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

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Keywords

animal personality, corticosterone, exploratory behavior, social network, house finch (*Haemorrhous mexicanus*)

Disciplines

Animal Sciences | Behavior and Ethology | Ecology and Evolutionary Biology | Natural Resources Management and Policy

Comments

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**Exploratory behavior is linked to stress physiology and social network
centrality in free-living house finches (*Haemorhous 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.

Keywords: animal personality, corticosterone, exploratory behavior, social network, house finch (*Haemorrhous mexicanus*)

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 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 is 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 (*Haemorhous 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 hours after capture before banding, marking, and releasing them. In line with the patterns found in many species of songbirds, we predicted that more exploratory house finches would have lower baseline and stress-induced CORT concentrations than less exploratory conspecifics. We then test whether exploratory behaviors in wild house finches is linked to inter-individual variation in foraging behaviors, aggressive behaviors, and social network metrics. Because exploratory behavior could be linked to movement across the landscape or to risk-taking behaviors (e.g. Quinn et al., 2011; Stuber et al., 2013) such as foraging at feeders in open habitat (Dunn and Tessaglia, 1994), we predicted that more exploratory house finches would visit more unique feeders in our study population. We also predicted that exploratory birds would spend more overall time on bird feeders than less exploratory birds, either due to functional linkages between boldness and energetic requirements (Careau et al., 2008), or because bolder songbirds typically have higher social dominance (e. g. David et al., 2011; Drent et al., 1996; Favati et al., 2014), which should allow bolder individuals greater access to bird feeders. Similarly, because exploration has been positively correlated with aggression in several taxa (e.g. Huntingford, 1976; Sih et al., 2004; Verbeek et al., 1996), we predicted that more exploratory birds would engage in more aggressive interactions than less exploratory birds. Lastly, as has been shown in great tits (Aplin et al., 2013), we predicted that more exploratory birds would hold a more central position within social networks (e.g. interact with more individuals, engage in more interactions, etc.) in the wild than less exploratory birds.

Materials and Methods

Field Captures

Wild house finches (n=184) were captured between October 2012 and March 2013 on and around the Virginia Tech campus in Blacksburg, VA. We trapped twice per week throughout this time period, rotating through six field sites so that each site was trapped at once per week. The six sites were located within close enough proximity of each other that finches could feasibly visit all of the locations (maximum distance between feeders = 2.3 km). One tube-shaped bird feeder was installed at each of our field sites for the duration of our field season. All birds were caught using wire traps suspended around bird feeders or mist nets placed in close proximity of bird feeders. Because both CORT levels and behavior are influenced by *M. gallisepticum* infection in house finches (Love et al., 2016), we did not include any of the 18 birds (out of 184 individuals in total) that were caught with clinical signs of mycoplasmal conjunctivitis in either the CORT, or exploratory behavior studies.

Quantification of circulating corticosterone concentrations

We quantified the concentrations of circulating CORT in a subset of 20 birds captured during our field season for which we were able to obtain both a baseline and stress-induced blood sample. Because not all of the 20 birds that we obtained CORT samples for remained in the social network for long enough (≥ 7 days) to be included in the field study (see below), there is very small overlap (n=8) in the individuals for which we had CORT, exploratory behavior, and social network data on. Thus, the two overarching research questions (how CORT relates to exploratory behavior, and how exploratory behavior relates to social and feeding behaviors) were analyzed separately using largely distinct individuals.

For birds bled for CORT, initial blood samples were taken within three minutes of entry into the trap or net to quantify baseline CORT concentrations, and a subsequent blood sample was taken at 30 minutes post-capture to quantify stress-induced CORT concentrations (Romero and Reed, 2005). Blood was collected by puncturing the brachial vein with a sterile 26-gauge needle, and then collecting the pooled blood (~50-100 microliters) using a heparinized capillary tube. Samples were stored on ice for up to six hours until centrifugation and plasma extraction. Plasma was stored at -20°C. CORT concentrations were quantified using direct radioimmunoassay following extraction in re-distilled dichloromethane (Bonier et al., 2011). We used the corticosterone antibody from Esoterix Endocrinology (catalogue number B3-163) and labeled corticosterone from New England Nuclear Research Products (catalogue number NET-399). Samples were corrected individually for extraction efficiency, and average extraction efficiency was 72.0%. Within-assay variation among four known-concentration standard samples was 9.65%, and the detection limit was ~1.4 ng/ml.

