

EXPLORATORY BEHAVIOR OF FOREST BIRDS AND THE INFLUENCE OF TUFTED
TITMOUSE (*BAEOLOPHUS BICOLOR*) ANTI-PREDATOR VOCALIZATIONS

By

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To my family

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TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS.....	4
LIST OF TABLES.....	7
LIST OF FIGURES.....	8
ABSTRACT	9
CHAPTER	
1 INTRODUCTION	12
2 INTERSPECIFIC DIFFERENCES IN EXPLORATORY BEHAVIORS AMONG FOREST BIRDS	15
Introduction	15
Intra-specific Variation in Exploratory Behavior	15
Neophobia and Interspecific Assessments of Exploration and Personality	18
Interspecific Characterization of Exploratory Behavior	20
Study System.....	21
Research Design	23
Objectives and Experimental Design.....	23
Predictions.....	24
Methods	25
Capture and Handling	25
Testing protocol.....	26
Measuring Exploratory Behaviors.....	27
Statistical Analysis.....	28
Results.....	29
Interspecific Comparison	29
Foraging Guild Comparison.....	30
Social Group (Flocking Behavior) Comparison.....	30
The Performance of Exploratory Score versus Component Behaviors	31
Discussion	31
Measuring Exploratory Behavior	31
Social Roles and Exploratory Behavior	34
Behavior Syndromes, Neophobia and Exploration	37
Flexibility, Plasticity, or Behavioral Diversity in a Changing World	39
3 TUFTED TITMOUSE (<i>BAEOLOPHUS BICOLOR</i>) ANTI-PREDATOR VOCALIZATIONS ALTER HETEROSPECIFIC EXPLORATORY BEHAVIOR	57
Introduction	57
Animal Ecology and Information-driven Decision-making	57

Social Information and Its Influences.....	57
Using Social Information to Navigate Landscapes of Fear.....	59
Study System.....	61
Research Design	63
Objectives and Experimental Design.....	63
Predictions.....	64
Methods.....	65
Capture and Handling	65
Playback Treatments.....	65
Testing Protocol and Exploratory Behavior Measurements.....	66
Statistical Analysis.....	67
Results.....	68
Temporal Patterns in Movement Types.....	68
Temporal Patterns in Thoroughness of Exploration	69
Temporal Patterns in Scanning Behavior	69
Discussion	70
Interspecific Social Cues with Known Information Content.....	70
Exploratory Behavior under Socially Conveyed Threat of Predation	71
Information, Spatial Behavior and Future Implications	73
4 CONCLUSION.....	81
LIST OF REFERENCES	87
BIOGRAPHICAL SKETCH.....	101

LIST OF TABLES

<u>Table</u>	<u>page</u>
2-1	List of components of exploratory behavior, their definitions/ measures and how data were transformed for analysis. 48
2-2	Mean and coefficients of variation (CV) of 8 component exploratory behaviors for 6 species..... 49
2-3	Comparison among species and between groups based on each component of exploratory behavior 50
2-4	Results of Kendall’s Tau-b Correlation Analysis between component behaviors and body size..... 51
2-5	Tukey Test results for between-species comparison. WEVI = white-eyed vireo, CACH = Carolina chickadee, TUTI = tufted titmouse, CAWR = Carolina wren, NOCA = Northern cardinal, and EATO = Eastern towhee. MD = Mean Difference = Spp 1 – Spp 2. 52
2-6	Factor loadings of the 8 component behaviors on the 2 principal components. Eigenvalues and amount of variance explained by the respective components are given at the bottom. MAN(C)OVA results are shown in the bottom two panels. 54
2-7	Structure coefficients/ discriminant loadings of the 8 component behaviors on the function(s) from canonical discriminant function analysis of the different group comparisons. Eigenvalues and amount of variance explained by the respective components are at the bottom..... 55
2-8	Foraging behavior of 6 species based on different references. 56
3-1	Prediction of influence of 4 different vocalization trials through time. Sign → means no changes at all, ↓ means decreasing, and ↑ means increasing. The number of signs indicates the strength of the influence..... 79
3-2	Factor loadings of the 8 component behaviors on the 3 principal components after varimax rotation. Eigenvalues and amount of variance explained by the respective components are given at the bottom. MANOVA results from these three principal components for different comparisons are shown in the bottom panel..... 80

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1	The design of the testing cage (novel environment). The releasing cage, covered by camouflage fabric, is in the lower left corner. The tripod (at right) held the video camera set to record all behaviors inside the cage. One perch (of 5: see Figure 2-2) is visible inside the cage..... 42
2-2	The assignment of volume within the cage into 27 cubes (9 ground calls × 3 strata) for exploration by test subjects. Perching substrates (sticks) intercepted a total of 21 of the 27 total volume cells..... 43
2-3	Results of the discriminant function analysis for (A) species (1 st two discriminant functions used; WEVI = white-eyed vireo, CACH = Carolina chickadee, TUTI = tufted titmouse, CAWR = Carolina wren, NOCA = Northern cardinal, and EATO = Eastern towhee), (B) foraging guilds, and (C) flocking groups showing, for each, the two component behaviors with the highest weights on the single discriminant function generated. The factor loadings for DF analyses are listed in Table 2-4..... 44
2-4	Scatter plots of mean coefficients of variation (CV) across all 8 component behaviors vs. (A) max. latitudinal range (degrees) in geographical distribution, (B) max. longitudinal range (degrees) in geographical distribution, and (C) ratio of insect to plant food types in the diet of each species. In Panels A and B, the assumption is that generalists are on the right side, and in Panel C, they are on the left side. WEVI = white-eyed vireo, CACH = Carolina chickadee, TUTI = tufted titmouse, CAWR = Carolina wren, NOCA = Northern cardinal, and EATO = Eastern towhee. 46
3-1	Bar graphs showing changes in 8 components of exploratory behaviors over the three trial periods (before, during and after broadcasting) for each treatment (control, low-risk mobbing, high-risk mobbing, and seet call): (A) flight number, (B) hop number, (C) prop. of perches explored, (D) prop. of ground explored, (E) active scan number, (F) average active scanning time, (G) still scan number, and (H) average still scanning time. Bars show mean values with 95% confidence intervals. 76
3-2	The relationship among social information, animal behavioral ecology, and functional connectivity. 78
4-1	Linking knowledge from this study to future researches and application goals. . 86

Abstract of Thesis Presented to the Graduate School
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Exploratory behavior is the gathering of information about objects or other aspects of the environment not reflected in the satisfaction of immediate needs. Exploratory behavior is heritable and repeatable, and has a strong connection with animal personality, or behavior syndromes. The first goal of my study was to increase understanding of how bird species differ in their exploratory behavior based on their natural history characteristics (e.g., foraging guilds and social roles; Chapter 2). Additionally, I applied a novel multivariate approach to characterizing interspecific exploratory behavior not previously used, that increases the level of detail with which exploratory behavior can be analyzed. Second, I tested whether and how heterospecific social information concerning predation risk may influence exploratory behavior (Chapter 3).

In the first experiment, I recorded the exploratory behavior exhibited by 6 different forest bird species in 10 minute trials inside a novel testing cage. Different species showed different patterns across eight component behaviors of exploration that I identified and measured on each individual. Interspecific differences were generally related to natural history characteristics (foraging guild and social roles in winter

foraging flocks). In discriminant function analysis, foraging guild (species grouped into either insectivore lower-canopy / shrub gleaner vs. omnivore ground gleaner) allowed a 72.8% correct classification of the species; insectivores exhibited longer active scanning times while omnivores tended to explore a higher proportion of the ground inside the cage. When species were classified as either winter foraging flock participants or non-flocking species, discriminant function analysis achieved 96.3% correct classification. Species attending mixed-species foraging flocks in winter used flight in exploration, whereas non-flocking species stayed on the ground to explore. A multivariate approach based on the 8 component behaviors I identified was more useful in describing interspecific differences in exploratory behavior than a single exploratory score that has been used most commonly to characterize intraspecific variation in exploratory behavior.

In a second experiment, I tested whether and how social information cues (predation threat encoded in anti-predator vocalizations of the tufted titmouse, *Baeolophus bicolor*) influence the exploratory behavior of Northern cardinals (*Cardinalis cardinalis*). Both species are common and widely distributed in Eastern North America, and titmouse anti-predator calls encode highly specific types of information concerning predation risk, that cause anti-predator behaviors in a variety of taxa. I determined socially derived information (titmouse anti-predator calls) encoding known predation information influenced exploration and movement in the Northern cardinal. Cardinals interpreted the anti-predator signals encoded in the calls I broadcast to them correctly and responded accordingly via adjusting their activities in the novel environmental cage. When the predation threat level encoded in titmouse vocalizations increased, cardinals exhibited less active movements but increased their scanning frequency and time. And,

even though I found that cardinals rarely exhibit still scanning during normal exploration, broadcasts of social cues from titmice indicating high predation risk stimulated cardinals to exhibit significant levels of this behavior. Thus, titmouse calls that conveyed higher risks of predation caused cardinals to decrease their overall activity levels (exploration and movement).

Since exploratory behavior is genetically related to natal dispersal ability of birds, the results of this study could have implications for the study of functional connectivity of landscapes at large scales. Given that the degree of exploratory behavior exhibited in a small cage, like the one I used, is directly linked to dispersal ability (more active explorers disperse further), my results suggest that social information use, in addition to species traits, may also influence large-scale movements of birds. Physical landscapes with known habitat connectivity of bird species will contain bird communities that produce labile “landscape of information.” Through invisible to the eye, I propose, based on this work, that social information, and the environmental conditions it reflects, may have important influences on the functional connectivity of landscapes for forest birds not reflected in physical habitat configurations.

CHAPTER 1 INTRODUCTION

Exploratory behavior is the gathering of information about objects or other aspects of the environment that does not satisfy immediate needs; and it varies with sex, age, social status, ecological traits, and experience of the individual. Exploratory behavior is linked to dispersal ability, animal personality (or behavior syndrome), and various social roles (e.g., dominance; Greenberg, 2003). Information gathering is of crucial importance in managing uncertainty in the everyday lives of organisms. Information is gained from personal experience through exploring the environment directly; or via the use of social information provided by other individuals (advertently or inadvertently) in decision-making (Danchin et al., 2008). Since animals rely on information to make decisions, learning more about the landscape of information available to animals at the landscape scale, and how animals filter and then use the information in decision making regarding landscape-scale behaviors is therefore necessary (Fletcher and Sieving, 2010).

I sought to understand, first, how exploratory behavior at a small spatial scale (in a novel cage environment) correlated with certain natural history traits of forest birds. Since exploratory behavior is highly correlated with movement ability at larger scales, this information could prove useful in understanding species differences in susceptibility to forest fragmentation (Dingemanse et al., 2003). Second, I also sought to understand the influence of heterospecific social information (in the form of anti-predator alarm calls) on the exploratory behavior of one species. Social information use may strongly influence spatial behavior at larger scales (Fletcher, 2009; Fletcher and Sieving, 2010; Sieving et al., 2004). Therefore, I sought to test how social information influences

exploratory behavior at a small scale (novel cage environment) in order to guide investigations of information use and behavioral connectivity at larger scales.

Specifically, in Chapter 2 I addressed the following: (1) how exploratory behavior in a novel environment generally varies among 6 different bird species using a detailed breakdown of exploratory behavior into 8 component behaviors I identified; (2) major species traits correlated with exploratory behavior, namely foraging guild and behavior syndrome (as expressed in social roles exhibited in winter foraging flocks), and (3) how my, more detailed multivariate approach to describing exploratory behavior compared to the standard exploratory score currently in use by others. I established that the 6 species tested exhibited different exploratory behavior in a novel cage environment. Foraging guild was loosely correlated with exploratory behavior, but whether a species commonly participated in winter foraging flocks or not was tightly correlated with exploratory behavior traits (discriminant function analysis). Using a multivariate approach provided a more complete picture for describing exploratory behavior and comparing it across multiple species.

In Chapter 3, I explored how social information use may influence exploratory behavior. Northern cardinals experienced vocalization playback trials in the same novel cage environment as in Chapter 2. I presented 4 experimental playback treatments to cardinals, including tufted titmouse alarm calls (given to different live predators under controlled conditions; Hetrick, 2006; Sieving et al., 2009) that encoded known but distinct predation threats. I found that cardinals interpreted the encoded information appropriately and adjusted their exploratory behavior in ways that would decrease their susceptibility to predation threats represented in the playback treatments. As perceived

risk of predation increased with the degree of danger encoded in titmouse calls, cardinals reduced overall activity levels, expressed in active components of exploratory behavior, but increased overall vigilance-related components. In particular, treatments conveying the highest risk of predation elicited significant amounts of “still scanning”; a behavior not commonly observed in cardinals (Chapter 2).

