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Risk of parasite transmission influences perceived vulnerability to disease and perceived danger of disease-relevant animals

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ABSTRACT

Adaptationist view proposes that emotions were shaped by natural selection and their primary function is to protect humans against predators and/or disease threat. This study examined cross-cultural and inter-personal differences in behavioural immune system measured by disgust, fear and perceived danger in participants from high (Turkey) and low (Slovakia) pathogen prevalence areas. We found that behavioural immune system in Turkish participants was activated more than those of Slovakian participants when exposed to photographs depicting disease-relevant cues, but not when exposed to disease-irrelevant cues. However, participants from Slovakia, where human to human disease transmission is expected to be more prevalent than in Turkey, showed lower aversion in Germ Aversion subscale supporting hyper-sensitiveness of the behavioural immune system. Having animals at home was less frequent both in Turkey and in participants who perceived higher danger about disease relevant animals. Participants more vulnerable to diseases reported higher incidence of illness last year and considered perceived disease-relevant animals more dangerous than others. Females showed greater fear, disgust and danger about disease-relevant animals than males. Our results further support the finding that cultural and inter-personal differences in human personality are influenced by parasite threat.

1. Introduction

Evolution by natural and sexual selection is considered as the origin of domain-specific psychological mechanisms that include the structure of human personality (reviewed by Michalski and Shackelford, 2010). Natural selection which operates on survival of an individual, forms specific behavioural mechanisms that help us escape or avoid from predators (reviewed by Öhman and Mineka, 2001) and/or pathogens (reviewed by Oaten et al., 2009; Schaller and Duncan, 2007).

Most of parasites causing current diseases emerged in the last 11,000 years. Wolfe et al. (2007) argue that this is because of a shift to living in larger groups that are able to sustain epidemic diseases and because of close contact with animals via domestication and agriculture (Wolfe et al., 2007). Both historical evidences (Dobson and Carper, 1996; Guerra, 1993; McNeill, 1976; Murray and Schaller, 2010) and recent reports (Crompton, 1999; Macpherson, 2005; Sachs and Malaney, 2002) suggest that usually parasites cause human morbidity and mortality and, thus, they are powerful mechanism of natural selection. There are evidences showing that adjustments of life history traits (Michalakis and Hochberg, 1994) are a classical phenomenon in front of parasitic constraints. This theory provides a framework that addresses how, in the face of trade-offs; organisms should allocate time and energy to tasks and traits in a way that maximizes their fitness. Research showed that human populations living under severe parasitic constraints have increased reproductive investment, represented by increases in both the size (Thomas et al., 2004) and the number of offspring (Guégan et al., 2001). This suggests that natural selection favours heavier newborns (who are less susceptible to parasitic diseases) and larger number of offspring in areas where parasite-driven mortality is high.

The primary role of the immune system is to identify and defend an organism against harmful parasites when those parasites come into contact with the body. Comparative research revealed that human populations from pathogen rich environments have more diverse genes determining the recognition and recognition of antigens than humans who are under low pathogen threat (Prugnolle et al., 2005). The behavioural immune system is defined as a set of mechanisms that allow individuals to detect the potential presence of parasites in objects (or individuals) and/or to prevent contact with those objects (or individuals) (Schaller, 2006; Schaller and Duncan, 2007; Schaller and Murray, 2010). Evolutionary psycholo-

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gists agree that there are two compatible emotions that represent the core of the behavioural immune system in humans: disgust, that helps us avoid from certain animals, ill humans, faeces, vomit, sexual substances and other harmful substances or events (Prugnolle et al., 2009; Oaten et al., 2009; Rozin et al., 2000) and fear that motivates avoidance and escape (Epstein, 1972; Gerdes et al., 2009; Öhman and Mineka, 2001; Rachman, 2004).

The link between risk of parasite transmission and behavioural immune system predicts both inter-personal and cross-cultural differences in human personality. With respect to the former, it was found that behavioural immune system is activated especially in immunologically compromised individuals because there is higher cost of parasite threat compared to healthy individuals (Navarrete et al., 2007). People who feel especially vulnerable to parasite transmission have greater aversive responses against physically disabled individuals (Park et al., 2003), towards older adults (Duncan and Schaller, 2009), immigrants (Faulkner et al., 2004), or disease-relevant animals or microorganisms (Porzig-Drummond et al., 2009; Prokop et al., 2010; Stevenson et al., 2009; Tybur et al., 2009). Physical contact with all these groups of people increases the probability of transmission of a novel, infectious disease. Most recently, Schaller et al. (in press) found that visual perception of disease-connoting cues elicited aggressive immunological responses in humans. There is a general agreement that females are more disgust sensitive than men (reviewed by Oaten et al., 2009), because a choice of a mate with low resistance to parasites can results in low parental investment. Also, females bear a care for infants who need to be protected from infectious diseases.