Temporary Housing

Immediately following capture, all birds were fitted with a United States Geological Survey aluminum band stamped with a unique ID number, determined the sex of each bird through their sexually dimorphic plumage, and several morphometric measurements were taken (mass, wing length, tarsus size, and pectoral muscle index—a metric of the robustness of the pectoralis major relative to the carina of the sternum, where each bird was assigned a score from 1-4 with larger numbers indicating more muscle volume (Gosler, 1991). A blood sample was taken from all individuals before being temporarily housed, but only the individuals for which we were able to obtain a blood sample within three minutes of capture were included in the CORT study. Following processing, all birds were temporarily housed within an indoor animal

care facility on the campus of Virginia Tech for approximately 24 hours. Birds were held individually in visually isolated small cages (46 x 46 x 76cm) and provided *ad libitum* food and water. All birds were housed in the same indoor room at a constant light cycle (12L:12D) and temperature (22-24°C). Individuals captured with clinical signs of mycoplasmal conjunctivitis (swelling, redness, or exudate in either eye) were not held overnight to avoid contaminating the novel environment arena. All such individuals were released at the site of capture after banding and processing (see below) and were not included in this study.

Response to Novel Environment

After temporary overnight housing (as per Aplin et al., 2013), we placed each bird (n=52) individually into a small wooden refuge (25.4 x 25.4 x 25.4cm), placed the refuge inside a novel environment arena, and left the room. After approximately five minutes within the refuge, a sliding door on the refuge was remotely opened using a pulley system, allowing the bird access to the closed observation arena (2 x 2.3 x 2.6m). The observation arena contained five identical wooden trees, each with four branches of varying heights (as per Verbeek et al., 1994). A video camera located just outside of the arena recorded the behavioral response of each bird for 15 minutes to quantify exploratory behavior via response this novel environment (Verbeek et al., 1994).

To quantify behavioral response to a novel environment, the following non-independent behaviors were quantified and incorporated into a principal components analysis (as per Dingemanse et al., 2002): latency to exit the refuge, latency to perch on first tree, number of trees visited, number of inter-tree flights, total number of flights, number of inter-perch hops, number of unique perch visits, total number of perch visits, number of refuge returns, and the number of times the bird perched on any other surface other than a tree or perch (mesh

boundaries of observation arena, etc.). Principal components analysis of behavioral response to a novel environment was performed using R (R Development Core Team, 2014, see analysis below).

Banding, PIT Tagging, and Release

After completing the novel environment assay, all birds were given a unique combination of color bands, and fitted with a passive integrative transponder (PIT) tag. Each 0.1-gram PIT tag was fastened to the color bands on the right leg using colored electrical tape (as per Bonter et al., 2013). Birds then had their conjunctiva swabbed for a separate study (Adelman et al., 2015b) and were released at their site of capture.

Monitoring Behavior of PIT-Tagged Birds

At each of our field sites, we placed bird feeders equipped with Radio Frequency Identification (RFID) reading technology to monitor the social and foraging behavior of PIT-tagged birds at our feeders (as per Aplin et al., 2013; Bridge and Bonter, 2011). Each tube-shaped feeder had two ports, each with an RFID antenna affixed below the perch. These antennas, which functioned independently of one another, logged the presence of PIT-tagged birds at a resolution of one data point per second. This allowed us to collect data on the social interactions between PIT-tagged individuals, as well as feeding behaviors at RFID-equipped feeders from November 11th, 2012 through March 5th, 2013. We estimate that we PIT-tagged approximately 49% of the population (Adelman et al., 2015b).

Extracting Behavioral Metrics Using Radiofrequency Identification Data

We extracted three categories of behavioral metrics: social network metrics, aggressive interactions, and foraging behaviors, all of which have been shown to predict disease