My results revealed, in greater detail than previously examined, how exploratory behavior varies among different species, and how social information about predation risk can bring about changes in exploratory behavior at a small scale. Given that exploratory behavior is highly correlated with dispersal ability (Dingemanse et al., 2003; Johnson, 1988), my findings suggest expectations for how species traits and information use can together affect spatial behavior at larger scales. For example, the functional connectivity of landscapes, or portions of them, where social information conveys a high degree of predation risk, movement by species that can use the information to mediate their own risk of predation may be slower in such areas.

CHAPTER 2 INTERSPECIFIC DIFFERENCES IN EXPLORATORY BEHAVIORS AMONG FOREST BIRDS

Introduction

Uncertainty poses significant challenges in animal decision making and carries important fitness consequences for wildlife in rapidly changing human-dominated landscapes. For an animal to best exploit potential opportunities and avoid dangers, it must anticipate changeable environments, including variation in distribution and kinds of resources and risks. Information gathering is crucial for managing uncertainty and changes affecting critical activities, including: mate choice (Candolin, 2003; Drullion and Dubois 2008); habitat selection (Arlt and Part, 2008; Forsman et al., 2009; Parejo et al., 2007); assessing food availability (Fletcher and Miller, 2008; Valone and Templeton, 2002); whether to disperse (Enfjall and Leimar, 2009; Ward, 2005) and how far to go (Long et al., 2005); and choosing safe paths when moving (Roche et al., 1999). In movement decisions, information about habitat and resource distributions and about predator location and predation risk is actively sought and used by vertebrates, often via active exploration or investigation to obtain information (Blumstein, 1999; Schmidt et al., 2008).

Intra-specific Variation in Exploratory Behavior

Exploration, and related exploratory behavior, is an important way for animals to obtain information about their environments. Exploratory behavior is the gathering of information about objects or other aspects of the environment that does not satisfy immediate needs (Dall et al., 2005). Exploratory behavior has been characterized for a number of organisms and is particularly well-studied

in certain vertebrate animals including Eastern chipmunk (*Tamias striatus*; Wolfe, 1969), goldfish (*Carassius Auratus*; Kleerekoper et al., 1974), guppy (*Poecilia reticulata*; Budaev, 1997), rat (*Rattus norvegicus*; Smith et al., 2009; Raud et al., 2007), and a number of bird species. Major correlates of intra-specific differences in exploratory behavior include sex, age, social status, environmental conditions, experience of the individual, personality, and dispersal capability (Arakawa, 2005; Lodewijckx, 1984; Mettke-Hoffmann et al., 2002; Mettke-Hoffman et al., 2006). Exploratory behavior can be highly variable among individuals of the same species depending on the combined effects of these various correlated conditions (e.g., Dingemanse and de Goede, 2004; Dingemanse et al., 2002).

Dispersal success is one potential consequence of exploratory movement, because exploration allows an animal to compare its possible success elsewhere with that of its present location (Johnson, 1988). In great tits, exploratory behavior is heritable and has a strong positive relationship with natal dispersal ability. Daughters of males with higher exploratory behavior scores (exhibit more flights and hops in novel environments) tend to disperse further (Dingemanse et al., 2003). But exploratory behavior in adult birds can also be influenced by environmental exposures during the exploratory juvenile phase of development (Hopf, 1985), and this has also been linked to differential dispersal success in forest birds (C. Cornelius, personal communication). Thus species with heritable but developmentally flexible exploratory and dispersal capabilities may adapt better to disturbed landscapes with complex patterns of habitat fragmentation that naturally increase the isolation of habitat patches for forest birds (Desrocher

and Hannon, 1997; Greenberg and Mettke-Hofmann, 2001; Grubb and Bronson, 2001; Grubb and Doherty, 1999).

Exploratory behavior is also strongly connected with animal personality, or behavior syndromes. A behavioral syndrome is a suite of correlated behaviors expressed either within a given behavioral context or across different contexts (Sih et al., 2004). Established examples of behavior syndromes include “activity” (Sih et al., 2003) and “shyness” or “boldness” (Bell and Sih, 2007; Both et al., 2005). Individuals with different personalities can perform differently under different types of stress, and the type of personality is usually highly correlated with an individual’s exploratory skills. In bluegill sunfish (*Lepomis macrochirus*), bolder individuals exhibit higher-scoring exploratory behavior (Wilson and Godin, 2009). In great tits, individuals with higher exploratory scores recover from being startled sooner and thus their latencies to return to a feeding table are shorter, and slow exploring tits exposed to intruders spend more time in agonistic displays and take longer to attack (Carere et al., 2005). This suggests exploratory behavior may be an indicator of personality as it relates to ‘risk-taking’ behavior (van Oers et al., 2005). Finally, breeding pairs with opposite exploratory scores (e.g., fast-exploring male and slow-exploring female) exhibit the highest reproductive success for great tits (Both et al., 2005). Authors speculate the contrasting parental personalities may combine the best of both worlds for reproduction. The fast-explorer more effectively defends a high quality territory (Dingemanse and de Goede, 2004) and the slow-exploring parent can respond

more quickly to food distribution change due to more continuous exploration of alternative feeding options (Verbeek et al., 1994).

In sum, exploratory behaviors documented in novel caged environments (such as flight and hop numbers) have repeatedly been highly correlated with personality (Dingemanse and Réale, 2005; Dingemanse et al., 2004) and, in turn, with consequential vital responses of interest. Links between exploratory behavior and large-scale spatial behaviors, such as natal dispersal and gap-crossing in fragmented landscapes, are of increasing interest in conservation biology. Recent definitions of landscape connectivity for animals are primarily behavior-based. For example ‘functional connectivity’ is defined as the combined effects of landscape configuration and species behavioral reactions to landscape elements (e.g., matrix and corridors between habitat patches) and assumes that different species will move differently in the same landscapes (Belisle, 2005). Thus, linking interspecific variation in exploratory score to landscape-level variation in distributions is a future goal of this line of work. However, recent exploratory behavior analyses only address intraspecific variation. Our best understanding of species’ variation in personality, spatial movements, and links to potential conservation implications derives from work on “neophobia” in wild species.

Neophobia and Interspecific Assessments of Exploration and Personality

Neophobia is the fear of novel stimuli in the immediate environment (Greenberg, 1983), and is highly variable in its intensity among bird species. For example, when 6 warbler species are presented with a positive, but novel foraging stimulus (a cup full of mealworms), bay-breasted warblers (*Dendroica*

castanea) are the least hesitant, and chestnut-sided warblers (*Dendroica pensylvanica*) show significantly greater hesitation (latency to approach; Greenberg, 1983). As with exploratory behavior variation within species, the difference in neophobic responses among species has been related to bold vs. shy personality and fast vs. slow exploration that, in turn, have been linked to different life-histories and habitat associations (Greenberg, 2003). For example, resident Sardinian warblers (*Sylvia melanocephala*) are less neophobic and more exploratory than migrant garden warblers (*Sylvia borin*; Mettke-Hofmann et al., 2005). Parrot species that utilize complex habitats or that feed on buds show the shortest latencies to approach a novel subject in exploratory tests (Mettke-Hofmann et al., 2002). Those findings suggest that exploratory behaviors (and their correlated personalities, such as neophobia) reflect a complex of adaptations to different environmental conditions that vary between species (Greenberg, 2003). More importantly, both exploratory scores in novel environments (within species) and neophobic latencies (between species) vary similarly with personality and risk-taking behaviors. That is bold species and individuals take greater risks in aggression and food-finding (van Oers et al., 2005); suggesting that bolder species (like individuals) should be more active explorers, and potentially better dispersers. Interspecific comparisons of exploratory behavior are needed to make these links.

One potential limiting factor in assessing exploratory behavior across species and ecosystems or landscapes is the very simplicity of current measures of exploration. Different species move and explore in unique ways, and the

current measurement standard for exploratory behavior (the combined number of flights and hops within 2-10 minutes in a novel cage environment) may not be universally applicable to interspecific comparisons. Animals can explore (gather information) using diverse cues (sounds, scents, visual and tactile stimuli) that can be gathered via active behaviors (hopping, flying, looking), but also via still scanning or listening for cues and signals that may come from further away than short hops and flights would indicate (Fletcher et al., 2009; Grim, 2008; Martin and Lopez, 2009). A major goal of this work is to clarify measurement of interspecific exploratory behavior in order to facilitate comparative work.

Interspecific Characterization of Exploratory Behavior

In this study, I took a systematic approach to characterizing interspecific differences in exploratory behavior (in a novel cage environment) with the goal of identifying species traits that are most highly correlated with, both, individual components and synthetic (multivariate) measures of exploratory behavior. I selected a variety of bird species from different taxonomic groups that vary markedly in at least two ways relevant to spatial exploration or personality; (1) foraging guilds (diet breadth, and prey search, pursuit, and capture techniques) and (2) social roles with respect to winter flocking. Since foraging entails intense spatial exploration in birds (Mettke-Hofmann et al., 2002), comparison of species exhibiting different foraging modes should ensure some variation in style and propensity to explore. Similarly, I selected species with different social roles related to winter foraging flocks as a surrogate for variation in personality syndromes under the following reasoning. Flock leaders are often characterized as vocal, intraspecifically gregarious, bold (socially dominant), and more vigilant

toward predators than flock satellites (species that follow the leader) and non-flocking species (Farley et al., 2008; Hutto, 1994; Munn and Terborgh, 1979). Using these two groupings (foraging guilds and flocking behavior) I could address whether interspecific variation in exploratory behavior could be used to predict larger ecological patterns in bird communities. My specific goals with this work are to help standardize ways to characterize the exploratory behavior of diverse species, and to increase understanding of the complex of factors that influence exploratory behavior of different species. I am particularly interested in exploratory behavior, and its causes and correlates, as an indicator of spatial behavior, more broadly, for informing the conservation of behaviorally complex species in a rapidly changing world.

Study System

I selected 6 understory forest bird species common in the South-eastern United States, including the tufted titmouse, white-eyed vireo (*Vireo griseus*), Carolina chickadee (*Poecile carolinensis*), Carolina wren (*Thryothorus ludovicianus*), Northern cardinal, and an endemic yellow-eyed sub-species of the Eastern towhee (*Pipilo erythrophthalmus*). All six species are permanent residents, occupying year-round territories. A large proportion of the forest bird community participates at some level in winter foraging flocks, including the titmouse, vireo, and chickadee (above, the other three study species do not; Farley et al., 2008).

In North-central Florida, titmouse is a year-round resident species, and in winter is reliably associated with mixed-species flocks, serving as the flock leader (nuclear species; Farley et al., 2008; Waite and Grubb, 1988). Titmice have bold

personalities and dominant social status. They facilitate flock formation, initiate and guide flock movement (Farley et al., 2008; Greenberg, 2000), and reduce predation risk and food stress for satellite species (Dolby and Grubb, 1998; Ragusa-Netto, 2002; Sridhat et al., 2009). A central mechanism underlying the benefit to satellites of following titmice is the amount and precision of threat-appropriate signals encoded in their alarm calls (Sieving et al., 2010). Species that participate in flocks, even if they do not lead them, may exhibit different personality types than species that do not join flocks. For example, flock territories in winter are larger than individual birds' or pair territories (Jullien and Thiollay, 1998; Munn and Terborgh, 1979), suggesting that flocking species may use space differently than non-flocking species. Further, flock participants gain benefits through coordination including reduced predation risk and potentially increased foraging efficiency (King and Rappole, 2000; Powell, 1985; Pulliam, 1973; Sridhar et al., 2009). In order to keep up with flock movements, deal with agonistic encounters that occur at higher frequencies in mixed flocks (Griffin et al., 2005; Morse, 1977; Terborgh, 1990), and maintain awareness of visual and vocal cues from a variety of species, flocking species personality syndromes are likely to be distinct from solitary foragers.

My 6 bird species represented variation in foraging guilds, and in both level of participation in winter foraging flocks. These six species fall into two foraging guilds. Titmouse, chickadee, vireo and wren classify as insectivores (& lower-canopy/ shrub gleaners), whereas, cardinal and towhee are omnivores (& ground gleaners; de Graaf et al., 1985). Three species are flock participants: tufted

titmice (nuclear), white-eyed vireo, and Carolina chickadee (satellites). And 3 species do not follow foraging flocks: Carolina wren, Northern cardinal and Eastern towhee. Chickadees (in the same family as titmice; Paridae), have the same complex anti-predator communication system as titmice (Freeberg et al., 2003, Sieving et al., 2010), but they are subordinate to titmice when the two species co-occur in flocks (Cimprich and Grubb, 1994).

Research Design

Objectives and Experimental Design

The objectives of this study are three-fold: (1) to understand how exploratory behavior in a novel environment generally varies among different bird species, (2) to test (via correlation) for major species traits linked to exploratory behavior, namely foraging guild and personality (as expressed in social roles in winter foraging flocks), and (3) to compare my measures of exploratory behavior to the standard exploratory score used by others (the accumulative number of flights and hops inside the novel environment).

