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Essay

Impact of infection on mate choice

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Sexual selection predicts that mate choice increases individual fitness. Infection by parasites (from eukaryotes to bacteria or viruses) can reduce this individual fitness, altering the infected individuals' sexual traits and molecular cues. In this case, one would expect to observe mechanisms for avoiding infection during mate choice. The vast majority of host responses to infection in terms of mate choice are intended to avoid infection, but the costs of mate choice can also hinder infection avoidance. This paper highlights the main limitations in current knowledge and empirical experiments, and summarizes the key factors that should be taken into account to test the hypothesis of infection avoidance in mate choice: the time of host–parasite coevolution in the biological interaction implied, the choosy sex tested (male, female or both) and the genetic background of the individuals tested.

Sexual selection is a key evolutionary process that occurs through competition over mates and/or for mating, implying mechanisms of mate choice and reproductive outcome. In some species, sexual selection involves competition between individuals of the same sex who fight each other to win their mate (Wyatt, 2008). A wealth of studies about sexual selection have also been carried out investigating mate choice, a common behaviour in which members of one sex put themselves on display to be chosen by a member of the other sex. Mate choice is generally based on phenotype, allowing the choosy sex to assess individual condition, only high-quality individuals being able to display the most extravagant phenotype (e.g. ornaments). According to the handicap principle, this extravagant phenotype is maintained because the relative cost of producing the signal is lower for high-quality individuals (Zahavi, 1977).

Phenotype expressions used in mate choice are correlated with several parameters of individual condition, such as body weight and parasitic load (Andersson, 1994). Therefore, in a given population, the best male (with the best genetic qualities) displays a better phenotype than the males that are more sensitive to parasites or diseases.

Mate choice benefits are explained by a variety of evolutionary mechanisms offering indirect and direct benefits (Andersson, 1994; Wyatt, 2008). On the one hand, indirect benefits include the transmission to offspring of genes for both fitness quality and mating preference (Kokko, Brooks, Jennions, & Morley, 2003). On the other hand, direct benefits can be gained by mating with partner(s) with the highest fitness, as a result of better parental care, foraging efficiency, fecundity or fertility (Andersson, 1994). Direct benefits also include avoiding parasitized mates, as this could affect both the partner's fitness benefits and direct parasite transmission (Hillgarth, 1996; Martinez-Padilla, Vergara, Mougeot, & Redpath, 2012). In this way and according to the 'contagion indicator' hypothesis, male secondary sexual characters are correlated with the intensity of transmittable parasites (Able, 1996). Avoiding parasitic infection by choosing a healthy male confers to females and their offspring direct benefits, decreasing the risk of parasite acquisition (Able, 1996). In the case of contagious diseases, many species use odour cues as phenotypes to choose healthier mates (Arakawa, Cruz, & Deak, 2011; Penn & Potts, 1998a). The mechanisms of mate choice can determine whether parasites (eukaryotes, bacteria or viruses) affect the processes underlying mating decisions and whether they can be considered as agents of selection.

An individual's infection status can alter how its health status is perceived by its conspecifics: notably in the context of sexual behaviour, mate choice (Sharon et al., 2010) and recognition (Richard, Holt, & Grozinger, 2012). The effect of infection on mate recognition and mate choice can be investigated on two different levels: (1) at the proximate level to find out which signals

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individuals use to discriminate between mates and which molecular mechanisms and chemical cues play a role in mate choice in infection conditions; and (2) at the ultimate level to understand how host responses to infection drive sexual selection and, in particular, mate choice.

The aim of this paper is to provide new insights to improve our understanding of the link between infection and mate choice. We examine this link at the proximate and ultimate levels of understanding in the light of the existing literature.

PROXIMATE LEVEL

Effect of Infection on Sexual Traits

Some traits (e.g. ornaments, coloration, calling song, odours) are altered by simple or multiple infections and correlate with these (Biard, Saulnier, Gaillard, & Moreau, 2010; Hamilton & Poulin, 1999; Hamilton & Zuk, 1982; Horak et al., 2004; Potti & Merino, 1996; Ryder & Siva-Jothy, 2000). For example, bill colour, plasma carotenoid levels and body mass are strongly related to the relative abundance of parasite species in blackbirds, *Turdus merula* (Biard et al., 2010).

Infection can have a negative impact on phenotypic traits, such as sexual ornaments and displays. For example, in red junglefowl, *Gallus gallus*, males infected by the nematode *Ascaridia galli* showed less-developed secondary traits (Zuk, Thornhill, Ligon, & Johnson, 1990). In the same way, coccidian infection reduced plumage coloration in infected greenfinches, *Carduelis chloris*, by decreasing carotenoid levels (Horak et al., 2004). Mite nest ectoparasites also have a negative impact on the growth of the tarsus in flycatchers, *Ficedula hypoleuca*, potentially linked to the host's hormone regulation and immune system (Potti & Merino, 1996). According to the Hamilton and Zuk parasite hypothesis, the expression of particular male traits can be associated with resistance to parasites, and so females can use these male traits as indicators of heritable parasite resistance (Hamilton & Zuk, 1982). For example, in red grouse, *Lagopus lagopus scoticus*, the nematode *Trichostrongylus tenuis* is an intestinal parasite that reduces its host's ability to reproduce (Hudson, 1986). According to the handicap principle applied to parasite resistance, the expression of male sexual displays informs about the capacity to fight against parasite infection (Aguilar, Maia, Santos, & Macedo, 2008; Ahtiainen, Alatalo, Kortet, & Rantala, 2004; Hamilton & Zuk, 1982). In this way, sexual ornaments can provide cues reflecting individual condition when parasites are abundant in the population (Vergara, Mougeot, Martinez-Padilla, Leckie, & Redpath, 2012).