With respect to the latter, it was found a positive association between pathogen prevalence and the cultural value of collectivism (Fincher et al., 2008) and religious diversity (Fincher and Thornhill, 2008). Females living in parasite-rich environments show lower mean levels of extraversion and openness and more restricted sexual behaviour (Schaller and Murray, 2008). Proximate mechanisms of such anti-pathogen avoidance lay in human avoidance of strangers, who may host a novel potentially infectious disease, to which the intruded community (in-group) has no immunity.

Recent evidence revealed that in tropics, where parasite prevalence and richness is generally higher (Guernier et al., 2004): (1) a higher proportion of diseases is transmitted by insect vectors compared to temperate zone, (2) animal reservoirs are more frequent and (3) a lower proportion of diseases is strictly confined to humans (Wolfe et al., 2007). We hypothesised that the behavioural immune system could be influenced by different evolutionary pressures in temperate zones compared with tropics which suggest that in areas with high parasite prevalence the disgust of disease-relevant insects and other animals (e.g., rodents) should be higher than in humans living in low parasite prevalence (Prokop et al., 2010). In contrast, animal avoidance (e.g., avoid having animals at home) should be more frequent in areas with high pathogen prevalence, because risk of disease transmission is higher. An avoidance of stimuli that indicate human to human parasite transmission should be higher in temperate zone because diseases transmitted from human to human are more frequent. With respect to inter-individual differences in human emotions, we predict that the behavioural immune system will be more activated in less healthy participants who perceive more vulnerable to disease. Furthermore, we predict that if other components of disgust (not only pathogen disgust, but also moral disgust that refers to sensitivity to non-normative, often antisocial activities such as lying, cheating, and stealing that harm others directly and/or have costs on one's social group, see Tybur et al., 2009) are associated with pathogen disgust and emotions that were determined by natural selection to protect ourselves against predators and/or parasites (Curtis et al., 2004; Fessler and Navarrete, 2003; Öhman and Mineka, 2001), then both these components of disgust have the same evolutionary origin (Schaich Borg et al., 2008; Tybur et al., 2009). Finally, the behavioural immune system should be more activated in females whose paternal concern is higher than those of males.

2. Materials and methods

2.1. Participants

A total of 120 Slovakian and 136 Turkish students (50 males and 206 females) with mean age 21.79 (SE = 0.11) years (range = 19–30 years) attending two universities participated in the study. Mean age of Slovakian and Turkish participants show only weak difference (mean ± SE, 22.04 ± 0.16 vs. 21.56 ± 0.15, $t = 2.19$, df = 254, $p = 0.03$, respectively). Because our research was conducted in educational faculties where a strong female bias in both countries historically exists, it was impossible to adjust the female to male ratio more accurately. The participants were recruited on a voluntary basis, and were not compensated for their participation. These countries were chosen because historical and recent data show that the prevalence of major parasites in Slovakia is significantly lower than in Turkey. Especially, serious parasitic diseases such as leishmaniasis, filiariasis, malaria, leprosy and schistosomiasis were almost never reported in Slovakia, but are significantly more prevalent in Turkey (Schaller and Murray, 2008; Prokop et al., 2010).

Students have been studying to become primary or secondary school teachers. However, all of them enrolled biology course at various level. The participants responded to questions related to (1) age/grade, (2) gender, (3) whether they have any animals as pets or farm animals, and, if yes, (4) what animal species they have as pets or farm animals and (5) the illness frequency during the last year.

The types of animal kept were categorized into pets (dogs, cats, fish, tortoises, parrots, rabbits, small rodents and invertebrates) and farm animals (poultry, livestock, pigs/sheeps). These two categories of animals are however strongly related, because only 4 students (1.6%) reported to have exclusively farm animals, but not pets.

