis' image set; and (v) exhibit larger differences between the pathogen-salient and pathogen-free sets compared to Curtis's set. Our results showed clearly that this cross-cultural, multi-staged, bottom-up process has produced a new set of disgust images that meet these requirements. We suggest that our image set is an effective instrument for consistently and reliably eliciting pathogen disgust and measuring pathogen disgust sensitivity across cultures. Moreover, it does so along four distinct pathogen disgust factors – something not previously done.

The C-DIS was subsequently employed in each of the following studies of this thesis.

Chapter 3: Pathogen stress and MHC preference

3.1 Introduction

Mating is arguably the oldest social behaviour in sexually reproducing species. In order to mate and reproduce, an individual must first choose or be chosen as a mating partner. Due to anisogamy and the disparity between males and females in obligatory investment in reproduction, females have evolved to be the more discriminating of the sexes in mate choice (Trivers, 1972). Females choose mates based on the direct benefits a mate(s) can provide to self and offspring, e.g. resources such as food, protection, and care, and indirect benefits to the offspring produced from that mate pairing, such as genetic quality and health (Andersson, 1994). They have evolved preferences for mates who exhibit cues that suggest the ability to confer these benefits. For example, women express adaptive preferences for partners who exhibit indicators of willingness to invest time, care, energy and finances in long-term relationships and offspring, as well as for partners who exhibit indicators of phenotypic and genetic quality, i.e. 'good genes' that would be passed on to resulting progeny (Andersson, 1994; Gangestad & Simpson, 2000; Trivers, 1972; Williams, 1966; Zahavi, 1975).

However, the extent to which they prefer one over the other in a partner is thought to be a trade-off formulated on costs-benefits analysis influenced by, among other things, the local ecological environment (Gangestad & Simpson, 2000; Thornhill & Fincher, 2014b). That is, the priority or value given to one type of benefit over the other in a potential mate is condition-dependent. Thornhill and Fincher propose in their parasite-stress theory of values and sociality that this trade-off is contingent upon the level of pathogen prevalence in the local ecological environment, which is thought to activate the behavioural immune system (BIS). They theorise that high parasite stress activates the BIS and causes women to adapt their mate preferences to be more concerned with and thus hold more value in the health and genetic quality of a mate at the expense of other benefits. The higher the stress, the stronger preferences for phenotypic and genetic indicators of these qualities in them they have. The significance of this trade-off becomes clearer when considering that indicators of genetic quality are also associated with negative personality traits which afford less investment in offspring and partners and poorer relationship and parenting qualities (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010).

As noted in subsection 1.3.1 of this thesis, the three main indicators of health and genetic quality in males are sexually dimorphic (masculine), average, and symmetrical physical characteristics (Gangestad & Scheyd, 2005; Scheyd et al., 2008; Thornhill &

Gangestad, 1993). These indicators combine to form a main part of what is termed as physical attractiveness. Through the parasite-stress theory of sexual selection, Hamilton and Zuk (1982) reasoned that physical attractiveness is an indicator of 'good genes' – specifically, genes that indicate strong resistance to parasites and thus afford developmental stability. Based on this and Thornhill and Fincher's theory, the value individuals hold toward physical attractiveness should be reflective of BIS-activation via the level of pathogen prevalence in the local region. As individuals are the constituent parts of a society, a society's cultural values regarding physical attractiveness should vary with the level of pathogen prevalence in the local ecological environment. In addition to the research and evidence presented in subsection 1.3.1 (e.g. Gangestad & Buss, 1993), there is an expanding body of evidence to support this notion.

For example, Lee and Zietsch (2011) conducted a study to test the theorised trade-off by women in their preference for indirect versus direct benefits. They recruited women to complete one of three questionnaires, each of which primed them with a different type of environmental threat: either pathogen prevalence, resource scarcity, or an unrelated threat as a control. The women then engaged in a forced trade-off task. They were shown a list of 10 traits, 5 representing 'good-genes' traits (indicators of genetic quality) and 5 representing 'good-dad' traits (indicators of resource attainment and parental investment) and were assigned a limited amount of 'mate dollars' with which they could invest in the traits to create the ideal partner. Results showed that women who were primed with the pathogen prevalence invested significantly more mate dollars in the 'good-genes' traits, which directly reduced investment in 'good-dad' traits, thus illustrating the theorised trade-off.

Facial attractiveness is perhaps one of the more obvious features of physical attractiveness, and perhaps the easier to use in studies on the topic. Facial attractiveness – that is, facial masculinity, averageness, and symmetry, is an indicator of phenotypic and genetic quality (Gangestad & Scheyd, 2005; Scheyd et al., 2008; Thornhill & Gangestad, 1993). In addition to odour, facial attractiveness and masculinity are phenotypic traits thought to be indicators of robust immune systems in potential partners that would confer benefits through disease resistance in potential offspring. Studies show that the value in facial attractiveness, particularly masculinity, held by individuals and cultures correlates with pathogen stress in the ecological environment as well as health measures of countries (DeBruine, Jones, Little, Crawford, & Welling,

2011; DeBruine, Little, & Jones, 2012). Moreover, DeBruine et al. (2010) found that pathogen disgust in women predicted their preferences for facial masculinity in men. Particularly relevant to the study presented in this chapter, Little, DeBruine, and Jones (2011) found that women who viewed pathogen-relevant images preferred more masculine and symmetrical faces than women who viewed control images. Ainsworth and Maner (2019) and Young et al. (2011) generated similar findings in that participants in the disease-relevant conditions preferred more symmetrical faces than those in the control conditions.

It is unclear whether physical attractiveness is a reflection of 'good genes' or actually a reflection of heterozygosity at specific loci of the major histocompatibility complex (MHC) – that is, genetic quality may be defined as MHC heterozygosity (Brown, 1997; Brown, 1998). MHC heterozygosity is associated with symmetry, developmental homeostasis, parasite resistance and better immune systems (Brown, 1997; Brown, 1998; Folstad & Karter, 1992). MHC-dependent mating preferences are thought to confer adaptive benefits to self and potential progeny in that it aids in kin recognition and the avoidance of inbreeding, and MHC disassortative mating produces offspring with MHC heterozygosity which may enhance their immunocompetence with higher resistance to parasites (Havlíček & Roberts, 2009; Penn & Potts, 1999; Roberts & Little, 2008; Tooby, 1982). But it is difficult to ascertain how MHC genes are expressed in physical attractiveness and whether heterozygosity is associated with facial attractiveness or the phenotypic traits that influence it. Roberts et al. (2005) conducted a study to investigate whether there is a link between facial attractiveness and MHC heterozygosity as a measure of genetic quality. They recruited 50 women to rate the faces of men who had previously had their genomic DNA typed at three key loci in the MHC for attractiveness and skin healthiness. They found that women rated men who were heterozygous at these loci as significantly more attractive and their skin as significantly healthier looking than men who were homozygous.

These studies, along with the studies described in Chapter 1, represent a non-exhaustive list of research and evidence that suggests women's preferences for indicators of genetic quality are to some extent influenced by and contingent upon pathogen related cues and concerns, and the advantages availed by mates who are heterozygous at MHC loci. This is the focus of the study presented in this chapter.

3.1.1 Study rationale

Based on previous theory and evidence, Thornhill and Fincher (2014b) propose that variation in parasite stress in the ecological environment imposes causal influence on MHC-dependent mate preferences, such as facial attractiveness and masculinity. However, much of the supporting evidence is correlational and the studies that are not correlational by design, i.e. the experimental studies, arguably have their own methodological issues. For example, Lee and Zietsch (2011) employ a form of semantic priming to activate the BIS in their mate preference trade-off study. However, it may be more ecologically valid to employ visual priming given that perceiving, tracking and processing phylogenetically relevant stimuli in the environment is necessarily a visual medium (Öhman & Mineka, 2001). Visual processing of threatening stimuli such as pathogen-related cues is more evolutionarily ancient than semantic processing of words. Similarly, Lee and Zietsch employ a forced trade-off, budget-allowance paradigm to metaphorically build an ideal mate. But mate choice via cues of physical attractiveness is also necessarily a visual medium. Therefore, having participants view and rate masculine versus feminine men's facial images would offer a more ecologically valid design to study trade-off behaviour related to MHC-driven mate choice via visual indicator traits. Little et al. (2011) do employ both facial images and disgust priming images for this purpose. However, their study employed Curtis et al.'s (2004) disgust image set which was not effectively constructed or validated, and they only consider preferences for masculinity versus femininity of the faces. They do not consider preferences for the attractiveness of the faces or its relationship with MHC zygosity. Roberts et al. (2005) employ facial images and do consider preferences for attractiveness and its relationship with MHC zygosity but do not test the group differences relating to cues of pathogen threat.

Finally, there are only a small handful of studies (known to the researcher) which employ a pre-test/post-test or mixed factorial design to effectively and directly test the proposed causation. However, their methods differ slightly, and even the ones that employed disease- or disgust-relevant images contain the same issues with the chosen visual stimuli as those mentioned in section 2.1.1. Moreover, none of them explicitly set out to test Fincher and Thornhill's proposal. The current study combined components of the studies described here to experimentally test Fincher and Thornhill's proposal. I employ facial images from Roberts et al. (2005) and paired masculine/feminine facial images from Little et al. (2011) and Little et al. (2013). Further, I employ the Culpepper Disgust Image Set (C-DIS: Culpepper et al., 2018) to

visually generate variation in BIS-activation. This study employs a mixed factorial design to test the hypothesis that variation in visual pathogen threat will generate variation in mate preferences for masculinity and MHC heterozygosity as indicated by facial attractiveness. Interactions were predicted, in that participants who view the pathogen-salient images would show a larger increase in preferences for masculine versus feminine faces and in attractiveness ratings for MHC-heterozygotes versus homozygotes than those who view the control images. These interaction effects were predicted to be more prominent in women. In the context of this thesis, such findings would suggest it is possible for cultures to diverge in beliefs about what is attractive as a causal effect of variation in parasite stress in the ecological environment.

3.2 Method

Ethics statement

This study received ethical approval from the General University Ethics Panel at the University of Stirling and adhered to the ethical guidelines of the British Psychological Society. All participants provided prior informed consent and viewed a debriefing page after participation. No reward was offered for participation. The stimuli employed in this study were used with permission from the original researchers.

3.2.1 Participants

A total of 96 participants (70 women, 26 men) with an overall mean age 22.82 ± SD 6.82 (range 18-56) were recruited through various university connections and social media outlets, e.g. Facebook, email. Eighty reported to be heterosexual (83.3%), four homosexual (4.2%), seven bisexual (7.3%), and five 'other' (5.2%). Ninety reported to be White (93.8%), two Black or of African descent (2.1%), three Asian (3.1%), and one 'other'. Forty-three reported to be Christian (44.8%), thirty-six (37.5%) Atheist or Agnostic, twelve (12.5%) 'other', one Muslim, and one Buddhist. Sixty-three of these were from the UK (65.6%), six from the Czech Republic (6.3%), two from Canada, two from Sri Lanka, and one each from Argentina, Australia, Finland, Germany, Ireland, Italy, and Romania.

3.2.2 Materials

The survey consisted of several demographic questions, e.g. age, gender, sexuality, religion. Participation included the Perceived Vulnerability to Disease scale

(PVD: Duncan et al., 2009), a face rating task, a face selection task, and the C-DIS rating task.

Perceived Vulnerability to Disease

This study employed the 15-item PVD scale, which is designed to measure the extent to which individuals perceive themselves as vulnerable to infectious diseases. The scale included statements such as 'If an illness is 'going around', I will get it' and 'It really bothers me when people sneeze without covering their mouths'. See Appendix B for complete PVD scale. An overall mean PVD score was calculated for each individual. Cronbach's *alpha* was conducted on the mean scale scores, $\alpha = .777$. *Alpha* could not be increased to more than .782 by the deletion of any scale items. The PVD scale is comprised of two subscales: the Germ Aversion (PVD_{GA}) and Perceived Infectability (PVD_{PI}) subscales, and evidence from previous studies suggests that strong BIS responses are associated more particularly with heightened vulnerabilities related to the PVD_{GA} subscale (see Ackerman, Tybur, & Mortensen, 2018; Makhanova, Miller, & Maner, 2015). Therefore, mean scores were also calculated for the subscales for each individual to be included in the analysis. Cronbach's was conducted on these mean subscale scores as well, PVD_{GA}: $\alpha = .702$, and PVD_{PI}: $\alpha = .873$. *Alpha* could not be increased to more than .718 and .878 (respectively) by the deletion of any scale items.

Facial image stimuli

This study included the use of two sets of facial images from previous studies.

Facial attractiveness: MHC zygosity

The first set of images consisted of 40 men's faces from Roberts et al. (2005). Roberts and colleagues genetically typed 92 men to determine their zygosity at specific MHC loci. In the second part of that study, they randomly selected a subset of 20 heterozygous and 20 homozygous men from that sample. Those facial images were employed in this study. Mean scores were calculated for participants' ratings of the complete set of 20 homozygous faces and for the complete set of the 20 heterozygous faces, both pre- C-DIS manipulation and again for post- C-DIS manipulation.

Cronbach's was conducted on the ratings for each of the four categories. Pre- C-DIS: homozygous, $\alpha = .960$; heterozygous, $\alpha = .957$. Post- C-DIS: homozygous, $\alpha = .968$; heterozygous, $\alpha = .953$. These could not be increased by any image deletion.

(Images are of actual people therefore for ethical reasons they are not be presented here.)

Facial preference: Masculine versus feminine

The second set of images (borrowed from Little et al., 2011, and Little et al., 2013) consisted of 10 paired images of men's faces (i.e. 20 total). These images are digital composites of a collection of facial photographs each made into one average image. That is, the researchers used a compilation of 5 groups of neutrally posed male and female faces to create composite faces by generating 20 average male and female facial images from the individual photographs. They then delineated 174 feature points on each face and calculated the linear difference between these points for the average male and female face shapes to construct a continuum of 11 face shapes which ranged from +50% masculinised to +50% feminised for both male and female faces (see Perrett, Lee, Penton-Voak, & Rowland, 1998). This generated 10 individual test faces for each sex, each on the 11-point masculine-feminine shape continuum. For the purposes of the current study, only the 10 male facial composites were employed, only utilising the end-points of the shape continuum for each of the test faces, i.e. the most masculinised and the most feminised versions of each. This left 10 paired male facial images – one masculinised and feminised version of each different male face (Fig. 3.1). (For further details on the digital techniques, see Benson & Perrett, 1993; Tiddeman, Burt, & Perrett, 2001).
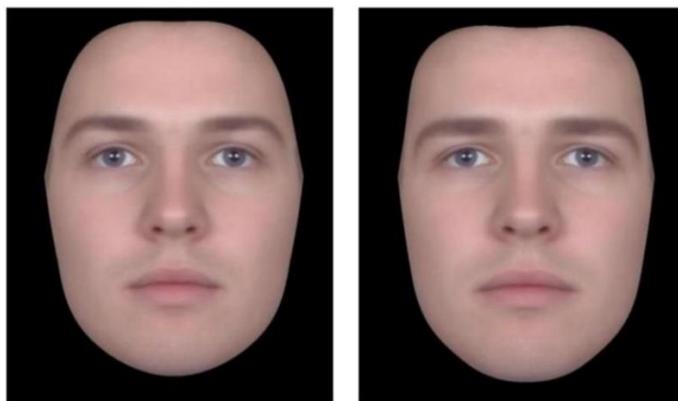
Figure 3.1 Paired images of digitally feminised (L) and masculinised (R) men's faces viewed for preference by participants. (With permission from Little et al., 2013)

Cronbach's was also performed on participants' selections of each paired set, both pre- C-DIS and post- C-DIS: pre- C-DIS selections, $\alpha = .773$; post- C-DIS, $\alpha =$

.787. Neither of these could be increased by any image-pair deletion. For the purpose of analysis, percentages were calculated for each participant based on the number of times they selected the masculine faces over the feminine faces from the ten pairs. This was done individually for both the ten pre- C-DIS image pairs and the 10 post C-DIS image pairs.

Manipulation of pathogen threat

BIS manipulation was conducted via the C-DIS. Half of the participants rated the pathogen-salient images while the other rated the control images on a 7-point scale (0=*not disgusting at all*, 6=*extremely disgusting*). Mean disgust scores were calculated for each C-DIS set. Cronbach's was conducted on both sets: pathogen-salient set, α = .932, and pathogen-free set, α = .895. These could not be increased to more than .935 and .898, respectively, by any item deletion.

3.2.3 Procedure

After completing the demographic questions, participants completed the PVD scale, where they rated how much they agreed or disagreed with the statements on a 7-point scale (1=*strongly disagree*, 7=*strongly agree*). Participants then sequentially viewed and rated the randomised set of 40 men's faces for attractiveness on a 7-point scale (0=*not at all attractive*, 6=*very attractive*). Next, they viewed the 10 pairs of men's faces (sequentially in pairs) and selected which face they found more attractive of the two faces for each pair. Participants were then randomly assigned to view and rate either the C-DIS pathogen-salient image set or the C-DIS control set, after which participants completed the face rating and face selection tasks a second time so that any changes in their preferences as a result of visual pathogen stress could be analysed.

3.3 Results

This section will include descriptions of data preparation, including statistical analyses to check the effectiveness of the C-DIS manipulation on BIS-activation, and the results for analyses on both facial attractiveness ratings and preferential selection of facial masculinity versus femininity. Analyses were conducted on the sample as a whole (women and men), but also for women and men separately. Normal distribution of the data was assumed according to the Central Limit Theorem, which states that sample sizes of ≥ 30 are likely to be normally distributed (Field, 2013; Lumley, Diehr, Emerson, & Chen, 2002). Parametric tests were therefore used for analysis.

3.3.1 Manipulation check

Participants who viewed the C-DIS pathogen-salient images were predicted to show an increase in their ratings of attractiveness toward the heterozygous faces and an increased preference for masculinity compared to participants who viewed the C-DIS control images. It was therefore imperative to test whether the C-DIS images had the intended manipulation effect, i.e. that the pathogen-salient images sufficiently evoked the BIS and the control images left the BIS sufficiently inactive. First, the ratings of C-DIS images were averaged to create a mean disgust score for each participant. I then standardised the disgust scores for each condition into z scores and assessed these data for outliers. Two outliers (females) were found to be > 2 standard deviations larger than the mean ratings in the control condition, suggesting that the control images likely evoked disgust for these participants. Whereas, three outliers (two males and one female) were found to be < 2 standard deviations smaller than the mean ratings in the pathogen-salient condition, suggesting that these images likely did not sufficiently activate the BIS in these participants. These participants were therefore excluded from the analysis, leaving N=91.

An independent samples t-test was then conducted on the disgust scores for both C-DIS image sets to determine whether the pathogen-salient images were rated as significantly more disgusting than the control images. Significantly larger disgust ratings for the pathogen-salient images would suggest that these images sufficiently activated the BIS for the experimental group in comparison to the control group. The pathogen-salient images (5.46 ± 0.88) were rated as significantly more disgusting than the control images (1.93 ± 0.65), a statistically significant difference of 3.53 (95% CI, $3.20 - 3.85$), $t(89) = 21.93$, $p < .001$, $d = 4.56$. This suggests the C-DIS images effectively manipulated participants' BIS as intended.

3.3.2 Analysis of facial attractiveness and MHC zygosity

A three-way mixed ANOVA was conducted with image condition (pathogen-salient and control) as the between-participants factor, exposure (pre- and post-manipulation) as a within-participants factor, and two levels of zygosity (homozygous and heterozygous) as a within-participants factor, with the mean attractiveness ratings for each face as the dependent variable. Assessment of Box's test showed sufficient homogeneity of covariance ($p = .108$) and Levene's test showed sufficient homogeneity of variance for all four pre- and post- manipulation face rating measures (ps > .181). Analysis revealed no significant interaction effect between attractiveness

ratings, exposure, and image condition, $F(1, 87) = 0.049$, $p = .825$, $\eta p^2 = .001$. However, there was a significant main effect of exposure, $F(1, 87) = 8.84$, $p = .004$, $\eta p^2 = .092$, and a significant main effect of zygosity, $F(1, 87) = 79.05$, $p < .001$, $\eta p^2 = .003$, on attractiveness ratings. Attractiveness ratings for both types of faces were significantly higher prior to the C-DIS task than after it, and participants rated heterozygous faces as significantly more attractive than homozygous faces.

Women's ratings of facial attractiveness and MHC zygosity

A three-way mixed ANOVA was again performed with the same variables, this time on women's data only. Results were similar to those reported above. Box's test showed sufficient homogeneity of covariance ($p = .090$) and Levene's test showed sufficient homogeneity of variance for all four pre- and post- manipulation face rating measures (ps > .082). Again, there was no significant interaction effect between attractiveness ratings, exposure, and image condition, $F(1, 63) = 0.55$, $p = .815$, $\eta p^2 = .001$. There was again a significant main effect of exposure, $F(1, 63) = 7.10$, $p = .010$, $\eta p^2 = .092$, and a significant main effect of zygosity, $F(1, 63) = 60.55$, $p < .001$, $\eta p^2 = .490$, on attractiveness ratings. This followed the same pattern as reported for the participant sample as a whole (women and men combined).

Covariation: attractiveness ratings, exposure, MHC zygosity and PVD

To investigate the lack of interaction between attractiveness ratings, exposure, and image condition, I conducted three-way mixed ANCOVAs on both the full set of data (women and men combined) and also on women's data only, including overall PVD scores, and PVD_{GA} and PVD_{PI} scores as covariates. For women's data, I also included women's reported day in their ovulatory cycle.

Full data set: results showed no significant covariation of overall PVD scores ($p = .202$), PVD_{GA} ($p = .200$), or PVD_{PI} ($p = .204$).

Women's data only: results showed no significant covariation of overall PVD scores ($p = .852$), PVD_{GA} ($p = .858$), PVD_{PI} ($p = .863$), or day in cycle ($p = .876$).

3.3.3 Analysis of preference for facial masculinity

A two-way mixed ANOVA was conducted with image condition (pathogen-salient and control) as the between-participants factors, and exposure (pre- and post-manipulation) as the within-participants factor, with the number of masculine faces preferred out of each of the ten pairs as the dependent variable. Box's test suggested sufficient homogeneity of covariance ($p = .520$) and Levene's test showed sufficient

homogeneity of variance for masculine faces preferences both pre- and post-manipulation face rating measures ($p = .051$, $p = .557$, respectively). There was no significant interaction effect between image condition and exposure, $F(1, 86) = 0.141$, $p = .708$, $\eta p^2 = .002$, no main effect of exposure, $F(1, 86) = 2.87$, $p = .094$, $\eta p^2 = .023$, and no main effect of image condition, $F(1, 86) = 1.18$, $p = .281$, $\eta p^2 = .014$, on preference for masculine faces. There was no statistically observable pattern of increased preference for masculinity.

Women's preference for facial masculinity

A two-way mixed ANOVA was conducted again on women's data only using the same variables. Box's test suggested sufficient homogeneity of covariance ($p = .569$) and Levene's test showed sufficient homogeneity of variance for masculine faces preferences both pre- and post- manipulation face selection measures ($p = .059$, $p = .646$, respectively). There was no significant interaction effect between image condition and exposure, $F(1, 62) = 2.27$, $p = .136$, $\eta p^2 = .035$, no main effect of exposure, $F(1, 62) = 0.12$, $p = .915$, $\eta p^2 < .001$, and no main effect of image condition, $F(1, 62) = 3.03$, $p = .087$, $\eta p^2 = .047$, on preference for masculine faces. Again, there was no statistically observable pattern of increased preference for masculinity.

Covariation: facial preferences, exposure and PVD

The lack of interaction between facial preferences and exposure was further investigated via two-way mixed ANCOVAs. These were conducted on both the full set of data (women and men combined) and again on women's data only, including overall PVD scores, and PVD_{GA} and PVD_{PI} scores as covariates. Women's reported day in their ovulatory cycle was again included for women's data.

Full data set: results showed no significant covariation of overall PVD scores ($p = .398$), PVD_{GA} ($p = .405$), or PVD_{PI} ($p = .398$).

Women's data only: results showed no significant covariation of overall PVD scores ($p = .655$), PVD_{GA} ($p = .670$), PVD_{PI} ($p = .654$), or day in cycle ($p = .414$).

3.3.4 Noteworthy findings

Based on previous theory and research, I conducted a paired-samples *t*-test on the initial (pre-manipulation) ratings of the full data set (men and women combined) for homozygous and heterozygous faces. Results showed that heterozygous faces (2.67 ± 0.99) were rated as significantly more attractive than homozygous faces (2.39 ± 0.92), a statistically significant difference of 0.28 (95% CI, $0.22 - 0.35$), $t(90) = 8.35$, $p <$

.001, $d = 0.29$. I split the file by gender and found this pattern also held for both women's and men's ratings individually (ps $< .001$).

Then for the facial preference analysis, I converted the number of times out of ten each participant preferred the masculine versus the feminine face in the initial preference task (pre-manipulation) into mean percentage scores and conducted a paired-samples t-test on these scores. Results showed that the masculine faces were preferred at a significantly larger percentage rate (M=62%) than feminine faces (M=38%), $t(88) = 4.12$, $p < .001$. I then split the file by gender and found that women preferred the masculine faces (M=63%) at a significantly larger percentage rate than feminine faces (M=37%), $t(64) = 3.86$, $p < .001$, $d = 0.93$. Men showed no significant difference in facial preference ($p = .145$).

3.3.5 Correlational analysis

Due to the lack of significant interactions, I ran Pearson's one-tailed correlations on PVD scores with the initial (pre-manipulation) facial attractiveness ratings and percentages of preferences for facial masculinity for the whole sample (women and men) (Table 3.1) and the data split by gender (Table 3.2). No significant correlations were found between PVD scores (including subscales) and MHC-dependent preferences for either sample grouping. As an aside, day of ovulatory cycle was included in the analysis for women's data – no significant correlation with any other variable was found.

Table 3.1 Correlations for perceived vulnerability to disease scores (PVD, overall and by germ aversion and perceived infectability subscales), initial mean attractiveness ratings for MHC homozygous and heterozygous faces, and percentages of preferences for masculine faces (whole sample).

