



Exploratory behavior is linked to stress physiology and social network centrality in free-living house finches (*Haemorrhous mexicanus*)

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ABSTRACT

Animal personality has been linked to individual variation in both stress physiology and social behaviors, but few studies have simultaneously examined covariation between personality traits, stress hormone levels, and behaviors in free-living animals. We investigated relationships between exploratory behavior (one aspect of animal personality), stress physiology, and social and foraging behaviors in wild house finches (*Haemorrhous mexicanus*). We conducted novel environment assays after collecting samples of baseline and stress-induced plasma corticosterone concentrations from a subset of house finches. We then fitted individuals with Passive Integrated Transponder tags and monitored feeder use and social interactions at radio-frequency identification equipped bird feeders. First, we found that individuals with higher baseline corticosterone concentrations exhibit more exploratory behaviors in a novel environment. Second, more exploratory individuals interacted with more unique conspecifics in the wild, though this result was stronger for female than for male house finches. Third, individuals that were quick to begin exploring interacted more frequently with conspecifics than slow-exploring individuals. Finally, exploratory behaviors were unrelated to foraging behaviors, including the amount of time spent on bird feeders, a behavior previously shown to be predictive of acquiring a bacterial disease that causes annual epidemics in house finches. Overall, our results indicate that individual differences in exploratory behavior are linked to variation in both stress physiology and social network traits in free-living house finches. Such covariation has important implications for house finch ecology, as both traits can contribute to fitness in the wild.

1. Introduction

Animal personalities, or consistent inter-individual differences in behavior (Réale et al., 2010; Sih et al., 2004), influence the ways in which an individual interacts with conspecifics, other species, and the environment (e.g. Aplin et al., 2013; Boyer et al., 2010; Favati et al., 2014; Pruitt and Modlmeier, 2015). One of the most commonly studied behavioral heterogeneities in the context of animal personalities is response to novelty, wherein individuals are often placed on a behavioral spectrum that ranges from “bold” (displaying exploratory behaviors) to “shy” (displaying neophobic behaviors) based on their responses to novel environments, objects, and/or conspecifics (e.g. Dingemanse et al., 2007; Drent et al., 2002; Sih et al., 2004; Verbeek et al., 1994). This central axis of personality has the potential to link consistent

differences in individual stress physiology (Carere et al., 2010), interactions with conspecifics (e.g. social network position; Aplin et al., 2013; McCowan and Griffith, 2015; Snijders et al., 2014), and interactions with the environment (e.g. Boon et al., 2008; Boyer et al., 2010). While previous studies have explored different aspects of these links between physiology and behavior, none have simultaneously examined stress physiology, exploratory tendencies, and other potentially correlated behaviors (e.g. social behaviors) in the wild, thus limiting our ability to understand how these traits interact to influence individual fitness.

Because of the pleiotropic effects of hormones on diverse traits (McGlothlin and Ketterson, 2008), numerous recent studies have examined how personality traits such as exploratory behavior are linked to endocrine physiology, and in particular, to reactivity of the

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hypothalamic-pituitary-adrenal (HPA) axis, which produces glucocorticoids (Carere et al., 2010; Hau et al., 2016). Although the directionality of these links is challenging to unravel, experimental selection for fast exploration in great tits resulted in lower baseline corticosterone concentrations in both adults and nestlings relative to lines selected for slow exploration (Baugh et al., 2012; Stöwe et al., 2010). By contrast, zebra finches selected for higher stress-induced corticosterone concentrations showed greater risk-taking behavior relative to birds in other lines (Martins et al., 2007). Thus, exploration behavior and HPA reactivity appear to be strongly linked, and at least in some cases, genetically correlated. However, the direction of relationships between stress hormones (glucocorticoids) and boldness behaviors is not always consistent across taxa. For many species of mammals, such as mice, rats, and pigs, shy individuals show higher stress-induced glucocorticoid concentrations than bold individuals (reviewed in Carere et al., 2010). However, for birds, the relationship between personality and concentrations of the glucocorticoid corticosterone (CORT) is less clear. Higher stress-induced CORT concentrations have been correlated with slow exploration tendencies in great tits (*Parus major*) (Baugh et al., 2013, 2012; Carere et al., 2010), house sparrows (*Passer domesticus*) (Lendvai et al., 2011), and dark-eyed juncos (*Junco hyemalis*) (Atwell et al., 2012). However, for captive zebra finches (*Taeniopygia guttata*) selectively bred to have low corticosterone production, individuals with higher stress-induced circulating CORT concentrations exhibited more exploratory behaviors than individuals with lower circulating CORT concentrations, though this pattern was not present in the high corticosterone production selection line (Martins et al., 2007). Overall, while shy or slow-exploring individuals generally harbor higher stress-induced CORT concentrations in the taxa studied to date, more studies are needed to determine the generality of this pattern (at least within birds) or to explore environmental or life-history differences underlying the directionality of this relationship.