Effect of Infection on Molecular Cues

Parasites often alter the body odour of infected animals, including humans, with evolutionary consequences for both the parasite's and the host's strategies (Prugnolle et al., 2009). Infection could affect the host's attractiveness and decrease its reproductive success. Several odour preference experiments have revealed that females not only discriminate the odour of uninfected males but are also more attracted to it than that of experimentally infected males (Ehman & Scott, 2001; González Quiñónez, Pirela di Vincenzo, De Jesús de Durán, & Muñoz-Romo, 2011; Kavaliers et al., 2006; Kavaliers & Colwell, 1995a, 1995b; Kavaliers, Colwell, Braun, & Choleris, 2003; Klein, Gamble, & Nelson, 1999; Penn, Schneider, White, Slev, & Potts, 1998; Willis & Poulin, 2000; Worden, Parker, & Pappas, 2000).

Molecular compounds seem to be involved in discrimination between individuals according to their infection status. Mate recognition and preference thus appear to be induced by proximate factors. Chemical cues may be used by males or females to detect complex information about potential mates, such as size, body condition, parasite load, immunocompetence, familiarity, reproductive status, degree of relatedness and individual health (Arakawa et al., 2011; Coleman, 2009; Johanson & Jones, 2007; Richard et al., 2012).

Paradoxically, few experimenters have tried to identify the chemical compounds involved in mate choice linked to infection. The ever-improving performance of the 'omic tools' in chemistry and molecular genetics (transcriptomics, proteomics and genomics) should offer an ideal means for improving our understanding of the topic (McFall-Ngai et al., 2013). Focusing on the molecular scale could thus lead to a better understanding of the proximate factors underlying mate choice linked to infection. In this context, some chemical compounds, proteins and genes have been identified as being directly or indirectly involved in mate recognition or mate choice (Andersson & Simmons, 2006; Hammer, Zhou, & Cheung, 1994; Kavaliers, Colwell, Ossenkopp, & Perrot-Sinal, 1997; Sharon et al., 2010).

In *Drosophila*, gene loci and proteins of seminal fluids have been shown to be involved in postcopulatory sexual selection, inducing changes in the female (i.e. increased egg laying and decreased receptivity to other males) that are beneficial for the male (Andersson & Simmons, 2006). In the same species, commensal bacteria also play a role in mating preference, which is linked to changes in the host's cuticular hydrocarbon profiles (Sharon et al., 2010).

In mice, *Mus musculus domesticus,* males infected with a virus decrease in attractiveness (Penn et al., 1998). When females are exposed to the urine of an infected male (which has lost its attraction), the levels of some endogenous opioids increase, which inhibits the female's sexual receptivity (Hammer et al., 1994). Certain categories of endogenous opioids increase sexual interest whereas others decrease it (Kavaliers et al., 1997). In this case, it is the reorganization and the regulation of the levels of endogenous opioids that induce the sexual interest rather than the presence or the absence of one molecule (Kavaliers et al., 1997). Changes in female behaviour could also be the result of compounds missing from the urine of infected males, as male androgen levels decline in infected individuals (Arakawa et al., 2011; Dunlap & Schall, 1995 and references therein). Moreover, the mechanisms responsible for individual recognition have also been investigated and appear to be mediated by major urinary proteins (MUPs) that bind and release small volatile pheromones (Hurst et al., 2001).

Major histocompatibility complex (MHC) genes encode the proteins that present foreign peptides to T-cells. Associated with a high level of individual polymorphism, these proteins may play a role in pathogen resistance. Producing soluble proteins or protein-binding volatile molecules, the MHC also plays a role in individual odour and recognition (Arakawa et al., 2011). However, exactly how individuals choose a mate according to MHC remains unclear (reviewed in Tregenza & Wedell, 2000). Some MHC proteins are expressed in sperm, which means mate choice may take place at the gametic level based on MHC genotype (reviewed in Tregenza & Wedell, 2000). Although the MHC proteins are the molecules most often cited as being involved in mate choice (Penn & Potts, 1998b), other proteins appear to be involved.

Genomics, transcriptomics, proteomics and metabolomics make it possible to determine the molecules and molecular pathways involved in multiple levels of animal interactions (McFall-Ngai et al., 2013), and more specifically in sexual selection mechanisms such as mate choice, and should be able to clarify the proximate factors involved in mate choice. In all the studies previously cited in this essay, certain chemical compounds, proteins and/or genes were identified as being altered by infection, with consequences for