	PVD Scores	PVD$_{GA}$ Scores	PVD$_{PI}$ Scores	MHC HomoZ	MHC HeteroZ
MHC Homozygous	-.007	-.064			
MHC Heterozygous	.004	.048	.053	.946**	
Masculine faces	-.038	-.048	-.010	.067	.085

*. Correlation is significant at the 0.05 level (1-tailed).
**. Correlation is significant at the 0.01 level (1-tailed).

Table 3.2 Correlations for perceived vulnerability to disease scores (PVD, overall and by germ aversion and perceived infectability subscales), initial mean attractiveness ratings for MHC homozygous and heterozygous faces, and percentages of preferences for masculine faces (split by gender).

	PVD Scores	PVD_{GA} Scores	PVD_{PI} Scores	MHC HomoZ	MHC HeteroZ
Women					
MHC Homozygous	.007	-.018	.023		
MHC Heterozygous	.006	-.026	.029	.940**	
Masculine faces	-.081	-.124	-.001	.052	.096
Men					
MHC Homozygous	.101	-.099	.212		
MHC Heterozygous	.126	-.044	.194	.960**	
Masculine faces	-.140	.001	-.177	.145	.091

*. Correlation is significant at the 0.05 level (1-tailed).

**. Correlation is significant at the 0.01 level (1-tailed).

3.4 Discussion

This study experimentally tested the proposal laid out in Thornhill and Fincher's (2014b) parasite-stress theory, that variation in pathogen threat causes variation in mate preferences. Previous studies and evidence (Fincher et al., 2008; Fincher & Thornhill, 2008a; Fincher & Thornhill, 2012; Thornhill & Fincher, 2014b) has shown a strong relationship between pathogen stress and various components of social behaviour, arguably causal, but none have tested a direct causal relationship via a pre-test/post-test, or mixed factorial design. As far as I am aware, this study is the first to do so. The results of this study do not provide support for the parasite-stress theory. Analysis revealed no interaction effects between groups and image condition. There was no three-way interaction. Participants exposed to the pathogen-salient images did not show a larger increase in facial attractiveness ratings for MHC heterozygotes versus homozygotes compared to participants exposed to the control images. There was also no two-way interaction. Participants exposed to the pathogen-salient images did not show a larger increase in preference for facial masculinity versus facial femininity compared to those exposed to the control images. Several issues may account for these findings, including for example, carry over effects and progressive error.

For example, there was a significant main effect of exposure for the facial attractiveness rating task for the full sample (women and men combined) and for the genders individually. The pre-manipulation ratings were higher than post-manipulation ratings. The ratings dropped after manipulation, regardless of which image condition

was viewed. One explanation is that there may have been some type of second viewing effect occurring across both condition groups. That is, seeing the same facial images a second time may have generated some level of recognition or familiarity in general. Viewing the images a second time may have given participants more time to analyse the faces in more detail or even second guess their initial responses. This may occur independently but also may be related to fatigue effects. Participants rated 40 faces for attractiveness, followed by 10 paired masculine/feminine images (20 faces), followed by 20 C-DIS images, followed by the initial 40 plus 10-paired facial images again – a total of 120 images (120 faces total, not including the faces within C-DIS). This may have been mentally overwhelming to complete in one sitting.

Although the interaction predictions were not supported, analysis did reveal support for the evolutionary foundations on which the parasite-stress theory model and subsequent hypotheses were constructed, as well as support for findings from previous related research. There was a main effect of MHC zygosity for the facial attractiveness rating task. The MHC-heterozygous faces were rated significantly more attractive than the homozygous faces. This supports the theory and evidence regarding the link between the MHC and genetic quality as indicated by physical attractiveness, and suggests that there are indeed some adaptive benefits to be gained from preferring and mating with partners who are heterozygous in MHC loci (Brown, 1997; Brown, 1998; Folstad & Karter, 1992). Importantly, this replicates the findings of Roberts et al. (2005) and suggests that facial attractiveness is likely an indicator of some degree of MHC heterozygosity. Interestingly, men's ratings showed the same pattern. They rated the heterozygous faces as significantly more attractive as well. It is difficult to say whether men contain the same degree of MHC-concerned preference as women, but at the very least this finding supports the notion of mutual mate choice in humans (Miller, 2013) and illustrates that men also have the evolved cognitive mechanisms involved in tracking MHC zygosity via physical attractiveness.

There were similar findings for the masculine/feminine face preferences analysis, in that there were no significant interactions but the results provide some support for evolutionary theory and previous related research. The findings do not converge with the findings of the research on which the rationale of the current study is formed (Lee & Zietsch, 2011; Little et al., 2011). Nor do they converge with other similarly grounded studies (e.g. Ainsworth & Maner, 2019; Little et al., 2011; Young et al., 2011) that predicted and found pathogen-driven increases in preference for facial

symmetry – which, like sexual dimorphism (i.e. masculinity), is another putative honest signal of immunocompetence. Instead, as in McIntosh et al. (2017), the direction of preferences for masculinity was not causally influenced by BIS-activation via variation in exposure to pathogenic cues.

However, although there was no significant increase in preference for masculine faces versus feminine faces as a result of manipulation, initial selections (pre-manipulation) showed that masculine faces were preferred significantly more than feminine faces by women. This is important in that it supports long-held understanding of the evolution of sexual dimorphism and preference for genetic quality, which is more impactful when considering that the men showed no significant difference in facial preference. But it also supports previous research which shows that women prefer men with masculine faces in general (Little et al., 2011; McIntosh et al., 2017), albeit the degree to which is often contingent upon various factors (discussed further in subsection 3.4.1).

Based on the absence of the predicted interactions for both sets of analyses, it was important to consider the potential impact of covariates on the corresponding results. Ackerman et al. (2018) noted the impact that chronic germ aversion (as scored on the PVD_{GA} subscale) had on BIS-related behaviours in previous studies. In their self-image studies, they themselves found that individuals who scored higher on the PVD_{GA} subscale demonstrated significantly greater concern with regards to their own physical appearance when exposed to pathogen cues than individuals who scored lower. However, in the current study, to control for the potential impact of germ aversion, perceived infectability, and overall perceived vulnerability to disease, ANCOVAs were conducted including the PVD scores of these variables as covariates. Analysis revealed no significant impact on the MHC-zygosity or facial masculinity preference interactions by any of them. No correlations were found between any of the variables either. Both the full and women's-only data sets lacked these expected covariations and correlations. This is difficult to explain given the preponderance of previous research that highlight strong relationships between the PVD scale (and other similar BIS measures) and mate preferences, e.g. facial attractiveness, masculinity and symmetry (Ackerman et al., 2018; DeBruine et al., 2010; DeBruine et al., 2012; Little et al., 2011; Welling, Conway, DeBruine, & Jones, 2007; Young et al., 2011). Limitations discussed in subsection 3.4.1 may provide some explanation.

3.4.1 Limitations and future directions

Generally speaking, there were several limitations to the current study. Several extraneous variables were not considered in the analysis that may explain the lack of interactions but that also may have confounded the results. For example, information about relationship status, environment, hormonal contraceptive use, day in ovulatory cycle (only partially considered), self-perceived attractiveness, and self-resemblance were not considered in the analysis. Theory and evidence suggest that these factors can affect mate preferences. Little et al. (2002) found that, individuals in or seeking short-term relationships showed increased preference for sexual dimorphism as a function of maximising potential for 'good genes' benefits. Further to this, they found that the use of hormonal contraception negated these effects. Whereas Little et al. (2007) found that this relationship was contingent upon the 'harshness' of environmental conditions. Other studies have also found similar effects of hormonal contraceptive use on MHC-dependent mating behaviour (e.g. Klapilová et al., 2014; Little et al., 2013; Roberts et al., 2014). Moreover, studies show that women's preferences for symmetry and masculinity fluctuate based on where they are in their ovulatory cycle (Little, Jones, Burt, & Perrett, 2007; Little, Jones, & Burriss, 2007). Additionally, self-perceived attractiveness (Little, Burt, Penton-Voak, & Perrett, 2001) and facial resemblance (Alvarez & Jaffe, 2004; DeBruine, 2004) also affect an individual's perceptions and beliefs about facial attractiveness in others.

Finally, variance in geographical location of upbringing, and the corresponding related aspects of ontogeny, may have generated location-specific (and thus perhaps even cultural) variation between participants in their responses. The sample size was too small (or each country was not represented enough in the sample) to analyse the data split by country of origin. Larger representation from each country may have, for example, offered more power to explain at least some of the variance or noise in the data potentially arising from geographical variation in preferences for location-specific advantages of optimal inbreeding. That is, when parasite stress (particularly nonzoonotic) is high in the local ecological environment it may be adaptive to engage in some level of inbreeding to retain coadapted gene complexes associated with resistance to those parasites, even at the risk of inbreeding depression (see Denic & Nicholls, 2007; Hoben, Buunk, Fincher, Thornhill, & Schaller, 2010; Kokko & Ots, 2006; Thornhill & Fincher, 2014b). This may, for example, influence the extent to which MHC heterozygosity or homozygosity, and/or the associated phenotypes, is preferred by individuals. This could not be considered in this analysis.

Considering the design issues mentioned in section 3.4, it may be useful for future studies to consider reducing the number of faces to rate for attractiveness to 10 heterozygous and 10 homozygous, and the number of paired masculine/feminine images to 5 pairs, and maybe even employ a smaller selection of images from C-DIS. Although mixed factorial designs are likely the most valid for testing causation, focus and attention can be lost in repeating the same tasks, which can also facilitate fatigue effects. Future researchers may benefit from considering these issues in their study design and analysis, if and where possible.

3.4.2 Conclusions

The aim of this study was to experimentally test Thornhill and Fincher's (2014b) parasite-stress theory proposing that pathogen stress imposes causal effects on the social behaviour of mate choice and preferences. They suggest that this causation explains to some extent regional variation in mate preferences. There is a considerable amount of evidence to support this proposal, however, only a small collection of previous studies employ designs that allow for direct causal assessment. This study attempted to contribute to this small collection using a mixed factorial design. The results of the current study do not provide support for the hypothesised interaction effects, and therefore do not provide support for the causal relationship proposed in the parasite-stress theory. The pathogen-salient images imposed no increase on the MHC-dependent preferences for facial attractiveness or masculinity, compared to the control images or otherwise. However, the results do not disconfirm their proposal either. Responses to the pre-manipulation tasks support and even replicate the evolutionary theory and evidence on which this study was founded. This suggests that the noted limitations, as well as the design, may have confounded the results. Future studies may obtain more reliable findings by employing a mixed factorial design for true experimental testing but with proper consideration of the limitations and appropriate design modifications.

Chapter 4: Pathogen stress and cultural divergence

4.1 Introduction

The behavioural immune system (BIS) acts as a first line of defence against infection before it comes in contact with the body by motivating avoidance behaviours that distance the self from sources that connote potential threat of infection (Schaller, 2006; 2011); however, a major potential source of infection is other humans. As noted in section 1.2.2, the notion of geographical localisation suggests that the highest risk of morbidity and mortality comes from infections that derive from out-group individuals, i.e. individuals who are perceived to deviate from the norms of the in-group (Terrizzi et al., 2013). In-group members share both immunological adaptedness to local pathogens and culturally developed norms that are, in part, designed to reduce disease transmission, such as culturally specific customs, practices and laws regarding food preparation and hygiene-related behaviour. Out-group individuals pose the risk of carrying novel pathogens to which the locals are not adapted, and they are more likely to violate local norms of which they may be unware (Schaller & Murray, 2008; Schaller & Neuberg, 2008).

According to Thornhill and Fincher's parasite-stress theory, activation of the BIS motivates intra-group embeddedness, cohesion and protectionism and out-group avoidance which are expressed through in-group assortative social behaviours, which then encourage more socially and culturally conservative values (Thornhill & Fincher, 2014b; Fincher & Thornhill, 2008a; 2008b; 2012; Fincher et al., 2008). They argue that these behaviours lead to group isolation in which norms, traditions, attitudes and beliefs of groups arise and evolve differently and independently of each other (e.g. directions, times, rates, due to temporal and geographical differences in environmental pressures). As noted throughout this thesis, a main crux of Thornhill and Fincher's theory is that degree of in-group assortative sociality falls along a continuum, whereby it is dependent on and covaries with levels of parasite stress in the local ecological environment. Groups living in environments with high parasite stress will tend to exhibit a stronger degree of conservatism, traditionalism, and collectivism, while groups living in environments of low parasite stress will tend to exhibit a stronger degree of liberalism, progressivism, and individualism. However, in addition to these group differences, it is also argued that individual BIS strength variation within the group produces within-group differences such as polarised politics (see Aarøe et al., 2017; Tybur et al., 2016). BIS activation (or strength) results in stronger in-group assortative sociality among individuals, which results in a more socially and culturally conservative value system; whereas, BIS inactivation (or weakness) results in stronger

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omni-group prosociality among individuals, leading to a more socially and culturally liberal value system.

The values of a culture are heavily influenced by its religion, and thus a culture and its society is somewhat shaped by its foundational religious beliefs and practices (Cohen, 2011). Religious conservatism is also viewed as another form of social conservatism which may share a relationship with the BIS and parasite stress (Terrizzi et al., 2012). Thornhill and Fincher (2014b) further predict that the importance of religiosity should be positively related across regions to respective levels of parasite stress. Religious behaviour (e.g. participation, rituals) functions to signal costly hard-to-fake allegiance and commitment to the in-group (Alcorta & Sosis, 2005; Sosis & Alcorta, 2003; Sosis et al., 2007), and motivate in-group cohesion and out-group avoidance. Variation in pathogen stress across regions should be predictive of the magnitude of the costs associated with religiosity, as well as of the degree to which people in a region find religion important, and therefore of their willingness to engage and incur the associated costs. Therefore, individuals and groups will adhere to local religious systems (e.g. sacred texts, traditions, customs) to a stronger degree in regions of higher parasite stress than individuals and groups in regions with low parasite stress, due to the notion that values in low parasite stress regions would allow for people to be more flexible in their degree of religious adherence.

There is a growing body of evidence to support the parasite-stress theory. For example, PVD is correlated with negative attitudes towards individuals perceived as out-group members, including disabled and obese individuals (Navarrete & Fessler, 2006; Park, Faulkner, & Schaller, 2003; Park, Schaller, & Crandall, 2007). Disgust sensitivity is also correlated negatively with openness to experience and positively with neuroticism (Druschel & Sherman, 1999), and positively with prejudice against homosexuals (Inbar, Pizarro, Knobe, & Bloom, 2009; Terrizzi, Shook, & Ventis, 2010). Research has also found that BIS sensitivity is a predictor of anti-immigration attitudes (Aarøe et al., 2017). Moreover, pathogen prevalence has been shown to positively correlate to various related values and behaviours. A recent study found that in US regions with higher infectious disease rates (pathogen prevalence) express higher implicit and explicit racial prejudice, in both White and Black individuals (O'Shea, Watson, Brown, & Fincher, 2019). Pathogen prevalence positively correlates to cultures with collectivist value systems and which focus on teaching collectivist values (Fincher et al., 2008; Cashdan & Steele, 2013, respectively), and also to regions with

autocratic versus democratic governmental systems (Thornhill et al., 2009). Furthermore, Schaller and Murray (2008) found that people report lower levels of sociosexuality, extraversion, and openness to experience in regions with historically high disease prevalence. Disgust priming studies have also shown that BIS activation can affect intergroup categorisation (Makhanova et al., 2015) and increase participants' xenophobia and ethnocentrism (Faulkner et al., 2004; Navarrete & Fessler, 2006; Navarrete, Fessler, & Eng, 2007, respectively), as well as conformity to the perceived in-group (Wu & Chang, 2012).

With regards to religiosity, Fincher and Thornhill (2008a) found that religion diversity positively correlated to infectious disease stress across the globe, and Fincher and Thornhill (2012) found a positive association between religiosity and parasite stress, both cross-nationally and between the states across the US. Similarly, pathogen and sexual disgust sensitivity were found to correlate with religious conservatism (Terrizzi et al., 2012). But also, Ritter and Preston (2011) found that disgust was elicited simply by contact with out-group religious beliefs, an example of neophobia – or fear of new, non-traditional or non-conformistic ideas and beliefs (Thornhill & Fincher, 2014b). Terrizzi, Shook, & McDaniel (2013) conducted a meta-analysis on 24 BIS-related studies and found that BIS strength was positively correlated to social conservatism via measurements of ethnocentrism, collectivism, political conservatism, right-wing authoritarianism, social dominance orientation, and religious fundamentalism and orthodoxy. Tybur et al. (2016) found that, across 30 nations, national parasite stress and pathogen avoidance positively relate to traditionalism – that is, political conservatism that motivates adherence to local norms, which would include rules, taboos, rituals, and religiosity.

The evidence suggests that people with a stronger BIS response, or who live in environments of high parasite stress, express stronger in-group assortative sociality and hold and adhere to more socially, politically, and religiously conservative values; and vice versa for people with a weak BIS response, or who live in environments of low parasite stress (Terrizzi et al., 2013). Therefore, BIS sensitivity and/or activation via parasite stress appears to have profound implications for the expression of individual and social behaviour, including attitudes, norms, morals, and beliefs, which have far-reaching implications for religiosity, politics, government, society, and thus culture. This may, to a large extent, explain not only the emergence of culture, but also the divergence of and variation between cultures via human values and beliefs.

One of the main issues with the parasite-stress theory is that a substantial portion of the supporting evidence is correlational, from which causal conclusions cannot be conclusively drawn. Moreover, the experimental studies to date do not directly test whether parasite stress plays a causal role in the diversification and variation of cultures via their values and beliefs. Therefore, the current study set out to test this theory experimentally.

4.1.1 Study rationale

A society's cultural values and beliefs may perhaps be most overtly reflected in its governing laws, i.e. its rules. The governing rules of a society are formed around the group's socially and historically derived norms, morals, traditions, taboos and practices, which are collectively determined, driven, shared and enforced by the group as a society. For example, governing rules in western societies are somewhat guided by the Ten Commandments (Exodus 20; King James Bible). Therefore, if parasite stress can indeed affect the cultural values of a society, then it should impose observable causal effects on the governing rules the individuals of the society select. BIS activation by perceived pathogen threat should cause individuals of a society to favour rules that represent more socially conservative values. This raises the following question: Can BIS activation, via pathogen stress, influence the ontogeny and trajectory of a culture's values by affecting the governing rules individuals choose for their society? If so, then there would be good evidence to argue that pathogen stress can indeed lead to the divergence of and variance between cultures.

To test this, participants were asked to consider the premise: 'What if humans had the opportunity to start over with a new society founded on a newly developed set of basic social rules – around what rules would we choose to build this new society?' Serving as variation in pathogen stress, participants were exposed to the Culpepper Disgust Image Set (C-DIS: Culpepper et al., 2018). Half of the participants rated the C-DIS 20 pathogen-salient images depicting scenes involving pathogenic threats of infection, while the other half rated the C-DIS control images – 20 matching images without the pathogen-relevance. They then selected 15 rules (i.e. their 'Fifteen Commandments') from a predetermined list of 60 rules and ranked their selected rules in order of importance. The 60-rule list included: 20 liberal-leaning *prosocial rules* designed to provide all-inclusive protection of the rights of citizens, immigrants, and foreign visitors, putting all individuals above the in-group community and beliefs; 20 *pathogen-management rules* designed to manage and minimise contact and spread of

pathogenic infection within the community; and 20 conservative-leaning *assortative social rules* designed to protect and preserve the in-group community's traditional values and beliefs at the expense of the concern for out-group individuals and communities.

Based on the cited literature, I formed the umbrella hypothesis that increased perceived parasite stress will emphasise the perceived importance of pathogen-management and assortative social rules over prosocial rules. I predicted that participants who viewed the pathogen-salient images would selectively favour pathogen-management and assortative social rules more than prosocial rules compared to participants who viewed the pathogen-free control images, and that participants who viewed the pathogen-free images would selectively favour the prosocial rules more. I measured this in two ways: selection and prioritisation, i.e. the total number of selected rules by rule-type and the ranked order of importance of their selected rules by rule-type. Finally, I tested the potential moderating effects of religiosity with the prediction that rule selection and prioritisation would be independent of participants' level of religiosity or religious affiliation. Again, in the context of this thesis, such findings would illustrate that it is possible for cultures to become isolated and diverge in beliefs about what types of rules would be most appropriate for a society to follow as a causal effect of variation in parasite stress in the ecological environment.

4.2 Method

Ethics statement

This study received ethical approval from the General University Ethics Panel at the University of Stirling and adhered to the ethical guidelines of the British Psychological Society. All participants provided prior informed consent and viewed a debriefing page after participation. Participants were compensated £5 for participation.

4.2.1 Participants

A total of 40 participants (20 women, 20 men) with an overall mean age 39.65 ± SD 13.17 (range 18-76) were recruited via the Qualtrics Panel system in the UK. All were UK residents. Thirty (75%) listed their country of origin as the UK, four others listed their origin as Poland, Bulgaria, Nigeria, and Pakistan, and six did not provide their origin. Thirty-seven reported their ethnicity as White (92.5%), two Asian (.05%), and one Black (.025%). Religious orientation included twenty-four Christians (60%),

eleven Atheists (27.5%), two Muslims (5%), two Agnostics (5%), and one did not provide their religion.

4.2.2 Materials and procedure

The study employed the use of a Qualtrics online survey consisting of a set of demographic questions (age, gender, religion, and ethnicity), as well as two scales, an image-rating task, and an item-selection task.

PVD and religiosity scales

Participants first completed the 15-item PVD scale (Duncan et al., 2009) and rated the extent to which they agreed or disagreed with the PVD statements on a 7-point scale (1=*strongly disagree*, 7=*strongly agree*). PVD was calculated as a single score. An overall mean PVD score was calculated for each individual. Cronbach's *alpha* was conducted on the means scale scores, $\alpha = .740$. *Alpha* could not be increased to more than .769 by the deletion of scale items. As in Chapter 3, the same was done for the Germ Aversion (PVD_{GA}) and Perceived Infectability (PVD_{PI}) subscales. PVD_{GA}: $\alpha = .577$, and could not be increased above .611 with the deletion of any item; and PVD_{PI}: $\alpha = .598$, and could not be increased above .668 with any item deletion.

Participants then completed a 9-item scale designed to assess levels of religiosity, henceforth referred to as the religiosity scale. The scale comprised the full 8 items from Valdesolo and Graham (2014), and assessed belief in supernatural forces with items such as 'It is feasible that God, or some type of non-human entity, is in control, at least in part, of the events within our universe' and 'I am a confident believer in God'. I included one additional item which I considered to be particularly related to the topic of this thesis - belief in supernatural control and causation of environmental events such as disease and disasters: 'To what extent do you believe that events such as tornados, earthquakes, floods, diseases, etc. are caused by God, the devil, demons, spirits, or curses?'. See Appendix A for the complete scale. Participants rated how much they agreed with these statements on a 7-point scale (0=*not at all*, 6=*very much*). Responses were averaged to provide overall mean individual religiosity scores. Cronbach's *alpha* was conducted on the scale scores, $\alpha = .951$. *Alpha* could not be increased by any item deletion.

Manipulation of pathogen threat

After completing the scales, participants were then randomly assigned to one of two conditions: 10 men and 10 women viewed the pathogen-salient images and 10 men

and 10 women viewed the pathogen-free images. See Table 4.1 for descriptive statistics split by condition. To experimentally manipulate the BIS, I employed the C-DIS. Participants rated the images for disgust on a 7-point scale (0=*not disgusting at all*, 6=*extremely disgusting*). Mean disgust scores were calculated for each C-DIS set. Cronbach's *alpha* was conducted on both sets: pathogen-salient set, α = .957, and pathogen-free set, α = .965. These could not be increased by any item deletion.

Table 4.1 Descriptive statistics for participants split by condition: total N, gender (male=M, female=F) mean age, PVD score, and religiosity score, and religion affiliation. (SD in brackets)

Condition	N & Gender	Age	PVD	Religiosity	Religion
Pathogen-Salient	10M / 10F	39.75 (14.17)	3.85 (0.89)	3.73 (1.80)	6 Atheism 12 Christianity 2 Islam
Pathogen-Free	10M / 10F	39.55 (12.45)	3.80 (0.77)	3.28 (1.72)	2 Agnosticism 5 Atheism 12 Christianity

Social rule-building task

After completing the image-rating task, participants were then asked to consider a 'what if' premise: what if humans had the opportunity to start a new society founded on a new set of social rules – what rules do you think would be best for the new society to follow? They were told that they and other potential leaders of the new society (the other participants) were asked to select 15 rules, from a list of 60, that they think would be best for the society. Each participant was also asked to rank their selected 15 rules in order of importance. They were told that a democratic election would then be held whereby the potential members of the new society would then vote on which of the sets of rules they would be most willing to follow.

For this task, I prepared a list of sixty social rules: twenty prosocial rules, twenty assortative social rules, and twenty rules related to pathogen avoidance and/or management (see Appendix E for the complete 60-rule list). The *prosocial rules* included liberal-oriented restrictive items designed to provide protection and limitations and promote all-inclusive cooperation to the society's citizens, immigrants and foreign visitors, as well as to the broader human civilisation. These included rules such as 'All Citizens, immigrants and foreign visitors must be considered equal in the eyes of the law', 'Citizens, immigrants and foreign visitors must not kill any other

person(s)', and 'The well-being of human civilisation must take priority over the well-being of any one community'. The *assortative social rules* included conservative-oriented restrictive items designed to protect the in-group community (society), its citizens, and its social and cultural heritage over and above non-citizens and out-group communities. These included rules such as 'The rights, life and safety of citizens must always take priority over any non-citizen (immigrants and foreign visitors)', 'The well-being of the community must take priority over the well-being of all other communities', and 'Citizens must not diminish or undermine the preservation of the community's native culture and traditions'. The *pathogen-management rules* included items designed to protect the community by preventing or minimising contact with pathogens and reducing the spread of infectious disease within the community. These included rules such as 'Food products sold to the public must be produced, prepared and distributed according to specific health codes', 'Sanitation waste (rubbish and sewage) must be removed to a safe distance from the local population', and 'Immigrants and foreign visitors must be screened for infectious diseases before entering the community'.