There is also accumulating evidence that animal personality and components thereof (i.e. exploratory behaviors) are linked to social interactions among conspecifics (both non-aggressive and agonistic). However, studies linking personality to social behaviors have also yet to yield broad patterns. For some species, such as grey kangaroos (*Macropus giganteus*) and zebra finches, shy animals tend to associate with larger groups (Best et al., 2015; L. S. McCowan and Griffith, 2015), presumably because there is safety in numbers (Best et al., 2015). In contrast, shy three-spined sticklebacks (*Gasterosteus aculeatus*) associate with fewer individuals (Pike et al., 2008), and less exploratory great tits hold more peripheral (less central) positions within social networks in the wild (Aplin et al., 2013; Snijders et al., 2014), but maintain more stable social relationships (Aplin et al., 2013). Animal personality can also influence the nature of the social interactions that individuals experience, as exploratory behavior has been linked to aggression in several studies (reviewed in Sih et al., 2004). Additionally, boldness and aggression have been shown to be positively correlated with social dominance in a number of taxa (Dingemanse and de Goede, 2004; Drent et al., 1996; Favati et al., 2014). Finally, exploration has been positively associated with the degree of habitat exploration (e.g. van Overveld and Matthysen, 2010), which may impact the type and extent of social interactions that individuals experience. Investigating how differences in exploratory behavior correlate with the degree and nature of social interactions can give us a broader understanding of how behavioral heterogeneity at the individual level can influence the patterns of how groups of conspecifics interact with one another, i.e. the social structure or social network.

Overall, exploratory behavior has been linked to traits potentially relevant for both susceptibility to pathogens (e.g., stress hormone levels, which can cause immunomodulation) and the likelihood of individual exposure to pathogens (e.g., social behaviors, habitat exploration). Thus, this axis of personality has been associated with increased or decreased individual risk of some parasites and pathogens, although the relative roles of individual variation in susceptibility

versus exposure in driving these patterns are often difficult to discern (Barber and Dingemanse, 2010). In general, studies have found a positive relationship between individual boldness and parasite or pathogen risk: bolder or more exploratory individuals had higher ectoparasite loads than shy individuals in both Siberian chipmunks (*Tamias sibiricus*) and firebugs (*Pyrrhocoris apterus*) (Boyer et al., 2010; Gyuris et al., 2016), and bolder feral cats (*Felis catus* L.) and deer mice (*Peromyscus maniculatus*) showed higher seroprevalence of viral and bacterial pathogens, respectively (Dizney and Dearing, 2013; Natoli et al., 2005). In a study that tracked transmission using a labeled, inert bacterium (and thus isolated effects of exploratory behavior on exposure alone), bold female social spiders (*Stegodyphus dumicola*) had a higher risk of acquiring a cuticular bacterial species (Keiser et al., 2016). Effects of personality traits on susceptibility to parasites and pathogens are less well understood (reviewed in Lopes, 2017), but firebugs that mount stronger immune responses behave more boldly (Gyuris et al., 2016), and wild-caught greenfinches (*Carduelis chloris*) with a calmer coping style while in captivity mount stronger antibody responses to a novel antigen (Sild et al., 2011). The causative role of stress hormones in underlying personality-related differences in susceptibility to pathogens is challenging to unravel, but because stress hormones induce immunomodulation or suppression in many systems (reviewed in Demas et al., 2011), these hormones have the potential to significantly alter host susceptibility to pathogens. For example, a recent study on wild-caught Belding's ground squirrels (*Urocitellus beldingi*) found that experimentally blocking the actions of glucocorticoid receptors eliminated relationships between CORT levels and both exploratory behavior and a metric of innate immunity (Dosmann et al., 2015). Overall, exploration behavior may be an example of a trait that integrates phenotypic covariation in both the likelihood of exposure to pathogens (via behavioral differences) and susceptibility to infection once exposed (via physiological differences), with important population-level consequences for infectious disease dynamics (Hawley et al., 2011). Understanding how exploratory behaviors link to both inter-individual differences in exposure-relevant behaviors and physiology within a single study population will shed light on this possibility.

In this study, we explored the relationships between exploratory behavior, hormonal stress physiology, and social and foraging behaviors in wild house finches (*Haemorrhous mexicanus*). House finches are common songbirds found across North America, and form loose winter flocks during their non-breeding season (Altizer et al., 2004; Thompson, 1960a). House finches can be regularly observed competing for access to food, with more dominant individuals aggressively displacing subordinate individuals at feeders, as well as successfully defending their positions from challengers (Hawley et al., 2006; Thompson, 1960b). House finches also largely forage at backyard bird feeders during the non-breeding season, which make them an excellent species for tracking social and foraging behaviors at radiofrequency identification (RFID) equipped feeding stations. Furthermore, the use of bird feeders by house finches has been linked to the risk of transmission of a naturally occurring bacterial pathogen, *Mycoplasma gallisepticum* (Adelman et al., 2015b; Dhondt et al., 2007a; Hartup et al., 1998), that causes annual outbreaks in eastern North American house finch populations during the non-breeding season (Altizer et al., 2004). This pathogen causes conjunctivitis in house finches and is associated with reduced overwinter survival (Faustino et al., 2004), likely due to a reduced ability to find food or evade predators (Adelman et al., 2017). Individual house finches that spend more time on feeders are both more likely to acquire and spread *Mycoplasma gallisepticum* (Adelman et al., 2015b) which suggests that foraging behaviors are important for disease risk in this system.

We first examine whether exploratory behavior is linked to stress physiology in the house finch. To do this, we caught wild house finches during the non-breeding season and assessed baseline and stress-induced CORT concentrations for a subset of birds at capture. We then assayed their response to a novel environment 24 h after capture before

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