To address species and group differences in exploratory behavior, individual birds of each species were captured from the wild and released into a novel cage environment. Birds were video-taped for 10 minutes and then released. Using previous work on exploratory behavior of birds in similar novel environmental settings, and some measures that I developed during preliminary examination of videos of my test subjects, I quantified how the different species moved around in, and visually inspected, the space within the cage. I then examined how each of 8 different component behaviors, associated with moving (hops, flights) and visual scanning, varied within and between the 6 species, 2

foraging guilds (insectivore/foilage gleaner and omnivore/ground gleaners), and 2 social groups (flocking and non-flocking) using univariate and multivariate statistics. I also 'scored' exploratory behavior similarly to previous work, using only hop and flight numbers, so that my assessments of interspecific exploratory behavior based on 8 components could be compared directly with previous intraspecific measures of exploratory behavior.

Predictions

Under objective (1) I had no specific predictions, just that each species would exhibit unique exploratory behavior with respect to variation within each of the 9 component measures of exploratory behavior, and across synthetic (multivariate) measures. But in general, based on general findings from similar studies (Dongemanse et al., 2003), I assumed the following: that high levels of movement (hopping and flying) and of visual scanning within the cage reflect high exploratory behavior, and also that if a bird actually visited a higher proportion of the volume of space within the cage then that also reflected high levels of exploration.

For objective (2), foraging and social group comparisons, I predicted that the ground omnivores might not scan as much as the insectivores (that need to locate active prey), and that the activity of the two groups would be different in kind (above ground insectivores would fly more and the ground foragers hop more). I also predicted that the socially dominant tufted titmouse would be the most vigilant (high scanning rates) and (along with) Carolina chickadees and the other satellite species (white-eyed vireo) would rank high in both exploration thoroughness and activity levels Non-flocking species (Northern cardinal, Eastern

towhee, and Carolina wren) should be less exploratory. Satellite species might explore less vigorously than non-flocking species; if they rely on the social group to watch for predators and rely fully on the vigilant tufted titmouse for scanning. But I expected that the ability to follow actively moving flocks would require satellites to exhibit similarly high levels of exploratory behavior as the titmice (Griffin et al., 2005).

Finally, for objective (3), while I predicted that the classic exploratory scores (hop number plus flight number) would generally be correlated with the more comprehensive measures I used above, I also expected that different component behaviors would be more or less useful for characterizing each species or group. I expected that the classic exploratory score may not be very useful, by itself, for describing complex interspecific differences in exploratory behavior.

Methods

Capture and Handling

I conducted field tests between May 2009 and January 2010 in Alachua and Putnam Counties in Florida. Eighty-one individuals of the target species were captured either by feeder trap (wire boxes with drop doors placed on platform feeders) or mist nets. Captured individual were then put into a small wire cage with a trap door (releasing cage), and that was placed inside the larger 3 × 3 × 2 m test cage. The releasing cage was covered with camouflage screen to provide semi-darkness for calming the test bird while blocking the view of the novel exploratory environment. Using a string attached to the trap door, birds could be released into the testing cage remotely. The testing process and bird- captures

took place at several different locations in Florida, including the Ordway-Swisher Biological Station in Melrose (Putman County), the USDA/APHIS/WS/NWRC Florida Field Station (United States Department of Agriculture, Animal & Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center; USDA lab) in Gainesville and 4 private yards in the city of Gainesville (all trap sites were at least 2 Km apart).

The design of the test cage (novel environment) was modified from Dingemanse et al. (2002), and constructed of 3 cm diameter poly vinyl chloride (PVC) pipes, plastic bird netting (mesh size = 12.7 mm), covered by white sheets. The sheets were used to block the test birds' view of the outside environment; this was important because it prevented escape behaviors that would confound observations of exploration. I placed 5 perches inside the test cage for birds to utilize during exploration that allowed birds to perch throughout the volume of space available for exploration (Figure 2-1).

Testing protocol

Captured birds were placed in a cloth bag for transport to the testing environment (usually on the same site or within a five-minute drive), then moved into the releasing cage. After a 10 min acclimation period in the darkened releasing cage (draped in a camouflaged fabric), the bird was released into the larger test cage (using the pulley string from a concealed location outside the cage). Once released, birds were allowed 10 min to explore the cage without disturbance. A video camera (Figure 2-1) recorded all movements within the cage.

Measuring Exploratory Behaviors

I used 8 component behaviors representing the exploratory behavior for analysis in objective (1) and (2): flight number, hop number, the proportion of perches explored, the proportion of ground explored, active scan number, average active scanning time, still scan number, and average still scanning time of the tested individual in the novel cage during the trial (Table 2-1). I used two measures of how thoroughly an individual moved throughout the space of the cage. I identified 9 ground cells that could be accessed via moving on the ground or between perches, and 3 vertical strata that could be accessed by moving up or down on the 5 perches inside the cage (different perches reached to different heights; Figure 2-2). Two of the perches reached as high as the top vertical stratum. Overall, the branching perches gave access to 21 of the 27 total cells of volume within the cage. Thus the other measure of thoroughness of exploration was the proportion of those 21 cells visited by each bird tested in the 10 min sample period. Finally, during my preliminary experiments, I found that test individuals frequently stopped at perches to look around to examine the novel environment. Therefore I included the number and average time of scanning behavior as traits of exploratory behavior. Active scanning was defined as when the individual moved its head and/ or body while looking around toward different directions. Still scanning was used to identify times the individual was clearly looking around, but only the eyes moved without any body movement. Both types of scanning were commonly observed.

Dingemanse et al. (2002) used the sum of flight number and hop number alone to score the exploratory behavior of great tits during a 2 min period

following release into the cage. In analyses, I treated flight and hop number independently but I also compared the performance of the exploratory score (flights plus hops) to the other measures.

Statistical Analysis

For objectives (1) and (2), I used a similar statistical approach. Individual component behaviors (Table 2-1) were compared among 6 species using analysis of variance (ANOVA) and Tukey multiple comparisons tests (t-tests for the foraging guild and social group comparisons). To determine how exploratory behavior varied across all 9 component behaviors simultaneously (i.e., in multivariate measures) I used the following sequence of analyses. To eliminate collinearity among the 9 component measures I used principal components analysis (PCA; varimax rotation on the correlation matrix) and then submitted the component scores with eigenvalues greater than 1 to multiple analysis of variance (MANOVA) to see whether the species, foraging guilds or flocking/ non-flocking groups were distinct. Because body size can influence behavior via metabolic rate and other species traits (Brown et al. 2004; Gillooly & Ophir 2009), I used it as a covariate in multiple analysis of covariance (MANCOVA) models for foraging guilds and flocking groups. Finally, discriminant function analysis (DFA) was used to characterize the interspecific and intergroup distinctions. Group or species misclassification rates were compared to determine the strongest discriminant model (species, foraging guild, versus social groupings). All statistical analyses were performed using SPSS 11.0 for windows; significance level was established at $\alpha = 0.05$.

To assess objective (3), the value of the classic exploratory score for interspecific characterization of exploratory behavior, I used t-test and MANOVA to test for inter-group differences.

Results

Interspecific Comparison

All 8 component behaviors of exploratory behavior varied significantly with species (ANOVA $p < 0.05$; Table 2-3) and only 3 of them were not correlated with body size (proportion of perches explored, active scan number and exploratory score; Table 2-4). Each component behavior of exploration differentiated between species (Tukey pairwise comparisons: $q_{0.05, 80, 5} = 4.16$, $p < 0.05$; Table 2-5). In PCA, the first principal component (PC1) was weighted most heavily on flight number, proportion of perches explored and active scan number (active above-ground exploration). PC2, however, was dominated by hop number and average still scanning time (active ground exploration; Table 2-6). The first two principal components explained 63.8% of the variance. Both components varied significantly with species (MANOVA $p < 0.05$; Table 2-6). In the DFA, two functions were generated for species identification. The first factor (F1) was mostly determined by proportion of ground explored, still scan number, and flight number, and F2 was determined mainly by average active scanning time (Table 2-7). The DFA produced 77.8% correct classification of the 6 species. The resulting graph (Fig. 2-3 A) shows 3 distinct clusters; the white-eyed vireo, Carolina chickadee and tufted titmouse (centroids 1-3) were in 1 group, the Northern cardinal was by itself (centroid 5) and the Eastern towhee and Carolina wren formed the third cluster (centroid 4 and 6).

Foraging Guild Comparison

Six out of 8 component behaviors differed significantly with foraging guilds (t-test $p < 0.05$; Table 2-3), but active scan number ($t_{79} = -0.98$, $p = 0.330$), average still scanning time ($t_{79} = -0.37$, $p = 0.710$), and exploratory score ($t_{79} = -0.37$, $p = 0.715$) did not. In MANOVA, component 1 (PC1) didn't vary significantly with foraging guilds ($F_{1, 80} = 2.26$, $p = 0.136$), but the second component (PC2) did (MANOVA $p < 0.05$; Table 2-6). However, in MANCOVA, after adding body size as a covariate, neither PC1 nor PC2 varied between guilds (MANCOVA $p = 0.44$ and 0.66 respectively; Table 2-6). In the DFA only one discriminant function was significant and was comprised mainly by the proportion of ground explored and average active scanning time (Table 2-7). The DFA produced a 72.8% correct classification of the groups. The scatter plot (Fig. 2-3 B) showed that the insectivore (& lower-canopy/ shrub gleaner) group differed most from the omnivore (& ground forager) guild based on proportion of the ground explored.

Social Group (Flocking Behavior) Comparison

Six out of 8 component behaviors varied significantly between the two groups (Flock vs. Non-flock; t-test $p < 0.05$; Table 2-3). The two groups did not differ in the proportion of perches explored ($t_{79} = 1.64$, $p = 0.106$), active scan number ($t_{79} = 0.36$, $p = 0.718$), or exploratory score ($t_{79} = -0.12$, $p = 0.907$). In MANOVA, PC1 and PC2 varied significantly with flocking group; and this was the same results for MANCOVA (with body size as covariate; all $p < 0.01$; Table 2-6). In DFA, only one discriminant function was used, defined primarily by proportion of the ground explored and flight number (Table 2-7). This DFA provided 96.3%

correct classification of flocking groups. Fig. 2-3 C shows how flocking/ non-flocking groups separated on flight number and proportion of ground explored. .

The Performance of Exploratory Score versus Component Behaviors

In the 6 species comparison (ANOVA), exploratory score varied significantly among species ($p=0.004$), but the degree of resolution between individual species was low. Multiple comparisons tests with exploratory score identified 2 subsets while other component behaviors grouped the 6 species into 2, 3 or 4 subsets (Table 2-5). The exploratory score did not vary between either the 2 foraging guilds or social groups (p value= 0.715 and 0.907 respectively).

Discussion

Measuring Exploratory Behavior

Four types of measures are commonly used to quantify behavior: latency (time to onset or cessation), frequency (number of occurrences), duration (time), and intensity (Martin and Bateson, 2007). While latency is the primary measure used to describe neophobia (Greenberg, 2001), both latency and frequency measures are commonly used to describe intraspecific exploratory behavior (Dingemanse et al., 2002; Verbeek et al., 1994). Drent et al. (2003) used latency to visit a given proportion of the perches whereas Dingemanse et al. (2002; 2003; 2004) set the total number of flights and hops within the first 2 minutes as an index of “exploratory score.” In this study I explored the utility and relevance of a larger diversity of measures of exploration in order to expose the richness of variation in how different species gather information immediately available in space. Greater complexity of measurement will better expose the potential complexity of behaviors that serve critical functions (Sieving et al., 2010). In this

case, exploratory behavior may best be characterized as “exploratory syndrome”, or a complex of individual measures of exploration that can vary differently across species, guilds, and ecological conditions. In taking this view, my work provided several key insights into behavioral variations not evident when only flight and hop number were used (Table 2-3; 2-6).

All 8 component behaviors provided ways to distinctively characterize individual species. For example, Carolina chickadees fly significantly more than any other species, and never stopped moving to scan while still (Table 2-2, 2-5). In contrast, the con-familial and socially dominant tufted titmouse spent more time scanning actively than any other species. Yet no single measure varied so much between species that more than 4 homogeneous sub-sets were detected in multiple comparisons tests (Table 2-5), suggesting that ecologically similar birds explore their environments in similar ways.