4.2.3 Analyses

I prepared the data for analysis in two ways. For the selection measurement, I calculated the total number of rules selected from each rule type by each participant. For the prioritisation measurement, each of the rules selected by each participant were assigned a value from 15-1 based on the order in which they were ranked, i.e. 15 for the highest and 1 for the lowest ranked rule for each participant's rule list. A mean rank score was calculated for the rules selected from each rule type by each participant.

4.3 Results

This section will describe statistical analyses conducted to test the effectiveness of the manipulation, and provide the results for rule selection and prioritisation. The data was first inspected to establish whether it was normally distributed. Both the Q-Q plots and the Shapiro-Wilk tests were unclear, therefore, I converted the skewness and kurtosis values for each of the three rule selection scores and each of the three prioritization scores into z scores. The z kurtosis and z skewness fell between -1.96 and 1.96 for four of six categories suggesting these data were normally distributed (Ghasemi & Zahediasl, 2012). Only the Prosocial rules (selected) and Prosocial rules

(ranked) data exhibited z kurtosis, 2.40 and 2.57, respectively. Based on these results, parametric tests were used for each analysis.

4.3.1 Manipulation check

Participants who viewed the C-DIS pathogen-salient images were predicted to favour pathogen-management and assortative social rules, whereas participants who viewed the C-DIS control images were predicted to favour the prosocial rules in comparison. It was therefore pertinent to test whether the C-DIS images had the intended manipulation effect the same way as in Chapter 3. I averaged the ratings of the C-DIS images together to create overall mean disgust scores for each participant and then standardised the disgust scores for each condition into z scores to assess them for outliers. Only one outlier was found to be > 2 standard deviations smaller than the mean ratings in the pathogen-salient condition, suggesting that the images likely did not evoke disgust for this participant. Due to the relatively small sample size, the data for this participant were retained for analysis.

Again, as in Chapter 3, an independent samples t-test was then performed on the disgust scores for both sets of C-DIS images to ascertain whether the pathogen-salient images were rated as significantly more disgusting than the control images, and therefore whether they sufficiently activated the BIS for the experimental group in comparison to the control group. The pathogen-salient images (5.48 ± 1.16) were rated as significantly more disgusting than the control images (2.84 ± 1.44), a statistically significant difference of 2.63 (95% CI, 1.79 – 3.47), $t(38) = 6.36$, $p < .001$, $d = 2.01$. This suggests the C-DIS images likely activated participants' BIS as intended.

4.3.2 Analysis on rule selection

A two-way mixed ANOVA was conducted with image condition (pathogen-salient, control) as the between-groups factor, the three levels of social rules as the within-participants factor, and the total number of selected rules from each rule type as the dependent variable. Assumptions of sphericity (Mauchley's: $p = .636$) and equality of error variances (Levene's: prosocial, $p = .326$; pathogen, $p = .706$; assortative, $p = .204$) were both met. I found a statistically significant main effect of rule type on number of rules selected, $F(2, 76) = 8.11$, $p < .001$, $\eta p^2 = .176$, whereby prosocial rules were more frequently selected and assortative social rules selected least often (Figure 4.1). There was no statistically significant interaction effect between image condition and rule-type selection, however, this approached significance, $F(2, 76) = 2.72$, $p < .072$, $\eta p^2 = .067$. Independent-samples t-tests were conducted to explore the group

differences in more detail. Analysis revealed that, surprisingly, group differences in pathogen rules were invariant, $t(38) = 0.65$, $p = .523$, $d = 0.20$, and group differences in prosocial rules were also nonsignificant, $t(38) = 1.71$, $p = .095$, $d = 0.54$; but participants selected a significantly larger number of assortative rules in the pathogen-salient condition than in the pathogen-free condition, $t(38) = 2.10$, $p = .042$, $d = 0.66$.
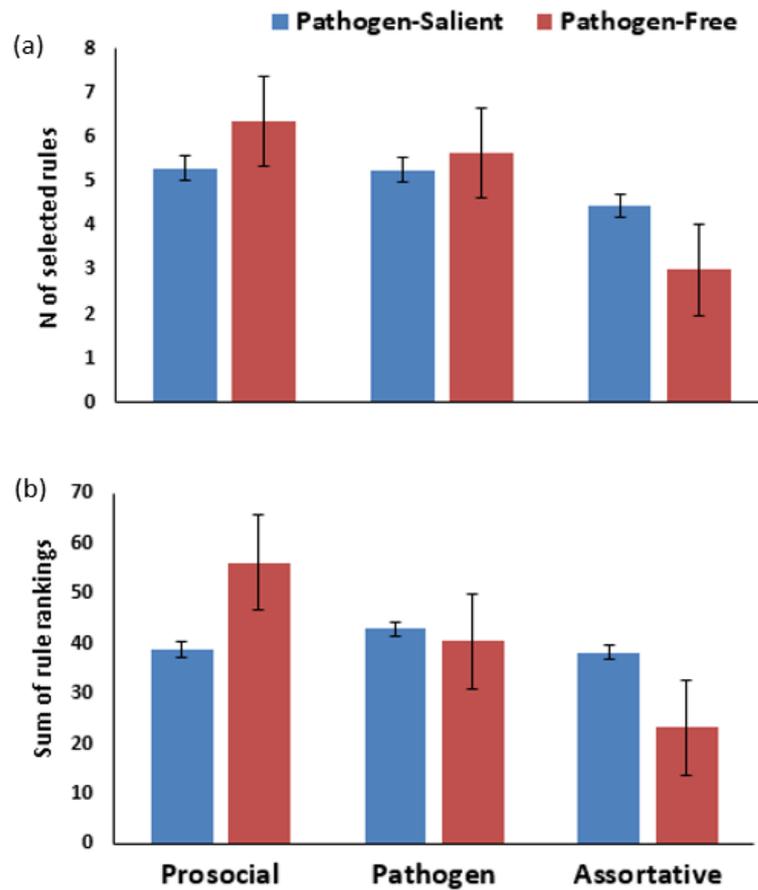
Figure 4.1 (a) The number (N) of rules of each type selected by participants in the pathogen-salient and pathogen-free conditions. (b) Sum of rankings for rule sets. Data show mean (± s.e.) for each measure.

4.3.3 Analysis on rule prioritisation

The same analyses were conducted on the rankings that participants gave to their rule selections. A two-way mixed ANOVA was conducted with image-condition as the between-groups factor, the three levels of social rules as the within-participants factor, with the mean ranking of the selected rules from each rule type as the dependent variable. Assumptions of sphericity (Mauchley's: $p = .889$) and equality of error variances (Levene's: prosocial, $p = .058$; pathogen, $p = .711$; assortative, $p = .350$)

were both met. Results showed a statistically significant main effect of rule type on rule rankings, $F(2, 76) = 5.04$, $p = .009$, $\eta p^2 = .117$, following the same pattern as for rule selection. However, here there was also a statistically significant interaction effect between image and rule types, $F(2, 76) = 4.64$, $p = .013$, $\eta p^2 = .109$. Post hoc independent-samples t-tests revealed that this was driven by lower prioritisation of prosocial rules, $t(38) = 2.75$, $p = .009$, $d = 0.87$, and higher prioritisation of assortative social rules, $t(38) = -2.38$ $p = .022$, $d = 0.75$, in those exposed to pathogen-salient images. Again, and rather surprisingly, no significant group difference was found in weight given to pathogen-management rules, $t(38) = -0.40$, $p = .688$, $d = 0.13$.

4.3.4 Religiosity, religion and PVD scores

Covariation

Finally, I investigated the independent effects of individual variation in religiosity, religious affiliation, and perceived vulnerability to disease (PVD). To do this, I repeated the two-way mixed ANOVA as described above, now including religiosity and PVD scores (including the two subscales PVD_{GA} and PVD_{PI}) as covariates (i.e. ANCOVAs). The analyses revealed no covariation between number of rules selected and either religiosity ($p = .502$) or PVD ($p = .348$), PVD_{GA} ($p = .770$) or PVD_{PI} ($p = .136$); nor between rule ranking and religiosity ($p = .262$), PVD ($p = .435$), PVD_{GA} ($p = .379$) or PVD_{PI} ($p = .064$).

Correlations

Correlations were analysed for the number and rankings of the selected rule types, with religiosity scores and PVD scores, including the PVD_{GA} and PVD_{PI} subscales (Table 4.2). Strong correlations were found between the number and rankings of all rule types, except between total of pathogen-management rules and ranking of prosocial rules. Interestingly, religiosity and PVD scores only positively correlated with each other, Pearson $r(40) = 0.343$, $p = .030$. The PVD subscales only correlated with each other and PVD overall.

Comparing groups

An independent-samples t-test was also conducted to analyse group differences in religiosity and in PVD scores, including the PVD_{GA} and PVD_{PI} subscales. Results showed no difference between the conditions in religiosity scores, $t(38) = -0.81$, $p = .423$, PVD scores, $t(38) = -0.20$, $p = .841$, PVD_{GA}, $t(38) = -0.406$, $p = .687$, and PVD_{PI}, $t(38) = 0.072$, $p = .943$.

Table 4.2 Correlations for the three rule types: prosocial, pathogen-management (pathogen), and assortative social (Totals and Rankings), and PVD (including PVD_{GA} and PVD_{PI}) and religiosity scores.

	Prosoc (Total)	Path (Total)	Assort (Total)	Prosoc (Rank)	Path (Rank)	Assort (Rank)	PVD Score	PVD_{GA} Score	PVD_{PI} Score
Pathogen (T)	-.331*								
Assortative (T)	-.590**	-.567**							
Prosocial (R)	.910**	-.216	-.610**						
Pathogen (R)	-.394*	.812**	-.351*	-.459**					
Assortative (R)	-.587**	-.495**	.935**	-.622**	-.410**				
PVD Score	-.048	-.197	.211	-.097	-.121	.206			
PVD_{GA} Score	-.070	-.081	.130	-.124	.032	.099	.906**		
PVD_{PI} Score	-.013	-.284	.255	-.044	-.266	.279	.879**	.595**	
Religiosity	-.226	.036	.166	-.291	.165	.153	.343*	.307	.306

*. Correlation is significant at the 0.05 level (2-tailed).

**. Correlation is significant at the 0.01 level (2-tailed).

Table 4.3 Descriptive statistics for mean totals and rankings of selected prosocial, pathogen-management (pathogen) and assortative social rules by participant religion. (SD in brackets)

	N	Prosocial Total	Pathogen Total	Assortative Total	Prosocial Ranking	Pathogen Ranking	Assortative Ranking
Christianity	24	5.38 (1.28)	5.87 (2.13)	3.75 (1.98)	42.17 (14.56)	48.50 (19.40)	29.33 (18.30)
Islam	2	5.50 (2.12)	4.00 (1.41)	5.50 (0.71)	42.00 (21.21)	27.00 (0.00)	51.00 (21.21)
Atheism	11	6.27 (2.41)	5.09 (1.58)	3.64 (2.87)	55.09 (28.87)	32.73 (13.05)	32.18 (24.45)
Agnosticism	2	8.00 (5.66)	4.00 (1.41)	3.00 (4.24)	65.50 (45.96)	24.50 (3.53)	30.00 (42.42)

Table 4.4 Comparisons between the totals (above) and rankings (below) of prosocial, pathogen-management and assortative rules selected by religious and non-religious participants. N=total participants in each group.

Rules	Religious (N=26)	Non-religious (N=13)	S.E.	t	df	p
Totals						
Prosocial	5.38	6.54	.822	1.40	37	.181
Pathogen-management	5.73	4.92	.666	1.21	37	.233
Assortative social	3.88	3.54	.893	.388	37	.703
Rankings						
Prosocial	42.15	56.69	8.74	2.06	37	.117
Pathogen-management	46.85	31.46	5.95	2.59	37	.014
Assortative social	31.00	31.85	7.24	.117	37	.908

Comparing religious groups

Descriptive statistics were calculated for number and of rankings of rule types selected based on the reported religions of the participants (Table 4.3). Although there was insufficient power to compare Christian and Muslim participants, or Atheists and Agnostics, I was able to test effect of identification with either religion or none. I therefore grouped Christian and Muslim participants as "Religious" participants and atheists and agnostics as "Non-religious" participants, and compared their selection and prioritisation of rules using independent-samples t-tests. There were no significant differences between groups for selection or ranking of prosocial and assortative social rules. However, religious participants ranked pathogen-management rules as significantly more important than the non-religious participants (Table 4.4).

4.4 Discussion

The results of the current study provide supporting evidence for the parasite-stress theory, in that the manipulation of perceived parasite stress affected the rules that individuals might select for their society. My hypothesis, that participants in the pathogen-salient condition would selectively favour assortative social rules more than prosocial rules compared to those in the pathogen-free condition, and that participants in the pathogen-free condition would selectively favour the prosocial rules more, was supported. Those in the pathogen-free condition selected a significantly larger number of prosocial rules than assortative social rules. Although there was no statistically significant interaction between the conditions and number of selected rule-types, participants in the pathogen-salient condition selected fewer prosocial and more assortative social rules than those in the pathogen-free condition. Results of the prioritisation analysis (rule rankings) followed the same pattern as the selection results, but to a stronger extent. Participants in the pathogen-free condition ranked the prosocial rules as significantly more important than the assortative social rules. Moreover, there was a significant interaction effect between the conditions and prioritisation of the selected rule-types. Participants in the pathogen-salient condition ranked the assortative social rules as significantly more important than those in the pathogen-free condition and ranked the prosocial rules as significantly less important than participants in the pathogen-free condition.

Surprisingly, there was no significant group difference in the selection or prioritisation of pathogen-management rules. This part of the hypothesis was not

supported. On one hand, this is peculiar in that, if the BIS is activated as a result of exposure to pathogen-salient images, then an increased concern over pathogen-management would be expected. Perhaps one explanation for this is that pathogen-management rules may be valued as equally important to fitness regardless of the degree of parasite stress, because of a consistent and therefore relatively invariant adaptive necessity for pathogen-management by individuals and societies throughout human evolution. Importantly, it was the main variables of relevance, prosocial and assortative social rules, which were causally affected by perceived parasite stress, as predicted.

The analyses suggest that rule selection and prioritisation were independent of participants' level of religiosity and PVD, including the two subscales: germ aversion and perceived infectability. These behaviours had no effect on the numbers of each rule type selected, nor on how the rules were ranked. This was expected, as the BIS should be sensitive to potential threats of infection regardless of these behaviours. Additionally, whereas previous studies suggest that there may be differential effects of germ aversion over perceived infectability (e.g. Ackerman et al., 2018; Makhanova et al., 2015), this was not supported here. These results did reveal a significant positive correlation between religiosity and PVD. Although this adds nothing to the argument of causation, it does provide more correlational evidence to further corroborate the parasite-stress theory (Terrizzi et al., 2013; Terrizzi et al., 2012; Thornhill & Fincher, 2014b). There may also be potential interaction effects of PVD and religiosity questions. For example, questions about PVD and religiosity may have interacted to influence rule-decisions more or less in religious or non-religious groups, and/or influence or moderate BIS responses to the C-DIS stimuli.

In the current study, variation in perceived pathogen stress led to differences in the types of rules that potential leaders of a would-be society selected for their society, and the priority they gave to the rules they selected. Variation in parasite stress affected the variation in liberal prosociality versus conservative in-group assortative sociality. Individuals who were exposed to images denoting conditions of parasite stress favoured a much more conservative set of social rules, which would reflect a more conservative society. I argue that this can be extrapolated to explain how the ontogeny of the values and beliefs of a society can be affected by perceived parasite stress. The rules of a society are formed upon, and are therefore somewhat reflective of, the values and beliefs of the individuals of the society, which are themselves products of

evolutionary processes. The BIS is activated in response to the pressures of the local environment, i.e. perceived parasite stress, and motivates the corresponding adaptive behaviour. This leads to out-group avoidance and thus group isolation. The norms, traditions, values, and beliefs of groups arise and evolve differently and independently in isolation, which then leads to differences in cultures and their religions. This further suggests that variation in geographical parasite stress within the same group, and individual variation in BIS strength, can lead to within-group differences in values and beliefs and thus to within-group social, religious, and political polarisation.

These findings suggest that pathogen-salient images, denoting conditions of higher parasite stress, activated the participants' BIS and motivated in-group assortative social behaviours, which then affected the expression of their values and beliefs and caused them to favour a more socially conservative set of governing rules. This not only provides evidence to support the parasite-stress theory, as well as corroborating other related research (e.g. Aarøe et al., 2017; Faulkner et al., 2004; Tybur et al., 2016), but it also has implications for other theories. For example, the moral foundations theory (Haidt & Graham, 2007) attempts to account for the differences between the moral views of liberals and conservatives through the five foundations of morality – Justice/Fairness, Harm/Care, In-group/Loyalty, Authority/Respect and Purity/Sanctity (i.e. disgust). They argue that political liberals are more morally concerned with the Justice/Fairness and Harm/Care foundations whereas political conservatives employ all five foundations. However, these findings suggest that moral values, at least those involved in determining a society's governing rules, may vary due to perceived parasite stress and might therefore affect the political leanings and polarisation of a society (Aarøe et al., 2017). As social and political conservatism correlates with religious conservatism, parasite stress may then also impose causal effects on the degree of religious adherence and conservatism (Fincher & Thornhill, 2012; Terrizzi et al., 2012). Indeed, research suggests that religious attendance is more predictive of moral foundations regarding In-group/Loyalty, Authority/Respect, and most strongly of Purity/Disgust than of the foundations most concerned with prosociality, i.e. Justice/Fairness and Harm/Care (see Shariff, 2015).

Further to this, previous studies have found (and replicated) the correlation between pathogen avoidance behaviour and moral values (Makhanova, Plant, Monroe, & Maner, 2019). Makhanova et al. found a strong association between chronic pathogen avoidance and endorsement of group-binding moral values – that is, Group-

binding (group-focused) versus Individualizing (individual-focused). The moral values employed in their study were based on the five from Haidt and Graham's (2007) moral foundations theory, with the 'Binding' values of Sanctity, Authority, and Loyalty; and with the 'Individualizing' values of Care and Fairness. In contrast to the current study, they did not find a causal link between situationally activated pathogen avoidance, i.e. experimentally primed disgust. This may be down to the differences in priming methods. However, the evidence again confirms the relationship between pathogen avoidance and moral, prosocial and ethnocentric behaviour.

Similarly, Norenzayan's (2013) 'Big Gods theory' of prosociality suggests that belief in the presence of morally concerned deities (i.e. Big Gods) may have functioned to facilitate prosocial behaviour in expanding groups and thus led to large-scale, anonymous, yet cooperative societies. However, here I show that degree of prosociality versus assortative sociality can vary as a result of perceived pathogen stress. Moreover, it is argued that religious prosociality is more akin to the in-group assortative social behaviour of ethnocentrism (Martin & Wiebe, 2014). Cultures and their religion are intrinsically linked, and therefore likely so is their origin and evolution. Their origin and evolution appears to be affected by parasite stress.

4.4.1 Limitations and future directions

One limitation of this study is the size and homogeneity of the sample. I recruited twenty participants per condition, predominately white and British. The results cannot therefore be generalised across human populations, and a larger sample size comprised of individuals from various regions around the world, and from more varied ethnic and religious backgrounds, would provide more insight into cross-cultural differences regarding evolutionary behaviour. It may also be useful to consider the differences in historical levels of parasite stress in the analysed regions when comparing the findings from each culture. Another limitation of this study to be considered in future research is the use of two conditions, pathogen-salient images and pathogen-free images. Follow-up studies might consider the use of a second type of existential threat as a third condition to determine if the effects are solely caused by pathogenic threat rather than just threats to fitness in general. For example, researchers could employ the use of fear-inducing scenarios (e.g. accidents, safety threats - see Faulkner et al., 2004; Wu & Chang, 2012), in addition to the pathogen salience. Finally, the religiosity scale I used was designed to measure the foundational aspects of religious cognition (i.e. belief in supernatural agents, control, and causation, Valdesolo & Graham, 2014). Future

researchers may find other religiosity scales more useful; for example, scales that consider other measures of religiosity such as value, commitment, or experience (e.g. Huber & Huber, 2012).

4.4.2 Conclusion

This study provides experimental evidence to support the parasite-stress theory of human values and sociality and is the first (to my knowledge) to show that parasite stress can affect the ontogeny and trajectory of a society's governing rules. I argue that this illustrates that parasite stress can affect an individual's values and beliefs, which, in addition to within-group variation, can potentially lead to group isolation and thus cultural divergence. Variation in parasite stress likely accounts, to some extent, for the variation and diversification of cultures and their religions. These findings have far-reaching implications for the understanding of social behaviour, including values, morals, politics, government, and religion, and subsequently on the related theoretical perspectives.

Chapter 5: Pathogen stress and assortative sociality

5.1 Introduction

The findings from Chapter 4 provide preliminary evidence to support Fincher and Thornhill's parasite-stress theory. Variation in parasite stress, via variation in BIS-activation, did produce variation in the degree of assortative sociality versus prosociality in the rule systems generated. More specifically, BIS-activation via visual pathogen threat generated a stronger degree of in-group assortative sociality. In the study described in this chapter, I tease apart the main components of in-group assortative sociality more specifically than in Chapter 4, to assess the effects that BIS-activation may have on the expression of each of them individually.

As described in Chapter 4, the BIS motivates intra-group embeddedness, cooperation, cohesion and protectionism, and out-group avoidance expressed through behaviours of in-group assortative sociality (Thornhill & Fincher, 2014b; Fincher & Thornhill, 2008a; 2008b; 2012; Fincher et al., 2008). I laid out multiple lines of converging evidence in Section 1.3 that collectively supports Fincher and Thornhill's argument that there is indeed a relationship between variation in parasite stress in the ecological environment and variation in the exhibited degree of various behavioural manifestations of collectivistic, conservative, traditional values. These include correlations between variables of pathogen prevalence and various measures of philopatry, ethnocentrism, xenophobia and religiosity, from various types of data, e.g. epidemiological and ethnographic data collected from national, inter-state, regional and cross-cultural samples (e.g. Cashdan & Steele, 2013; Fincher et al., 2008; Fincher & Thornhill, 2008a; Fincher & Thornhill, 2012; Morand & Walther, 2018). Additionally, I described several studies which found that measures of disgust sensitivity, perceived vulnerability to disease, disease worries, and religiosity correlated with various measures of ethnocentrism and xenophobia (e.g. Faulkner et al., 2004; Jackson & Hunsberger, 1999; Navarrete & Fessler, 2006; Terrizzi et al., 2012; Widman et al., 2009; Wu & Chang, 2012). However, more specific to the aim of this thesis, several of the cited studies include experimental paradigms designed to prime the disgust emotion – i.e. activate the BIS, to assess potential causal effects on measures of in-group assortative sociality.

For example, Navarrete and Fessler (2006) investigated whether priming the disgust emotion could increase participants' ethnocentric attitudes. In Study 2 they recruited 253 American participants online to take part in a between-subjects experiment containing two conditions: a disease-salient condition and a control

condition. Participants from the disease-salient condition were asked to first complete the Disgust Scale (Haidt et al., 1994), which semantically primed the psychological mechanisms associated with processing cues of pathogen threat – now understood to be the BIS. Then they were asked to evaluate two different essays – a positive, pro-American appraisal of the USA and American values, putatively authored by an American, and a negative, critical appraisal of the USA and American citizens, putatively authored by a foreigner. They were then asked to rate various characteristics of the two authors. Participants in the control condition were directed straight to the essays and were not primed with the Disgust Scale. Positive ratings of the pro-American author and the negative ratings of the anti-American author were calculated as measures of in-group attraction and out-group negativity, respectively. As reported in subsection 1.3.2, the results showed that these joint measures of ethnocentrism were increased by the disgust priming, suggesting a causal effect of BIS-activation.

Similarly, Wu and Chang (2012) conducted several studies to test whether pathogen threat could impose causal effects on conformity – a component of ethnocentrism. In study 2, they recruited 83 southern Chinese high school students to take part in a between-subjects experiment containing three conditions followed by a rating task to assess degree of conformity. Participants were first shown a 10-image slide show that depicted either pathogens (e.g. maggots, gory wounds), accidents (e.g. car accidents, derailed trains – but without wounds or blood), or buildings. Next, they engaged in a task (adopted from Renkema, Van Yperen, & Stapel, 2008) in which they were asked to rate 30 modern art drawings on a 10-point Likert scale (1=*dislike very much*, 10=*like very much*). However, below the drawings participants could see fictitious ratings described as being from previous students from China (in-group) and two other countries (out-groups). Wu and Chang measured conformity to the perceived in-group by the absolute score difference between the ratings given by participants and the fictitious ratings by the perceived in-group versus those of the two out-groups. Their results showed that inducing participants with pathogen threat led to significantly higher conformity to the in-group ratings than the accident or building conditions.

While the two experiments described above focus on aspects of ethnocentrism, Faulkner et al. (2004) conducted six studies, two of which were experiments designed to test the effects that pathogen threat may have on measures of xenophobia. In Study 5, they recruited 57 Canadian undergraduates which were then randomly assigned to one of two conditions. They either viewed an 11-image 'Disease' slide show which

induced the threat of pathogens, or an 11-image 'Accident' slide show which induced the threat of non-disease relevant danger. Participants were then randomly assigned to hear a passage being read aloud about a group of foreigners seeking to immigrate to the local area of Canada – Vancouver, either from Nigeria or Scotland (rated in a pre-test as most foreign and least foreign, respectively). They were then asked to complete a questionnaire designed to assess their attitudes regarding the potential of the target foreign group immigrating to Canada, their attitudes toward Canada's immigration policy in general, and their judgments about various traits of the target immigrant group. The results showed that participants in the disease-salient condition were significantly more likely to support the immigration of the Scottish group and less likely to support immigration of the Nigerian group, while there was relatively equal support for the immigration of each group by participants in the disease-irrelevant condition.

The researchers found something similar in Study 6 using a budget allocation paradigm. Again, Canadian undergraduates (N=45) were randomly assigned to the same slide show conditions as Study 5, they were asked how much financial resources the Canadian government should allocate to the advertisement of Canada as a destination for potential foreign immigration – to either Mongolians or Taiwanese (rated as most foreign and least foreign, respectively). Participants in the disease-salient condition allocated significantly more budget resources for advertising to the Taiwanese than to the Mongolian immigrants, while there was relatively equal allocation to both groups by participants who viewed the disease-irrelevant condition. The findings together show a causal effect of BIS-activation via visual pathogen threat on measures of xenophobia.