2.2. Research instruments

2.2.1. Perceived vulnerability to disease

The perceived vulnerability to disease scale (PVDS) (Duncan et al., 2009) was used to assess the participants' self-perceived vulnerability to disease. This scale consists of 15 items; one subscale assesses beliefs about one's own susceptibility to infectious diseases (Perceived Infectability [PI]; 7 items with actual Cronbach's alpha = 0.83); the second subscale assesses emotional discomfort in contexts that suggest an especially high potential for pathogen transmission (Germ Aversion [GA]; 8 items with actual Cronbach's alpha = 0.67). Items were rated on a five-point Likert scale from 1 (strongly disagree) to 5 (strongly agree). Negatively worded items were scored in reverse order. To support the validity of Perceived Infectability, we found that mean score of this subscale strongly correlated with how many times the students was ill during last year ($r = 0.59$, $p < 0.001$, $n = 256$). There was only marginal correlation between Germ Aversion subscale and frequency of illness ($r = 0.19$, $p < 0.01$, $n = 256$).

2.2.2. Pathogen and moral disgust

The Pathogen Disgust Scale and Moral Disgust Scale, each of which has 7 items, were adopted from Tybur et al. (2009). The Pathogen Disgust Scale (with actual Cronbach's alpha of 0.63) is designed to measure disgust elicitors caused by sources of various pathogens (e.g., stepping on dog poop). The Moral Disgust Scale (with actual Cronbach's alpha of 0.71) is a domain of disgust that pertains to social transgressions (e.g., deceiving of a friend). These social transgressions broadly include non-normative, often antisocial activities like cheating, stealing and so forth. Participants responded to items on a five-point Likert scale from not at all disgusting (1) to extremely disgusting (5).

2.2.3. Measurement of disgust, fear and perceived danger

A total of 20 colour pictures (6 disease-relevant adult insects, 4 disease-relevant vertebrates, 5 disease-irrelevant adult insects and 5 disease-irrelevant vertebrates) were presented to participants in lecture halls (see the Appendix A for a complete list of species). The animals present some kind of 2×2 factorial design, because the first two groups of animals are risky to humans in terms of decreased immunity and/or health problems, and the latter two groups served as controls. Disease-irrelevant adult insects were controls for disease-relevant adult insects, and disease-irrelevant vertebrates were controls for disease-relevant vertebrates. We adjusted picture sizes to a standard body length. Pictures had similar contrast and brightness. The pictures were presented in random order. Each picture was presented for 1 min. Using a five-point scale from not at all (1) to extremely (5), participants rated animals' fearfulness, disgustness and dangerousness according to their perceptions.

3. Results

3.1. Perception of animals

Nested design ANOVA (with gender nested in country as fixed factors) with mean scores of disgust, fear and perceived danger of control and disease-relevant vertebrates and invertebrates (defined as dependent variables) revealed that control animals were perceived similarly between Slovakian and Turkish students. Multivariate results revealed non significant effect of country ($F_{12,241} = 1.58$, $p = 0.09$). The effect of country explained 7% of the variability of the results. However, disgust, fear and perceived danger of disease-relevant invertebrates (Fig. 1) and vertebrates (Fig. 2) were higher in Turkey than in Slovakia. Mean values presented in Figs. 1 and 2 suggest that students showed greater disgust, fear and perceived danger of disease-relevant animals compared to control animals. Disease-relevant vertebrates were perceived more dangerous while disease-relevant invertebrates were perceived more disgusting.

Mean score of males was generally lower than mean scores of females ($F_{24,482} = 7.52$, $p < 0.001$) indicating that the level of disgust, fear and perceived danger was higher in females. This effect was relatively high and explained 27% of the variability of the results. Univariate results revealed that there were only three exceptions in gender differences that were not statistically significant: disgust and fear of disease-relevant insects ($F_{2,252} = 2.84$ and 1.22, $p = 0.06$ and 0.30, respectively), and disgust of control vertebrates ($F_{2,252} = 2.42$, $p = 0.09$). Other differences were significant at $p < 0.001$.

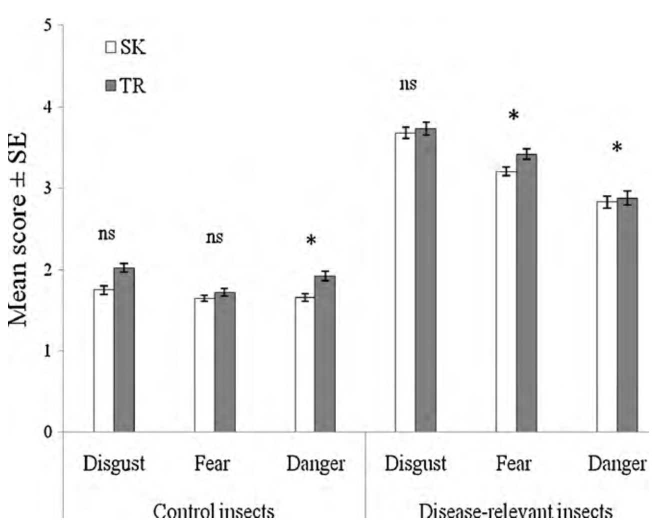

Fig. 1. Differences in perception of control and disease-relevant insects between Slovakian (SK) and Turkish (TR) students. ns = not statistically significant, $^{*}p < 0.05$.