transmission in house finches and/or other taxa (e.g. Barber and Dingemanse, 2010; Hamede et al., 2013; and MacIntosh et al., 2012, respectively), and are measurable using RFID technology. To test whether exploratory tendencies predicted a bird's relative centrality within a social network, we used the methods described in Adelman et al. (2015b) to construct foraging a network from our RFID data based on patterns of co-occurrence in foraging flocks (Psorakis et al., 2015, 2012) at our RFID-equipped feeders using the R package *asnipe* (Farine, 2013; Farine and Whitehead, 2015). Even though we only had exploration data from a subset of birds in our population (n=52), we used all birds in our population detected at RFID feeders (n=117) when constructing our social networks. Edges in our network were defined using the simple ratio index, or the probability of observing two individuals together given that one was observed. We used these networks to determine the two most commonly used social network metrics for each bird: weighted degree (a measure of an individual's direct or local connectedness, integrating both the abundance and strength of direct interactions with conspecifics) and eigenvector centrality (a measure of an individual's connectedness within a network, quantified as the sum of the centralities of each node to which an individual is connected; MacIntosh et al., 2012) using the *sna* package for R (Butts, 2014). More connected birds, or birds that are more central to the social networks, will have higher weighted degree and eigenvector centrality scores.

Aggressive inter-individual interactions at the feeder were inferred by quantifying each time two individuals were logged at the same feeder port within a two-second window of one another, suggesting that an aggressive displacement event occurred. This "two-second rule" was validated through video analysis. Using video cameras set up at bird feeders in the field, we recorded 9.6h of footage at four sites on two dates (25 January, 2013 and 1 February, 2013). From these videos we observed 175 instances in which one house finch arrived at a feeding port

within 2s of another departing. On all 175 occasions, the arriving finch exhibited aggression, defined as “a rapid movement...made directly at the other bird” (Adelman et al., 2015a).

Because not every individual was banded and not all color band combinations were identifiable on the videos, we cannot be entirely certain how many different individuals participated in these interactions. However, we estimated a minimum number of unique individuals, using several highly conservative assumptions. At each site on each day, we assumed that 1) every unbanded male was the same individual, 2) every unbanded female was the same individual, and 3) among banded birds, every individual of the same sex that shared even one color band in common was the same individual. Based on these strict assumptions, a minimum of 44 different individuals participated in these interactions.

To measure social dominance, for each inferred aggressive interaction, a bird was considered the winner if it displaced another individual; a bird was considered the loser if it was displaced by another individual. From these data, we calculated social dominance as each bird's Elo score. This score ranks each bird in terms of its propensity to displace others, be displaced by others, and the hitherto relative ranks of both individuals involved in the interaction, resulting in a larger score for more dominant birds and vice-versa (Neumann et al., 2011; Sánchez-Tójar et al., 2017). Elo score was computed in the AniDom package for R (Sánchez-Tójar et al., 2017). Finally, we used RFID data to extract two metrics of foraging behaviors in the wild. First, we quantified the average amount of time individuals spent on the feeders per day, because this behavior has been shown to predict the spread of *M. gallisepticum* in house finches (Adelman et al., 2015b). Second, we examined the average number of different bird feeders an individual visited per day, because this could be a relevant metric of spatial exploration in the wild. As the maximum distance between feeders was 2.3 km, which is below the maximum daily distance

traveled by free-living house finches between roost and foraging locations (Dhondt et al., 2007b), individual birds could potentially travel among multiple feeders throughout the course of a day.

Statistical Analyses

Exploratory Behavior

We used principal component analysis in R (R Development Core Team, 2014) to describe variation in the many non-independent behaviors we measured in response to the novel environment assay. All birds included in the CORT and Exploratory Behavior study and/or the Exploratory Behavior and Field Behaviors studies were included in this analysis (n=64). The first two principal components together explained 71.5% of the observed variation in behavioral response to a novel environment. Principal component 1 (PC1; *Exploration*), which explained 52.8% of variation, was essentially a metric of the amount of exploration, and was positively correlated with the number of unique perches visited, the number of trees visited, number of flights, total number of perch visits, and number of inter-perch hops (Table 1). Principal component 2 (PC2; *Exploration Latency*), which explained 18.7% of variation, was a metric of latency to explore and proclivity for sitting on the ground. PC2 was positively correlated with latency to exit the refuge and latency to perch on the first tree, as well number of visits to the ground. PC2 was negatively correlated with the number of times a bird perched on an object other than a tree or perch.

Corticosterone and Exploratory Behavior

We used general linear models in R (R Development Core Team, 2014) to assess relationships between stress physiology and response to a novel environment. The dependent

variable was either *Exploration* (PC1), or *Exploration Latency* (PC2). Our predictor variables were baseline CORT concentrations and stress-induced CORT concentrations, and we included several potential relevant covariates in each initial model (sex, mass, and pectoral muscle index). Initial models included all pairwise interactions, but interactions that were not significant at an alpha level of 0.05 were removed from the final model. Mass did not significantly predict either PC1 or PC2, and thus, was not included in the final models.