These experimental studies provide some evidence for causation of BIS-activation via pathogen threat on measures of both ethnocentrism and xenophobia, thus providing support for Fincher and Thornhill's parasite-stress theory. However, there are arguably some methodological and/or experimental issues with each of these studies – the most obvious of which were the methods of priming employed, which I addressed in Chapter 2 (subsection 2.1.1). Moreover, experimental studies on the potential causal effects of pathogen stress on philopatry or religiosity are lacking. Various correlational studies illustrate a relationship between pathogen prevalence and philopatric behaviour such as range size, mobility patterns, strength of family ties, etc. (e.g. Cashdan & Steele, 2013; Fincher & Thornhill, 2008a)., and religious behaviour

such as participation and commitment (e.g. Fincher & Thornhill, 2008a; Fincher & Thornhill, 2012). But these relationships have yet to be explored experimentally. Further to this, while there does seem to be plenty of correlational evidence to suggest the possibility of a causal relationship between pathogen stress and in-group assortative social behaviour, not all evidence supports the relationship. Some researchers note the difficulties of analysing the data with regards to pathogen stress, however, some note other types of issues.

To illustrate, Cashdan and Steele (2013) found evidence of correlation between pathogen stress and philopatry and obedience but no evidence for the correlation with their measures of ethnocentrism or xenophobia. They also point out the difficulties involved in analysing ethnocentrism and social support as responses to pathogen stress due to the value that these behaviours would provide in coping with sources of stress other than infectious disease. With respect to religiosity, Beit-Hallahmi (2012) questions the premise of Fincher and Thornhill's (2012) correlational predictions and the findings. He points to the issue of the proposed individual flexibility in religiosity throughout history, arguing that until recently there was little or no choice or option, particularly for children, for an individual in their religious identity. Atran (2012, p.79) further argues that the expansion and success of religions is largely due to the fact that they aim to include and recruit "as many genetic strangers as possible", and would therefore include out-group individuals and individuals without shared similar immunology. Experimental testing may help elucidate these ideas and issues.

Correlational evidence has laid the groundwork for a seemingly strong theoretical framework. Moreover, there are some experimental studies that appear to support it. Based on the issues and arguments briefly laid out here, more empirical research is needed. This will be the focus of the study described in this chapter.

5.1.1 Study rationale

The studies described in Section 1.3 and 4.1 provide correlational evidence that shows a relationship between various measures of each of the components of in-group assortative sociality and various BIS-related measures such as disgust sensitivity, perceived vulnerability to disease, chronic disease worries, as well as level of pathogen prevalence in the ecological environment. Additionally, in these sections I described several experimental studies which provide some provisional evidence to support the notion of a causal effect on in-group assortative social behaviours. However, there are several issues with these studies. For example, the correlational studies focus on

geopolitical regions as the primary unit of analysis; the experimental studies each individually focus on only one of the components of in-group assortative sociality, i.e. either measures of ethnocentrism or of xenophobia; and, as discussed, there are issues and limitations regarding the priming methods employed in these experiments. But also, none of them, or any others known to the researcher, directly test philopatry or religiosity. There is indeed a lack of experimental studies into the effects of pathogen stress or BIS-activation on philopatry and religiosity in general. Moreover, although there is an experimental study that shows that disgust can be increased by exposure to an out-group's religion (Ritter & Preston, 2011), there is debate about whether religiosity can be affected by pathogen stress. Therefore, I set out to address these issues here, through a kind of quasi-replication of the experimental studies described in Section 5.1.

In this quasi-replication study, I have adopted techniques and tasks from each of the previously described experimental studies on measures of ethnocentrism and xenophobia; however, I devised my own measures of philopatry and employed a previous scale for the measure of religiosity to account for the supernatural foundations of religiosity. But most importantly, to account for the issues and limitations of the priming methods used to manipulate the BIS in the previous experiments, here I employ the Culpepper Disgust Image Set (C-DIS: Culpepper et al., 2018) to test the potential causal effects of BIS-activation on specific behaviours of each of the individual components of in-group assortative sociality. The overall aim is to experimentally test Fincher and Thornhill's parasite-stress theory which proposes that variation in pathogen stress may be responsible for variation in in-group assortative sociality – that is to say, that parasite stress imposes causal effects on philopatry, ethnocentrism, xenophobia, and religiosity. Based on the parasite-stress theory and the evidence presented throughout this thesis, it was hypothesised that variation in the activation of the BIS via visual pathogen threat will motivate variation in the expression of each of these in-group assortative social behaviours. Such findings would draw a clearer line of evidence to suggest that cultures could become isolated and diverge through variation in the values and beliefs of the individuals within them as a result of the causal effects of variation in pathogen stress in the ecological environment.

5.2 Method

Ethics statement

This study received ethical approval from the General University Ethics Panel at the University of Stirling and adhered to the ethical guidelines of the British Psychological Society. All participants provided prior informed consent and viewed a debriefing page after participation. Psychology students received one token-credit for participation and non-psychology students received no reward.

5.2.1 Participants

A total of 449 undergraduate students were recruited from the University of Stirling to take part in a Qualtrics online survey. After excluding 274 respondents from analysis for either not completing all of the tasks, not stating their country of origin, or not being a Scottish native, data for 175 Scottish-born students were retained for analysis, including 147 women (84%) and 28 men (16%) (Mean age $\pm$ SD = 21.20 $\pm$ 6.24, range 18-56).

5.2.2 Materials and procedure

The survey consisted of several demographic questions, e.g. age, gender, sexuality, religion. Participants then completed several scales and judgment tasks designed to assess levels of perceived vulnerability to disease, religiosity, philopatry, ethnocentrism, and xenophobia, followed by the C-DIS rating task. After this rating task participants completed the initial scales and tasks a second time so that any changes in these behaviours as a result of pathogen stress could be analysed.

PVD and religiosity scales

Participants first completed the same scales described in sections 3.2 and 4.2. They completed the 15-item PVD scale (Duncan et al., 2009) and rated the extent to which they agreed or disagreed with the PVD statements on a 7-point scale (1=*strongly disagree*, 7=*strongly agree*). PVD was calculated as a single score. Cronbach's *alpha* was conducted, α = .710, and found that the alpha could be only minimally increased, α = .770 by removing scale item 3 ('I am comfortable sharing a water bottle with a friend'). As in the previous chapters, the same was done for the Germ Aversion (PVD$_{GA}$) and Perceived Infectability (PVD$_{PI}$) subscales. PVD$_{GA}$: α = .395, which could be increased to .612 with the deletion of item 3; and PVD$_{PI}$: α = .759, which could be increased to .844 with the deletion of item 6 ('I have a history of susceptibility to infectious diseases').

Next, participants completed the 9-item religiosity scale (Valdesolo & Graham, 2014, with added item - as in Chapter 4), and rated the extent to which they agreed with the statements on a 7-point scale (0=*not at all*, 6=*very much*). Cronbach's *alpha* was conducted on both pre- and post-manipulation religiosity scales: $\alpha = .915$ and $\alpha = .921$, respectively. Participants who viewed the pathogen-salient images were predicted to exhibit a larger increase in religiosity than those who viewed the control images.

Philopatry

Participants then answered two questions designed to assess participants' levels of philopatry. The first question was: 'If money was no object, which of these countries [Taiwan, Peru, Poland, Nigeria, Canada, Mongolia, Brazil, or Iceland] would you be most interested in moving to?' The selection of countries was adopted from Faulkner et al. (2004), in which Canadian student-participants rated eight immigrant groups from characteristically different climates and geographies (Taiwan, Peru, Poland, Nigeria, Scotland, Mongolia, Brazil, or Iceland) on several scales for how different the immigrants were to themselves as well as their differences in specific disease-relevant domains (e.g. food preparation, hygienic practices). The ratings were collectively computed to provide an average 'foreign-ness' score. Rated as most foreign to Canadians were immigrants from Nigeria, then Mongolia, Brazil, Peru, Iceland, Poland, and Taiwan, with the least foreign being Scotland. Based on this finding, as well as other notable similarities between Canada and Scotland, in the current Scottish-student study Scotland was reversed to Canada. The second question to assess philopatry was: 'If money was limited, where would you want to move to?' This question/task allowed participants to make a globally unrestricted selection as to which country they would choose to move.

The theory and evidence suggests that individuals who are more philopatric would likely choose to remain in country (in this case, Scotland) or be more interested in moving to somewhere more similar to their own culture. It was therefore predicted that when the participants were provided with a limited choice of countries to which they could move, the participants who viewed the pathogen-salient images would show a larger increase in their preference for a more culturally similar country to their own than participants who viewed the control images. Similarly, it was predicted that when they were provided with a globally unrestricted choice of countries, they would show a larger increase in their preference for a more culturally similar country to their own compared to countries preferred by control images viewers.

Ethnocentrism

Participants then completed a scale, a rating task and a budget allocation task to assess two measures of ethnocentrism – conformity and cooperation to the in-group.

Conformity: this was assessed as a measure of ethnocentrism using two different tasks adopted from Wu and Chang (2012). Participants completed the 13-item 'attention to social comparison information' subscale (Appendix C) from the revised self-monitoring scale (Lennox & Wolfe, 1984), which measures conformity in different situations (e.g. 'When I am uncertain how to act in a social situation, I look to the behaviour of others for cues'). They also rated 9 abstract modern art drawings on an 11-point scale (1=*ugly*, 11=*very nice*). Below the drawings, participants could see fictitious ratings described as being from previous students from Germany, Africa, and Scotland. The absolute score difference (ASD) between their ratings and that of the fictitious Scottish raters served as a measure of conformity to the perceived in-group.

Cooperation: prosocial cooperation with (or favourability toward) the in-group over out-groups is considered to be a form of ethnocentrism therefore ethnocentric cooperation was assessed via a form of budget allocation paradigm adopted from Faulkner et al. (2004). Participants were informed that the psychology department was considering a new idea for next year psychology participants and needed some feedback before implementing the idea. Participants were provided with the following statement regarding the new idea:

"Participants of each study will be entered into a draw with the potential of winning £25. The winners of each draw will also have the opportunity to donate a percentage of their winnings to a fund that will help other students in need (i.e. food, bills, tuition, etc.). We are interested to know if students think this is a good idea or not, and how much and to which groups students would prefer to donate any potential winnings."

Participants were asked if they thought this was a good idea (yes/no), then they were asked if this idea were to be put into place, what percentage of the £25 winnings (for each study) would they donate to Scottish-born, UK-born, and International-born students. The percentage to which these Scottish-born student-participants stated that they would in future studies donate to Scottish-born students over and above the other students served as a measure of ethnocentrism.

It was predicted that participants who viewed the pathogen-salient images would exhibit a larger increase in both conformity and cooperation to the perceived in-group than those who viewed the control images.

Xenophobia

Next, participants read a vignette regarding the potential immigration of an immigrant group, after which their levels of xenophobia were assessed using three different measures. The vignette and measures were adopted from Faulkner et al. (2004). One measure assessed attitudes towards potential immigrants seeking refugee status in Scotland from either Nigeria or Canada. These countries were again chosen based on the findings of Faulkner et al. (2004), in which Nigerians were rated by Canadians as the most foreign compared to seven other countries, and Scotland as the most similar – thus Scotland was reversed to Canada for the current study. A second measure assessed attitudes towards Scottish immigration policy in general. The third measure assessed participants' judgments on the characteristics of the target immigrant groups in general. Participants read the following vignette:

> *"As a result of the living conditions for the indigenous people of [Nigeria/Canada], a large number of refugees from native lands of [Nigeria /Canada] are seeking refugee status in Scotland. They have told Scottish immigration officials that the standard of living for the indigenous people is unacceptably low and that their health and social systems do not meet the needs of these [Nigerian/Canadian] people. The majority of these refugees are applying to live in the Central Scotland area."*

Half of the participants were randomly assigned to read the passage pertaining to Nigerian immigrants and half were assigned to read the passage pertaining to Canadian immigrants (participants were assigned the same immigrant passage after the experimental manipulation). After reading the passage, participants rated the extent to which they agreed or disagreed with three statements regarding the immigrant group: 'none of the [Nigerian/Canadian] immigrants should be allowed to immigrate to Scotland', 'there is a risk that [Nigerian/Canadian] immigrants will bring health problems to Scotland', and 'there is a risk that [Nigerian/Canadian] immigrants will bring criminal problems to Scotland'. Then they rated the extent to which they agreed or disagreed with three statements regarding Scotland's immigration policies: 'Scotland's immigration policies are too strict', 'all immigration to Scotland should be halted regardless of immigrant origin', and 'Scotland should accept refugees in need of

asylum'. The statements were rated on a 7-point scale (1=*completely disagree*, 7=*completely agree*). The first three items were combined into a single index for anti-immigration attitudes, and the second three items into a single index for pro-immigration attitudes (item two reverse coded). Participants were then asked to rate their assigned target immigrant group on 13 different characteristics on a negative 9-point scale. For example, to what degree they think the target group is sanitary, hygienic, likeable, and trustworthy. See Appendix D for complete list of questions.

A three-way interaction was predicted – that is, individuals who viewed the disgust images would show a larger increase in xenophobia along these three measures than individuals who viewed the control images; but additionally, that the increase would be larger for individuals who rated the Nigerian out-group than individuals who rated the Canadian out-group after viewing the disgust images.

Manipulation of pathogen threat

To manipulate the BIS, participants were randomly assigned to C-DIS image-type – approximately half viewed the pathogen-salient images and half viewed the control images. Participants rated the images for disgust on a 7-point scale (0=*not disgusting at all*, 6=*extremely disgusting*). Cronbach's *alpha* was conducted on both C-DIS sets: pathogen-salient set, $\alpha = .921$, and control set, $\alpha = .938$. After rating the C-DIS, participants completed the same initial scales and tasks as before the C-DIS task.

5.3   Results

This section will include descriptions of data preparation, including statistical analyses to check the effectiveness of the manipulation, and the results for each social behaviour. Normal distribution of the data for each analysis was assumed based on the Central Limit Theorem (Field, 2013; Lumley et al., 2002). Parametric tests were therefore used for each analysis.

5.3.1 Manipulation check

Participants who viewed the C-DIS pathogen-salient images were predicted to exhibit an increase in several measures of social behaviours compared to participants who received the C-DIS control images. Therefore, as in Chapters 3 and 4, I ran several tests to determine whether the C-DIS images had the intended manipulation effect. I averaged the ratings of the C-DIS images together to generate overall mean disgust scores for each participant, then standardised the scores for each condition into z scores

and assessed these data for outliers. Three outlier ratings were found to be > 2 standard deviations smaller than the mean ratings in the pathogen-salient condition, suggesting that the images likely did not evoke disgust for these participants as intended. Five outlier ratings were found to be > 2 standard deviations larger than the mean rating in the control condition, suggesting that the control images likely unintentionally evoked disgust for these participants. These eight outliers were therefore removed from all subsequent analyses, leaving $N = 167$.

As in Chapters 3 and 4, I conducted an independent samples t-test on the disgust scores for both C-DIS sets to determine whether the pathogen-salient images were rated as significantly more disgusting than the control images and thus whether the BIS for the experimental group was sufficiently activated in comparison to the control group. The pathogen-salient images (4.60 ± 0.83) were rated as significantly more disgusting than the control images (1.23 ± 0.92), a statistically significant difference of 3.36 (95% CI, $3.09 - 3.63$), $t(165) = 24.65$, $p < .001$, $d = 3.85$. This suggests that the images were effective at their intended manipulation.

5.3.2 Analysis of pathogen threat on religiosity

Responses to the religiosity scale were averaged to generate individual mean religiosity scores for the two religiosity scales (pre- and post- manipulation).

A two-way mixed ANOVA, with image condition (pathogen-salient, control) as the between-participants factor and religiosity score (pre- and post- manipulation) as the within-participants factor, was conducted to determine whether religiosity significantly increased for participants exposed to the pathogen threat compared to participants exposed to the control images. Assessment of Box's test and Levene's test showed sufficient homogeneity of covariance ($p = .295$) and homogeneity of variance (pre-image religiosity score, $p = .543$; post-image religiosity score, $p = .352$). There was no statistically significant interaction effect between image condition and religiosity, $F(1, 164) = .032$, $p = .858$, $\eta p^2 < .0001$ (Figure 5.1). There was also no statistically significant main effect of image condition on mean religiosity scores, $F(1, 164) = 1.95$, $p = .164$, $\eta p^2 = .012$. There was, however, a statistically significant main effect of religiosity, $F(1, 164) = 11.17$, $p = .001$, $\eta p^2 = .064$. Pairwise *post hoc* tests showed no significant difference in religiosity between image conditions, with a religiosity difference of $.310$, $p = .164$, 95% CI [0.128-0.748]. Religiosity scores slightly reduced after exposure in both conditions (Figure 5.1). Furthermore, an

independent-samples t-test showed no significant group difference between groups in pre-manipulation religiosity scores, $t(165) = 1.56$, $p = .120$.

5.3.3 Analysis of pathogen threat on philopatry

In order to analyse the philopatry data it was more useful to generate an overall philopatry score. To do this, I assigned a value to the eight countries offered as responses to the restricted choice question: 'If money was no object, which of these countries [Taiwan, Peru, Poland, Nigeria, Canada, Mongolia, Brazil, or Iceland] would you be most interested in moving to?' Canada, the most similar country of the eight to Scotland, was assigned the highest value (=8) as this would represent the least foreign culture and therefore the most philopatric choice, followed by Taiwan (=7), Poland (=6), Iceland (=5), Peru (=4), Brazil (=3), Mongolia (=2), and Nigeria (=1). I then calculated a cultural similarity score for the open choice question: 'If money was limited, where would you want to move to?' The cultural similarity of the choices was scored using the following criteria. A 'remain' (in Scotland) response was scored as *Same Culture* =4; countries that are British-settled, English-speaking, predominately white, Judeo-Christian, were scored as *High Cultural Similarity* =3 (e.g. Australia, Canada, USA); countries that have any smaller combination of these and/or were included as EU members were scored as *Medium Cultural Similarity* =2 (e.g. Spain, Norway, Italy, Sweden, France); and, countries that were not part of the EU and did not match the majority of the criteria were scored as *Low-No Cultural Similarity* =1 (e.g. South Korea, Bali, Jamaica). The scores from each of these two measures were tallied to compute an overall philopatry score for each participant, with the highest scores representing high philopatry and lowest scores representing low philopatry.

A two-way mixed ANOVA was again conducted, with image condition (pathogen-salient, control) as the between-participants factor but with philopatry score (pre- and post- manipulation) as the within-participants factor, to determine whether philopatry significantly increased for participants as an effect of pathogen threat compared to participants viewing the control images. Box's test ($p = .405$) and Levene's test (pre-image philopatry score, $p = .993$; post-image philopatry score, $p = .725$) suggest sufficient homogeneity of covariance and homogeneity of variance. There was no significant interaction effect between image condition and philopatry, $F(1, 164) = 1.20$, $p = .273$, $\eta p^2 = .007$. No significant main effect of philopatry, $F(1, 164) = .317$, $p = .574$, $\eta p^2 = .002$ was found. Nor was there a significant main effect of image condition on philopatry scores, $F(1, 164) = .279$, $p = .598$, $\eta p^2 = .002$. Pairwise

comparisons showed no significant difference between image conditions, with a mean philopatry difference of .156, $p = .598$, 95% CI [0.427-0.738]. The trend suggests the philopatry scores were moving in the opposite direction than predicted for the conditions (Figure 5.2). The two philopatry measures analysed separately also revealed no significant effects.

5.3.4 Analysis of pathogen threat on ethnocentrism
Conformity

Scale measure: Participant responses to the 13-item conformity scale were averaged to generate individual mean scores for both pre- and post- manipulation conformity scales. A two-way mixed ANOVA was conducted, again with image condition as the between-participants factor but with conformity scale score (pre- and post- manipulation) as the within-participants factor, to assess the effects of pathogen threat in comparison to control images. Box's ($p = .426$) and Levene's tests (pre-image conformity, $p = .400$; post-image conformity, $p = .839$) suggest sufficient homogeneity of covariance and homogeneity of variance. The analysis revealed a statistically significant main effect of conformity (scale), $F(1, 165) = 7.04$, $p = .009$, $\eta p^2 = .041$, however, there was no significant interaction effect between image condition and conformity, $F(1, 165) = .162$, $p = .688$, $\eta p^2 = .001$. There was also no significant main effect of image condition on conformity, $F(1, 165) = .005$, $p = .944$, $\eta p^2 < .001$. Pairwise comparisons again showed no significant difference between image conditions, with a mean conformity difference of .005, $p = .944$, 95% CI [0.146-0.156].

Art drawings measure: The ASD between participant ratings and the bogus Scottish ratings of the art drawings was calculated individually as a measure of conformity for both pre- and post- manipulation. A two-way mixed ANOVA was again conducted, with image condition as the between-participants factor and ASD scores (pre- and post- manipulation) as the within-participants factor, to assess the effects of pathogen threat in comparison to control images. Tests again suggest sufficient homogeneity of covariance (Box's: $p = .191$) and homogeneity of variance (Levene's: pre-image ASD, $p = .236$; post-image ASD, $p = .112$). There was no significant interaction effect between image condition and ASD, $F(1, 165) = 3.32$, $p = .069$, $\eta p^2 = .020$, and no significant main effect of ASD, $F(1, 165) = 3.08$, $p = .081$, $\eta p^2 = .018$. Nor was there a significant effect of image condition on ASD, $F(1, 165) = 1.19$, $p = .276$, $\eta p^2 = .007$. Again, pairwise comparisons showed no significant difference between image conditions, with a mean difference of .227, $p = .276$, 95% CI [0.183-0.636].
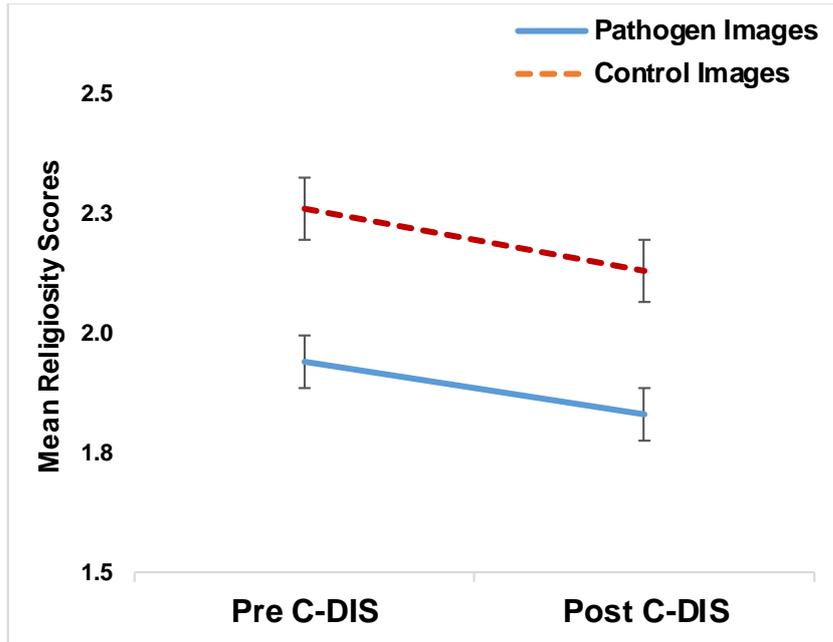
Figure 5.1 The mean pre- and post- manipulation religiosity scores in the pathogen-salient and pathogen-free image conditions. Data show mean (± s.e.) for each measure. (C-DIS: Culpepper Disgust Image Set)
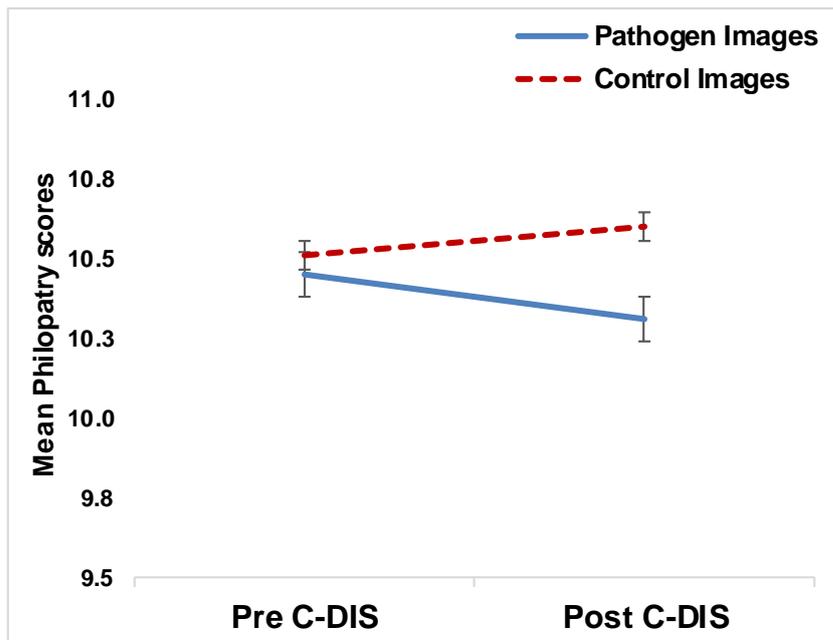

Figure 5.2 The mean pre- and post- manipulation philopatry scores in the pathogen-salient and pathogen-free image conditions. Data show mean (± s.e.) for each measure. (C-DIS: Culpepper Disgust Image Set)

Cooperation

As a measure of ethnocentrism two variables of cooperation were analysed: (1) the willingness for Scottish student-participants to donate their potential draw winnings to others, and (2) the percentage of these potential winnings they would be willing to donate to local (in-group) versus foreign (out-group) students, and whether these might change as an effect of pathogen stress. With regards to the first measure, 152 students (91%) initially stated 'yes' they thought the donation scheme was a good idea versus 15 (9%) who stated 'no'. Split by condition, 68 (87.2%) participants in the pathogen-salient condition and 84 (94.4%) in the control condition were in favour of the scheme. This remained basically unchanged after the C-DIS task, with 64 (82%) in the pathogen-salient condition and 82 (92.1%) in the control condition. Upon visual inspection of this data, aside from several missing responses only one participant changed their response (from 'yes' to 'no') after the manipulation and that participant was in the control condition.