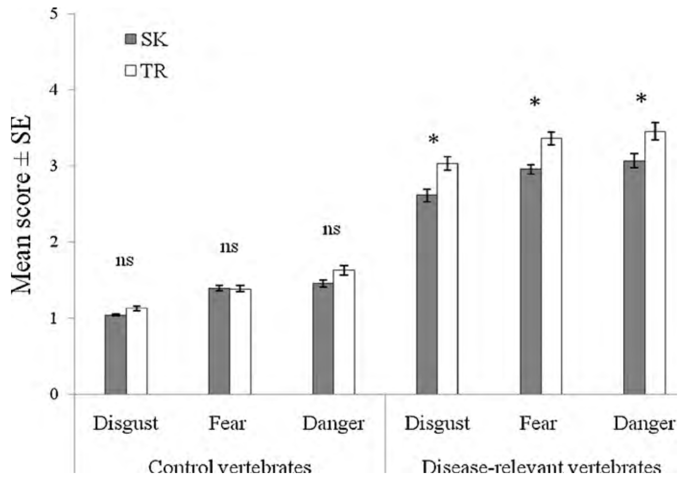

Fig. 2. Differences in perception of control and disease-relevant vertebrates between Slovakian (SK) and Turkish (TR) students. ns = not statistically significant, $^{*}p < 0.05$.

3.2. Perceived vulnerability to disease and disgust sensitivity

Nested ANOVA analysis with country and gender (gender nested in country as fixed factors) on mean scores of four dimensions (dependent variables) yielded significant effect of both predictors ($F_{4,249} = 11.51$ and $F_{8,498} = 4.88$, both $p < 0.001$, respectively). The effect of country and gender explained 16% and 7% of variability of results, respectively.

The effect of country is shown in Fig. 3. Perceived Infectability, Germ Aversion and Moral Disgust were significantly higher in Turkey, but Pathogen Disgust did not show any difference between countries. Females had higher mean scores than males in all four dimensions.

3.3. Having animals at home

Nested ANOVA with country and gender (gender nested in country as fixed factors) as fixed factors and total number of farm animals and pets as dependent variables revealed that Slo-

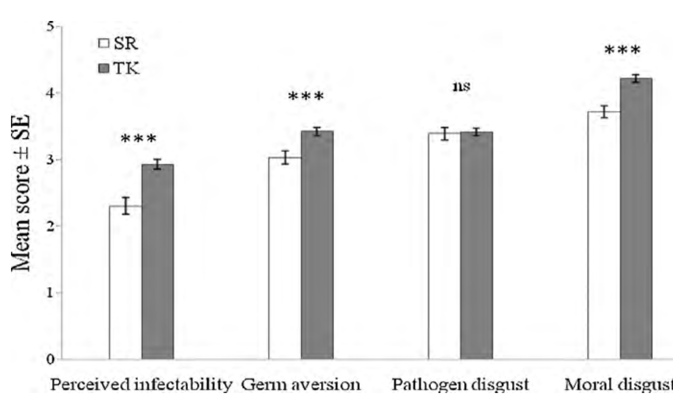

Fig. 3. Differences between countries in four dimensions. ns = not statistically significant, $^{*}p < 0.001$.

vakian students reported having more pets and tended to have also more farm animals than Turkish students ($F_{1,252} = 13.89$ and 3.52, $p < 0.001$ and $p = 0.06$, respectively). Females reported to have more pets and more farm animals than males ($F_{1,252} = 3.19$ and 4.03, $p = 0.08$ and $p = 0.046$, respectively). To examine whether an association between emotions and owning animals exists, additional multiple logistic regression was performed. Having at least one animal at home (farm animals mixed with pets) was dependent variable and country and gender were fixed categorical predictors. The mean scores of disgust, fear and perceived danger of disease-relevant and control animals were defined as continuous predictors. The significant effect of country and gender corroborate results reported above (Wald's $\chi^2 = 16.06$ and 13.57, both $p < 0.001$, respectively). However, perceived danger of disease-relevant animals was also associated with owning animals (Wald's $\chi^2 = 12.67$, $p < 0.001$) which means that students who perceived disease-relevant animals more disgusting owned animals less frequently than other students. Other predictors were not significant (all $ps > 0.18$).