My analysis also identified behavioral measures that would be useful (or not) for intra-specific examination of exploratory behavior. For example, the proportion of ground explored or still scanning behavior would be useless for intraspecific studies with chickadees, because they did not stay still or touch the ground (Table 2-2). Additionally, there were large differences in inter-individual variation across species and traits that could help guide species and trait selection for future studies. Eastern towhees and Carolina wrens both exhibited high means for proportion of the ground explored (80%) with low variation (CV = 25%), whereas, Northern cardinals had both the highest mean active scan number (12.6) and highest CV for that same trait (47.6%). Thus, we identified

species and traits with demonstrably low and high intraspecific variation – knowledge useful for designing studies involving response to selection on spatial behaviors (Greenberg, 2003).

With respect to comparisons of groups of ‘like’ species, not all 8 component behaviors varied significantly between groups (foraging and flocking). This suggests that for inter-guild comparisons of exploratory behavior, the choice of components to measure may be critical. And I found that the classic “exploratory score” based on the combined number of hops and flights would largely be useless for making inter-group comparisons, and somewhat less powerful for inter-species comparisons than the other 8 component behaviors I used (Table 2-3). Additionally, over half of the traits were significantly correlated with body size suggesting that this needs to be considered in selection of behaviors for interspecific comparisons (Table 2-4; Gillooly and Ophir, 2010). Overall, we required multiple analyses with component behaviors to provide clearer understanding of how species and ecological groupings of species differed with respect to exploratory behavior (or syndrome; Figure 2-3; Table 2-6). As is the case in other aspects of behavioral ecology (e.g., acoustic communication) multivariate analytical approaches to tracking behavioral variation will limit understanding less than univariate approaches (Arnold et al., 2008; Dawson et al., 2006; Sieving et al., 2010) and, therefore, should be incorporated into the design of future comparative studies of exploratory (and other complex) behaviors (intra- and inter-specific, and inter-group).

Social Roles and Exploratory Behavior

I identified that a social grouping (flocking versus non-flocking) of the 6 species generated the best discriminant model of the three I compared (96.3% correct classification vs. 77.8% for the species model and 72.8% for foraging guilds). This likely relates to the necessity of flocking species to move in similar ways; species that flock together have a similar set of behaviors that relate to the ones we measured. In subtropical and temperate forests, species attending flocks utilize the same forest strata (Ghizoni and Guimaraes Azevedo, 2006; Herzog et al., 2002; Jullien and Thiollay, 1998; Munn and Terborgh, 1979; Thiollay and Jullien, 1998; Tubelis, 2007). This may derive from a potential cost for species attending flocks; that is whether they have to compromise their optimal foraging speed in order to follow the flock (Hutto, 1988; Jones, 1977). For example, a slow exploring (hopping) ground gleaner cannot participate in a sub-canopy foliage-gleaning flock that flies between microsites. Actively foraging above-ground flocks move very quickly, relative to solitary foragers (Chen and Hsieh, 2002). I found that flocking species have many very similar behaviors related to rate of movement. An important component that separated flocking and non-flocking species in this study was flight number (Figure 2-3 C; Table 2-3); flocking birds exhibited significantly higher numbers of flights than non-flocking species. Another shared trait for flocking species appeared to be their vigilance rates; flocking species actively scanned the cage (for predators or other information; Figure 2-3 A; Table 2-7). Overall, my analysis identified the 3 flocking species as active (flying, active scanning) above-ground explorers

(Figure 2-3A; Table 2-7), whereas, non-flocking species were mostly ground explorers.

My findings underscore the linkage between the two central hypotheses regarding the formation of mixed-species foraging flocks; namely, the anti-predator (e. g. Gaddis, 1980; Thiollay and Jullien, 1998) and foraging efficiency hypothesis (e. g. Macdonald and Henderson, 1977; Powell, 1985; Pulliam, 1973). The anti-predator hypothesis is based on the high degree of alertness observed in nuclear species around which mixed flocks form (Gaddis, 1980; Greig-Smith, 1981; Munn and Terborgh, 1979; Ragusa-Netto, 2002). In concert with alertness, nuclear species tend to provide abundant and specific vocal information (Sieving et al., 2010) that satellite species use to locate both the flocks and nearby predators (Goodale and Kotagama, 2005; King and Rappole, 2000). Most flocking species exhibit high levels of vigilance toward potential predators (Chen and Hsieh, 2002; King and Rappole, 2000; Latta and Winderle, 1996) and vigilance levels can be very high, especially in the flock leaders (commonly they are parids in the Holarctic; Farley et al., 2008; Langham et al., 2006; Tubelis, 2007). Interestingly, vigilance often decreases with group size (Beauchamp, 2001; Lima et al., 1999), suggesting the existence of shared vigilance (more eyes together decreases the need for individual vigilance; Treves, 1998). High vigilance among all flock members will also enhance collective detection of predator attack; when all members of feeding group can be alerted quickly to an attack if at least one group member detects and alters its behavior in a way that signals the detection has been made (via fleeing or freezing; Lima, 1995). Having

similar capabilities for high scanning frequency would insure that all flock members could share vigilance and predator detection, thus providing the benefits underlying the facilitative social interactions in flocks (biological markets theory; Hoeksema and Schwartz, 2001). I found that the three flocking species I tested exhibited significantly higher average active scanning (Function 2 was weighted heavily on this component; Figure 2-3 A), supporting the functional links that have been proposed between how species move and scan, and their propensity to participate in close, actively moving, interspecific foraging associations (flocks).

The performance of the foraging guild model was not as good as the flocking model (Figure 2-3 B, C). Rather than concluding that foraging modes have little relationship to exploratory behavior, this result may relate more to the inconsistent and incomplete guild classifications that are available in the literature. I elected to use foraging guilds to test for similarities in exploratory behavior because species placed in the same foraging guilds tend to exhibit similar responses to spatial variation in their environments (e.g., toward landscape fragmentation; Klingbeil and Willig, 2009; Varasteh Moradi and Zakaria, 2009). But guild construction is a difficult task and not very precise (Jones and Sieving, 2006; Somasundaram and Vijayan, 2008). With respect to foraging guilds, bird species exhibit a great deal of intra-annual variation in food types (e.g., insectivorous during breeding, frugivorous during migration) not accounted for in terminology that captures the mean or modal food types over the annual cycle (e.g., Ehrlich et al., 1988; de Graaf et al., 1985; Rule, 1993). In my study, the

Carolina Wren readily classified as an insectivore, but it is likely to share omnivorous habits with other ground foragers (Table 2-8; Ehrlich, 1988; Rule, 1993). In contrast, my determination of flock participation was very precise and locally determined for my study species (Farley et al., 2008). Hence the precision of 'like' groupings was different for the foraging and flocking guilds I used to classify species exploratory tendencies. Finally, phylogenetically related species may share similar behaviors (Dobsen, 1984; Skinner, 1984); but these relationships were not considered here. Applying the comparative method (Harvey and Pagel, 1993) in future interspecific studies of exploratory behavior should prove fruitful.

Behavior Syndromes, Neophobia and Exploration

Individuals usually show consistent differences in their behavioral tendency (Gosling, 2001), and this can influence individual fitness of the individuals through adult survivorship, reproduction, parental care behavior (Both et al., 2005; Réale and Festa-Bianchet, 2003). Similar suites of correlated behaviors with fitness effects are referred to as behavioral syndromes (Sih et al., 2004). Both mechanistic and functional studies are applied to behavior syndromes in order to understand how the variation persists, how it results from the combined effects of genetic and environmental factors, and how selection operates on the personality (Dingemanse et al., 2002; Stamps, 2003). Neophobia is the avoidance of novel objects or environments, defined by their dissimilarity from what the individual has previously explored (Greenberg, 1983). Exploration is defined as an individual's search pattern for, and active investigation of, novel situations in the absence of pressing physiological need (Immelmann and Beer,

1989; similar to neophilia or curiosity). Neophobia and neophilia together provide important conceptual implications for how an individual organism deals with the changing world. Neophobia and neophilia are often studied by novel object testing. Researchers examine neophobia by measuring latency and number of unsuccessful approaches to feed when novel objects are placed near a familiar feeding cup or plate filled with preferred food (Greenberg, 1983; Mitchell, 1976). While studying neophilia, objects are presented without food so that their intrinsic attractiveness to the individual can be measured (Mayeaux and Mason, 1998; Mettke-Hoffman et al., 2002; Negro et al., 1996). In reality, attraction to explore novelty and the opposite (avoidance or neophobia) are distinct responses that, when they interact in an individual's behavior, result in ambivalence (Greenberg and Mettke-Hoffman, 2001). In the wild, animals do not face simplified situations of either/or; dangers and attractive resources are mixed in time and space. Yet animals must constantly collect all types of information through exploration (Danchin et al. 2008), and if we are to understand how exploratory syndromes are related to ultimate responses, such as fitness and personality in a heterogeneous world, we need a framework for characterizing the variety of related proximate responses, such as curiosity, avoidance, and neutral exploration. The approach developed here, based on identifying finer component behaviors that characterize more complex responses (exploratory or personality syndrome) could contribute to advancing understanding of animal ecology in changing landscapes (Greenberg, 2003).

Flexibility, Plasticity, or Behavioral Diversity in a Changing World

Behavioral flexibility is viewed as unlimited and allows individuals to maximize their fitness in the many different environments they encounter during life (Sih et al., 2004). Ecological stereotypes (Klopfer, 1967), on the other hand, describe those behaviors that remain specialized even in the face of environmental change. However, as Greenberg and Mettke-Hodmann (2001) point out, ecological plasticity and stereotypy could be traits with identifiable physiological underpinnings determining the capacity for behavioral change in the face of resource changes driven by anthropogenic forces acting on landscapes (Greenberg and Droege, 1999; Morton, 1998). Therefore, an understanding of species' tendencies toward behavioral stereotypy or plasticity could be important for conservation. Access to this understanding may be had through studies of neophobia and exploratory behavior. Neophobia and exploration have been related to ecological plasticity (Klopfer, 1967), innovative behavior (Lefebvre et al., 1997), whether a species classifies as a specialist or generalist (Greenberg, 1992; Webster and Lefebvre, 2000), and even to food preference and geological origins (Mettke-Hoffman et al., 2002).

Identifying ecological specialist versus generalist species is critical in ecology, evolution and conservation (Devictor et al., 2010). Efforts to quantify species' niches in order to identify their status as specialists or generalists have a long history in ecology (Bazzaz, 1991; Hutchinson, 1957; Levins, 1968; Whittaker, 1956). Attempts to classify species according to their degree of specialization are often problematic because choices of environmental gradients that define a species' niche are somewhat subjective and also because of the high variability

of existing definitions and methods (Devictor et al., 2010; Fridley et al., 2007; Witkowski and Lamont, 1997). Even so, ecological specialization is classically viewed as a constraint on a species' ability to adapt to environmental changes and, therefore, as a strong contributor to extinction risk (McKinney, 1997). Specialists have even been labeled the "great losers" of past and current global change (Colles et al., 2009). As Colles et al. (2009) point out however, useful understanding of how a species degree of specialization affects its success in this changing world, integration of different approaches (ecology, paleobiology and phylogeny) will be necessary.

In the behavioral arena, generalist birds are characterized as less neophobic than specialists (Greenberg, 1984; 1990; 1992). Webster and Lefebvre (2000) show that differences in ecological specialization are linked to variation in neophobia those, in turn, allow prediction of a species' ecological plasticity. My results may reflect similar relationships if I assume that the coefficient of variation (CV) in each species' exploratory behavior reflects their ecological plasticity (Table 2-2; Greenberg, 2003). Two ecological axes of specialization commonly used for birds include diet (diversity of food types consumed) and geographic range (Mettke-Hoffmann et al., 2002). Plotting each of my species' mean exploratory CV (summarized across all 8 components of exploratory behavior) on the Y axis, versus (respectively; Fig. 2-4 A-C) latitudinal, longitudinal range, and diet specialization, Northern cardinal and tufted titmouse stand out as the most behaviorally variable/flexible (highest CVs) and with the broadest geographic ranges and diets. These two species are identified as

extreme generalists in major references (e.g., Birds of North America Online; <http://bna.birds.cornell.edu/bna/>), and they exhibited extreme intraspecific variation in exploratory behavior. On the other end of the spectrum is the Eastern towhee; the distribution range displayed in Fig. 2-4 is for the “white-eyed” (pale straw yellow iris) subspecies that is largely endemic to Florida, and all towhees used in this study were of this particular morphological form (Batten, 2008; Dickinson, 1952). My data suggest that this subspecies may exist in a limited geographical area, in part, because of the lack of variation (plasticity) in exploratory behavior (Fig. 2-4A, B); though we note its diet is not particularly specialized (Fig. 2-4 C). Keeping in mind the caveat that this study was designed to detect interspecific (not intraspecific) variation, my findings do seem to support the idea that behavioral diversity (or plasticity) may be linked to species’ locations along ecological axes of specialization. In conclusion, my findings parallel other avenues of study linking behavioral plasticity with key traits relevant to survival and reproduction, as exploratory behavior surely is, and continued work should prove fruitful for understanding animal species responses to Earth’s diverse axes of environmental change.