A three-way mixed ANOVA was conducted on the donation data, with image condition (pathogen-salient, control) as the between-participants factor, exposure (pre- and post- manipulation) as a within-participants factor, and the three levels of donation (Scottish-born, UK-born, and International-born) as a within-participants factor, with the mean percentage of winnings donated to each group as the dependent variable. Levene's test showed sufficient homogeneity of variance for all pre- and post-manipulation donation measures (ps > .186) except one, post-manipulation donation to Scottish-born students ($p < .012$). According to Mauchly's test of sphericity, the assumption of sphericity was violated, $\chi2(2) = 37.331$, $p < .001$, with $\varepsilon = .831$; therefore, Greenhouse-Geisser correction was applied. Analysis revealed no significant interaction effect between donation, exposure, and image condition, $F(1.662, 274.182) = .528$, $p = .557$, $\eta p^2 = .003$.

Further analysis on the data split by image condition also revealed no significant interaction between donation and exposure. Mauchly's test of sphericity indicated that the assumption of sphericity was violated for both image conditions: pathogen-salient, $\chi2(2) = 63.589$, $p < .001$, with $\varepsilon = .683$; pathogen-free, $\chi2(2) = 33.354$, $p < .001$, with $\varepsilon = .758$; therefore, Greenhouse-Geisser correction was applied to both. Analysis showed no statistically significant simple two-way interaction effect for the pathogen-salient condition, $F(1.276, 98.286) = 2.654$, $p = .097$, $\eta p^2 = .033$, or for the pathogen-free

condition, $F(1.517, 133.490) = .025$, $p = .947$, $\eta p^2 < .001$. See Figure 5.3 for visual representation of this data split by condition.
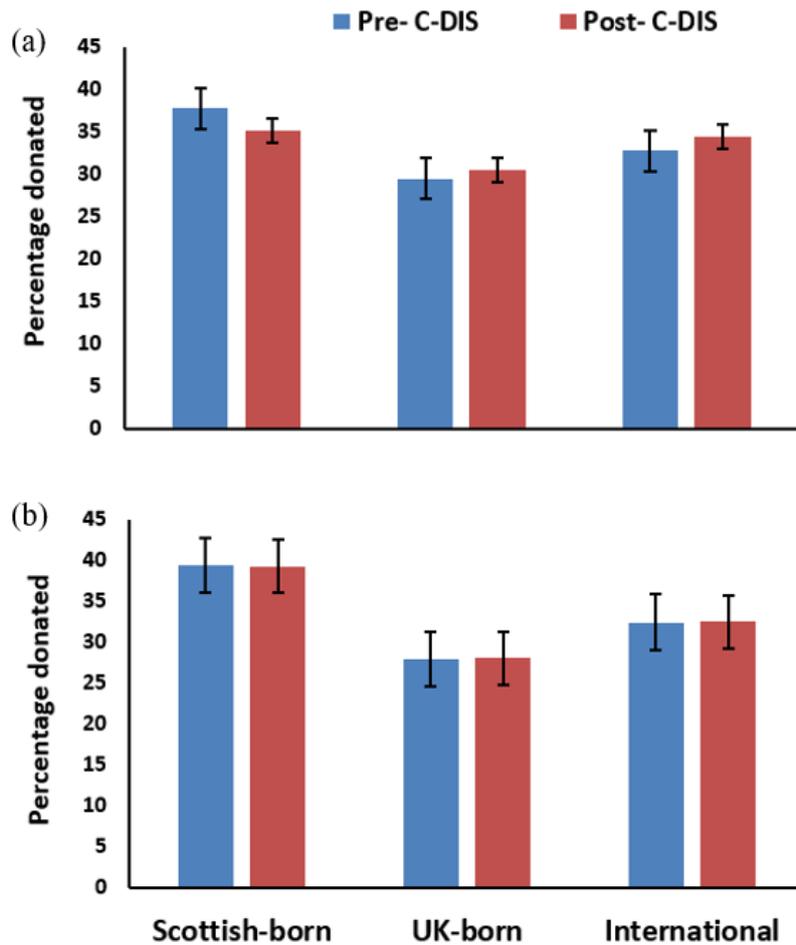
Figure 5.3 (a) The percentage of winnings participants in the pathogen-salient condition offered to donate to each of the potential groups of students. (b) Percentage participants in the pathogen-free condition offered to donate. Data show mean (± s.e.) for each measure.

5.3.5   Analysis of pathogen threat on xenophobia

The following analyses tested the corresponding interactions – that is, whether the Scottish participants' (1) anti-immigration attitudes towards the potential immigration of the target out-groups, (2) attitudes towards Scotland's pro-immigration policies in general, and (3) negative judgments of the characteristics of each target immigrant group increased as an effect of pathogen threat compared to the control images and whether they increased more toward the Nigerian group versus the Canadian group. In order to test the predicted interactions regarding these three

measures, I conducted 3 separate three-way mixed ANOVAs on each of these three measures as dependent variables, with image condition (pathogen-salient and control) as one between-participants factor, immigrant group (Canadian and Nigerian) as the second between-groups factor, and exposure (pre- and post- manipulation) as a within-participants factor.

Anti-immigration attitudes towards potential immigration of target group

Assessment of Box's test showed sufficient homogeneity of covariance (p = .853), and Levene's test showed sufficient homogeneity of variance (pre-image attitude score, p = .439; post-image attitude score, p = .364). Analysis revealed no significant three-way interaction effect between immigrant group, exposure, and image condition, $F(1, 163) = 2.703$, p = .102, ηp^2 = .016.

Attitudes towards Scotland's pro-immigration policies

Homogeneity of covariance was found to be insufficient (Box's test: p = .013). Levene's test indicated sufficient homogeneity of variance for pre-image attitude scores (p = .282), but not for post-image attitude scores (p = .031). Analysis again revealed no significant three-way interaction effect between immigrant group, exposure, and image condition, $F(1, 163) = 0.331$, p = .566, ηp^2 = .002.

Negative judgments of immigrant group characteristics

Again, homogeneity of covariance was found to be insufficient (Box's test: p < .001), while Levene's test suggested sufficient homogeneity of variance (pre-image attitude score, p = .913; post-image attitude score, p = .080). Analysis revealed no significant three-way interaction effect between immigrant group, exposure, and image condition, $F(1, 161) = 0.993$, p = .321, ηp^2 = .006.

Further analyses

Analyses were conducted on baseline group differences regarding anti-attitudes towards the potential immigration of each group, attitudes about Scotland's pro-immigration policies, and negative judgment of the characteristics of the target groups.

Three independent-samples t-test were conducted on the initial scores for each attitude measure. Initial attitudes towards the potential immigration of each target group showed no significant difference between the groups, $t(165)$ = -1.53, p = .129, d = 0.24. There was no significant group difference in participants' initial attitudes towards Scotland's pro-immigration policies, $t(165)$ = 1.14, p = .256, d = 0.18. However, initial judgments about the characteristics of the Nigerian group were

significantly less positive than those of the Canadian group, $t(163) = -2.52$, $p = .013$, $d = 0.40$.

5.3.6 Correlational and covariation analyses

For each of the measures of in-group assortative social behaviour (except xenophobia – see next paragraph), ANCOVAs were conducted with the two PVD subscales as covariates to ascertain whether the measures covary with either PVD_{GA} or PVD_{PI}. Results of the ANCOVAs showed that none of the measures significantly covaried with either PVD_{GA} or PVD_{PI} (all $ps > .238$).

Similar to Chapter 3, due to the lack of significant interactions, and thus of support for predicted causal effects, I thought it necessary to test whether the relationships found in the previous studies were present in the current data. The data were analysed for correlations between PVD, and the initial (pre-manipulation) scores of religiosity, philopatry, and ethnocentrism. Correlational analysis could not be conducted on the measures of xenophobia as participants were split by target immigrant group and by image condition.

A Pearson's one-tailed correlational analysis was conducted on PVD (and subscales) and the initial religiosity and philopatry scores, and the two ethnocentric measures of conformity: the conformity scale scores and the ASD of the art drawing ratings. Results indicated a positive relationship between religiosity and PVD, Pearson $r(167) = 0.190$, $p = .007$, and both PVD_{GA} ($r = .165$, $p = .017$) and PVD_{PI} ($r = .156$, $p = .022$). Religiosity also correlated in the direction implicitly predicted with both conformity measures: positively with conformity scale scores, $r(167) = 0.164$, $p = .017$, and negatively with ASD Art drawing ratings, $r(167) = -0.134$, $p = .043$ (Table 5.1).

Table 5.1 Correlations for PVD (including the PVD_{GA} and PVD_{PI} subscales), religiosity, and philopatry scores, and two measures of conformity (ethnocentrism): conformity scale scores and absolute score difference (ASD of the art drawing ratings.

	PVD	PVD_{GA}	PVD_{PI}	Religiosity	Philopatry	Conformity
Religiosity	.190**	.165*	.156*			
Philopatry	.035	.058	.009	-.096		
Conformity Scale	-.042	.047	-.097	.164*	-.041	
ASD Art Ratings	.078	.045	.080	-.134*	-.051	-.053

*. Correlation is significant at the 0.05 level (1-tailed).
**. Correlation is significant at the 0.01 level (1-tailed).

5.3.7 Analysis of gender differences

Due to the larger percentage of women participants and the potential effects of gender differences on in-group assortative social behaviours, I ran independent *t*-tests on men and women's pre-manipulation scores on religiosity, philopatry, the conformity measure of ethnocentrism, and the three xenophobia attitude measures. Women scored significantly higher than men in PVD (including each subscale) and religiosity, and men judged the characteristics of Nigerians significantly more negatively than did women (Table 5.2).

Table 5.2 Descriptive statistics from independent-samples *t*-tests on pre-manipulation scores for men and women on PVD, religiosity, philopatry, two conformity measures of ethnocentrism, and three measures of xenophobia: attitudes towards Scottish immigration policy, negative attitudes towards immigration of a foreign group and negative attitudes towards the characteristics of a foreign group (Nigerian; Canadian).

| | Mean scores | | | | |
Measures	Women	Men	*df*	*t*	*p*
PVD	4.17	3.52	165	4.14	< .001*
PVD$_{GA}$	4.10	3.56	165	3.36	< .001*
PVD$_{PI}$	4.24	3.49	165	4.25	< .001*
Religiosity	2.20	1.52	165	2.29	.023*
Philopatry	10.50	10.38	164	.281	.779
Ethnocentrism					
Conformity Scale	2.21	2.21	165	.014	.988
ASD Art Drawing ratings	-1.48	-1.54	165	.234	.815
Xenophobia *(attitudes towards)*					
Scottish pro-immigration policy	4.89	4.82	165	.282	.779
Anti-Immigration of Nigerians	2.53	3.15	92	1.77	.090
Judgments of Nigerians *(negative)*	3.31	4.10	91	2.24	.027*
Anti-immigration of Canadians	2.43	1.88	71	1.61	.111
Judgments of Canadians *(negative)*	2.90	3.20	70	.833	.408

5.4 Discussion

The aim of this study was to investigate whether variation in BIS-activation can produce variation in in-group assortative social behaviour, i.e. various measures of philopatry, ethnocentrism, xenophobia, and religiosity. The prediction was that participants whose BIS was activated would show a larger increase in measures of in-group assortative sociality than participants whose BIS remained inactivated, and that participants assigned to the most foreign immigrant group would show a larger increase

than participants in the least foreign group. The predicted interactions were not supported therefore the causal effects implied by the parasite-stress theory were not supported in this study.

Religiosity

For the first behaviour, religiosity, the results suggest that the pathogen-salient images did not elicit a larger increase in religiosity compared to the control images, i.e. there was no interaction effect of BIS-activation on the measure of religiosity. Interestingly, the analysis showed that viewing either set of images had a similar effect on religiosity. Religiosity scores showed a nonsignificant decrease for participants whether they viewed pathogen-salient or control images. The most obvious explanation for this finding would be that the length of the study and engagement in the various tasks may have generated some consistent reduction in participant accuracy and precision in the completion of the second (post-manipulation) religiosity scale across both image groups.

A second explanation could involve the scale I used to measure religiosity. Fincher and Thornhill (2012) analysed correlations of religious variables based on religious affiliation and commitment (participation and value). These variables are more related to the costly signalling of religious allegiance to the group (Alcorta & Sosis, 2005; Sosis & Alcorta, 2003; Sosis et al., 2007); however, they are unlikely, if not impossible, to alter over the course of a 25-minute experimental study. But further to this, they do not consider the adaptive cognitive mechanisms and strategies on which religiosity is founded, and which are particularly relevant to evolutionarily ancient, supernatural reasoning about infectious disease and illness. Therefore, I employed the religiosity scale based on supernaturality. But perhaps this was not the appropriate measure either. Religiosity is a difficult concept to measure in and of itself, but selecting the most appropriate measurement of religiosity for a specific approach and/or design is even more challenging. It would be useful for future studies to test this parasite-stress theory prediction with the consideration of other religiosity measures and perhaps over a longitudinal design. An individual's religiosity is typically founded on long-held, culturally and family cultivated and often imposed beliefs, which may only change with extended ontogenetic experience. Even if one's religiosity could change within a brief study, some individuals may be reluctant to admit it as they may view it (or fear it) as blasphemous to state otherwise even in a questionnaire.

More studies on the effects that ecological factors may have on religious behaviour are required. Most of the research on priming and religiosity focuses on testing whether priming religious concepts impacts other behaviours, e.g. conformity, morality, prosociality, rather than how factors may affect religiosity (see Shariff, Willard, Andersen, & Norenzayan, 2016, for review and meta-analysis of religious priming research). Moreover, there does seem to be a relationship between pathogen stress, and other BIS-related measures, and religiosity. Since there were no interaction effects, I conducted correlational analysis on religiosity scores and PVD scores (including the two PVD subscales) in this study to double-check the correlational findings in Fincher and Thornhill's work and found similar results. Religiosity positively correlated with PVD scores, and with the scores from each subscale. This consistent finding cannot be ignored and is yet to be explained by any other factor or phenomena. Having said this, in the current studies PVD scores showed no significant covariation with other measures, and the two PVD subscale scores had no significant differential association with stronger responses on any of the other measures, as found in other studies (e.g. Ackerman et al., 2018).

Philopatry

Results were similar for philopatry in that there were no interaction effects caused by BIS-activation – that is, participants who viewed the pathogen-salient images did not show a larger increase in measures of philopatry than participants who viewed the control images. There are several possible reasons for this result. First, the measures of philopatry may be problematic. For the first philopatry question I employed the use of countries that were determined and employed by a previous study and for a different purpose – testing differences in xenophobic attitudes, and on a different international sample of participants – Canadians (Faulkner et al., 2004). I tested Scottish participants and switched Scotland on the list of countries with Canada. I switched places between these countries based on the similarities between them in culture, climate, and geography, as well as because of Scotland's historical connection with and impression on Canada. However, Scottish people may not come to the same conclusion about which countries are more or less foreign as Canadians did in the Faulkner et al. study. The Scottish population is part of the UK and EU, each of which is arguably more cosmopolitan and more heavily exposed to international visitors than perhaps British Columbia, Canada. This would also suggest that they have the potential to be exposed to more non-local parasites, which may account for their high initial

philopatry scores. This may have led to a type of ceiling effect on philopatry, allowing little to no room for increase after manipulation.

There was also a much larger percentage of women in the sample (84%). This may have also had an effect on the results. Females tend to be the more philopatric sex across most social living mammalian species – that is, these species engage in a male-biased dispersal strategy (see Lawson Handley & Perrin, 2007 for review), and for several additional reasons to parasite stress, e.g. differences in energetic investment and differential effects on reproductive success (Clutton-Brock & Lukas, 2012). In addition to this, the mean age of the participants was 21 years and they were undergraduate students. International movement is not likely something many of them would have considered. But similar to the issue with religiosity, decisions about whether someone wants to move abroad or not are unlikely to change over the course of a brief experimental study. Again, some type of longitudinal design may be more useful in measuring changes in this behaviour stemming from BIS-related input.

Ethnocentrism

For ethnocentrism, I employed two measures of conformity and one measure of cooperation to the in-group. As in the religiosity and philopatry components, the results showed no interaction effects of BIS-activation on the conformity scale scores or for the absolute score difference of art drawings ratings. Participants who viewed the pathogen-salient images did not show a larger increase in this self-reported measure of conformity, nor did these participants show a larger increase in their conformity to the perceived in-group art ratings, than participants who viewed the control images. This is a peculiar result. The findings do not provide support for the parasite-stress theory nor do they corroborate the findings of the study on which the current study was modelled (Wu & Chang, 2012). Their study found significant group difference for the ASD conformity measures between participants who viewed the pathogen-salient condition versus those who viewed the building or accident conditions.

However, there were several notable differences between our studies. Their study was a simple between-participants design and did not employ a within-participants (pre/post) component, and they employed two non-disgust related conditions as controls; whereas the current study employed a mixed factorial design and pathogen-free control condition in which participants were still asked to rate these images for disgust. Furthermore, I was only available to 9 art drawings from Renkema et al. (2008) for use in my study, whereas Wu and Chang used the complete set of 30 art

drawings. There may have been some image-specific issues in the ones I used that may have been reduced or lost when using the complete image set. For example, the 9 images I used may have been the least likely to generate difference in ASD. The differences between the studies may account for the differences in the results.

With regards to the budget allocation cooperation task, no three-way interaction effects were found. Participants who viewed the pathogen-salient images did not show a larger increase in donations toward the in-group compared to participants who viewed the control images. Over 90% of the participants stated that they thought the donation scheme was a good idea, and participants did initially (pre-manipulation) offer to donate a significantly larger percentage of their potential winnings to the in-group versus the UK and international groups. This illustrates the nature of ethnocentrism in general, i.e. preferences for and cooperation toward the in-group, but it does not corroborate the findings from the study after which this study is modelled (Faulkner et al., 2004), and it says nothing about the proposed relationship between pathogen stress and ethnocentrism. Interestingly, participants were willing to donate a larger percentage to international students than to UK students who are technically more a part of the in-group than international students. This may be a result of Scotland's history with England. However, it does not explain why there was no increase in donation toward the in-group versus either of the two out-groups as a result of BIS-activation. I think the budget allocation paradigm was sound but like the conformity component of this study, perhaps the difference between these findings and the results from the model study stems from the difference in design. Faulkner et al. employed an independent-samples design (i.e. between-participants), whereas I employed a mixed factorial design to assess between-participants and within-participants differences.

Unlike the religiosity and philopatry components of the study, the ethnocentrism component was founded on a previous study which did find a causal relationship between pathogen threat and measures of ethnocentrism. Therefore, it would be prudent to test the causal prediction again, but instead using a between-participants design. If this were to provide support then it would suggest that the mixed factorial design needs amending before conducting another study.

Xenophobia

The results corresponding to this component of the current study also showed no three-way interaction effects of BIS-activation on the three measures of xenophobia.

Anti-immigration attitudes towards the target immigrant groups, attitudes towards Scotland's pro-immigration policies, and negative judgments towards the characteristics of the target immigrant groups did not exhibit a larger increase for participants who viewed the pathogen-salient images versus the control images, nor did they increase more in the more foreign immigrant group (Nigerian) than in the less foreign group (Canadian). These findings again do not provide support for the causal findings of the model study (Faulkner et al., 2004). Similar to the previous components, this may be a result of ceiling effects, which itself may also be a product of the study design as previously noted, which itself may also lend to fatigue effects.

Yet, the findings of this component do not disconfirm the findings of the model study or of foundational theory either. Further analysis was conducted using independent-samples t-tests to test initial xenophobia scores on the three measures. It was expected that participants would hold stronger anti-immigration attitudes towards the potential immigration of the more culturally foreign group than the less foreign group, but this was not the case. This may be explained by the fact that both groups were relatively in agreement from the start with Scotland's pro-immigration policies, which was to be expected since this is likely culturally driven. However, there was a significant difference between groups in the judgment of the characteristics of the immigrant groups. The characteristics of Nigerians were judged significantly more negatively than those of Canadians. Although this finding does not offer insight into causation, it does somewhat fit the theory. According to the theory, individuals should prefer the least foreign group over the most foreign. Again, there may have been potential interaction effects of PVD, religiosity questions, and statements regarding outgroup scenarios. These may have interacted to some extent to influence or moderate BIS responses to the C-DIS stimuli.

Interesting findings

Some evidence to support aspects of previous theory and evidence were found in this study. For example, religiosity significantly correlated with PVD and both conformity measures of ethnocentrism. This makes sense in that religiosity calls for high conformity to the group's strict taboos, rules, and rituals. Interestingly, many of these are designed around and focused on signalling allegiance to the in-group and avoiding real and supernatural related infections, whether to the body or the soul. This supports findings from Fincher and Thornhill's work (e.g. 2012) and further illustrates the proposed religiosity-BIS connection described in section 5.1. But further to this,

women also scored significantly higher in religiosity and in PVD than men. Both of these results are found throughout many previous studies. There are evolutionary reasons why women should express higher disgust than men (Fessler & Navarrete, 2003; Fessler, Eng, & Navarrete, 2005) but it is not yet clear why women are more religious (see Culpepper, 2014, for overview). Perhaps the evolutionary origins and the coevolutionary relationship between religiosity and the need to avoid disease is the key. A final interesting finding is that men expressed significantly more negative baseline judgments of the Nigerian immigrant group than women, but there was no gender difference for the Canadian immigrant group. This does not make sense from the disgust perspective. Considering that women express higher levels of disgust they should then be more concerned than men about the most foreign group.

5.4.1 Limitations and future directions

There are several limitations to this study that future studies could take into consideration. The most important of which is the design, as noted throughout the discussion. The experimental studies the current study is modelled after each employed a between-participants design rather than incorporating a within-participants factor. Among other things, the design of this study may have increased the potential of ceiling effects and fatigue effects. Future work should consider this design issue. Different measures of philopatry and religiosity could also be employed in the future and these behaviours could be analysed longitudinally. Additionally, researchers should conduct a pre-test to assess which countries the participant cohort considers least and most foreign to be used in the tasks for the philopatry and xenophobia components, as done by Faulkner et al. (2004).

Another limitation was the women-men ratio. Over 90% of the participants were women. This is problematic for several reasons, the first of which is that many women, for evolutionary reasons, express higher levels of disgust than men therefore a more equal gender representation may be useful. Another reason is that many of the women participants may have been taking hormonal contraception. I did not analyse this data but hormonal contraception has effects on the menstrual cycle and the corresponding hormones (i.e. progesterone) that modulate disease avoidance behaviour (Fleischman & Fessler, 2011). This could be controlled for in future analysis. These are just a few of the most obvious limitations and issues to be considered in future research.

5.4.2 Conclusions

The findings of this study – that is, the lack of interaction effects, do not offer evidence to support the causal relationship between pathogen threat and in-group assortative social behaviour predicted in the parasite-stress theory. But these findings also do not disconfirm the parasite-stress theory and its underlying hypotheses. The lack of support for the predictions may be explained by issues with the design of this study rather than with the theory itself. In fact, secondary analyses provided some evidence to support aspects of the theory but also to corroborate the correlations between BIS-related measures and religiosity found by Fincher and Thornhill. This finding is yet to be explained by any other means and just creates further mystery and intrigue. Research into the BIS and its potential causal effects on human behaviour must continue.

Chapter 6: General Discussion

6.1 Introduction

As described in Chapter 1 and throughout various sections of this thesis, there is a plethora of evidence from a wide range of studies which shows a relationship between a variety of BIS-related, disease-relevant input and output, i.e. in-group assortative sociality. This evidence converges to provide the framework and support for Thornhill and Fincher's (2014b) parasite-stress theory of human values and sociality, which proposes that variation in parasite stress lends to variation in in-group assortative sociality. Fincher and Thornhill propose that these causal effects on human values, which are expressed through in-group assortative social behaviour, can lead to cultural isolation and divergence, and thus to a form of cultural 'speciation'. However, the majority of the supporting evidence for this theory is correlational at the group level of analysis, and critics argue that caution should be taken about attributing causal mechanisms. Therefore, the main aim of this thesis was to experimentally test the plausibility of Thornhill and Fincher's theoretical proposal. To do this, three individual studies were designed and conducted with the aim of generating variation in visual activation of the BIS at the individual level to analyse resulting variation in specific measures of in-group assortative social behaviour. Results from the studies in this thesis were mixed.

6.2 Summary: Chapter 2

In order to test the effects of BIS-activation on in-group assortative social behaviours, I first needed to decide which set of visual priming stimuli I would employ. Upon reviewing the relevant literature to undertake the research within this thesis, I found that there were problematic limitations and issues with the methods employed to activate the disgust emotion and the BIS proper. Some studies employed the use of semantic priming and others used unrealistic cartoon images; while others employed more ecologically valid images but which included non-matching images as controls (e.g. Faulkner et al., 2004; Navarrete & Fessler, 2006; Wu & Chang, 2012). The only set of images that were specifically devised to prime pathogen disgust I could find was the set devised by Curtis et al. (2004) – arguably the most well-known in disgust-related research for more than the past decade. Oddly, this set of images was not used in any of the studies testing effects on ethnocentrism or xenophobia. However, upon further inspection I discovered that this image set also contains some limitations and weaknesses, including that it depicts only a limited range of disgust elicitors and omits many of the most commonly cited sources of disgust. Further to this, it was constructed

in a subjective top-down fashion, and was not effectively validated for cross-cultural application. Therefore, in the study presented in Chapter 2, I aimed to devise a new set of disgust images designed specifically to account for the limitations and issues of Curtis et al.'s (2004) image set, and which could subsequently be employed in the experiments that followed. Chapter 2 was based on the published manuscript by Culpepper, Havlíček, Leongómez, & Roberts (2018) in which I led the collaborative cross-cultural research effort to devise an image set that could be considered an improvement to the set by Curtis and colleagues. The study resulted in the Culpepper Disgust Image Set (C-DIS), a four-factored set of 20 images along with matching pathogen-free control images.