Exploratory Behavior and Field Behaviors

We tested whether exploratory behavior in a novel environment was related to two metrics of social network position. Because of issues with non-independence in network data, standard statistical practices are not suited analyses of animal social networks (Croft et al., 2011; Farine and Whitehead, 2015). We therefore used randomization tests to assess relationships among exploratory behaviors and social network metrics in the field. First, using our observed social networks, we fit separate general linear models in R (R Development Core Team, 2014) for weighted degree and eigenvector centrality. Although all observed birds (including 62 PIT-tagged birds for which we did not have novel environment assay data) were included in developing the network, only birds with ≥ 7 days of RFID data ($n=52$) were included in these analyses to exclude transient individuals for which we lacked repeated observations (Adelman et al., 2015b). Our initial predictor variables were *Exploration* (PC1), *Exploration Latency* (PC2), sex, and the two-way interactions with sex. To determine whether each of these parameters significantly predicted the dependent variable, we conducted 25,000 permutations of our network in the *asnipe* package in R (Farine and Whitehead, 2015; Farine, 2013), generating an increasingly random set of networks following the permutation procedure described by Bejder et al. (1998) and restricting swaps to happen within feeder within day. We then ran the same

general linear models as above on each of these networks, generating a null distribution for each parameter estimate. If a given variable's parameter estimate from our observed network fell outside of the 95% range of the estimates from the random networks, the effect of that variable was considered significant. P values calculated using randomizations are denoted P_{rand} . Interactions not meeting the significance criterion were removed from the models by backwards elimination.

To determine whether exploratory behaviors were related to other behaviors in the field, we performed general linear models in R (R Development Core Team, 2014). As above, only birds with ≥ 7 days of RFID data ($n=52$) were included in these analyses. The dependent variables examined were: aggressive interactions per day and relative social dominance (metrics of aggressive behavior), and time spent on feeders per day and the number of unique feeders visited per day spent within the study area (metrics of foraging behavior). We defined the number of days spent within the study area as the total number of days elapsed from an individual's first detection at an RFID-equipped feeder, to its last detection. Our predictors were Exploration (PC1) and Exploration Latency (PC2), and sex was included as a fixed effect in all models. Our aggression analysis also included each individual's average number of feeding bouts per day as an additional covariate. Initial models included all pairwise interactions, but interactions that were not significant at an alpha level of 0.05 were removed from the final model.

Permits

Both studies were conducted under the following permits: Virginia Tech Institutional Animal Care and Use Committee, Virginia Department of Game and Inland Fisheries (038781

and 044569), United States Fish and Wildlife Service (MB158404-1), and United States Geological Survey Bird Banding Lab (23513).

Results

Circulating corticosterone concentrations and exploratory behavior

We found that baseline CORT concentrations at capture, as well as pectoral muscle index, significantly predicted the extent of exploration in the novel environment assay. In contrast to our prediction, house finches that had higher baseline CORT concentrations exhibited more exploratory behaviors (aka had higher *Exploration* values (higher PC1) in our novel environment assay; baseline CORT: $\beta=0.78\pm0.24$, $F_{1,16}=7.56$, $P=0.015$) (Figure 1). Additionally, we found that finches that had a higher pectoral muscle index exhibited more exploratory behaviors (higher PC1) than birds with lower pectoral muscle index (pectoral muscle index: $\beta=3.09\pm1.31$, $F_{1,16}=5.56$, $P=0.032$). Stress-induced CORT concentrations (sample taken 30 minutes post-capture) did not significantly predict individual responses to a novel environment (stress-induced CORT: $\beta=-0.023\pm0.025$, $F_{1,16}=0.059$, $P=0.81$). For the subset of birds included in our CORT study, sex did not significantly predict *Exploration* in our novel environment assay (sex: $\beta=-0.19\pm1.00$, $F_{1,16}=0.035$, $P=0.85$).