Figure 2-1. The design of the testing cage (novel environment). The releasing cage, covered by camouflage fabric, is in the lower left corner. The tripod (at right) held the video camera set to record all behaviors inside the cage. One perch (of 5: see Figure 2-2) is visible inside the cage.

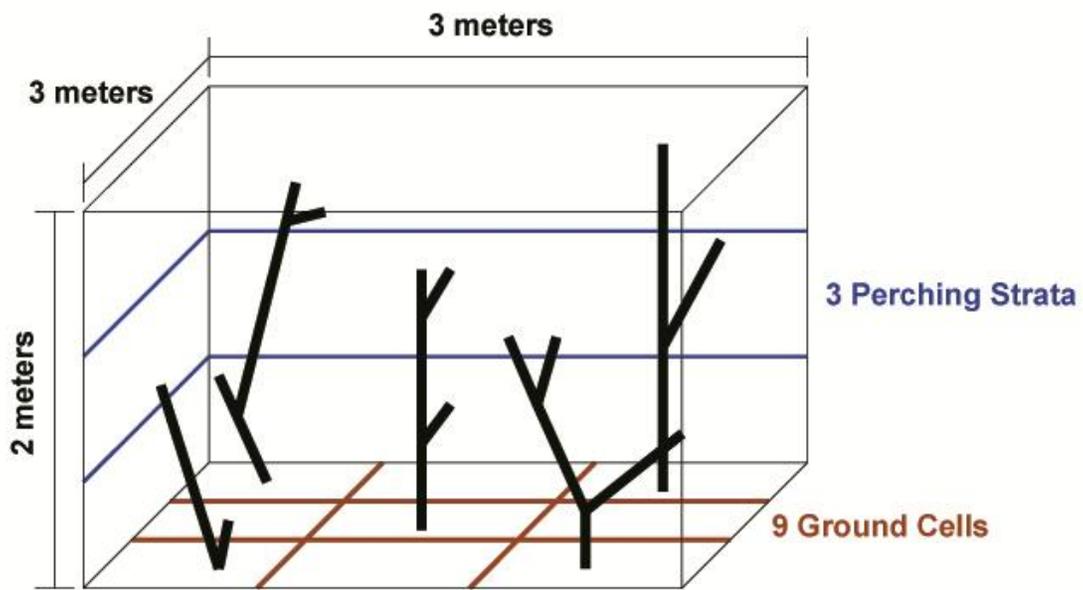
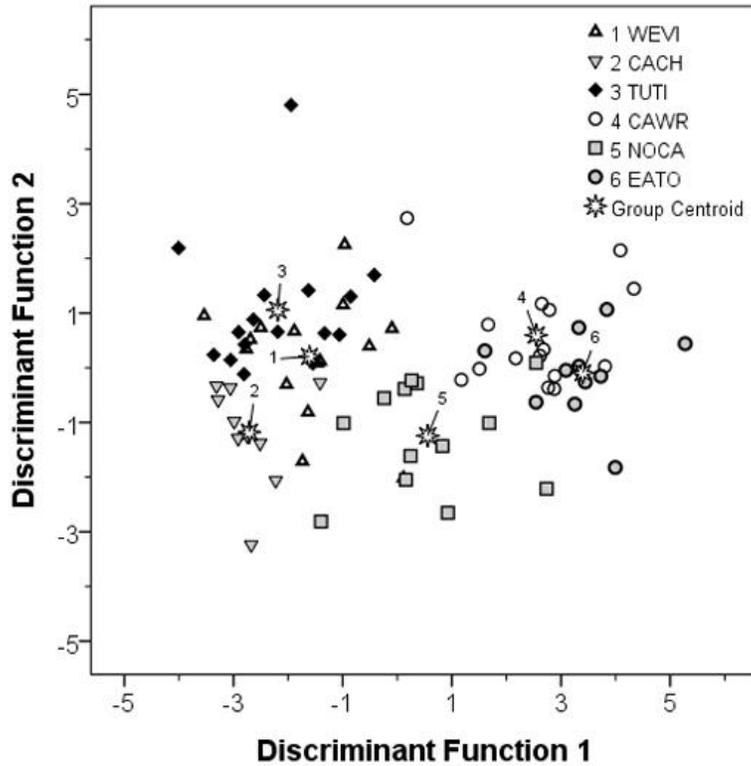
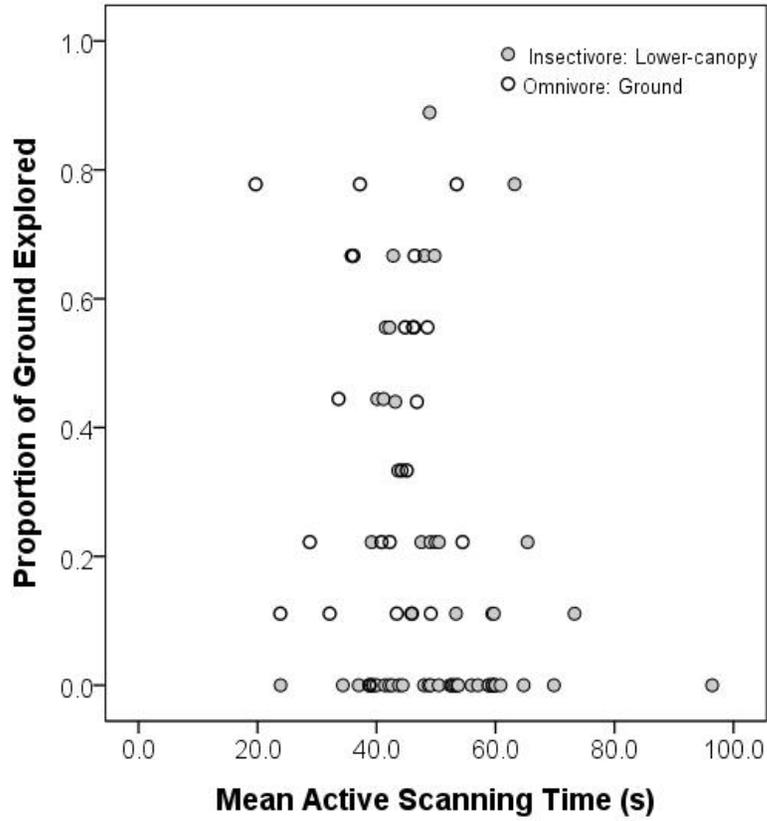


Figure 2-2. The assignment of volume within the cage into 27 cubes (9 ground cells \times 3 strata) for exploration by test subjects. Perching substrates (sticks) intercepted a total of 21 of the 27 total volume cells.

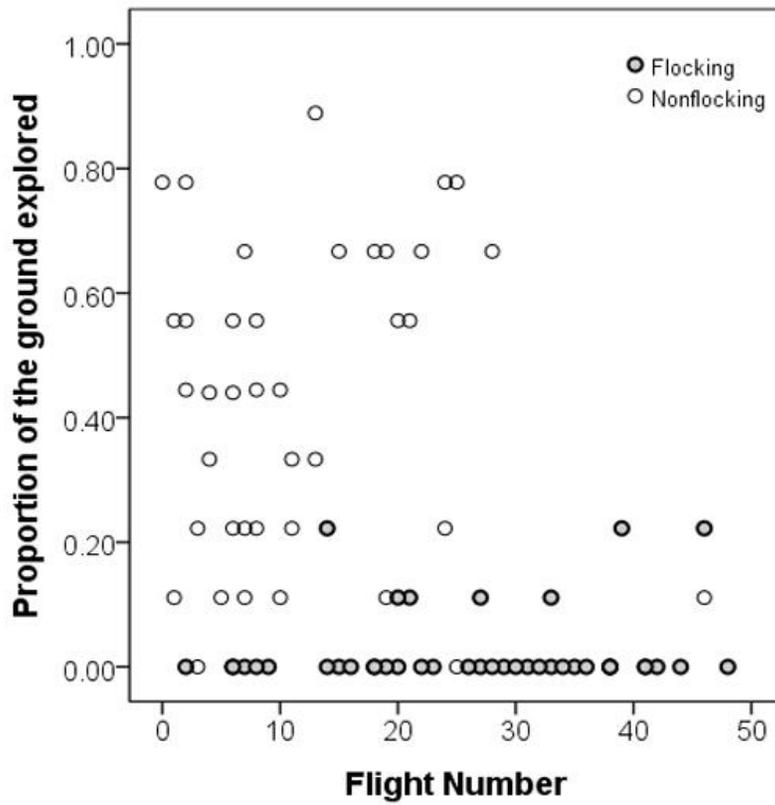


(A)

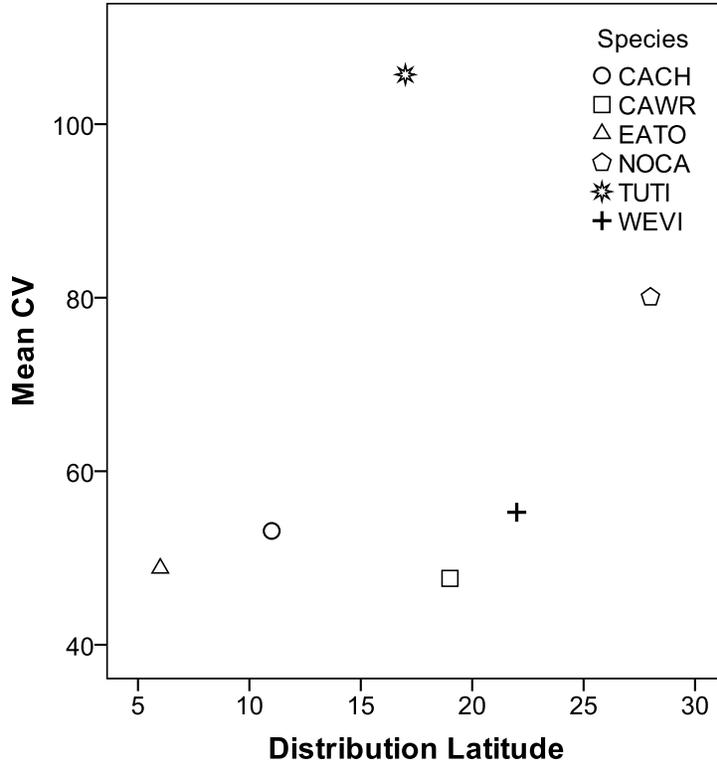
Figure 2-3. Results of the discriminant function analysis for (A) species (1st two discriminant functions used; WEVI = white-eyed vireo, CACH = Carolina chickadee, TUTI = tufted titmouse, CAWR = Carolina wren, NOCA = Northern cardinal, and EATO = Eastern towhee), (B) foraging guilds, and (C) flocking groups showing, for each, the two component behaviors with the highest weights on the single discriminant function generated. The factor loadings for DF analyses are listed in Table 2-4.



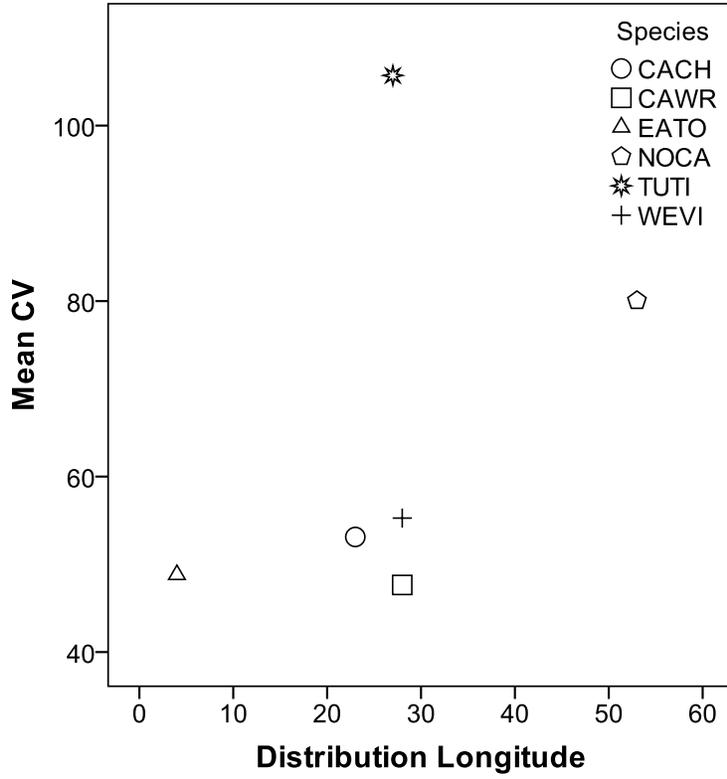
(B)



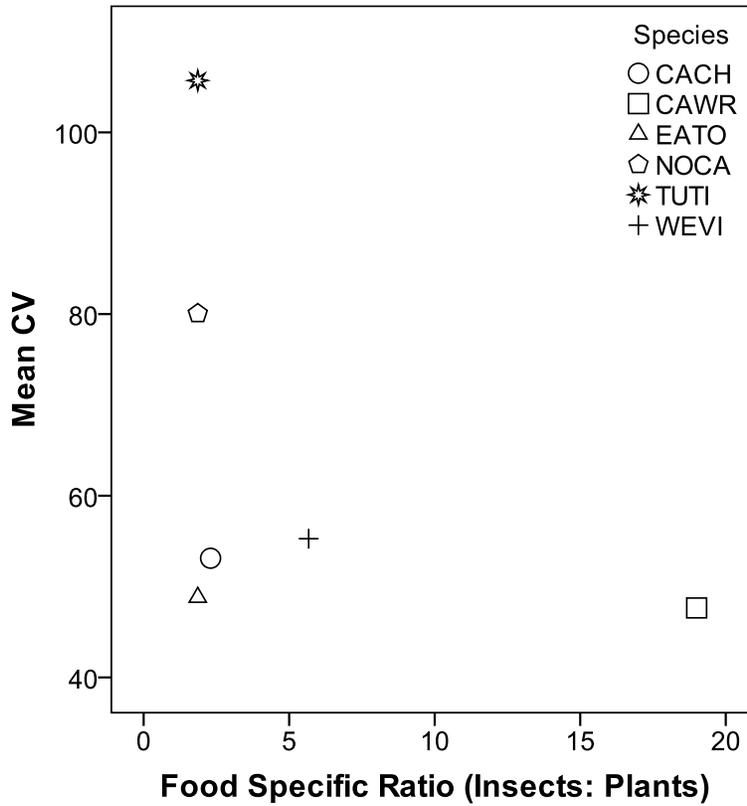
(C)
Figure 2-3. Continued.