The main issue we observed regarding the Curtis et al. (2004) image set was that the items and scenarios selected to be depicted in the images were not derived through objective population sampling. The study makes no mention of precisely how they were chosen, but presumably they were subjectively decided upon by the researcher(s) and did not pass through any data collection or validation steps or process. This not only generated a subjective set of a limited number of items and scenarios as well as a limited range of items and scenarios, but it also limited the potential for application in cross-cultural research. Having said this, I am not certain that Curtis and colleagues devised their image set with the intention or purpose of future widespread application. It seems that they may have just put a small set of images together for the simple purpose of testing the specific hypothesis that disgust is indeed an adaptation evolved to help avoid pathogens, after which the images were then employed by researchers in subsequent studies around the topic. However, their image set provided us with a starting point from which to consider the need and value of developing a new pathogen disgust instrument by methods of proper data collection and validation procedures, particularly an instrument that addresses the observable issues of the Curtis et al. set.

To address the issues of the Curtis et al. (2004), we modelled the development of our study specifically on previous multi-stage, item-generation procedures carried out by other researchers (Ferdenzi et al., 2011; Haidt et al., 1994; Tybur et al., 2009), with particular attention to Haidt et al. (1994) and Tybur et al. (2009) which developed earlier disgust scales. However, we also sought to improve upon these procedures. For example, in the initial stage of Haidt et al.'s study, they only asked 20 American participants to describe three disgusting life experiences, yielding a total of 221 descriptions from which to begin instrument development. In the initial stage of Tybur

et al.'s study, they only asked 14 students from one major university (unnamed) to list 15 things they found disgusting, yielding a total of 105 items. Whereas, in our initial stage we asked 461 participants from multiple regions and cultures, including from within North America, South America, the UK and Europe, to each list 5 of the most disgusting items or scenarios they could think of, yielding a more diverse, cross-cultural foundation of 2,287 items from which to begin instrument development. Moreover, their studies and resulting scales included domains other than pathogen disgust (e.g. sexual and moral disgust), whereas we included a stage designed to reduce the items down to only those that represent the pathogen disgust domain. Haidt et al.'s study led to 8 domains (66 questions) and Tybur et al.'s led to 3 domains (21 questions). Our study led to 4 factors within one domain – pathogen disgust (20 items). Interestingly, and particularly relevant to Fincher and Thornhill's parasite-stress hypothesis of religiosity, Haidt et al.'s Disgust scale includes a magic domain which illustrates the correlation between magical thinking around contagion concerns and disgust.

One issue with the development and validation procedure we employed in our study is that we did not compare our images set with other validated constructs for the purposes of assessing convergent and discriminant validity as done by the researchers for the other scales. For example, Tybur et al. (2009) conducted comparative analysis on their Three-Domain Disgust Scale with the PVD scale (Duncan et al., 2009), the Primary Psychopathy scale (Levenson, Kiehl, & Fitzpatrick, 1995), the Big Five personality scale (Benet-Martínez & John, 1998), and the Disgust Scale-revised version (Olatunji et al., 2007). Haidt et al. (1994) conducted comparative analysis on their Disgust scale with the Eysenck Personality Questionnaire (Eysenck & Eysenck, 1975), the Self-monitoring scale (Snyder, 1974), the Sensation Seeking scale (Zuckerman, 1979), and the Fear of Death scale (Boyar, 1964). Ferdenzi et al. (2011) compared their Liverpool and Singaporean odour perception scales to the validated Geneva Emotion and Odor Scale (GEOS: Chrea et al., 2009) after which they were modelled. Here, we compared our C-DIS only with the non-validated Curtis et al. (2004) image set. Comparisons between the C-DIS and other scales and/or image sets may have provided stronger convergent and discriminant validity with and against other constructs.

That being said, other validated image sets currently available were not devised and validated for the specific purpose of studying disgust, e.g. the IAPS (Lang et al., 2008), the NAPS (Marchewka et al., 2014), the GAPED (Dan-Glauser & Scherer,

2011), and the EmoPicS (Wessa et al., 2010). To our knowledge, only one other image set was devised for this purpose – the DIRTI picture set designed by Haberkamp et al. (2017). However, this set suffers from the same issues and limitations our study was attempting to address – namely, it was also developed through a top-down approach along preselected disgust categories. Moreover, it was not available at the time of our procedures and analyses. Therefore, the foremost important aspects for us in our analysis of the C-DIS were that it showed strong evidence of convergent and discriminant validity with Curtis et al.'s (2004) image set, and that it met three predetermined measures of improvement against the Curtis et al. set – all of which it did.

There was another limitation of our development process. Although we sampled and validated our data cross-culturally, it would have been even more useful to have drawn from a wider range of regions and cultures. For example, it would have been particularly useful to have collected data from various non-Western groups such as peoples from the South Pacific and the Middle Eastern regions, the San and Hadza of Africa, the Yanomami of South America, and even the Inuit people distributed across the circumpolar regions of Russia, Alaska, Canada, Greenland, and Denmark. This may have added more specific insight into the evolutionary foundations of disgust.

Ultimately, by employing a 7-stage bottom-up approach, our study overcame the shortcomings of the Curtis et al. (2004) image set and resulted in an image set that can be considered an improvement to their set. Further to this, the initial stage of our study – the item-generation stage – can also be considered an improvement on the initial stages of other related scales. There were some limitations to our development process which researchers should consider in future attempts to improve upon the C-DIS, but overall our C-DIS provides an instrument that should be a useful asset to disgust-related research.

6.3 Summary: Chapters 3, 4, 5

Chapters 3, 4, and 5 each presented individual studies designed to experimentally test components of Thornhill and Fincher's (2014b) parasite-stress theory of values and sociality using the C-DIS as visual pathogen threat to evoke variation in BIS-activation and response.

Chapter 3 presented a study founded on evolutionary theory regarding the condition-dependent trade-offs that drive women's preferences between mate qualities.

Researchers propose that women adapt their mate preferences to value indicators of genetic quality and health more than indicators of parental and relationship investment in response to pathogen stress in the ecological environment (e.g. Folstad & Karter, 1992; Gangestad & Simpson, 2000; Gangestad & Scheyd, 2005; Hamilton & Zuk, 1982; Thornhill & Gangestad, 1993; Trivers, 1972; Zahavi, 1975). Thornhill and Fincher (2014b) incorporate this into their parasite-stress theory to explain how and why cultures differ in their values and beliefs about physical attractiveness, and how cultural divergence in these values and beliefs is part and parcel of regional variation in pathogen stress. As discussed throughout subsection 1.3.1 and Chapter 3, there is much theoretical and correlational evidence to support these views. In these sections I also described a small selection of experiments that support the evolutionary theory on which the parasite-stress theory is founded. However, these experiments do not directly test the causal relationship proposed by Thornhill and Fincher. The study I presented in Chapter 3 is formed on a combination of several of these previous experiments (e.g. Lee & Zietsch, 2011; Little et al., 2011; Roberts et al., 2005) and was designed to test whether variation in visual pathogen threat could cause variation in preferences for facial attractiveness and masculinity, which would evidence the proposed benefits trade-off. Facial attractiveness and masculinity are both thought to be indicators of genetic quality and health, which are thought to be indicators of MHC heterozygosity.

The study in Chapter 3 did not provide evidence to support the proposed hypothesis and therefore did not provide support for the overarching proposal by the parasite-stress theory. That is, the predicted interaction effects did not occur. Participants did not exhibit variation in mate preferences for MHC heterozygosity as indicated by facial attractiveness, or in preferences for facial masculinity – another MHC-related phenotypic trait. The lack of interaction effects does not in and of itself disconfirm the parasite-stress theoretical proposal. Analysis revealed main effects and initial (pre-manipulation) response patterns that fall in line with the evolutionary theory on which the parasite-stress theory and the previous experiments were founded. Moreover, the results of the facial attractiveness ratings replicated the findings from Roberts et al. (2005), further strengthening the theoretical link between facial attractiveness and MHC heterozygosity. In addition to this, facial masculinity was significantly more preferred than feminine faces by women but not men, which makes sense in light of the evolved gender differences in mating psychology.

The fact that these patterns were found in the data suggests that the lack of interaction effects is likely a result of various issues inherent in the design, e.g. extraneous variables, carry over effects, progressive error, rather than issues with the parasite-stress theory. Future studies into this topic would benefit from controlling for various extraneous variables and design issues such as those discussed in section 3.4.1. But perhaps more importantly, the observed patterns illustrate the ability for individuals to track MHC zygosity in potential mates and thus appears to confirm the notion that there is an adaptive advantage to preferring MHC heterozygotes, as indicated by physical attractiveness. It would be interesting to find out whether facial masculinity is also linked to heterozygosity as previously proposed. Since the masculine and feminine facial images were digital composites in this study, no information can be gleaned as to whether preference for masculinity is relative to MHC zygosity. Further studies could consider this in the design. For example, researchers could ask participants to rate the same MHC facial images (from Roberts et al., 2005) for masculinity to see if masculinity ratings map onto heterozygosity as clearly as physical attractiveness ratings. But in the context of this thesis, there is more research that can be done regarding MHC-heterozygosity and the parasite-stress theory. Future studies should consider the potential effects of differences in preferences as they relate to optimal inbreeding.

Chapters 4 and 5 both focused on Thornhill and Fincher's proposal that temporal and geographical variation in parasite stress in the ecological environment causes variation in the ontogeny and trajectory of social and cultural value systems by activating the BIS and motivating, to differing degrees, in-group assortative sociality. They argue that high level of parasite stress motivates stronger expression of philopatric, ethnocentric, and xenophobic behaviour in groups, leading to group isolation from which distinctly different values and beliefs arise and evolve – i.e. evoked culture. Previous research has provided an extensive amount of evidence to show correlations between both BIS-related input and cognition with the expressed degree of a broad range of individual and social values and behaviour, such as personalities, attitudes, norms, morals, taboos, practices, and beliefs, that make up a culture's value system. These are to a large extent reflected in the rules collectively formed and enforced by the citizens and social and governmental institutions of a society. Religious, political and government systems of societies in regions of stronger parasite stress are expressive of more conservative, traditional, and collectivistic values than those in regions of lower parasite stress.

Based on this, I presented a novel study in Chapter 4, designed to experimentally test the proposal that variation in visual pathogen threat can motivate variation in the values and beliefs that impact the type of governing rules (laws) individuals might favour for their society, and therefore impact the ontogeny and trajectory of the overarching culture. More specifically, the study investigated whether generating variation in BIS-activation in individuals could cause a divergence in the sets of values on which they form their beliefs about morality as expressed through legality, which may increase isolationist ideology. These include beliefs about rights, freedoms, group cohesion, patriotism, nationalism, protectionism, egalitarianism, liberalism, globalism. For example, which individuals can or cannot have rights (or have their rights protected), how individuals must or must not behave, what beliefs individuals must or must not hold, whether and how much individuals must conform to the norms of the social group, which individuals are included or excluded from the social group, and the criteria on which these decisions are made.

In this study participants viewed either the pathogen-salient images or the control images and selected and prioritised 15 rules from a 60-rule list, with 20 each of pathogen-management, prosocial and assortative rules. The general hypothesis was for the most part supported. Participants who viewed the pathogen-salient images favoured assortative social rules over prosocial rules and those who viewed the control images favoured prosocial rules over assortative social rules. This suggests that pathogen stress can cause differences in values that motivate stronger in-group assortative sociality in individuals. An interesting finding was that the groups did not differ in their favouring of pathogen-management rules. It was expected that participants exposed to the pathogen-salient images would show more concern with these rules as a result of BIS activation than participants exposed only to the control images. This is difficult to explain. It may be a result of the pathogen-management rule list itself (see following paragraph). The data also revealed a correlation between religiosity and PVD score. This supports the theory and evidence put forward by previous researchers (Terrizzi et al., 2013; Terrizzi et al., 2012; Thornhill & Fincher, 2014b). But the findings also bring into question other theories, such as the moral foundations theory (Haidt & Graham, 2007) and the 'Big Gods theory' of prosociality (Norenzayan, 2013). The findings of the study in Chapter 4 suggest that moral values are not static – they can fluctuate and vary as a response to BIS activation. Similarly, so can the extent to which individuals express assortative versus prosocial behaviour, suggesting that rather than Big Gods promoting prosociality it may instead be little parasites motivating assortative sociality.

Having said all this, there were issues with this study – the first of which is the sample. The sample was small and homogenous, i.e. predominately white and British. The small sample size may be the biggest issue. It may be best to consider this a pilot study when considering the sample size, but a pilot which provides ample rationale for recruiting a larger sample for replication. The homogeneity of the sample may not be problematic for the purposes of this thesis study. On one hand, the results cannot be generalised across populations. But, on the other hand, the homogeneity acts as a control for the potentially confounding variable of ontogenetic differences between cultures with varying levels of parasite stress in the ecological environment that may influence the responses of corresponding participants differently. Another issue may be the rules constructed for the task. These were subjectively drawn up by myself to be a depiction of each of the three list topics. Although this would not account for the differences exhibited by the condition groups in rule selection and prioritisation, it still may be useful for researchers to construct a cross-culturally validated set of rules for each of the three rule lists to employ in future studies.

Aside from these minimally concerning issues, the findings of this study appear to provide preliminary support for the parasite-stress theory and suggest that BIS activation can lead to individual differences in values involved in the formation of what people consider right and wrong. Pathogen stress seems to have inspired individuals to favour social rules that promoted, in this instance, values which motivate conformity to and protection of the in-group's members, norms, ways, and beliefs, to the exclusion and avoidance of out-group individuals and isolation from outside groups. Further investigation with a validated set of rules and a larger cross-cultural sample which can be analysed by independent groups and by group comparisons will likely be more informative.

Finally, the study presented in Chapter 5 also investigated the effects of visual pathogen threat on the individual components of in-group assortative sociality more specifically. In this study I combined several previous experiments (Faulkner et al., 2004; Navarrete & Fessler, 2006; Wu & Chang, 2012) into one to test the proposal that variation in visual pathogen threat can generate variation in responses to measures of philopatry, ethnocentrism, xenophobia, and religiosity. Participants responded to tasks and scenarios corresponding to each type of assortative social component, were then randomly split into either the pathogen-salient group or the control group, after which they completed the corresponding tasks and scenarios again. Interaction effects were

predicted for each of the measures in that, participants in the pathogen-salient group were expected to show a significantly larger increase in each of the measures than participants in the control group. The interaction effects did not occur and therefore the predictions were not supported. Thus, this study did not provide any evidence to support the causal relationship proposed in the parasite-stress theory. However, similarly to the study in Chapter 3, these findings may be a result of design issues. I employed a mixed factorial design for this study as well, which may have also resulted in issues such as carry over effects and progressive error, e.g. fatigue effects. Whereas, the studies on which this study was modelled each employed a between-participants design. But aside from these design issues there may have been other extraneous variables as well.

For example, the lack of interaction effects on religiosity may have been a result of the scale employed to measure religiosity. Future studies may offer more insight with the use of a different religiosity scale. Additionally, due to the nature of the enculturation and fear of punishment enveloped in abruptly admitting lack of or change in religious belief, a longitudinal study may be more appropriate for measuring this type of behaviour. The lack of effects on philopatry may have been a result of the large proportion of women in the sample. This may have lent to ceiling effects due to women arguably being the more philopatric sex in general (see Lawson Handley & Perrin, 2007 for review). This would leave little room for increase in philopatric behaviour as an effect of pathogen stress. Another issue may have been the assumptions I made about the relationship between Scotland and the countries utilised in Faulkner et al. (2004). This study was the first (known to me) to test direct causal effects of pathogen stress on measures of religiosity and philopatry. These are just a few considerations but the wrinkles in this study need some ironing before conducting any form of replication, but this was a useful start. One interesting finding that supported previous parasite-stress theory-based predictions and evidence was that religiosity and PVD scores positively correlated. This recurrently found phenomena suggests an underlying connection that demands further investigation.

The lack of interaction effects on the two measures of ethnocentrism, conformity and cooperation, also provides no evidence to support the parasite-stress theory. The lack of corroboration for the findings of Wu and Chang (2012) regarding effects of pathogen threat on conformity may be a result of the differences in the set of art images used in their study versus what I was able to find. Interestingly, conformity scores did

correlate with religiosity and PVD scores, as would be expected if the parasite-stress theory is accurate. The lack of effects for in-group cooperation in the budget allowance paradigm is to some extent likely due to the historical issues between Scotland and England that are embedded into Scottish society. However, the initial percentages of winnings donated by the participants did further support long-held understanding of ethnocentrism and in-group versus out-group preferences in that, individuals were willing to donate significantly higher percentages of winnings to fellow Scottish students.

With regards to the measures of xenophobia, again there were no interaction effects. Participants in the pathogen-salient condition did not show larger increase in the measures of xenophobia than participants in the control condition. Again, this may be due to ceiling effects, carry over effects and progressive error. However, somewhat contradictorily, analysis of initial responses on attitudes towards the immigration of the two foreign groups revealed that participants did not hold stronger anti-immigration attitudes towards the most foreign versus the less foreign group. There was however a significant group difference in the ratings of the characteristics of the two foreign groups. Participants rated the most foreign group most negatively. This supports Faulkner et al. (2004) and the theoretical basis for the parasite-stress theory.

The goal of chapters 3 and 5 were to offer quasi replications of previous experimental studies that found effects of pathogen threat on measures of in-group assortative sociality, but by employing mixed factorial designs to more effectively test direct causation than between-participants designs can offer. In doing so, I may have incurred different extraneous input which had their own implications on the outcomes. However, various analyses did provide evidence to corroborate or support previous evolutionary theory and studies on which the parasite-stress theory is founded. If nothing else, this merits further investigation on this evolutionary topic but with modifications to the design of my studies as well as the studies after which my studies were modelled.

6.4 Limitations and future directions

There are several issues and limitations enveloped in research into the BIS topic. One issue, or collection of issues, brought to attention by Tybur et al. (2014) is chosen methodology and the interpretations of findings obtained from such methodology. For example, they note the issues of making inferences about individual-level processes from cross-population (group-level) observations, e.g. correlations. The studies within

the current thesis were designed specifically to overcome this issue. They also discuss issues regarding covariation, or lack thereof, in the various instruments designed to assess individual differences across BIS-related research. Although I employed the use of the PVD scale, the main focus of this thesis was experimental priming, therefore this issue will not be addressed here. The third and most relevant issue noted by Tybur and colleagues is that of experimental priming. They illustrate how employing different types of priming can have distinct effects on individuals based on a variety of factors. They specifically address the question of whether different pathogen cues activate different goal states.

To simplify this question in the context of the current thesis, priming cues to pathogens from different modalities may activate different goal states which then may affect individuals differently based on their own state or condition. For example, olfactory, tactile, visual and verbal (e.g. semantic) priming may activate the BIS differently as they affect attention and memory systems differently, and the differences may also be dependent on the individual's condition state (e.g. health) or stage of life (e.g. age). This may explain the differing results between the results of Chapter 3 and 4 (visual priming) with those of Lee and Zietsch (2011) and Navarrete and Fessler (2006) (semantic priming). It may be useful for researchers to test which types of experimental primes are most reliable for a variety of factors – for example, for different ages, but also for different concerns, and employ them accordingly. Disgust images may not be the best way to activate concerns regarding in-group/out-group relationships. This thesis aimed to test whether mere activation of the BIS by variation in visual pathogen threat was enough to differentially motivate change in measures of in-group assortative social behaviour, but perhaps yet another instrument needs to be constructed for this task.

Another limitation to interpreting the findings of the studies within this thesis derives from experimental design. As noted throughout this thesis, there are a handful of experimental studies in the literature that have been conducted on a variety of aspects of the parasite-stress theory, both directly and indirectly (e.g. xenophobia: Faulkner et al., 2004; mate preferences: Lee & Zietsch, 2011; Little et al., 2011; ethnocentrism: Navarrete & Fessler, 2006). However, each of the experimental studies that provide support for the parasite-stress theory employs a between-participants design. While this is of course a valid experimental paradigm, it cannot show direct causation – that is, causal change. Differences between groups on the dependent

variable must to some extent be inferred as caused by the independent variable. Mixed factorial designs can show direct within-participant change while also comparing any change between groups, e.g. the control group. Having said this, there are potential issues with mixed factorial designs. For example, in any form of pre-test/post-test design, participants can experience carry over effects and progressive error, e.g. practice effects, fatigue effects and context effects. These are less likely in between-groups only designs (i.e. no within-participants factor). Upon reflection, I do not think it is a coincidence that the only study within this thesis that supported the hypothesis was the study that did not employ a mixed factorial design. Future experiments endeavouring to replicate the studies within this thesis, or any of the model studies for that matter, should conduct a between-participants study first. If the results suggest a possible causal effect, the researchers should then retest with the inclusion of the with-participants factor to validate the original findings.

Either way, I do think that experimental studies are imperative to further test the parasite-stress theory. As strong as the correlational evidence is, illustrating a direct, unfalsifiable causal link between parasite-stress and assortative social behaviour would quell the critics and solidify years of research. Finding unfalsifiable evidence which shows that there is no causal link would allow researchers to lay this weight down and move onto something else. Either would be an advancement of science. Until then, critics will always argue that causation cannot be inferred from correlation. Thornhill and Fincher (2014b) themselves understand this completely and note that it is important to be cautious when interpreting correlational evidence. However, they also make an excellent point by illustrating that technically all scientific findings are correlational and that evidence from correlational studies should not necessarily be considered less convincing than experiment-driven evidence. They argue that the important determining factor as to whether any scientific evidence can show causation is the extent to which the researchers were able to control for confounding variables. I agree with Thornhill and Fincher but I also argue that it is more difficult to control for confounds in group-level analysis than individual-level analysis, particularly regarding ecological factors. Moreover, experimentation allows for more direct testing of the effects of BIS-activation on the values and subsequent behaviour of individuals, which is the foundation of the group-level output. I do not argue against the value or interpretation of the correlational evidence by Thornhill and Fincher. In fact, I find it compelling. It also provides valid reason for experimentation.

Final considerations: Religiosity and Material Security

Religiosity

Fincher and Thornhill's work focuses on the putative effects of parasite stress on components of in-group assortative sociality and religion – that is, its effects on the adoption and maintenance of values associated with these behaviours. Their research does no not (nor claim to) explain the part that parasite stress has potentially played in the evolutionary origins of religiosity in general. They focus on behavioural out-put such as religious affiliation and commitment and the genesis of religion diversity (Fincher & Thornhill, 2008a), rather than other cognitions (e.g. thoughts, beliefs) on which religious behaviour such as affiliation and commitment are founded. But religions world-wide share universal commonalities that reflect evolved cognitive mechanisms and strategies that form supernatural thinking and reasoning about the world. For example, humans engage in aetiological reasoning about the world, whereby they apply causal explanations to natural events that appear to have no other explanation; they infer design or purpose in nature through teleological reasoning; and, they believe in supernatural causality to events through superstition. This is especially relevant and observable regarding infectious disease. For instance, humans in all regions of the world have historically viewed disease and illness to be a result of supernatural causation through elements such as sorcery, the breaching of taboos, disease-object intrusion, spirit intrusion, and soul loss (Clements, 1932; Last, 1993; Tylor, 1871). Evidence from traditional societies in Africa and South America offers a window into the origins of religiosity and into the overlap (and likely co-evolution) between religiosity and historically older, more traditional concepts and beliefs about disease, and the corresponding BIS-related behaviour.

According to Marshall (1962), the !Kung bushmen from Africa believe that sickness is put upon them by gods and mischievous spirits, either for wrongdoing or just for the sake of it. To them, sickness is the "greatest tool of the death-bringers and they kill mostly by it" (p.244). They also believe that illness can be cured through ritualistic curing dances. The Hadza people have two main supernatural beliefs about the cause of disease (Marlowe, 2010). One cause is the violation of specific taboos and rules. The main rule is associated with proper ritualistic preparation and ceremony regarding *epeme* meat. The other belief is that illness within the group is sent from neighbouring out-groups through witchcraft. Whereas the Yanomami people in South America believe that the soul is directly linked to sickness (Chagnon, 1983). They believe that there is a component of the soul that resides in the thoracic cavity, called

the *möama*, and when it is lost the person becomes ill and dies. They also believe that shamans can use the *möama* to retrieve others' lost souls and also to attack the souls of enemies in neighbouring communities.

Contemporary religions hold similar beliefs. Traditional Christianity is founded on belief in evil and evil spirits (or demons), and that loss/lack of belief in God can leave the soul open for contamination or infection by them – otherwise known as sin. And this sin can only be cleansed or cured by accepting God and/or by rituals such as baptism, communion, and even exorcism. Similarly, traditional Islam holds the belief in *jinns* – creatures that work for Satan and cause illness in humans that disobey the will of Allah. Many of these ideas and behaviours focus on motivating conformity to specific in-group beliefs, rules, and rituals, and avoiding the beliefs, rules and rituals from out-groups.

These are but a few examples, but they show that much of religious behavioural out-put (e.g. practices, rituals) rests on cognitions – beliefs and explanations about the natural world, especially about disease – and is aimed at avoiding or removing it. The elements of religiosity described here appear to map onto the relationship between parasite stress, BIS and the individual and collective components of in-group assortative sociality almost perfectly. This is not to say that there are no other factors that likely contributed to the origins of religiosity. Indeed, throughout history and across cultures religiosity (and subsequent religions) also incorporates other types of cognition and corresponding input and output - for example, forms of animism, ancestor worship, and spirit worship. But with regards to parasite stress, as theorised by Fincher and Thornhill, it is reasonable to think that the degree to which religious behaviour is seen as important to a society (e.g. adopted and maintained) may shift with the coming and going of, for example, epidemics. However, what may be even more interesting is the extent to which parasite stress, the BIS, and other cognitive strategies may be responsible for the origins and emergence of religiosity. More research in this area is encouraged and welcomed.

Material security

Another competing (or arguably overlapping) hypothesis to the parasite-stress hypothesis, which attempts to explain cross-population variation in in-group assortative sociality, is the material (or existential) security hypothesis. This hypothesis predicts a relationship between institutions (i.e. existence, quality and effectiveness) and measures of in-group favouritism (Hruschka & Henrich, 2013). The prediction is

formed on the notion that humans have evolved and are constantly under varying levels (across populations) of material insecurity – that is, material threats to survival, e.g. pathogen stress, environmental extremes, resource scarcity, and inter-group conflict. However, humans engage in social niche construction, whereby they have adaptively constructed social institutions which mitigate these material threats. These institutions are thought to reduce levels of uncertainty and insecurity. This perspective proposes that in societies with higher quality and effective institutions (including public services, social safety nets, etc.) that reduce the deleterious effects of material threats, people would rely less on and invest less in the local group, and interact impartially with strangers. Whereas, in areas where these institutions are not in place, or are not effectively conducted, people would prefer to rely more on and invest more in the local group.