Exploration Latency (PC2) was not significantly predicted by either baseline or stress-induced CORT concentrations (baseline CORT: $\beta=-0.003\pm0.17$, $F_{1,16}=0.00$, $P=0.98$; stress-induced CORT: $\beta=-0.034\pm0.017$, $F_{1,16}=3.89$, $P=0.067$). In contrast to results for *Exploration*, pectoral muscle index did not significantly predict *Exploration Latency* ($\beta=-1.24\pm0.91$, $F_{1,16}=1.87$, $P=0.19$). Sex predicted *Exploration Latency* in the subset of birds assayed for CORT

concentrations ($\beta=1.49\pm 0.69$, $F_{1,16}=4.65$, $P=0.048$), with males showing lower exploration latency than females.

Exploratory behavior and feeding behaviors in the wild

Throughout our study, we recorded a total of 79,079 feeding bouts at our RFID-equipped feeders. The 52 individuals for which we have both exploratory behavior and ≥ 7 days of RFID data were responsible for 53,011 of these bouts. Overall, response to a novel environment did not predict foraging behaviors in free-living house finches. *Exploration* (PC1) was not associated with the average time (in minutes) individuals spent on bird feeders per day ($\beta=-0.029\pm 0.55$, $F_{1,51}=0.003$, $P=0.96$), nor was *Exploration Latency* (PC2) ($\beta=-1.32\pm 0.91$, $F_{1,51}=2.12$, $P=0.15$). Sex was also not a significant predictor of average time spent on feeders per day ($\beta=-2.54\pm 2.44$, $F_{1,51}=1.08$, $P=0.30$).

The birds for which we have both exploratory behavior and ≥ 7 days of RFID data visited a mean of 0.078 feeders per day within the study area (minimum=0 feeders, maximum=3 feeders). *Exploration* (PC1), *Exploration Latency* (PC2), and sex were not significant predictors of the average number of feeders that house finches visited per day (PC1: $\beta=-0.009\pm 0.005$, $F_{1,51}=3.21$, $P=0.080$; PC2: $\beta=-0.003\pm 0.009$, $F_{1,51}=0.126$, $P=0.72$; Sex: $\beta=0.00\pm 0.023$, $F_{1,51}=0.00$, $P=0.99$).

Exploratory behavior and aggression in the wild

The number of feeder visits an individual made per day was a strong predictor for the average number of aggressive interactions an individual experienced (as an initiator or a receiver) per day ($\beta=0.11\pm0.011$, $F_{1,50}=104.05$, $P<0.001$). However, we found no relationship between *Exploration* (PC1), *Exploration Latency* (PC2), or sex and the number of aggressive interactions per day at our RFID equipped feeders (PC1: $\beta=0.075\pm0.048$, $F_{1,50}=2.48$, $P=0.122$; PC2: $\beta=-0.035\pm0.082$, $F_{1,50}=0.18$, $P=0.68$; Sex: $\beta=-0.063\pm0.21$, $F_{1,50}=0.089$, $P=0.77$). Furthermore, *Exploration* (PC1) and *Exploration Latency* (PC2) were not positively correlated with Elo score, a measure of relative social dominance at bird feeders (PC1: $\beta=2.13\pm1.86$, $F_{1,50}=1.31$, $P=0.26$; PC2: $\beta=-1.25\pm3.23$, $F_{1,50}=0.15$, $P=0.70$). While not significant, females tended to have lower Elo scores, and thus be less dominant than males ($\beta=-16.37\pm8.33$, $F_{1,50}=3.86$, $P=0.055$).

Exploratory behavior and social network metrics in the wild

Our permutation analyses detected significant effects of both *Exploration* and *Exploration Latency* on weighted social network degree in the wild. The effects of *Exploration* (PC1) were sex-specific (sex(F) x PC1: $\beta=0.018\pm0.049$, $P_{\text{rand}}=0.028$). The positive relationship between *Exploration* (PC1) and weighted degree, indicating that more exploratory house finches interacted with more unique conspecifics than less exploratory house finches, was stronger for females ($\beta=0.062$) than it was for males ($\beta=0.044$) (Figure 2). The main effect of sex was also significant in our model, with female house finches having a higher weighted degree ($\beta=0.069\pm0.086$, $P_{\text{rand}}=0.0003$). A significant relationship between *Exploration Latency* (PC2) and weighted degree was present for both sexes: consistent with our prediction, birds that

exhibited higher exploration latencies (higher PC2 = less exploratory) had lower weighted degrees ($\beta=-0.04\pm 0.034$, $P_{\text{rand}}=0.004$).