(A)
 Figure 2-4. Scatter plots of mean coefficients of variation (CV) across all 8 component behaviors vs. (A) max. latitudinal range (degrees) in geographical distribution, (B) max. longitudinal range (degrees) in geographical distribution, and (C) ratio of insect to plant food types in the diet of each species. In Panels A and B, the assumption is that generalists are on the right side, and in Panel C, they are on the left side. WEVI = white-eyed vireo, CACH = Carolina chickadee, TUTI = tufted titmouse, CAWR = Carolina wren, NOCA = Northern cardinal, and EATO = Eastern towhee.



(B)



(C)

Figure 2-4. Continued.

Table 2-1. List of components of exploratory behavior, their definitions/ measures and how data were transformed for analysis.

Component Name (ID)	Definition	Transformation
Flight number (FN)	Number of flights in ten minutes	
Hop number (HN)	Number of hops in ten minutes	
Prop. of perches explored (PP)	The number of perch spaces one individual explored in ten minutes divided by the total number of perch spaces (3 strata × 9 cells where a segment of perches is present = 21 cells with perch segment out of 27 total)	Arcsinsqrt
Prop. of ground explored (PG)	The number of ground cells one individual explored in ten minutes divided by the total number of cells	Arcsinsqrt
Active scan number (ASN)	The number of active scans (looking around with head or body movements) in ten minutes	
Average active scanning time (AAST)	Accumulated active scanning time divided by the active scan number	
Still scan number (SSN)	The number of still scans (looking around with no head or body movements, merely the eye activities) in ten minutes	
Average still scanning time (ASST)	Accumulated still scanning time divided by the still scan number	

Table 2-2. Mean and coefficients of variation (CV) of 8 component exploratory behaviors for 6 species.

Species Name (Species ID)		FN	HN	PP	PG	ASN	AAST	SSN	ASST
White-eyed vireo (WEVI)	Mean	16.9	5.9	0.3	0.0	7.3	54.5	1.5	9.1
	CV	58.0%	54.2%	33.3%	N/A	23.3%	15.8%	106.7%	95.6%
Carolina chickadee (CACH)	Mean	37.7	17.9	0.5	0.1	12.0	39.2	0.0	0.0
	CV	15.6%	33.0%	40.0%	200.0%	15.0%	15.1%	N/A	N/A
Tufted titmouse (TUTI)	Mean	27.7	12.4	0.5	0.1	8.8	58.0	0.5	12.5
	CV	39.7%	52.4%	40.0%	200.0%	26.1%	20.3%	160.0%	307.2%
Carolina wren (CAWR)	Mean	10.5	26.0	0.5	0.8	7.5	48.3	2.8	33.4
	CV	64.8%	76.5%	20.0%	25.0%	25.3%	18.6%	32.1%	118.9%
Northern cardinal (NOCA)	Mean	16.9	20.1	0.4	0.4	12.6	37.3	1.1	6.3
	CV	72.8%	74.1%	50.0%	75.0%	47.6%	23.9%	127.3%	169.8%
Eastern towhee (EATO)	Mean	8.4	32.9	0.2	0.8	6.1	44.8	3.4	29.6
	CV	96.4%	59.6%	100.0%	25.0%	29.5%	14.3%	50.0%	68.2%
Total	Mean	19.2	18.7	0.2	0.2	8.9	48.0	1.6	15.8
	CV	68.8%	84.5%	50.0%	150.0%	41.6%	24.0%	106.3%	177.2%

Table 2-3. Comparison among species and between groups based on each component of exploratory behavior

Statistical Analysis: ANOVA			
Comparison	Trait	Results	
		F _{df}	p value
Species	Flight number	16.4 _{5,80}	≤ 0.01
	Hop number	7.0 _{5,80}	≤ 0.01
	Proportion of perches explored	6.8 _{5,80}	≤ 0.01
	Proportion of ground explored	41.9 _{5,80}	≤ 0.01
	Active scan number	10.0 _{5,80}	≤ 0.01
	Average active scanning time	11.7 _{5,80}	≤ 0.01
	Still scan number	15.0 _{5,80}	≤ 0.01
	Average still scanning time	3.4 _{5,80}	0.01
	Exploratory Score	3.8 _{5,80}	≤ 0.01
Statistical Analysis: T-Test			
Comparison	Trait	Results	
		t _{df}	p value
Foraging Guild	Flight number	3.0 ₇₉	≤ 0.01
	Hop number	-3.0 ₇₉	≤ 0.01
	Proportion of perches explored	3.0 ₇₉	≤ 0.01
	Proportion of ground explored	-4.5 ₇₉	≤ 0.01
	Active scan number	-1.0 ₇₉	0.33
	Average active scanning time	4.0 ₇₉	≤ 0.01
	Still scan number	-2.3 ₇₉	0.02
	Average still scanning time	-0.4 ₇₉	0.71
	Exploratory Score	-0.4 ₇₉	0.72
Flocking Group	Flight number	5.8 ₇₉	≤ 0.01
	Hop number	-4.8 ₇₉	≤ 0.01
	Proportion of perches explored	1.6 ₇₉	0.11
	Proportion of ground explored	-11.6 ₇₉	≤ 0.01
	Active scan number	0.4 ₇₉	0.72
	Average active scanning time	3.5 ₇₉	≤ 0.01
	Still scan number	-5.2 ₇₉	≤ 0.01
	Average still scanning time	-2.5 ₇₉	0.01
	Exploratory Score	-0.1 ₇₉	0.91

Table 2-4. Results of Kendall's Tau-b Correlation Analysis between component behaviors and body size.

	Flight number	Hop number	Prop. of perches	Prop. of ground	Active scan number	Average active scanning time	Still scan number	Average still scanning time	Exploratory score
Body size									
Correlation	-0.30	0.32	-0.07	0.55	-0.06	-0.21	0.26	0.23	-0.74
Significance (2-tailed)	≤ 0.01	≤ 0.01	0.40	≤ 0.01	0.49	0.02	0.01	0.01	0.40

Table 2-5. Tukey Test results for between-species comparison. WEVI = white-eyed vireo, CACH = Carolina chickadee, TUTI = tufted titmouse, CAWR = Carolina wren, NOCA = Northern cardinal, and EATO = Eastern towhee. MD = Mean Difference = Spp 1 – Spp 2.

Spp 1	Spp 2	Flight Number		Hop Number		P. of Perches Explored		P. of Ground Explored		Active Scan Number	
		MD	p value	MD	P value	MD	p value	MD	p value	MD	p value
WEVI	CACH	-20.8	≤0.01	-12.0	0.26	-0.2	0.09	-0.1	0.99	-4.7	≤0.01
	TUTI	-10.8	0.03	-6.4	0.76	-0.2	0.04	-0.2	0.36	-1.4	0.77
	CAWR	6.5	0.42	-20.1	≤0.01	-0.1	0.21	-0.8	≤0.01	-1.3	1.00
	NOCA	0.0	1.00	-14.1	0.07	-0.1	0.64	-0.5	≤0.01	-5.3	0.88
	EATO	8.5	0.19	-27.0	≤0.01	0.1	0.35	-0.8	≤0.01	1.3	≤0.01
CACH	TUTI	10.0	0.10	5.5	0.91	0.0	1.00	-0.1	0.85	3.3	0.08
	CAWR	27.2	≤0.01	-8.1	0.68	0.1	0.99	-0.7	≤0.01	4.5	0.01
	NOCA	20.8	≤0.01	-2.2	1.00	0.1	0.82	-0.4	≤0.01	-0.6	1.00
	EATO	29.3	≤0.01	-15.0	0.11	0.3	≤0.01	-0.8	≤0.01	5.9	≤0.01
TUTI	CAWR	17.2	≤0.01	-13.6	0.06	0.0	0.98	-0.6	≤0.01	1.3	0.83
	NOCA	10.8	0.04	-7.7	0.64	0.1	0.76	-0.3	≤0.01	-3.9	0.01
	EATO	19.3	≤0.01	-20.5	≤0.01	0.3	≤0.01	-0.7	≤0.01	2.7	0.19
CAWR	NOCA	-6.5	0.47	5.9	0.85	0.0	0.99	0.3	≤0.01	-5.2	≤0.01
	EATO	2.1	0.99	-6.9	0.77	0.3	≤0.01	-0.1	0.96	1.4	0.83
NOCA	EATO	8.5	0.23	12.8	0.17	0.2	0.01	0.4	≤0.01	6.5	≤0.01
Subsets		2		3		2		3		3	

Table 2-5. Continued.

Spp 1	Spp 2	Average Active Scanning Time		Still Scan Number		Average Still Scanning Time		Exploratory Score	
		MD	p value	MD	p value	MD	p value	MD	p value
WEVI	CACH	15.3	≤0.01	1.5	0.03	9.1	1.00	-32.7	≤0.01
	TUTI	-3.5	0.88	1.0	0.18	-3.4	1.00	-17.2	0.13
	CAWR	6.2	0.42	-1.3	0.06	-24.3	0.12	-13.6	0.37
	NOCA	17.2	≤0.01	0.5	0.92	2.8	1.00	-14.1	0.37
	EATO	9.7	0.07	-1.9	≤0.01	-20.5	0.34	-18.5	0.13
CACH	TUTI	-18.8	≤0.01	-0.5	0.91	-12.5	0.84	15.5	0.33
	CAWR	-9.1	0.13	-2.8	≤0.01	-33.4	0.03	19.1	0.14
	NOCA	1.9	1.00	-1.1	0.29	-6.3	0.99	18.6	0.19
	EATO	-5.6	0.68	-3.4	≤0.01	-29.6	0.10	14.3	0.49
TUTI	CAWR	9.7	0.04	-2.3	≤0.01	-20.9	0.24	3.6	1.00
	NOCA	20.7	≤0.01	-0.6	0.80	6.2	0.99	3.1	1.00
	EATO	13.2	≤0.01	-2.9	≤0.01	-17.1	0.53	-1.3	1.00
CAWR	NOCA	11.0	0.02	1.7	≤0.01	27.1	0.08	-0.5	1.00
	EATO	3.5	0.91	-0.6	0.78	3.8	1.00	-4.9	0.99
NOCA	EATO	-7.5	0.29	-2.3	≤0.01	10.5	0.24	-4.3	0.99
Subsets		4		4		2		2	

Table 2-6. Factor loadings of the 8 component behaviors on the 2 principal components. Eigenvalues and amount of variance explained by the respective components are given at the bottom. MAN(C)OVA results are shown in the bottom two panels.