There is evidence to support this proposal. For example, Hruschka and Henrich (2013) found that in geopolitical regions with weaker institutions and high material insecurity, people demonstrated stronger in-group preferences. Other studies found similar results at the community and national levels (e.g. Hruschka et al., 2014). Hadley and Hruschka (2017) found that in samples of young Ethiopian people food insecurity was associated with intolerant mate preferences. That is, they found that people who were chronically food-insecure or under threat of becoming food-insecure were more likely to prefer to marry a co-ethnic (in-group) individual. Moreover, ecological harshness and uncertainty are associated with cooperative breeding (e.g. in birds) and other forms of group living in mammals (Botero et al., 2014). Interestingly, these studies also tested the relationship with in-group assortative sociality proposed in the parasite-stress hypothesis and either found no evidence to support it, or found that it could not explain the variation in assortative sociality as well as the material security hypothesis.

Additionally, some researchers argue that prosocial behaviour is influenced by the relationship between religiosity and measures of ecological harshness and duress (Botero et al., 2014). Botero et al. argue that societies who have historically experienced high ecological harshness and duress are more likely to believe in moralistic religions with moralising high gods. This is thought to be because high gods concerned with morals promote prosociality, which in turn motivates support for in-group members experiencing difficulty. They found evidence to suggest that global distribution of beliefs in moralising high gods was predicted by levels of ecological

harshness and duress. While researchers argue that greater material security, economic equality, and education predict lower levels of overall religiosity, Purzycki et al. (2018) found no evidence to support a relationship between these components and individual-level religious beliefs and behaviours, including toward moralistic religions in particular.

This was only a brief side note to acknowledge the existence of another of the more promising competing theories. This thesis has not considered the material security hypothesis within any of the studies conducted; however, evidence suggests that it is a compelling alternative theory to the parasite-stress theory in explaining assortative social behaviours of ethnocentrism, xenophobia, and religiosity. Future research should focus on teasing apart parasite stress and the relevant components of material security and subjecting them to more scrutiny and comparison.

6.5 Conclusion

The main aim of this thesis was to experimentally test components of Thornhill and Fincher's (2014b) parasite-stress theory of values and sociality. I specifically tested the plausibility of their proposal that variation in parasite stress in the ecological environment causes variation in values and behaviour which then drives a wedge between groups and leads to cultural isolation and divergence. Much of the supporting evidence is correlational, from which, critics argue, causation cannot be unequivocally concluded. The goal of this thesis was to contribute experimental evidence to the debate. Only one of the three theory-focused studies within this thesis provided evidence to support their proposal. In Chapter 4, the findings showed that activation of the BIS via visual pathogen stress can impose causal effects on the types of rules individuals selected and prioritised for the hypothetical start of a new society. This illustrates how the values and beliefs individuals hold about judicial and moral issues can diverge based on differences in exposure to pathogen stress. But chapters 3 and 5 did not provide experimental support for the theory. However, they did not necessarily disconfirm the theory either. The fact that foundational evolutionary theory was supported by the pre-manipulation responses suggests that the lack of theoretical support may more likely be a result of issues with the design of the studies rather than issues with the parasite-stress theory itself. Future experimental research on the topic would do well to consider the implications of methodology, both study design and priming techniques.

There was at least one piece of valuable output produced by this thesis, in that my colleagues and I made a useful contribution to BIS-related research with the introduction of the Culpepper Disgust Image Set. However, the studies within this thesis did not find valid evidence to disconfirm Thornhill and Fincher's parasite-stress theory and they may do little to sway its critics. Thus, the parasite-stress theory and the considerable amount of evidence that supports it will continue to intrigue and inspire researchers. One thing seems certain, the host-parasite interaction is more involved in human and animal behaviour than most people could venture to even fathom. The coevolutionary arms race between host and parasite is the most evolutionarily ancient relationship in living organisms and covers the broadest spectrum of human psychology. Some may even argue that the adapted mind (Barkow, Cosmides, & Tooby, 1992) is largely founded on the disgusted mind.

References

Aarøe, L., Petersen, M. B., & Arceneaux, K. (2017). The behavioral immune system shapes political intuitions: Why and how individual differences in disgust sensitivity underlie opposition to immigration. *American Political Science Review, 111*(2), 277-294.

Ackerman, J. M., Tybur, J. M., & Mortensen, C. R. (2018). Infectious disease and imperfections of self-image. *Psychological Science, 29*(2), 228-241.

Ainsworth, S. E., & Maner, J. K. (2019). Pathogen avoidance mechanisms affect women's preference for symmetrical male faces. *Evolutionary Behavioral Sciences, 13*(3), 265-271.

Alcorta, C. S., & Sosis, R. (2005). Ritual, emotion, and sacred symbols: The evolution of religion as an adaptive complex. *Human Nature, 16*(4), 323-359.

Alesina, A., & Giuliano, P. (2010). The power of the family. *Journal of Economic Growth,* (2), 93.

Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2014). Human emotions: An evolutionary psychological perspective. *Emotion Review, 8*, 173-186.

Alvarez, L., & Jaffe, K. (2004). Narcissism guides mate selection: Humans mate assortatively, as revealed by facial resemblance, following an algorithm of "self seeking like". *Evolutionary Psychology, 2*(1), 177-194.

Andersson, M. B. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Atran, S. (2012). Parasite stress is not so critical to the history of religions or major modern group formations [peer commentary on "parasite-stress promotes in-group assortative sociality: The cases of strong family ties and heightened religiosity]. *Behavioral and Brain Sciences, 35*(2), 79-80.

Barber, I., & Dingemanse, N. J. (2010). Parasitism and the evolutionary ecology of animal personality. *Philosophical Transactions: Biological Sciences, 365*(1560), 4077-4088.

Barkow, J. H., Cosmides, L., & Tooby, J. (1992). *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford: Oxford University Press.

Barrett, D. B., Kurian, G. T., & Johnson, T. M. (. (2001). *World Christian Encyclopedia* (2nd ed.). Oxford, UK: Oxford University Press.

Behringer, D. C., Butler, M. J., & Shields, J. D. (2006). Avoidance of disease by social lobsters. *Nature, 441*(7092), 421.

Beit-Hallahmi, B. (2012). Connecting biological concepts and religious behavior [peer commentary on parasite-stress promotes in-group assortative sociality: The cases of strong family ties and heightened religiosity]. *Behavioral and Brain Sciences, 35*(2), 80-81.

Benet-Martínez, V., & John, O. P. (1998). Los Cinco Grandes across cultures and ethnic groups: Multitrait multimethod analyses of the big five in Spanish and English. *Journal of Personality and Social Psychology, 75*(3), 729-750.

Benson, P. J., & Perrett, D. I. (1993). Extracting prototypical facial images from exemplars. *Perception, 22*(3), 257-262.

Botero, C. A., Gardner, B., Kirby, K. R., Bulbulia, J., Gavin, M. C., & Gray, R. D. (2014). The ecology of religious beliefs. *Proceedings of the National Academy of Sciences of the United States of America, 111*(47), 16784-16789.

Boyar, J. I. (1964). *The construction and partial validation of a scale for the measurement of the fear of death.* (Unpublished UMI, Ann Arbor, Michigan; Dissertation Information Service.

Boyd, R., & Richerson, P. J. (2004). *The origin and evolution of cultures*. New york: Oxford University Press, Inc.

Boyer, P., & Bergstrom, B. (2011). Threat-detection in child development: An evolutionary perspective. *Neuroscience and Biobehavioral Reviews, 35*(4), 1034.

Boyer, P. (2003). Religious thought and behaviour as by-products of brain function. *Trends in Cognitive Sciences, 7*(3), 119-124.

Brown, J. L. (1997). A theory of mate choice based on heterozygosity. *Behavioral Ecology, 8*(1), 60-65.

Brown, J. L. (1998). The new heterozygosity theory of mate choice and the MHC. *Genetica, 104*(3), 215-221.

Bulbulia, J., & Mahoney, A. (2008). Religious solidarity: The hand grenade experiment. *Journal of Cognition and Culture, 8*(3-4), 295-320.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12*(1), 1-49.

Calder, A. J., Keane, J., Manes, F., Antoun, N., & Young, A. W. (2000). Impaired recognition and experience of disgust following brain injury. *Nature Neuroscience, 3*(11), 1077-1078.

Caldwell, C. A., & Millen, A. E. (2008). Studying cumulative cultural evolution in the laboratory. *Philosophical Transactions: Biological Sciences,* (1509), 3529.

Cashdan, E., & Steele, M. (2013). Pathogen prevalence, group bias, and collectivism in the standard cross-cultural sample. *Human Nature, 24*(1), 59-75.

Cattell, R. B. (1966). The scree test for the number of factors. *Multivariate Behavioral Research, 1*, 245-276.

Chagnon, N. A. (1983). *Yanomamo: The fierce people* (3rd ed.). New York: Holt, Rinehart and Winston.

Chrea, C., Grandjean, D., Delplanque, S., Sander, D., Scherer, K. R., Cayeux, I., . . . Velazco, M. I. (2009). Mapping the semantic space for the subjective experience of emotional responses to odors. *Chemical Senses, 34*(1), 49-62.

Clayton, D., Koop, J., Harbison, C., Moyer, B., & Bush, S. (2010). How birds combat ectoparasites. *The Open Ornithology Journal, 3*, 41-71.

Clements, F. E. (1932). Primitive concepts of disease. *American Archaeology and Ethnology, 32*(2), 185-252.

Clutton-Brock, T. H., & Lukas, D. (2012). The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology, 21*(3), 472-492.

Cohen, A. B. (2011). Religion and culture. *Online Readings in Psychology and Culture, 4*(4).

Cohen, D. (2001). Cultural variation: Considerations and implications. *Psychological Bulletin, 127*(4), 451-471.

Cohen, J. (1992). A power primer. *Psychological Bulletin, 112*, 155-159.

Culpepper, P. D. (2014). *Agent detection and religious behaviour: Sex differences in evolved psychological mechanisms that predispose religiosity.* (Unpublished Dissertation for MSc in Evolutionary Psychology). Brunel University London, UK,

Culpepper, P. D., Havlíček, J., Leongómez, J. D., & Roberts, S. C. (2018). Visually activating pathogen disgust: A new instrument for studying the behavioural immune system. *Frontiers in Psychology, 9*(1397).

Curtis, V. (2014). Infection-avoidance behaviour in humans and other animals. *Trends in Immunology, 35*(10), 457-464.

Curtis, V., Aunger, R., & Rabie, T. (2004). Evidence that disgust evolved to protect from risk of disease. *Proceedings of the Royal Society B, 271*, S131-S133.

Curtis, V., & Biran, A. (2001). Dirt, disgust, and disease - is hygiene in our genes? *Perspectives in Biology and Medicine, 44*, 17-31.

Dan-Glauser, E., & Scherer, K. R. (2011). The Geneva affective picture database (GAPED): A new 730-picture database focusing on valence and normative significance. *Behavior Research Methods, 43*(2), 468-477.

DeBruine, L. M. (2004). Facial resemblance increases the attractiveness of same–sex faces more than other–sex faces. *Proceedings of the Royal Society B, 271*(1552), 2085-2090.

DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L. M., & Little, A. C. (2010). The health of a nation predicts their mate preferences: Cross-cultural variation in women's preferences for masculinized male faces. *Proceedings: Biological Sciences, 277*(1692), 2405-2410.

DeBruine, L. M., Jones, B. C., Little, A. C., Crawford, J. R., & Welling, L. L. M. (2011). Further evidence for regional variation in women's masculinity preferences. *Proceedings of the Royal Society B, 278*, 813-814.

DeBruine, L. M., Jones, B. C., Tybur, J. M., Lieberman, D., & Griskevicius, V. (2010). Women's preferences for masculinity in male faces are predicted by pathogen disgust, but not by moral or sexual disgust. *Evolution and Human Behavior, 31*, 69-74.

DeBruine, L. M., Little, A. C., & Jones, B. C. (2012). Extending parasite-stress theory to variation in human mate preferences. *The Behavioral and Brain Sciences, 35*(2), 86-87.

Del Giudice, M. (2019). Invisible designers: Brain evolution through the lens of parasite manipulation. *The Quarterly Review of Biology, 94*(3), 249-282. doi:10.1086/705038

Denic, S., & Nicholls, M. G. (2007). Genetic benefits of consanguinity through selection of genotypes protective against malaria. *Human Biology, 79*(2), 145-158.

Druschel, B. A., & Sherman, M. F. (1999). Disgust sensitivity as a function of the big five and gender. *Personality and Individual Differences, 26*(4), 739-748.

Duncan, L. A., Schaller, M., & Park, J. H. (2009). Perceived vulnerability to disease: Development and validation of a 15-item self-report instrument. *Personality and Individual Differences, 47*, 541-546.

Ekman, P., & Friesen, W. V. (1975). *Unmasking the face: A guide to recognizing emotions from facial clues*. Oxford, England: Prentice-Hall.

Ekman, P., Friesen, W. V., & Hager, J. C. (2002). *Facial action coding system* (2nd ed.). Salt Lake City, UT: Research Nexus eBook.

Elliott, A. C., & Woodward, W. A. (2007). *Statistical analysis quick reference guidebook; with SPSS examples* (1st ed.). London: Sage Publications.

Eysenck, H. J., & Eysenck, S. B. G. (1975). *Eysenck Personality Questionnaire.* San Diego, CA: Educational and Industrial Testing Service.

Ezenwa, V. O. (2004). Selective defecation and selective foraging: Antiparasite behavior in wild ungulates? *Ethology, 110*(11), 851-862.

Faulkner, J., Schaller, M., Park, J. H., & Duncan, L. A. (2004). Evolved disease-avoidance mechanisms and contemporary xenophobic attitudes. *Group Processes & Intergroup Relations, 7*, 333-353.

Ferdenzi, C., Schirmer, A., Roberts, S. C., Delplanque, S., Porcherot, C., Cayeux, I., . . . Grandjean, D. (2011). Affective dimensions of odor perception: A comparison between Swiss, British, and Singaporean populations. *Emotion, 11*, 1168-1181.

Fessler, D. M. T., Eng, S. J., & Navarrete, C. D. (2005). Elevated disgust sensitivity in the first trimester of pregnancy - evidence supporting prophylaxis the compensatory hypothesis. *Evolution and Human Behavior, 26*, 344-351.

Fessler, D. M. T., & Navarrete, C. D. (2003). Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evolution and Human Behavior, 24*(6), 406-417.

Field, A. (2013). *Discovering statistics using IBM SPSS statistics* (4th ed.). London: Sage Publications, Ltd.

Fincher, C. L., & Thornhill, R. (2008a). Assortative sociality, limited dispersal, infectious disease and the genesis of the global pattern of religion diversity. *Proceedings of the Royal Society B, 275*, 2587-2594.

Fincher, C. L., & Thornhill, R. (2008b). A parasite-driven wedge: Infectious diseases may explain language and other biodiversity. *Oikos, 117*(9), 1289-1297.

Fincher, C. L., & Thornhill, R. (2012). Parasite-stress promotes in-group assortative sociality: The cases of strong family ties and heightened religiosity. *Behavioral and Brain Sciences, 35*, 61-79.

Fincher, C. L., Thornhill, R., Murray, D. R., & Schaller, M. (2008). Pathogen prevalence predicts human cross-cultural variability in individualism/collectivism. *Proceedings of the Royal Society B, 275*, 1279-1285.

Flegr, J., & Kuba, R. (2016). The relation of toxoplasma infection and sexual attraction to fear, danger, pain, and submissiveness. *Evolutionary Psychology, 14*, 1-10.

Fleischman, D. S., & Fessler, D. M. T. (2011). Progesterone's effects on the psychology of disease avoidance: Support for the compensatory behavioral prophylaxis hypothesis. *Hormones and Behavior, 59*(2), 271-275.

Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist, 139*(3), 603.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology, 14*(2), 89-96.

Gangestad, S. W., Haselton, M. G., & Buss, D. M. (2006). Evolutionary foundations of cultural variation: Evoked culture and mate preferences. *Psychological Inquiry, 17*(2), 75-95.

Gangestad, S. W., & Scheyd, G. J. (2005). The evolution of human physical attractiveness. *Annual Review of Anthropology, 34*, 523-548.

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences, 23*(04), 573-587.

Gangestad, S. W., & Thornhill, R. (1997). Human sexual selection and developmental stability. In J. A. Simpson, & D. T. Kenrick (Eds.), *Evolutionary Social Psychology* (pp. 169-195). Mahwah, N.J.: Erlbaum.

Ghasemi, A., & Zahediasl, S. (2012). Normality tests for statistical analysis: A guide for non-statisticians. *International Journal of Endocrinology and Metabolism, 10*(2), 486-489.

Gurven, M. (2015). Book review: The parasite-stress theory of values and sociality: Infectious disease, history and human values worldwide. *American Journal of Human Biology,* (5), 740.

Haberkamp, A., Glombiewski, J. A., Schmidt, F., & Barke, A. (2017). The DIsgust-RelaTed-images (DIRTI) database: Validation of a novel standardized set of disgust pictures. *Behaviour Research and Therapy, 89*, 86-94.

Hadley, C., & Hruschka, D. (2017). Stability and change in in-group mate preferences among young people in Ethiopia are predicted by food security and gender attitudes, but not by expected pathogen exposures. *Human Nature, 28*(4), 395-406.

Haidt, J., & Graham, J. (2007). When morality opposes justice: Conservatives have moral intuitions that liberals may not recognize. *Social Justice Research, 20*(1), 19-19.

Haidt, J., McCauley, C. R., & Rozin, P. (1994). Individual differences in sensitivity to disgust: A scale sampling seven domains of disgust elicitors. *Personality and Individual Differences, 16*, 701-713.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science, 218*(4570), 384-387.

Hart, B. L. (1990). Behavioral adaptations to pathogens and parasites: Five strategies. *Neuroscience and Biobehavioral Reviews, 14*(3), 273-294.

Havlíček, J., & Roberts, S. C. (2009). MHC-correlated mate choice in humans: A review. *Psychoneuroendocrinology, 34*(4), 497-512.

Helman, C. G. (2007). *Culture, health and illness* (5th ed.). New York: Oxford University Press, Inc.

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences, 33*, 61-135.

Hertenstein, M. J., & Campos, J. J. (2004). The retention effects of an adult's emotional displays on infant behavior. *Child Development, 75*(2), 595.

Hoben, A. D., Buunk, A. P., Fincher, C. L., Thornhill, R., & Schaller, M. (2010). On the adaptive origins and maladaptive consequences of human inbreeding: Parasite prevalence, immune functioning, and consanguineous marriage. *Evolutionary Psychology, 8*(4), 658-676.

Hruschka, D., Efferson, C., Jiang, T., Falletta-Cowden, A., Sigurdsson, S., McNamara, R., . . . Henrich, J. (2014). Impartial institutions, pathogen stress and the expanding social network. *Human Nature, 25*(4), 567-579.

Hruschka, D., & Henrich, J. (2013). Institutions, parasites and the persistence of in-group preferences. *PLoS ONE, 8*(5), e63642.

Huber, S., & Huber, O. W. (2012). The centrality of religiosity scale (CRS). *Religions, 3*(3), 710-724.

Inbar, Y., Pizarro, D. A., Knobe, J., & Bloom, P. (2009). Disgust sensitivity predicts intuitive disapproval of gays. *Emotion, 9*(3), 435-439.

Jackson, L. M., & Hunsberger, B. (1999). An intergroup perspective on religion and prejudice. *Journal for the Scientific Study of Religion,* (4), 509.

Klapilová, K., Cobey, K. D., Wells, T., Roberts, S. C., Weiss, P., & Havlíček, J. (2014). Current hormonal contraceptive use predicts female extra-pair and dyadic sexual behavior: Evidence based on Czech national survey data. *Evolutionary Psychology, 12*(1), 36-52.

Kokko, H., & Ots, I. (2006). When not to avoid inbreeding. *Evolution, 60*(3), 467-475.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International affective picture system (IAPS): Affective ratings of pictures and instruction manual.* (Technical Report No. A-8). University of Florida, Gainesville, FL.:

Last, M. (1993). Non-western concepts of disease. In W. F. Bynum, & R. Porter (Eds.), *Companion Encyclopedia of the History of Medicine* (pp. 634-660). New York: Routledge.

Lawson Handley, L. J., & Perrin, N. (2007). Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology, 16*(8), 1559-1578.

Lee, A. J., & Zietsch, B. P. (2011). Experimental evidence that women's mate preferences are directly influenced by cues of pathogen prevalence and resource scarcity. *Biology Letters, 7*(6), 892-895.

Lee, J., Lee, Y., & Hatchwell, B. J. (2010). Natal dispersal and philopatry in a group-living but noncooperative passerine bird, the vinous-throated parrotbill. *Animal Behaviour, 79*, 1017-1023.

Legare, C. H., Wellman, H. M., & Gelman, S. A. (2009). Evidence for an explanation advantage in naïve biological reasoning. *Cognitive Psychology, 58*(2), 177-194.

Lennox, R. D., & Wolfe, R. N. (1984). Revision of the self-monitoring scale. *Journal of Personality and Social Psychology, 46*, 1349-1364.

Lester, T. (2002, February). Oh, gods! *The Atlantic Monthly,* 37-45.

Levenson, M. R., Kiehl, K. A., & Fitzpatrick, C. M. (1995). Assessing psychopathic attributes in a noninstitutionalized population. *Journal of Personality and Social Psychology, 68*(1), 151-158.

Lieberman, D., & Patrick, C. (2014). Are the behavioral immune system and pathogen disgust identical? *Evolutionary Behavioral Sciences, 8*, 244-250.

Little, A. C., Burriss, R. P., Petrie, M., Jones, B. C., & Roberts, S. C. (2013). Oral contraceptive use in women changes preferences for male facial masculinity and is associated with partner facial masculinity. *Psychoneuroendocrinology, 38*, 1777-1785.

Little, A. C., Burt, D. M., Penton-Voak, I., & Perrett, D. I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society B, 268*(1462), 39-44.

Little, A. C., Cohen, D., Jones, B. C., & Belsky, J. (2007). Human preferences for facial masculinity change with relationship type and environmental harshness. *Behavioral Ecology and Sociobiology, 61*(6), 967-973.

Little, A. C., DeBruine, L. M., & Jones, B. C. (2011). Exposure to visual cues of pathogen contagion changes preferences for masculinity and symmetry in opposite-sex faces. *Proceedings of the Royal Society B, 278*, 2032-2039.

Little, A. C., Jones, B. C., & Burriss, R. P. (2007). Preferences for masculinity in male bodies change across the menstrual cycle. *Hormones and Behavior, 51*(5), 633-639.

Little, A. C., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007). Preferences for symmetry in faces change across the menstrual cycle. *Biological Psychology, 76*(3), 209-216.

Little, A. C., Jones, B. C., & DeBruine, L. M. (2011). Facial attractiveness: Evolutionary based research. *Philosophical Transactions: Biological Sciences, 366*(1571), 1638-1659.

Little, A. C., Jones, B. C., Penton-Voak, I., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society B, 269*(1496), 1095-1100.

Loehle, C. (1995). Social barriers to pathogen transmission in wild animal populations. *Ecology, 76*(2), 326-335. doi:10.2307/1941192

Low, B. S. (1990). Marriage systems and pathogen stress in human societies. *Integrative and Comparative Biology, 30*(2), 325-340.

Lumley, T., Diehr, P., Emerson, S., & Chen, L. (2002). The importance of the normality assumption in large public health data sets. *Annual Review of Public Health, 23*(1), 151-169.

Makhanova, A., Miller, S. L., & Maner, J. K. (2015). Germs and the out-group: Chronic and situational disease concerns affect intergroup categorization. *Evolutionary Behavioral Sciences, 9*(1), 8-19.

Makhanova, A., Plant, E. A., Monroe, A. E., & Maner, J. K. (2019). Binding together to avoid illness: Pathogen avoidance and moral worldviews. *Evolutionary Behavioral Sciences, 13*(2), 182-204.

Marchewka, A., Zurawski, L., Jednoróg, K., & Grabowska, A. (2014). The Nencki affective picture system (NAPS): Introduction to a novel, standardized, wide-range, high-quality, realistic picture database. *Behavior Research Methods, 46*(2), 596-610.

Marks, I., & Nesse, R. M. (1994). Fear and fitness: An evolutionary analysis of anxiety disorders. *Ethology and Sociobiology, 15*(5), 247-261.

Marlowe, F. W. (2003). The mating system of foragers in the standard cross-cultural sample. *Cross-Cultural Research, 37*(3), 282-306.

Marlowe, F. W. (2010). *The Hadza: Hunter-gatherers of Tanzania* (1st ed.) University of California Press.

Marshall, L. (1962). ! Kung bushman religious beliefs. *Africa, 32*(3), 221-252.

Martin, L. H., & Wiebe, D. (2014). Pro- and assortative-sociality in the formation and maintenance of religious groups. *Journal for the Cognitive Science of Religion, 2*(1), 1-12.

McIntosh, T. L., Lee, A. J., Sidari, M. J., Stower, R. E., Sherlock, J. M., & Dixson, B. J. (2017). Microbes and masculinity: Does exposure to pathogenic cues alter women's preferences for male facial masculinity and beardedness? *PLoS ONE, 12*(6)

McPherson, M., Smith-Lovin, L., & Cook, J. M. (2001). Birds of a feather: Homophily in social networks. *Annual Review of Sociology,* 415.

Miller, G. F. (2013). Mutual mate choice models as the red pill in evolutionary psychology: Long delayed, much needed, ideologically challenging, and hard to swallow. *Psychological Inquiry, 24*(3), 207-210.

Mitchell, I. J., Heims, H., Neville, E. A., & Rickards, H. (2005). Huntington's disease patients show impaired perception of disgust in the gustatory and olfactory modalities. *Journal of Neuropsychiatry and Clinical Neurosciences, 17*(1), 119-121.

Morand, S., & Walther, B. A. (2018). Individualistic values are related to an increase in the outbreaks of infectious diseases and zoonotic diseases. *Scientific Reports, 8*(1)

Mullett, T. L., Brown, G. D. A., Fincher, C. L., Kosinski, M., & Stillwell, D. (2019). Individual-level analyses of the impact of parasite stress on personality: Reduced openness only for older individuals. *Personality & Social Psychology Bulletin,* 146167219843918.