3.4. Associations between disgust, fear and perceived danger of animals and PVD

Because mean scores of control animals were generally dissimilar to mean scores of disease-relevant animals (Figs. 1 and 2), we used overall mean scores of disgust, fear, and perceived danger of control animals [vertebrates and invertebrates] and disease-relevant animals [vertebrates and invertebrates] as predictors of Perceived Infectability (dependent variable). Further predictors were gender and country. Backward stepwise multiple regression resulted in significant model ($R^2 = 0.14$, $F_{2,253} = 21.19$, $p < 0.001$). However, only two predictors remained in the model: country and perceived danger of disease-relevant animals ($\beta = 0.30$ and 0.20, $t(253) = 5.10$ and 3.48, both $p < 0.001$, respectively). Other variables were removed from the model. These results indicate that Turkish students perceived disease-relevant animals more dangerous than Slovakian students. Students who perceived themselves more vulnerable to infectious diseases considered disease-relevant animals more dangerous than students who felt healthier.

When the mean score of the Germ Aversion was defined as dependent variable, the model was also significant but explained less variance than the previous model ($R^2 = 0.08$, $F_{1,254} = 22.43$, $p < 0.001$) with the only danger of disease-relevant animals remaining in the model ($\beta = 0.28$, $t(254) = 4.74$, $p < 0.001$). Inclusion of Pathogen Disgust score fully corroborated the latter finding ($R^2 = 0.15$, $F_{1,254} = 43.65$, $p < 0.001$), because only danger of disease-relevant animals remained in the backward stepwise multiple regression model ($\beta = 0.38$, $t(254) = 6.61$, $p < 0.001$). When the mean score of Moral Disgust was defined as dependent variable, the model was again significant ($R^2 = 0.24$, $F_{2,253} = 40.73$, $p < 0.001$). In this case, only country and perceived danger of disease-relevant animals entered the multiple regression model ($\beta = 0.42$, and 0.22, $t(253) = 7.63$ and 3.99, both $p < 0.001$, respectively).

Analysis of correlation matrices revealed that although mean scores of all four dimensions (PI, GA, PD and MD) only modestly correlated (except for MD and PD which showed no correlation), because no correlation coefficient exceeded $r = 0.29$. This means that all these variables were more or less independent from each other.

4. Discussion

Differences in parasite prevalence between regions influence human personality (reviewed Schaller and Murray, 2010) and consequently human culture (Fincher et al., 2008; Thornhill et al., 2009). Our previous research (Prokop et al., 2010) provided some evidences showing that Turkish children have generally higher disgust, fear and perceived danger than Slovakian children and that perceived danger was associated with low health of participants.

The first focus of our study was to examine whether there were differences in the activation of the behavioural immune system in humans living in high and low pathogen prevalence regions. Namely, it is predicted that humans from high pathogen prevalence regions are (1) more aversive of disease-relevant vertebrates and invertebrates, (2) less prone to have animals at home and (3) less aversive of cues indicating human to human parasite transmission than humans from regions with low pathogen prevalence. The first two predictions were supported by the findings because Turkish participants who are more vulnerable to parasite showed significantly higher fear, perceived danger and disgust (except for disgust of disease-relevant insects) of disease-relevant, but not disease-irrelevant, animals. In addition, Turkish participants scored higher in Perceived Infectability and Germ Aversion subscales supporting our adaptationist view of human emotions. Although non-significant difference in Pathogen Disgust scale between participants from the two countries is surprising, it may be that items in Pathogen Disgust scale show no explicit disease threat than items in other subscales. Furthermore, Turkish participants reported to own less animals at home compared to Slovakian participants. Former finding supports the theories indicating that human personality is affected by parasite threat (Curtis et al., 2004; Lafferty, 2006; Fincher et al., 2008; Oaten et al., 2009; Park et al., 2003; Prokop et al., 2010; Schaller and Murray, 2008; Schaller, 2006; Schaller and Duncan, 2007; Stevenson et al., 2009; Thornhill et al., 2009). That is, risk of incautious behaviour is higher for humans living in environments with high parasite threat, favouring higher disgust sensitivity or fear or parasite connoting cues. Latter finding provides intriguing evidence about differences in owning animals between two distinct countries. From a perspective of social sciences ignoring effects of evolutionary pressures on human behaviour (Michalski and Shackelford, 2010; Öhman and Mineka, 2001), it would be argued that these differences can be attributed to cultural, rather than evolutionary differences. We argue, however, that these results seem not to be an artefact of "different culture", because only perceived danger of disease-relevant animals, country and gender (but not other variables) were significantly associated with keeping animals at home. Furthermore, our previous research in these two countries also revealed that owning animals is less frequent among Turkish students (Prokop et al., 2009) suggesting that results of our current research is valid.