Factor loadings				
Parameter	PC1		PC2	
1 Flight number	0.83		-0.16	
2 Hop number	0.05		0.86	
3 Prop. of perches explored	0.78		0.14	
4 Prop. of ground explored	-0.44		-0.59	
5 Active scan number	-0.74		0.28	
6 Average active scanning time	-0.71		-0.08	
7 Still scan number	0.67		0.11	
8 Average still scanning time	-0.33		0.88	
Eigenvalue	3.11		1.99	
% variance explained	38.9		24.9	

MANOVA results				
Comparison	PC1		PC2	
	F_{df}	p value	F_{df}	p value
Species	15.5 _{5,80}	≤ 0.01	23.0 _{5,80}	≤ 0.01
Foraging guild	2.3 _{1,80}	0.14	26.6 _{1,80}	≤ 0.01
Flocking group	13.5 _{1,80}	≤ 0.01	92.2 _{1,80}	≤ 0.01

MANCOVA results				
Comparison	PC1		PC2	
	F_{df}	p value	F_{df}	p value
Foraging guild	0.60 _{1,80}	0.44	0.20 _{1,80}	0.66
Body size	3.44 _{1,80}	0.07	7.83 _{1,80}	0.01
Flocking group	8.40 _{1,80}	≤ 0.01	37.38 _{1,80}	≤ 0.01
Body size	0.64 _{1,80}	0.43	0.07 _{1,80}	0.79

Table 2-7. Structure coefficients/ discriminant loadings of the 8 component behaviors on the function(s) from canonical discriminant function analysis of the different group comparisons. Eigenvalues and amount of variance explained by the respective components are at the bottom.

Parameter	Species		Foraging Guild	Flocking Group
	Function1	Function2	Function1	Function1
1 Flight number	-0.38	-0.20	0.23	-0.34
2 Hop number	0.21	0.05	-0.33	0.27
3 Prop. of perches Explored	-0.15	0.07	0.41	-0.14
4 Prop. of ground Explored	0.68	0.05	-0.62	0.68
5 Active scan number	-0.12	-0.29	0.11	-0.02
6 Average active scanning time	-0.12	0.92	0.55	-0.21
7 Still scan number	0.38	0.25	-0.28	0.31
8 Average still scanning time	0.04	0.29	-0.08	-0.02
Eigenvalue	5.72	0.77	0.68	3.68
% variance explained	79.6	10.8	100.0	100.0

Table 2-8. Foraging behavior of 6 species based on different references.

Species Name	De Graaf et al. 1985	Ehrlich et al. 1988	Rule 1993
White-eyed vireo (WEVI)	Insectivore: lower-canopy/ shrub gleaners	Insect: foliage gleaner	85% insects 15% plants
Carolina chickadee (CACH)	Insectivore: lower-canopy/ shrub gleaners	Insect, conifer seed, and fruit: foliage and bark gleaner	70% insects 30% plants
Tufted titmouse (TUTI)	Insectivore: lower-canopy/ shrub gleaners	Insect, seeds, and fruit: foliage and bark gleaner	65% insects 35% plants
Carolina wren (CAWR)	Insectivore: lower-canopy/ shrub gleaners	Insect: ground and foliage gleaner	95% insects 5% plants
Northern cardinal (NOCA)	Omnivore: ground forager	Insect, seeds, and fruit: ground gleaner	65% plants 35% insects
Eastern towhee (EATO)	Omnivore: ground forager	Insect, seeds, and fruit: ground and foliage gleaner	65% plants 35% insects

CHAPTER 3
TUFTED TITMOUSE (*BAEOLOPHUS BICOLOR*) ANTI-PREDATOR
VOCALIZATIONS ALTER HETEROSPECIFIC EXPLORATORY BEHAVIOR

Introduction

Animal Ecology and Information-driven Decision-making

Behavior is often defined as the way by which organisms adjust to environmental variation. Adjustment requires reactions to cues in the environment, signifying that organisms make decisions based on information they gather and process. Therefore, the study of behavior can thus be viewed as the study of decision-making, emphasizing information gathering, memory storage, and processing (Danchin et al., 2004; Danchin et al., 2008). The value of information resides in its power (accuracy and precision) to aid in identifying current conditions or to predict future conditions. Research efforts to understand information use are widespread across molecular, developmental and neurobiological contexts (Adami, 2004; Maynard Smith, 1999; Wagner, 2007). However, as Dall et al. point out (2005), information use in behavioral and evolutionary ecology has been narrowly restricted to particular contexts; e.g., foraging and mate choice and navigation. Given that information use is critical to animals' adaptive behavior, both Dall et al. (2005) and Danchin et al. (2008) emphasize an urgency to develop information-driven approaches across animal ecology in order to speed fundamental integration and enhance the predictive power of ecological theory.

Social Information and Its Influences

Biological information is defined as genetic and environmental cues that reduce uncertainty, potentially allowing a more adaptive response (Danchin et al.,

2004). Non-genetic information can be acquired in three ways: (1) parental effects on offspring phenotype; (2) personal information gathered by one individual's interaction with its environment; and (3) social information that is gathered by observing other individuals. Social information can be derived from "cues" produced inadvertently by individuals engaged in performance of activities or as "signals" exchanged intentionally between individuals (Danchin, 2008).

Obtaining and utilizing social information is increasingly recognized as a common and important mechanism underlying animal decision making, including foraging, habitat choice, and mate choice (Bonnie and Earley, 2007). Social information use can strongly influence both survival and fitness (Marzluff et al., 1996). For example, in an English raven (*Corvus corax*) roost, individuals follow successful foragers to food, which enhances their survival (Mennill et al., 2002). And even though most examples derive from intraspecific studies, social information is often exchanged between heterospecifics. For example, nine-spined sticklebacks (*Pungitius pungitius*) choose foraging patches based on the foraging preference of three-spined sticklebacks (*Gasterosteus aculeatus*; Coolen et al., 2003). Using information gathered from heterospecifics, through their unique sensory adaptations or greater experience, animals may be able to achieve more accurate information than they can obtain alone (Seppänen et al., 2007). Vigorous interspecific competitors, classically thought to have a globally negative influence on one another, apparently can provide exceptionally relevant information for each other about food resources or predation risk (Forsmann et al., 2007; Monkkönen and Forsmann, 2002; Templeton and Greene, 2007).

Therefore interspecific social information use is likely critical for understanding interactions among species; yet is a topic largely absent from community-ecological literature (Dall et al., 2005; Seppänen et al., 2007; but see Fletcher, 2008). One area where interspecific information use has been explored most fully, however, is regarding interspecific use of anti-predator alarm calls.

Using Social Information to Navigate Landscapes of Fear

Perhaps the most important of situations animals face is the risk of death or mortal injury by predator attack. Real probabilities of attack on prey organisms vary across landscapes in predictable ways based on changes in predator activity and abundance with changes in land cover, habitat types, and distances among habitats (e.g., Kuehl and Clark, 2003; Phillips et al., 2004; Sieving and Willson, 1998). While direct predation events obviously reduce individual fitness, the nonlethal (largely behaviorally-mediated) effects of predation risk also impact fitness in a variety of ways (Lima, 1998; Lima and Dill, 1990). Non-lethal predation effects, often termed “threat”, “fear”, “risk”, or “non-consumptive” effects, are now thought to play a major role in population and community dynamics, and potentially a much greater role even than direct predation (Creel and Christianson, 2008; Cresswell, 2008; Preisser et al., 2007). It follows that information about predators (location, type, hunger state) and the relative risk of predation would be a valuable commodity that individuals could share with others using various types of cues and signals (Caro, 2005; Hoeksema and Schwartz, 2001) with important consequences, including the determination of animal distributions at large scales (Goodale et al., 2010).

Social information use by animals has potentially profound influences on important spatial decisions of animals, including habitat selection. For example, the real or perceived presence and density of resident birds are used by migrants in breeding habitat selection; in part as indicators of breeding patch quality (Fletcher, 2008; Thomson et al., 2003). The perception of shared predation risk can also be transmitted between species (Ito and Mori, 2010; Sieving et al., 2010), and this can influence spatial behaviors at small (Schmidt et al., 2008) and larger scales (Manning et al., 2009; Plotnick et al., 2010; Sieving et al., 2004; Walker et al., 2007). The study of social information use in heterogeneous landscapes of fear is an active area of conservation, and is of great value to the study of animal spatial ecology more generally (Willems and Hill, 2009). In this study, I examined one of the mechanisms whereby a species use of socially-derived information about predation risk can influence spatial behavior in birds.

Exploratory behavior is the gathering of information about objects or other aspects of the environment that does not satisfy immediate needs (Dall et al., 2005), and can be characterized using a simple measures of movement and scanning behaviors in novel environments (Chapter 2). Exploratory behavior is both heritable and highly correlated with dispersal movements at large scales (Dingemanse et al., 2002; 2003). Therefore, exploratory behavior as described in experimental (novel) environments can be used as a surrogate for large-scale movement behaviors (e.g., natal dispersal; Dingemanse et al., 2003). Therefore, I experimentally manipulated exploratory behavior with interspecific socially-derived information about predation risk as a means to generate hypotheses

about how interspecific information use may be influencing landscape-level spatial behaviors such as exploration and habitat selection. Here, I used a selection of well-characterized anti-predator calls of the common, socially dominant tufted titmouse (*Baeolophus bicolor*), recorded under known predation threat contexts, as heterospecific social information and examined the effects of these calls on the exploratory behavior of sympatric Northern cardinals (*Cardinalis cardinalis*).

Study System

I selected 3 different anti-predator vocalization of tufted titmouse as the social information. As other species in the Paridae family, titmouse is a very vocal species (Harrap and Quinn, 1995). Its most common form of risk-related vocalization is the “chick-a-dee” call, a predator-mobbing call that is typical of most species in the same family and given when facing a non-immediate threat like a perched avian predator (e.g., the Eastern screech owl, *Megascops asio*; Otter, 2007). Individuals of closely-related black-capped chickadee (*Poecile artcapillus*) vary the composition of their notes in response to the presence of different predators, and these mobbing calls are displayed in a progressive manner consistent with the threat level of different predators – smaller raptors being perceived as more dangerous (Baker and Becker, 2002; Ficken, 1989; Gaddis, 1985; Templeton et al., 2005). Titmouse also exhibits the same mobbing call system, where the numbers of “chick” and “dee” notes per “chick-a-dee mobbing call” vary inversely with the perceived level of risk (Hailman, 1989; Sieving et al., 2010). They also give a different anti-predator call for actively attacking raptors – i.e., peak levels of mortality risk. These calls are commonly

identified as “seet” calls (high-frequency, low-amplitude calls; Hetrick, 2006; Sieving et al., 2010).

Acoustic information content in titmouse calls given to live predators clearly and appropriately distinguish the different threats they represent, and Carolina chickadee, another Paridae species, responses clearly and appropriately distinguish predation threats encoded in titmouse calls (Hetrick, 2006). Potentially many other species (birds and mammals) use the information from parid alarm calls across the Holarctic region in decision-making concerning anti-predator behaviors (Langham et al., 2006; Schmidt et al., 2008) and, potentially, in such spatial behaviors as boundary-crossing (Sieving et al., 2004). Previous works on the communication networks surrounding titmice and other parids provide strong indications that the vocalizations of parids represent important, community-level information sources that inform risk-appropriate decision-making. Here, I tested this hypothesis-directly by seeking to generate adjustments of behavior in one species toward the information provided by another. Auditory cues are among the most important forms of social information transmission (e. g. Clara et al., 2008; Grim, 2008; Welbergen and Davies, 2008), widely used within and between species (e. g. Griffin et al., 2005; Schmidt et al., 2008). This is especially the case in bird communities, where acoustic cues and signals carry the majority of social information available to interested con- and heterospecifics (Caro, 2005; Kroodsma and Miler, 1996; Langham et al., 2006; Sieving et al., 2008). In this study I tested whether and how acoustic information about predation threats, produced in known anti-predator contexts by one

species, influenced the exploratory behavior of another species known to participate in the same alarm-calling network.

I selected the Northern cardinal as a focal species for receiving the alarm calls of titmice for several reasons. My previous study suggests that they exhibit large intraspecific variation in certain components of exploratory behavior, providing the potential for detectable behavioral differences among treatments; the species is common, widely sympatric with titmice, and participates in the communication network centered on titmice (i.e., demonstrates appropriate responses to alarm calls of known context; Langham et al., 2006; Sieving et al., 2004).

Research Design

Objectives and Experimental Design

I hypothesized that the exploratory behavior of Northern cardinal will be influenced by tufted titmouse vocalizations, and such influence will be determined by the type of predation risk encoded in the titmouse vocalizations. This will be tested by comparing exploratory behavior of individual cardinals before, during, and after informational cues (titmouse alarm calls) are broadcasted to them while held in a novel environmental cage (Chapter 2). I exposed cardinals to 4 acoustic treatments: 1) control (no acoustic information); 2) low-risk mobbing calls (the proportion of chick/D notes was $\leq 3/2$); 3) high-risk mobbing calls (the proportion of D/chick notes was $\geq 3/2$ (using Hetrick, 2006; Sieving et al., 2010)); 4) seet call (comprised of several seet notes per call). Cardinal exploratory behaviors were video-taped for 9 minutes; 3-min before broadcasting, 3-min during broadcasting, and 3-min after broadcasting. I then quantified 8 component activities that reflect

key exploratory behaviors (Chapter 2) for each period (before, during, after) and examined whether and how exploratory behavior changed among treatments and among periods of each playback trial.

