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In house finches, *Haemorhous mexicanus*, risk takers invest more in innate immune function

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Consistent, stable behavioural differences in how individuals respond to novel situations can lead to variation in exposure to pathogens. To minimize the costs associated with pathogen infection, animals have evolved behavioural and immunological strategies to avoid infection. However, because both behavioural and immunological defences are costly, host individuals should benefit from balancing investment in these defence strategies. It has been suggested that one such behavioural defence strategy is hesitancy to engage with novel objects and environments. In particular, exploratory individuals appear more likely to be exposed to novel pathogens than less exploratory individuals. Here, we tested the hypothesis that immune function is inversely related to behaviours with the potential to decrease exposure to pathogens (i.e. forgoing exploratory behaviours). We found an inverse association between aspects of innate immune function and exploratory behaviours. These observations suggest that individuals that engage in low-risk behaviours when experiencing a novel situation may invest less in some aspects of innate immune function than individuals that engage in high-risk behaviours. This individual variation in pathogen defence strategy is expected to affect the dynamics of pathogen spread through populations, and ultimately the course of epidemics.

The distribution of infectious agents varies spatially (Hudson, Rizzoli, Grenfell, Heesterbeek, & Dobson, 2002); as a result, the extent and ways in which an individual interacts with its habitat are likely to affect pathogen exposure. Consistent, stable behavioural differences in how individuals respond to novel situations have been documented in a wide range of vertebrate species. Because behaviour can help determine the amount of exposure to parasites and pathogens that an individual experiences (Barber & Dingemanse, 2010; Hart, 1990), these consistent behavioural differences can lead to predictable individual variation in exposure to parasites and pathogens. For example, differences in foraging ecology and spatial distribution are reflected in differences in parasite fauna in distinct sympatric morphs of Arctic char, *Salvelinus alpinus*, and threespine stickleback, *Gasterosteus aculeatus* (Dorucu, Adams, Huntingford, & Crompton, 1995; Knudsen, Amundsen, & Klemetsen, 2003; MacColl, 2009). Variation in exploratory behaviour, which has received much attention (Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002; Drent & Marchetti, 1999; Marchetti & Drent, 2000; Verbeek, Drent, & Wiepkema, 1994), may be particularly important in determining individual variation in parasite and pathogen exposure.

Exploration provides individuals with vital information about their local environment, such as the location of food and water, hiding places and the presence of predators, and increased familiarity with a particular area can even provide an advantage in competitive interactions (Verbeek et al., 1994). However, it has been suggested that, because more exploratory individuals are more likely to approach novel objects or interact with novel environments, they should be more likely to come into contact with novel parasites or pathogens (Barber & Dingemanse, 2010). In addition, more exploratory individuals are likely to spend time in larger geographical areas (for example, see Boon, Réale, & Boutin, 2008; Kobler, Engelen, Knaepkens, & Eens, 2009; van Overveld & Matthysen, 2010), thereby increasing the number of pathogens or parasites that they can come into contact with. Few studies have examined the relationship between the extent of exploratory behaviour and pathogen exposure or parasite load. Nevertheless, there is some evidence that increased exploratory behaviour does indeed increase exposure to microbial pathogens and multicellular parasites. In a study of tick infestation in Siberian chipmunks, *Tamias sibiricus*, the extent of exploratory behaviour was an important explanatory factor in predicting tick load (Boyer, Réale,

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Marmet, Pisanu, & Chapuis, 2010). Similarly, pumpkinseed sunfish, *Lepomis gibbosus*, that show greater exploratory behaviour have significantly higher levels of infection with one species of trematode (Wilson, Coleman, Clark, & Biederman, 1993). Evidence from the ecological immunology literature lends further support to the idea that pathogen exposure increases in individuals that range over larger areas. For example, in birds, species with longer natal dispersal distances (and, thus, the potential for increased pathogen exposure) invest more in immune function (Møller, Martín-Vivaldi, & Soler, 2004; Snoeijs, Van de Casteele, Adriaensen, Matthysen, & Eens, 2004). The link between risk of pathogen exposure and investment in immune function could be the result of differences in early experience with pathogen exposure, which can impact the development of both adult immune response and personality traits, including exploratory behaviour, in mammals and birds (Butler, Toomey, McGraw, & Rowe, 2011; Galic, Spencer, Mouihate, & Pittman, 2009; Rico, Ferraz, Ramalho-Pinto, & Morato, 2010).