Neither *Exploration* (PC1) nor *Exploration Latency* (PC2) significantly predicted eigenvector centrality in the wild (PC1: $\beta=0.10\pm 0.13$, $P_{\text{rand}}=0.28$; PC2: $\beta=0.23\pm 0.22$, $P_{\text{rand}}=0.37$). Furthermore, sex did not significantly predict eigenvector centrality ($\beta=-0.47\pm 0.56$, $P_{\text{rand}}=0.24$). However, our certainty about these social network results, and eigenvector centrality in particular, are reduced by our sample size. In small social networks, or those containing few individuals, most individuals will have similar connections when combining their direct connections with those of their associates (as occurs with eigenvector centrality).

Discussion

Our results suggest that exploratory behavior in a novel environment is linked to both stress physiology and the patterns of social interaction with conspecifics in free-living house finches. We found that baseline CORT concentrations were positively associated with *Exploration* (PC1) in a novel environment, linking stress physiology to exploratory behaviors in this system. Additionally, we found links between exploratory behaviors and social network metrics, as *Exploration* (PC1) and *Exploration Latency* (PC2) both predicted weighted degree in the wild (though for PC1, the pattern was stronger in females than in males). However, we were unable to show a direct link between circulating CORT concentrations and social network metrics in the wild due to the small number of birds ($n=8$) for which we had sufficient data on both CORT concentrations and social behaviors in the field. Nevertheless, our data suggest a possible link between individual physiology and the ways in which individuals interact with one

another at the group level, mediated through inter-individual behavioral variation in free-living house finches. Thus, our study contributes to a broader understanding of the ecological consequences of individual variation in physiology and behavior.

We found that baseline circulating CORT concentrations predicted the extent of exploration of a novel environment in house finches. However, in contrast with our predictions and previous work done with great tits (Baugh et al., 2013; Stöwe et al., 2010), more exploratory birds (as measured by PC1) had higher baseline CORT concentrations than less exploratory birds at the time of capture. Although not statistically significant ($p=0.067$), birds that were slower to explore the novel environment (i.e., birds with lower PC2 values) tended to have higher stress-induced CORT levels than fast-exploring individuals, which is consistent with prior studies in songbirds (Atwell et al., 2012; Baugh et al., 2013, 2012; Carere et al., 2010; Lendvai et al., 2011). Because our small sample sizes for the CORT component of the study ($n=20$) may have limited our ability to detect significant relationships between stress-induced CORT and exploratory behavior, future studies with greater samples are needed to assess whether stress-induced levels of CORT are also associated with exploratory behavior in house finches. Further study is also needed to determine why the patterns we detected between baseline CORT concentrations and exploratory behaviors in free-living house finches differ from those of great tits, which have otherwise similar social systems during the non-breeding system.

Overall, our results suggest that exploratory behavior and stress hormone physiology are linked in house finches. However, because our study was observational, we are not able to establish a causal relationship between CORT concentrations and exploratory behavior. It is possible that birds with higher baseline CORT are able to better mobilize their energy stores, allowing them to engage in more exploratory behaviors. It is also possible that higher energy

mobilization could lead to an increased requirement for food intake, necessitating more exploratory behaviors in search of potential food sources. Although our data cannot distinguish between these and other non-mutually exclusive possibilities, we found that birds with higher pectoral muscle index exhibited more exploratory behaviors during the novel environment assay. This suggests that the relationship between CORT and exploratory behavior may be mediated in part by differences in body condition. We did not find any evidence that CORT was directly associated with pectoral muscle index in our study, but our sample sizes may have been insufficient to detect such relationships. Overall, experimental studies are needed to confirm any causation underlying the detected links, and thus to better understand the physiological mechanisms driving variation in individual exploration behavior.