Murdock, G. P., & White, D. R. (1969). Standard cross-cultural sample. *Ethnology, 8*(4), 329-369.

Navarrete, C. D., & Fessler, D. M. T. (2006). Disease avoidance and ethnocentrism: The effects of disease vulnerability and disgust sensitivity on intergroup attitudes. *Evolution and Human Behavior,* (4), 270.

Navarrete, C. D., Fessler, D. M. T., & Eng, S. J. (2007). Elevated ethnocentrism in the first trimester of pregnancy. *Evolution and Human Behavior, 28*(1), 60-65.

Nesse, R. (2005). Evolutionary psychology and mental health. In D. M. Buss (Ed.), *The Handbook of Evolutionary Psychology* (pp. 903-927). Hoboken, NJ: John Wiley and Sons.

Nettle, D. (2009). Ecological influences on human behavioural diversity: A review of recent findings. *Trends in Ecology and Evolution, 24*(11), 618-624.

Nettle, D., Grace, J. B., Choisy, M., Cornell, H. V., Guégan, J., & Hochberg, M. E. (2007). Cultural diversity, economic development and societal instability. *Plos One, 2*(9), e929-e929.

Norenzayan, A. (2013). *Big gods; how religion transformed cooperation and conflict* Princeton University Press.

O'Shea, B. A., Watson, D. G., Brown, G. D. A., & Fincher, C. L. (2019). Infectious disease prevalence, not race exposure, predicts both implicit and explicit racial prejudice across the United States. *Social Psychological and Personality Science,* 1948550619862319.

Oaten, M., Stevenson, R. J., & Case, T. I. (2009). Disgust as a disease-avoidance mechanism. *Psychological Bulletin, 135,* 303-321.

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review, 108*(3), 483-522.

Olatunji, B. O., Haidt, J., McKay, D., & David, B. (2008). Core, animal reminder, and contamination disgust: Three kinds of disgust with distinct personality, behavioral, physiological, and clinical correlates. *Journal of Research of in Personality, 42*(5), 1243-1259.

Olatunji, B. O., Williams, N. L., Lohr, J. M., Elwood, L. S., Tolin, D. F., Abramowitz, J. S., & Sawchuk, C. N. (2007). The disgust scale: Item analysis, factor structure, and suggestions for refinement. *Psychological Assessment, 19*(3), 281-297.

Park, J. H., Faulkner, J., & Schaller, M. (2003). Evolved disease-avoidance processes and contemporary anti-social behavior: Prejudicial attitudes and avoidance of people with physical disabilities. *Journal of Nonverbal Behavior, 27*(2), 65-87.

Park, J. H., Schaller, M., & Crandall, C. S. (2007). Pathogen-avoidance mechanisms and the stigmatization of obese people. *Evolution and Human Behavior, 28*(6), 410-414.

Penn, D. J., & Potts, W. K. (1999). The evolution of mating preferences and major histocompatibility complex genes. *The American Naturalist, 153*(2), 145-164.

Peoples, H. C., Duda, P., & Marlowe, F. W. (2016). Hunter-gatherers and the origins of religion. *Human Nature, 27*(3), 261-282.

Perrett, D. I., Lee, K., Penton-Voak, I. S., & Rowland, D. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature, 394*(6696), 884-7.

Poirotte, C., Massol, F., Herbert, A., Willaume, E., Bomo, P. M., Kappeler, P. M., & Charpentier, M. J. E. (2017). Mandrills use olfaction to socially avoid parasitized conspecifics. *Science Advances, 3*(4), e1601721.

Purzycki, B. G., Ross, C. T., Apicella, C., Atkinson, Q. D., Cohen, E., Willard, A. K., . . . McNamara, R. A. (2018). Material security, life history, and moralistic religions: A cross-cultural examination. *PLoS ONE, 13*(3), e0193856.

Quinlan, R. J. (2007). Human parental effort and environmental risk. *Proceedings of the Royal Society B: Biological Sciences, 274*(1606), 121-125.

Raden, D. (2003). Ingroup bias, classic ethnocentrism, and non-ethnocentrism among American whites. *Political Psychology,* (4), 803.

Renkema, L. J., Van Yperen, N. W., & Stapel, D. A. (2008). Go with the flow: Conforming to others in the face of existential threat. *European Journal of Social Psychology, 38*(4), 747-756.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution.* Chicago, IL, US: University of Chicago Press.

Ricoeur, P. (1967). *The symbolism of evil.* Boston, MA: Beacon Press.

Ritter, R. S., & Preston, J. L. (2011). Gross gods and icky atheism: Disgust responses to rejected religious beliefs. *Journal of Experimental Social Psychology, 47*(6), 1225-1230.

Roberts, S. C., Kralevich, A., Ferdenzi, C., Saxton, T. K., Jones, B. C., DeBruine, L. M., . . . Havlíček, J. (2011). Body odor quality predicts behavioral attractiveness in humans. *Archives of Sexual Behavior, 40*(6), 1111-1117.

Roberts, S. C., & Little, A. C. (2008). Good genes, complementary genes and human mate preferences. *Genetica, 132*(3), 309-321.

Roberts, S. C., Little, A. C., Burriss, R. P., Cobey, K. D., Klapilová, K., Havlíček, J., . . . Petrie, M. (2014). Partner choice, relationship satisfaction, and oral contraception: The congruency hypothesis. *Psychological Science, 25*(7), 1497-1503.

Roberts, S. C., Little, A. C., Gosling, L. M., Perrett, D. I., Carter, V., Jones, B. C., . . . Petrie, M. (2005). MHC-heterozygosity and human facial attractiveness. *Evolution and Human Behavior, 26*, 213-226.

Rottman, J. (2014). Evolution, development, and the emergence of disgust. *Evolutionary Psychology, 12*, 417-433.

Rozin, P., Haidt, J., & McCauley, C. R. (2000). Disgust. In M. Lewis, & J. M. Haviland-Jones (Eds.), *Handbook of Emotions* (2nd ed., pp. 637-653). New York: Guilford Press.

Rozin, P., Lowery, L., & Ebert, R. (1994). Varieties of disgust faces and the structure of disgust. *Journal of Personality and Social Psychology, 66*, 870-881.

Sarabian, C., Ngoubangoye, B., & MacIntosh, A. J. J. (2017). Avoidance of biological contaminants through sight, smell and touch in chimpanzees. *Royal Society Open Science, 4*(11), 170968.

Schaller, M. (2006). Parasites, behavioral defenses, and the social psychological mechanisms through which cultures are evoked. *Psychological Inquiry, 17*, 96-137.

Schaller, M. (2011). The behavioural immune system and the psychology of human sociality. *Philosophical Transactions of the Royal Society of London B, 366*, 3418-3426.

Schaller, M., & Duncan, L. A. (2007). The behavioral immune system: Its evolution and social psychological implications. In J. P. Forgas, M. G. Haselton & W. von Hippel (Eds.), *Evolution and the social mind: Evolutionary Psychology and Social Cognition* (pp. 293-307). New York, NY, US: Routledge/Taylor & Francis Group.

Schaller, M., & Murray, D. R. (2008). Pathogens, personality, and culture: Disease prevalence predicts worldwide variability in sociosexuality, extraversion, and openness to experience. *Journal of Personality and Social Psychology, 95*(1), 212-221.

Schaller, M., & Neuberg, S. L. (2008). Intergroup prejudices and intergroup conflicts. In C. Crawford, & D. Krebs (Eds.), *Foundations of Evolutionary Psychology* (pp. 401-414). New York, NY: Erlbaum.

Schaller, M., & Park, J. H. (2011). The behavioral immune system (and why it matters). *Current Directions in Psychological Science, 20*, 99-103.

Scheyd, G. J., Garver-Apgar, C. E., & Gangestad, S. W. (2008). Physical attractiveness: Signals of phenotype quality and beyond. In C. Crawford, & D. L. Krebs (Eds.), *Foundations of Evolutionary Psychology* (pp. 239-260). Mahwah, N.J.: Lawrence Erlbaum.

Schmitt, D. P. (2005). Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Sciences, 28*(2), 247-275.

Schmitt, D. P., Allik, J., Mccrae, R. R., Benet-Martinez, V., & et al. (2007). The geographic distribution of big five personality traits: Patterns and profiles of human self-description across 56 nations. *Journal of Cross-Cultural Psychology, 38*(2), 173-212.

Shapira, N. A., Liu, Y., He, A. G., Bradley, M. M., Lessig, M. C., James, G. A., . . . Goodman, W. K. (2003). Brain activation by disgust-inducing pictures in obsessive-compulsive disorder. *Biological Psychiatry*, *54*, 7, 751-756

Shariff, A. F. (2015). Does religion increase moral behavior? *Current Opinion in Psychology, 6*, 108-113.

Shariff, A. F., Willard, A. K., Andersen, T., & Norenzayan, A. (2016). Religious priming: A meta-analysis with a focus on prosociality. *Personality and Social Psychology Review, 20*(1), 27-48.

Sherman, P. W., & Billing, J. (1999). Darwinian gastronomy: Why we use spices: Spices taste good because they are good for us. *Bioscience, 49*(6), 453-463.

Snyder, M. (1974). Self-monitoring of expressive behavior. *Journal of Personality & Social Psychology, 30*(4), 526-537.

Soper, D. (2017). A-priori sample size calculator for student t-tests [software]. Retrieved from https://www.danielsoper.com/statcalc/

Sosis, R., & Alcorta, C. (2003). Signaling, solidarity, and the sacred: The evolution of religious behavior. *Evolutionary Anthropology: Issues, News, and Reviews, 12*(6), 264-274.

Sosis, R., Kress, H. C., & Boster, J. S. (2007). Scars for war: Evaluating alternative signaling explanations for cross-cultural variance in ritual costs. *Evolution and Human Behavior, 28*(4), 234-247.

Spector, P. E. (1992). *Summated rating scale construction: An introduction*. Thousand Oaks, CA, US: Sage Publications, Inc.

Sprengelmeyer, R., Young, A. W., Calder, A. J., Karnat, A., Lange, H., Hömberg, V., . . . Rowland, D. (1996). Loss of disgust: Perception of faces and emotions in Huntington's disease. *Brain: A Journal of Neurology, 119*(5), 1647-1665.

Sprengelmeyer, R., Young, A. W., Pundt, I., Sprengelmeyer, A., Calder, A. J., Berrios, G., . . . Przuntek, H. (1997). Disgust implicated in obsessive-compulsive disorder. *Proceedings: Biological Sciences, 264*(1389), 1767-1773.

Stearns, F. W., Tilmon, K. J., & Wood, T. K. (2013). Felsenstein's "one-allele model" of speciation: The role of philopatry in the initial stages of host plant mediated reproductive isolation in *Enchenopa binotata*. *Current Zoology, 59*(5), 658-666.

Stevens, J. P. (2002). *Applied multivariate statistics for the social sciences* (4th ed.). Mahwah, NJ, US: Lawrence Erlbaum Associates Publishers.

Stevenson, R. J., Case, T. I., & Oaten, M. J. (2009). Frequency and recency of infection and their relationship with disgust and contamination sensitivity. *Evolution and Human Behavior, 30*(5), 363-368.

Surguladze, S. A., El-Hage, W., Dalgleish, T., Radua, J., Gohier, B., & Phillips, M. L. (2010). Depression is associated with increased sensitivity to signals of disgust: A functional magnetic resonance imaging study. *Journal of Psychiatric Research, 44*(14), 894-902.

Terrizzi, J.,J.A., Shook, N. J., & Ventis, W. L. (2010). Disgust: A predictor of social conservatism and prejudicial attitudes toward homosexuals. *Personality and Individual Differences, 49*, 587-592.

Terrizzi, J.,J.A., Shook, N. J., & McDaniel, M. A. (2013). The behavioral immune system and social conservatism: A meta-analysis. *Evolution and Human Behavior, 34*, 99-108.

Terrizzi, J.,J.A., Shook, N. J., & Ventis, W. L. (2012). Religious conservatism: An evolutionarily evoked disease-avoidance strategy. *Religion, Brain & Behavior, 2*(2), 105-120.

Thompson, J. N. (2005). *The geographic mosaic of coevolution*. Chicago: University of Chicago Press.

Thornhill, R., & Fincher, C. L. (2014a). The parasite-stress theory of sociality, the behavioral immune system, and human social and cognitive uniqueness. *Evolutionary Behavioral Sciences, 8*(4), 257-264.

Thornhill, R., & Fincher, C. L. (2014b). *The parasite-stress theory of values and sociality: Infectious disease, history and human values worldwide*. Cham: Springer.

Thornhill, R., Fincher, C. L., & Aran, D. (2009). Parasites, democratization, and the liberalization of values across contemporary countries. *Biological Reviews, 84*(1), 113-131.

Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature, 4*(3), 237-269.

Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual behavior. *Psychological Science, 5*(5), 297-302.

Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics & Applications, 21*(5), 42-50.

Tooby, J. (1982). Pathogens, polymorphism, and the evolution of sex. *Journal of Theoretical Biology, 97*(4), 557-576.

Tooby, J., & Cosmides, L. (1992). Psychological foundations of culture. In J. H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind* (pp. 19-136). New York: Oxford University Press.

Trivers, R. L. (1972). Parental investment and sexual selection. *Sexual selection and the descent of man* (1871-1971 ed., pp. 136-172). Chicago, IL: Aldine.

Tybur, J. M., Bryan, A. D., Magnan, R. E., & Hooper, A. E. C. (2011). Smells like safe sex: Olfactory pathogen primes increase intentions to use condoms. *Psychological Science, 22*, 478-480.

Tybur, J. M., Inbar, Y., Aarøe, L., Barclay, P., Barlow, F. K., de Barra, M., . . . Zezelj, I. (2016). Parasite stress and pathogen avoidance relate to distinct dimensions of political ideology across 30 nations. *Proceedings of the National Academy of Sciences of the United States of America, 113*(44), 12408-12413.

Tybur, J. M., Lieberman, D., & Griskevicius, V. (2009). Microbes, mating, and morality: Individual differences in three functional domains of disgust. *Journal of Personality and Social Psychology, 97*, 103-122.

Tybur, J. M., Pollet, T. V., & Frankenhuis, W. E. (2014). Behavioral immune system methods: Surveying the present to shape the future. *Evolutionary Behavioral Sciences, 8*, 274-283.

Tylor, E. B. (1871). *Primitive culture: Researches into the development of mythology, philosophy, religion, art and custom.* London: John Murray.

Valdesolo, P., & Graham, J. (2014). Awe, uncertainty, and agency detection. *Psychological Science, 25*(1), 170-178.

Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory,* (1), 1-30.

Welling, L. L. M., Conway, C. A., DeBruine, L. M., & Jones, B. C. (2007). Perceived vulnerability to disease is positively related to the strength of preferences for apparent health in faces. *Journal of Evolutionary Psychology, 5*(1), 131-139.

Wessa, M., Kanske, P., Neumeister, P., Bode, K., Heissler, J., & Schönfelder, S. (2010). EmoPics: Subjektive und psychophysiologische evaluation neuen bildmaterials für die klinisch-biopsychologische forschung. *Zeitschrift Für Klinische Psychologie Und Psychotherapie, 39*(Suppl. 1/11), 77.

Wicker, B., Keysers, C., Gallese, V., Rizzolatti, G., Plailly, J., & Royet, J. -. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron, 40*(3), 655-664.

Widman, D. R., Corcoran, K. E., & Nagy, R. E. (2009). Belonging to the same religion enhances the opinion of others' kindness and morality. *Journal of Social, Evolutionary, and Cultural Psychology, 3*(4), 281-289.

Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought.* Princeton, N.J.: Princeton University Press.

Wu, B., & Chang, L. (2012). The social impact of pathogen threat: How disease salience influences conformity. *Personality and Individual Differences, 53*, 50-54.

Young, S. G., Sacco, D. F., & Hugenberg, K. (2011). Vulnerability to disease is associated with a domain-specific preference for symmetrical faces relative to symmetrical non-face stimuli. *European Journal of Social Psychology, 41*(5), 558-563.

Zahavi, A. (1975). Mate selection - a selection of handicap. *Journal of Theoretical Biology, 53*, 205-214.

Zuckerman, M. (1979). *Sensation seeking: Beyond the optimum level of arousal*. Hillsdale, NJ: Erlbaum.

Appendix A

Religiosity Scale

(adopted from Valdesolo & Graham, 2014)
*added item

1. To what extent do you believe in ghosts?

2. To what extent do you believe in angels?

3. To what extent do you believe in curses?

4. To what extent do you believe in miracles?

5. It is feasible that God, or some type of non-human entity, is in control, at least in part, of the events within our universe.

6. The events that occur in this world unfold according to God's, or some other non-human entity's plan.

7. There exists a spiritual order to the universe, such as Karma.

8. *****I believe that natural events (diseases, earthquakes, floods, etc.) are caused by God, the devil, demons, spirits, or curses.

9. I consider myself to be a… (0-6 scale from "confident atheist" to "confident believer in God")

1-4 (0-6 scale from "not at all" to "very much")
5-8 (0-6 scale from "tremendously doubtful" to "extremely likely")

Appendix B

Perceived Vulnerability to Disease Scale

(Duncan et al., 2009)

1. It really bothers me when people sneeze without covering their mouths.
2. If an illness is 'going around', I will get it.
3. I am comfortable sharing a water bottle with a friend. (R)
4. I don't like to write with a pencil someone else has obviously chewed on.
5. My past experiences make me believe I am not likely to get sick even when my friends are sick. (R)
6. I have a history of susceptibility to infectious diseases.
7. I prefer to wash my hands pretty soon after shaking someone's hand.
8. In general, I am very susceptible to colds, flu, and other infectious diseases.
9. I dislike wearing used clothes because you don't know what the past person who wore it was like.
10. I am more likely than the people around me to catch an infectious disease.
11. My hands do not feel dirty after touching money. (R)
12. I am unlikely to catch a cold, flu, or other illness, even if it is going around. (R)
13. It does not make me anxious to be around sick people. (R)
14. My immune system protects me from most illnesses that other people get. (R)
15. I avoid using public telephones because of the risk that I may catch something from the previous user.

Response format: 1 = Strongly Disagree ... 7 = Strongly Agree
(R) = Reverse scored
Subscale 1 (Perceived Infectability): Items 2, 5, 6, 8, 10, 12, 14
Subscale 2 (Germ Aversion): Items 1, 3, 4, 7, 9, 11, 13, 15

Appendix C

The Revised Self-Monitoring Scale

(Lennox & Wolfe, 1984)

1. In social situations, I have the ability to alter my behaviour if I feel that something else is called for.
2. I am often able to correctly read people's true emotions through their eyes.
3. I have the ability to control the way I come across to people, depending on the impression wants to give them.
4. In conversations, I am sensitive to even the slightest change in the facial expression of the person I am conversing with.
5. My powers of intuition are quite good when it comes to understanding others.
6. I can usually tell when others consider a joke in bad taste, even though they may laugh convincingly.
7. When I feel that the image I am projecting isn't working, I can readily change to something that does.
8. I can usually tell when I've said something inappropriate by reading it in the listener's eyes.
9. I have trouble changing my behaviour to suit different people and different situations.
10. I can adjust my behaviour to meet the requirements of any situation I am in.
11. If someone is lying to me, I usually know it at once from that person's manner or expression.
12. Even when it might be to my advantage, I have difficulty putting up a good front.
13. Once I know what the situation calls for, it's easy for me to regulate my actions accordingly.

Certainly, always false (0),
Generally false (1),
Somewhat false, but with exceptions (2)
Somewhat true, but with exceptions (3)
Generally true (4)
Certainly, always true (5)

Appendix D

Xenophobic attitudes questionnaire

(Adopted from Faulkner et al., 2004)

Responses rated from 'completely disagree' to 'completely disagree'

Anti-immigration attitudes towards target group (7-point scale)

1. None of the immigrants [Nigerians/Canadians] applying for citizenship should be allowed to immigrate to Scotland
2. There is a risk that [Nigerians/Canadians] immigrants will bring health problems to Scotland
3. There is a risk that [Nigerians/Canadians] immigrants will bring criminal problems to Scotland

Attitudes towards Scottish immigration policy in general (7-point scale)

4. Scotland's immigration policies are too strict
5. All immigration to Scotland should be halted, regardless of immigrant origin
6. Scotland should accept refugees in need of asylum

Characteristics rated from 'not at all' to 'extremely'

Negative judgment ratings characteristics of target immigrant group (9-point scale)

7. Sanitary (reverse coding for total)
8. Filthy
9. Hygienic (reverse coding for total)
10. Clean (reverse coding for total)
11. Dirty
12. Likeable (reverse coding for total)
13. Hostile
14. Trustworthy (reverse coding for total)
15. Open-minded (reverse coding for total)
16. Ignorant
17. Poor
18. Lazy
19. Unintelligent

Appendix E

The 60-rule list for selection and prioritisation: 20 pro-social, 20 assortative social, and 20 pathogen-management rules.

20 Pro-social-related rules

All Citizens, immigrants and foreign visitors must be considered equal in the eyes of the law

All citizens and immigrants must be provided with basic living standards

All citizens, immigrants, businesses, and establishments must pay designated share of taxes

Citizens, immigrants and foreign visitors must not commit acts of animal cruelty/abuse

Citizens, immigrants and foreign visitors must not commit child abuse (physical or sexual)

Citizens, immigrants and foreign visitors must not engage in bribery or payoffs

Citizens, immigrants and foreign visitors must not engage in dishonest and/or fraudulent business dealings (i.e. racketeering)

Citizens, immigrants and foreign visitors must not engage in human trafficking

Citizens, immigrants and foreign visitors must not falsely testify (lie) as witness (personally or in legal testimony)

Citizens, immigrants and foreign visitors must not kill any other person(s)

Citizens, immigrants and foreign visitors must not operate any type of vehicle (e.g. car, boat, plane, etc.) under the influence of drugs (alcohol, narcotics, etc.)

Citizens, immigrants and foreign visitors must not own or work any person(s) in slavery

Citizens, immigrants and foreign visitors must not harm any other person(s) (including physically or sexually)

Citizens, immigrants and foreign visitors must not slander the name or character of any other persons(s)

Citizens, immigrants and foreign visitors must not steal from any other person(s)

Citizens, immigrants and foreign visitors who break the rules of the community must be punished and rehabilitated accordingly

Community population level must be maintained at a safe level for the benefit of human civilisation

The rights, life and safety of children (citizen or foreign) must always take priority over any adult (citizen or foreign)

The well-being of human civilisation must take priority over the well-being of any one community

No belief system must be above the laws of the community or above the rights of the people (citizen or foreign)

20 Assortative social rules

Citizens and their families must remain in the community to maintain the community population, strength and solidarity

Citizens who leave the community must surrender their citizenship

Citizens must only marry someone of the same belief system (the community's belief system)

Citizens must only marry someone from within the community

The rights, life and safety of citizens must always take priority over any non-citizen (immigrants and foreign visitors)

Citizens and immigrants must take an oath of allegiance and patriotism to the community

Citizens must confirm and maintain the superiority of the community and its culture over any foreign community or culture

Citizens who are deemed unpatriotic to the community must be expelled from the community

Citizens must participate in or donate to caring for sick and/or elderly citizens only (not immigrants and foreign visitors)

The well-being of the community must take priority over the well-being of all other communities

The community must prevent or reduce the entrance and/or immigration of foreigners

Citizens must not trade or cooperate with foreign persons or communities

Citizens and businesses must not consume, sell or serve foreign products (e.g. foods, clothing, items)

Immigrants must convert to the community's belief system upon naturalisation

The community must only speak one language (the native language)

The community must follow only one belief system

Citizens and immigrants who do not believe in the community belief system must be expelled from the community

Immigrants must assimilate to the community's culture (e.g. language, dress, customs, traditions, etc.)

Citizens must not learn about or teach others about foreign belief systems

Citizens must not diminish or undermine the preservation of the community's native culture and traditions

20 Pathogen-management rules

Citizens and businesses must adhere to strict policies to protect natural resources from contamination

Food products sold to the public must be produced, prepared and distributed according specific to health codes

Immigrants and foreign visitors must be screened for infectious diseases before entering the community

Immigrants and foreign visitors with infectious diseases must not be allowed to enter the community until fully recovered (if recovery is possible)

Medical staff (doctors, dentists, nurses, etc.) must wear protective clothing (rubber gloves, masks, etc.) during all medical procedures and treatments

Sanitation waste (rubbish and sewage) must be removed to a safe distance from the local population

Water distributed to the public must be sanitized and purified before public distribution

Citizens who own pets must remove their animal's faeces from public places

Animals (living or dead) carrying infectious disease must be disposed of according to specific health codes (i.e. incinerated)

Citizens with deadly infectious diseases must be listed in a public medical database (e.g. Hepatitis C, Ebola, AIDS, HIV, etc.)

Citizens and businesses must not consume, sell or serve blood or blood-based products

Citizens must be kept up-to-date with current vaccinations for public safety

Citizens, immigrants and foreign visitors must not engage in cannibalism

Citizens, immigrants and foreign visitors must not spit, vomit, urinate or defecate in public places

Human bodies (deceased) carrying infectious disease must be disposed of according to specific health codes (i.e. incinerated)

Citizens with deadly infectious disease must be quarantined appropriately

Animals must be kept up-to-date with current vaccinations for public safety

Citizens with infectious illnesses (flu, cold, etc.) must not attend school, work or other public functions until fully recovered

All blood, organ and tissue (kidney, heart, limbs, etc.) donated for transfusions and transplants must be pre-screened for infectious diseases

Animals travelling with immigrants and foreign visitors must be screened for infectious diseases before entering the community

Electronic Supplementary Material

ESM1: Tables of descriptive statistics for Stages 1, 3, and 5. Word document file.

ESM2: Complete list of disgust items provided by participants in Stage1 (reported in Stage2). Excel file.

ESM3: Disgust-item rating task. Excel file.

ESM4: Item-categorisation and pathogen disgust inter-rater task for Stage 4. Excel file.

ESM1-4 are associated with the published study described in Chapter 2 and, along with the complete Culpepper Disgust Image Set, are also available at http://hdl.handle.net/11667/121.