The third prediction was not supported, because Turkish participants showed significantly higher mean scores in Germ Aversion subscale than Slovakian participants. Our current finding supports the idea suggesting that the behavioural immune system does not react to specific cues triggered by parasites, because these may greatly vary; instead, it responds, in a hypersensitive and overgeneral way, to the perceived presence of parasites in the sensory environment (Schaller and Duncan, 2007).

With respect to inter-personal differences, we predicted that perceived danger, disgust and fear will be more activated in less healthy participants who perceive more vulnerability to disease (Park et al., 2003; Prokop et al., 2010; Schaller, 2006; Schaller and Duncan, 2007; Schaller and Murray, 2010; Stevenson et al., 2009). In agreement with this prediction and with our former research, we showed that participants who perceive more vulnerability to diseases have higher incidence of illness. Moreover, these participants perceive disease-relevant animals (but not disease-irrelevant animals) more dangerous than participants who are less vulnerable to diseases.

Moral disgust is a domain of disgust pertaining to social transgression. Our study showed that the mean score of moral disgust was higher in participants living in areas with high parasite threat and that there was a significant association between moral disgust and perceived danger of disease-relevant animals. Although correlations between moral disgust and other subscales were only moderate suggesting that this scale is relatively independent from others (Tybur et al., 2009), the associations with danger of disease-relevant animals was the same for all subscales suggesting that the higher the disgust sensitivity is the higher perception of disease-relevant animals as dangerous. Our results support the findings of Schaich Borg et al. (2008) who found that pathogen related acts, incestuous acts, and socio-moral violations all activate a network of brain regions previously reported to be associated with disgust (e.g., the globis pallidus, putamen, caudate head, and amygdala). Other studies also indicate that disgust is linked to moral judgments (Marzillier and Davey, 2004; Wheatley and Haidt, 2005), further suggesting that disgust reflects a response toward multiple elicitors including infection, incest, and iniquity (Tybur et al., 2009). To conclude, our data suggest that moral disgust coincide with pathogen disgust supporting strong associations between these two domains of disgust.

Females are generally more disgust sensitive than men (Curtis et al., 2004; Fessler and Navarrete, 2003; Oaten et al., 2009; Porzig-Drummond et al., 2009; Prokop and Fančovičová, 2010; Tybur et al., 2009). This study extends previous research suggesting that females are the sex that has most to lose if they select a mate who is sick and then dies, leaving them to care alone for any offspring. Moreover, females bear care for infants, thus they need to protect their children from infectious diseases (Oaten et al., 2009). Further research is required to address whether the "paternal investment hypothesis" (assuming that females who invest more into reproduction should be more disease sensitive than those who invest less) or "costly signalling hypothesis" (assuming that males wish to demonstrate their fitness by displaying an indifference to disease signalling cues) (Oaten et al., 2009) is responsible for emotional differences between sexes.

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Appendix A

List of species used in Powerpoint presentation

Disease-relevant invertebrates: dengue mosquito (*Aedes aegpti*), tse-tse fly (*Glossina palpalis*), German cockroach (*Blatella germanica*), common tick (*Ixodes ricinus*), human flea (*Pulex irritans*), human louse (*Pediculus humanus*)

Disease-relevant vertebrates: common rat (*Rattus norvegicus*), house mouse (*Mus musculus*), red fox (*Vulpes vuples*), common Bent-wing bat (*Miniopterus schreibersii*)

Control invertebrates: rhinoceros beetle (*Oryctes nasicornis*), azure damselfly (*Coenagrion puella*), ladybird beetle (*Coccinella septempunctata*), duetting grasshopper (*Chorthippus biguttulus*), Old World swallowtail (*Papilio machaon*)

Control vertebrates: horse (*Equus ferus caballus*), Eurasian red squirrel (*Sciurus vulgaris*), European rabbit (*Oryctolagus cuniculus*), European roe deer (*Capreolus capreolus*) [female], common bottlenose dolphin (*Tursiops truncates*)

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