We also found that exploratory behaviors were predictive of the degree of interaction with conspecifics in the wild. House finches that exhibited more exploratory behaviors in response to a novel environment (higher PC1) had a higher weighted social network degree in the wild, but this relationship was stronger for female house finches. The positive relationship between exploration and weighted degree is consistent with our prediction and with past studies on great tits (Aplin et al., 2013; Snijders et al., 2014). However, further work is needed to determine why exploration was not as strongly linked to network degree in male house finches. Past work suggests that sexual selection could be a driver of network metrics for male house finches, but that study did not include female house finches (Oh and Badyaev, 2010), while ours did. For our other metric of exploratory behavior, *Exploration Latency*, we found that house finches that were slower to explore the novel environment had significantly lower weighted degree, and this pattern was not influenced by sex. This suggests that, as has been shown in great tits (Aplin et al., 2013; Snijders et al., 2014), birds that are very slow to begin exploring (or never

leave the refuge) during the novel environment assay interact significantly less often with unique conspecifics in the wild. Overall, our results indicate that both *Exploration* and *Exploration Latency* are linked with social network centrality in free-living house finches. Because there is increasing evidence that network centrality can influence disease transmission across a range of taxa (e.g. Bull et al., 2012; Drewe, 2010; Fenner et al., 2011; Keiser et al., 2016; Vanderwaal et al., 2013), exploratory house finches may be at higher risk of acquiring some directly-transmitted pathogens.

Surprisingly, neither relative social dominance (measured using Elo scores) nor the rate of aggressive interactions was significantly tied to exploration activity in our study. This unexpected result contrasts with behavioral patterns found in both great tits (e.g. Dingemanse and De Goede, 2004; Verbeek et al., 1996) and zebra finches (David et al., 2011), wherein more exploratory birds initiate and win more agonistic interactions than less exploratory birds. The discrepancy between our findings and those in other songbird species may be a result of the limitations inherent in using RFID-equipped feeders to measure social dominance and aggressive interactions. First, the only social dominance or agonistic interactions that can be inferred from RFID data are those in which a bird sitting on the feeder is successfully displaced by a more dominant bird, which we define as a unique bird being detected within two seconds of the prior bird's departure. Our definition of an aggressive interaction thus excludes instances where, for example, very shy or subordinate birds readily departed the feeder at any sign of approach made by a dominant conspecific. Second, our RFID data cannot identify instances where a bird sitting on the feeder is challenged by another, but asserts its dominance and does not abandon its position. Thus, our approach likely excludes interactions between dyads that include a very dominant or very subordinate bird. This combination of factors could truncate the variability of

social interactions that we were able to observe via RFID at both extremes of the social status spectrum. However, these limitations are likely to be outweighed by our ability to record many agonistic interactions over long periods of time by using automated technology, and the fact that relatively few observations are required to quantify robust dominance hierarchies (Sánchez-Tójar et al., 2017).

Finally, we predicted that more exploratory birds, which readily moved around and explored a novel environment, would move across the landscape more readily and visit more unique bird feeders per day. However, our data did not show a significant link between exploratory behaviors in a novel environment and the number of feeders used in the wild. It is possible that our feeders were placed far enough apart that we were not able to detect subtle variation in feeder use across a landscape, as the median number of feeders used by a bird in our study was two. Additionally, the use of bird feeders across a landscape could be determined at the flock level rather than at the individual level, thus obscuring differences in exploratory behaviors among individuals within a flock. Finally, exploratory behavior was also not a significant predictor of the amount of time that house finches spent on feeders, a behavior that has been shown to influence disease dynamics for house finches in the past (Adelman et al., 2015b). Together, these results suggest that exploratory behavior in free-living house finches does not predict inter-individual variation in how birds interact with feeders.

Conclusions

Our study highlights the importance of examining connections between individual physiology and behavior for understanding how these influence group-level dynamics, and in turn could potentiate population processes, such as disease transmission. Together, our results suggest that exploratory behavior may be linked to both behavioral and physiological traits

important for susceptibility to directly-transmitted pathogens. However, we did not find a link between exploratory behavior and the feeding behaviors that have been previously shown to influence transmission of *Mycoplasma gallisepticum*, a major pathogen of house finches. While our results suggest that exploratory behavior may not shape the likelihood of a house finch acquiring *M. gallisepticum*, the links between stress physiology, exploratory behavior, and the degree of direct interactions with conspecifics could work in concert to influence the dynamics of diseases transmitted primarily through social interactions.

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Tables and Figures

Table 1. Loading values for the two principal components used as measures of *Exploration* (PC1) and *Exploration Latency* (PC2).