To minimize the costs associated with parasite infestation and pathogen infection, animals have evolved behavioural and immunological strategies to avoid infection with pathogens and infestation with parasites (Brown & Brown, 1986; Franks, Hooper, Webb, & Dornhaus, 2005; Hart, 1990; Janeway, Travers, Walport, & Shlomchik, 2001). However, both of these strategies entail costs. For example, behavioural defences that minimize exposure to pathogens entail costs as a result of forgoing the benefits of exploration (Verbeek et al., 1994) or social interactions (i.e. reproduction opportunities, decreased predation risk; Alexander, 1974). Likewise, immune defences are costly in terms of energy expenditure, nutrient use, behavioural changes and risk of physical damage or death from an overactive or misdirected immune response (Bonneaud et al., 2003; Klasing & Leshchinsky, 1999). Because both behavioural and immunological pathogen defences are costly, it has been suggested that individuals may benefit from balancing investment in these two types of defences (Zylberberg, Klasing, & Hahn, 2013); for simplicity, we term this the pathogen defence optimization hypothesis (PDOH). We previously showed that, in a social context, house finches trade-off behavioural and immunological defences against pathogen infection (Zylberberg et al., 2013). Avoidance of pathogen-infected individuals is likely to be a highly effective technique in avoiding exposure to directly transmitted pathogens. Likewise, animals are able to use a variety of other behavioural defences to avoid exposure to pathogens that exploit other routes of transmission (i.e. vectorborne, or orally or environmentally transmitted pathogens: Darbro & Harrington, 2007; Ezenwa, 2004; Nunn & Heymann, 2005).

Here, we examined whether individuals balance investment in behavioural pathogen defences with immunological pathogen defences in a nonsocial context. Specifically, given the apparent importance of exploratory behaviour in pathogen exposure, we examined whether individuals balance investment in pathogen avoidance (forgoing exploratory behaviours) with investment in innate immune function. The PDOH suggests that individuals balance behavioural and immunological defences against pathogens; as a result, there should be an inverse relationship between behavioural and immunological pathogen defences. However, it is important to note that the immune system is a highly complex network made up of many partially overlapping components that vary in cost. All else being equal, the most expensive aspects of the immune system are the ones that should be balanced against behavioural pathogen defences and diminished when resources are scarce or when pathogen encounter rates are low or avoidable; the specific aspects of the immune system involved could also be influenced by the particular pathogens in a given system, the types of defences that are most effective against those pathogens, and the extent of specificity of the behavioural and immunological defences available to cope with those pathogens. We focused on innate immune function because the innate immune response has been shown to be substantially more costly than the adaptive immune response (Iseri & Klasing, 2013). The PDOH predicts that innate immune function will be inversely correlated with behaviours that minimize exposure to pathogens; for example, investment in innate immune function should decrease with increased investment in avoidance of novel objects, or in learning about a new environment prior to engaging with it (i.e. by surveying the environment). In contrast, innate immune function should not be related to behaviours that are not specifically tied to parasite or pathogen exposure in novel situations. Activity level is one aspect of behaviour that is frequently discussed in the context of exploratory behaviour (Barber & Dingemanse, 2010), although the relationship between activity and exploration can vary among species. While a high level of activity when exploring a novel environment could increase an individual's risk of exposure to parasites and pathogens, given that an individual spends the majority of its life in a familiar environment where activity level does not increase parasite or pathogen exposure, the PDOH does not predict that there will be a strong relationship between activity level and immune function.

An alternative set of hypotheses regarding the relationship between exploratory behaviour and immune function is that variation in individual condition underlies both variation in exploratory behaviour and investment in immune function. On the one hand, individuals in good condition may be able to invest more resources in both exploration and immune function. On the other hand, individuals in poor condition may be more motivated to explore due to their need for resources, but they may not be able to invest as much in immune function as individuals in better condition. Both of these hypotheses predict that individual condition will explain observed variation in exploratory behaviour between individuals, although the first predicts a positive relationship between condition and exploration while the second predicts a negative relationship between the two.

Here, we quantified individual behavioural variation in house finches in response to novel objects placed in the home cage and in response to a novel environment. We conducted a principal components analysis to elucidate and better describe the distinct modes of observed behavioural variation. We then tested whether variation in either condition or innate immune function explains variation in exploratory behaviour and whether innate immune function is inversely related to behaviours that have the potential to decrease exposure to pathogens.

METHODS

Study System

We conducted this study in house finches, which have become a model system for studying the dynamics of emerging infectious disease (Altizer, Davis, Cook, & Cherry, 2004; Bonneaud et al., 2011; Hotchkiss, Davis, Cherry, & Altizer, 2005). Twenty-seven male house finches were caught in mist nets or potter traps at four sites in Yolo and Solano counties in northern California, U.S.A., in June 2010. Individuals were brought into captivity, where they were individually housed in cages measuring 0.5 m in each dimension. Birds were able to see and hear other individuals, were kept on a natural photoperiod and were provided feed and water for ad libitum consumption (both before and during experiments). All birds were processed with the approval of Institutional Animal Care and Use Committee of University of California, Davis (IACUC protocol 12866) and in accordance with the ASAB/ABS guidelines for the use of animals in research; after the completion of this study,