Behavior	PC1 (‘Exploration’)	PC2 (‘Exploration Latency’)
Latency to Exit Refuge (s)	-0.48*	0.73*
Latency to First Tree	-0.60*	0.67*
Number of Trees Visited	0.94*	-0.03
Total Number of Flights	0.89*	0.21
Inter-Perch Hops	0.80*	0.37
Number of Unique Perches Visited	0.94*	0.17
Total Number of Perch Visits	0.89*	0.38
Number of Visits to Non-Perch	0.40*	-0.56*
Number of Ground Visits	0.13	0.19

*Significant loading values (values ≥ 0.4)

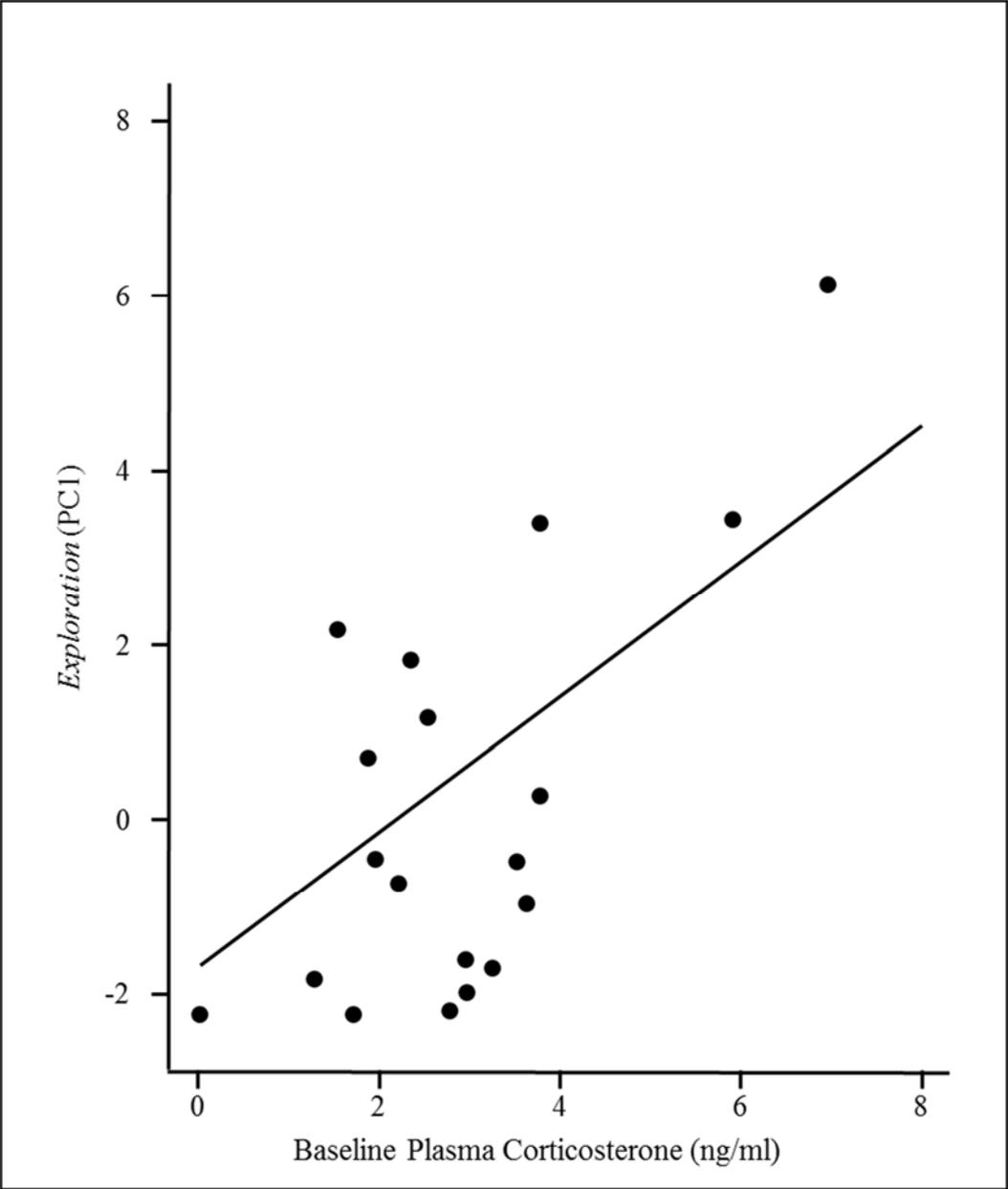


Figure 1. House finches with higher circulating baseline corticosterone concentrations at capture exhibited higher *Exploration* (PC1) in a novel environment assay, when accounting for pectoral mass index.