Predictions

Because no predators were visible to birds during trials, I assumed that individuals' active exploratory behaviors (flying, hopping) would generally be reduced as the level of threat of predation increased from control to low-risk – to high-risk mobbing to seet calls, respectively. Mobbing aggregations typically generate high amounts of movements by birds inspecting perched or ground predators that have been spotted, but when mobbing calls are given, responding individuals do not exhibit vigorous activity until the predator is spotted (Sieving et al., 2004). Thus, in this experiment, the mobbing call treatments represent the possibility that a perched predator is nearby, but invisible; therefore movement would be increasingly risky as the threat level encoded in titmouse calls goes up. And this response (less movement) should be extreme in the seet call treatment because parids use this call to identify a flying, potentially attacking, hawk in close proximity (Sieving et al., 2010). The most common response to this call by same and different species is to freeze in place until danger passes (Gaddis, 1985; Haftorn, 2000; Hetrick, 2006). With respect to the 4 treatments, then, I predicted generally less activity (hopping, flying, active scanning) from control to seet call treatment, and more still scanning. With respect to temporal changes in behavior across the treatment periods, I expected that exploration would decrease during the three titmouse treatments, and then rebound in the post manipulation period, but the rebound should be less with increasing threat level.

If still scanning increases during playback (as expected), it should reach its highest level in the set call treatment, and decrease again after playback stops but to a lesser degree with increasing threat level. A summary of predicted responses is in Table 3-1.

Methods

Capture and Handling

I conducted field tests from May, 2009 to March, 2010 in North-central Florida. Northern cardinals were captured either by feeder trap (wire boxes with drop doors placed on platform feeders) or mist nets. Field work took place at the Ordway-Swisher Biological Station in Melrose, FL (Putman County); the USDA/APHIS/WS/NWRC Florida Field Station (United States Department of Agriculture, Animal & Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center; USDA lab) and at 5 private yards in the city of Gainesville, FL (Alachua County; all sites where birds were trapped were at least 2 Km apart). Within 10 min of capture on average (up to 1 hour) Northern cardinals were placed in a small wire box with a swinging door, covered with camouflage cloth (to darken the cage, and hide its outline). This box was placed inside the test cage (Chapter 2) which served as a novel environment for recording exploratory behavior. The bird was released from the holding cage at the beginning of the trial (within 10 minutes of being placed there; see below).

Playback Treatments

All recordings were constructed to play titmouse calls in realistic sequences for 3 minutes, total, during each trial. Playback of each recording followed a "before" silent period of 3 minutes, followed by an "after" stimulus silent period

of observation lasting 3 minutes. To minimize pseudoreplication (Kroodsma, 1989), each recording played during a trial had calls from 3 different groups of 3 titmice presented with the same live predator stimulus under controlled aviary conditions (low- and high-risk mobbing and seet calls recorded by Hetrick, 2006). The 3 different sets of calls were played in random order on each playback recording, for a total of 6 possible recordings per treatment type to select for a given trial. For each cardinal captured and released within the test cage, treatment type was randomly selected from the 4 trials (high and low-risk mobbing, seet calls, and controls) to complete one full replication of treatments before completing the next replicate set (to maintain equal sample sizes among treatments as testing progressed). I applied *a priori* power analyses several times as data were collected to identify how many total samples were needed to detect the least difference of interest in analysis (using G*power 3.1; <http://www.psych.uni-duesseldorf.de/aap/projects/gpower/>).

Testing Protocol and Exploratory Behavior Measurements

Following capture and handling, each bird was given 10 min to acclimate to the small releasing cage (draped in a camouflaged fabric); then each bird was released into the larger test cage with perches (Figure 2-1, 2-2). The test individual experienced an initial 3-min period of silence, then 3 min of broadcast of one treatment type (control, low-risk mobbing call, high-risk mobbing call, and seet call), and then another 3-min of silence. Birds were kept in the cage for a total of 19 minutes. From the moment of placement into the release cage (opened via a string and pulley apparatus from 20 m away), test birds were not

exposed to sight or sound of human observers. A video camera recorded all movements of subjects within the cage (details described in Chapter 2).

I used 8 components of exploratory behavior (as in Chapter 2): flight number, hop number, the proportion of perches explored, the proportion of ground explored, active scan number, average active scanning time, still scan number, and average still scanning time. Summaries of all 8 behavioral components were produced for each period (before, during and after playback), and submitted to analyses.

Statistical Analysis

I conducted a principal component analysis (PCA) based on all 8 component behaviors of exploratory behavior, and pooling across the three periods of testing, to obtain the principal components (PC) having an eigenvalue greater than 1. Based on this given principal component model, I extracted the PC values of each treatment at every testing period as currency for later comparison. To test for the combined effects of treatment and time period (before, during, after), I first calculated the differences in the PCs for the two transitions of interest; During-Before (D-B), and After-Before (A-B). These differences would capture the magnitude of initial responses (during playback; D-B) and the degree to which those responses lasted during the post playback period (A-B). I then performed two MANOVAs on each of these PC differences, respectively, with treatment as the predictor. In the D-B analysis, I expected to see a general/significant decrease in movement (hops, flights, thoroughness, active scanning) with increasing predation threat (i.e., from control to low-, high-risk mobbing, to seet calls). In the A-B analyses, PC differences capturing movement

should not be so large, and treatment effects not so distinct (assuming rapid return to exploration following cessation of playbacks). But behaviors reflecting vigilance (i.e., scanning) should remain higher (differences between before and after periods should be greater) for the highest risk treatments (see Predictions, above, and Table 3-1).

Results

I tested a total of 32 cardinals (8 individuals per treatment type). The results of the PCA on the 8 component behaviors are summarized in Table 3-2. Only components with an eigenvalue greater than 1 were subsequently analyzed. The first principal component (PC1) was weighted most heavily on flight number and active scan number (active movement). The second component (PC2) was dominated by still scan number and average still scanning time (still scanning behavior). The third component (PC3) was dominated by hop number and proportion of ground explored (ground exploration). The first three principal components explained 78.4% of the variance. In MANOVA, all three principal components varied significantly with treatments in the Before – During analysis, and two of the three were significant in the After – Before analysis; PC3 did not vary among treatments anymore (p-value = 0.19; Table 3-2).

Temporal Patterns in Movement Types

The seet call treatment caused a significant decrease in flight number during broadcast, and following broadcast, flight number did not return to levels preceding broadcast. High-risk mobbing calls caused the same pattern but not as apparent as in the seet call treatment (Figure 3-1 A). In contrast, hop number dropped during, and then fully rebounded after playback, for all titmouse call

treatments, to levels observed before playback; the drop in hop number during playback was most significant in the seet call group (Figure 3-1 B).

Temporal Patterns in Thoroughness of Exploration

For the proportion of perches explored, both low-risk and high-risk mobbing caused a slight increase during the broadcast. Following broadcast, individuals kept exploring perches in low-risk mobbing treatment but not so much in the high-risk mobbing treatment. The seet call caused a decrease in the proportion, at first but then it largely rebounded post broadcast (Figure 3-1 C). Individuals explored a slightly smaller proportion of the ground for all experimental treatments during broadcasting. After broadcasting, cardinals explored either similar or greater proportions of the ground inside the cage (Figure 3-1 D).

Temporal Patterns in Scanning Behavior

Active scan number increased during broadcast then decreased slightly after the low-risk mobbing treatment was played. In contrast, the high-risk mobbing and seet call treatments caused a decrease and then an increase in active scan number; and the decrease during broadcasting was more significant in the seet call group (Figure 3-1 E). As for active scanning time, all three experimental treatments showed a quadratic pattern of change with an increase during and a decrease after broadcast (Figure 3-1 F).

Still scanning, on the other hand, in both high-risk mobbing and seet call treatments, increased during broadcast (both still scan number and time), and decreased after broadcast (both still scan number and time). The decrease after broadcast was less significant in the seet call treatment (Figure 3-1 G, H); still scanning remained pretty high.

Discussion

Interspecific Social Cues with Known Information Content

The basic function and structure of chick-a-dee calls is highly conserved across the Paridae family and has been well-described for several parid species (Langham et al., 2006; Templeton and Greene, 2007; Templeton et al., 2005; Sieving et al., 2009; Soard and Ritchison, 2009). The encoded information indicates different degrees of perceived predation threats from perched predators (avian, mammalian and/or reptilian; Sieving et al., 2010) and is expressed in the pattern of variation in chick and D notes per chick-a-dee call; more D notes per call signifies a more dangerous predator is being addressed by the signaler, and the greater the level of threat encoded in the call (Hetrick, 2006; Templeton et al., 2005; Sieving et al., 2010). In contrast, seet calls are given when attacking (nearby flying) predators are detected and these calls elicit escape or fearful responses (Hetrick, 2006; Lima and Dill, 1990; Templeton and Greene, 2007).

Appropriate responses to these calls, and to the different types of predator situations and threat levels encoded in the calls, can be generally classified into, first, escape or predator avoidance and, second, predator inspection or mobbing behaviors. Each, escape or inspection/mobbing, has associated predictable patterns in scanning (vigilance) or movement (hopping/flying) behaviors; all of which are components of exploratory behavior (Dugatkin and Godin, 1992; Lima, 1998; Chapter 2). Escape / avoidance behaviors, as from diving or flying hawks, would include an initial flight or hop into cover, followed by stillness in hiding and increased vigilance (Lima, 1998; Templeton and Greene, 2007). When cover is not readily available, freezing, and using still scanning in small birds has been

observed (Ficken and Witkin, 1977; Gaddis, 1985; Haftorn, 2000). Mobbing calls can generate increased activity levels (Langham et al., 2006; Templeton et al., 2005; Soard and Ritchison, 2009) associated with predator inspection and attack, but this may not always be the case when a perched predator has not been located. In this study (as in Hetrick, 2006), no predator is locatable; therefore depending on the perceived threat level represented by the predator, responses should vary from indifference to escape or avoidance behavior. Given the known level and kinds of threat known to be encoded in the calls that I broadcast, and given assumptions relating the different components of exploratory behavior I measured to appropriate types of responses to the calls, my results generally fit expected patterns. Northern cardinals showed significant changes on exploratory component behaviors across time at different treatments (Table 3-2).

Exploratory Behavior under Socially Conveyed Threat of Predation

As the encoded threat level in titmouse calls increased, levels of cardinal activity generally decreased, consistent with avoidance behaviors. Seet calls reduced the flight number and hop number of individuals during treatment broadcasts; high-risk mobbing generated the same but less distinct pattern of change while low-risk mobbing caused no specific changes (Figure 3-1 A, B). Similar patterns were observed for the measures of exploratory thoroughness (proportion of perches and ground explored; Figure 3-1 C, D). On the other hand, calls with higher threat-levels encoded in them induced marked expansion of time spent scanning the environment, either actively (with head/body turning) or via still scanning (head and body still, eyes moving) during broadcast of vocalizations (Figure 3-1 F, H). I therefore concluded that Northern cardinals not only

accurately interpreted the social information from tufted titmouse, but responded appropriately with finely tuned variations in diverse components of exploratory behavior. My analysis revealed the highest level of detail to date in understanding the various components of appropriate anti-predator behaviors.

Compared to the other 5 species tested in Chapter 2, Northern cardinals (as non-flocking omnivores) had average hop and flight numbers, thoroughness, and active scanning behaviors, but very low still scanning propensity in the unmanipulated novel exploratory cage (Table 2-1). In general, increasing risk of potential attack encoded in calls broadcast in this study decreased all component behaviors that involved active movement (hops, flights, thoroughness of ground and perch exploration and active scan number) while still scanning and active scanning time increased (Figure 3-1). Notable exceptions included an increasing proportion of perches explored (and slight increase in flight numbers) across time periods in the low-risk mobbing treatment, suggesting that slightly elevated predation risk caused cardinals to seek higher vantage points and potentially greater overall exploration of the cage, presumably to seek information on the threat before it becomes critical. This supports the general hypothesis that one function of mobbing aggregations is to locate a predator for future reference (Goodale and Kotagama, 2005; King and Rappole, 2000), while also suggesting the more specific hypothesis that cardinals used titmouse call structure to decide between two very different anti-predation strategies. When the encoded threat level is low (a large clumsy owl is near; Hetrick, 2006; Templeton et al., 2005), or perhaps a greater danger is still far away, it is a good time to search vigorously

for the threat (eliciting greater inter-perch movement), but once a threat becomes critical (e.g., titmice are signaling a dangerous predator is perched nearby; Sieving et al., 2010) the best bet is to make oneself less active (hide).

A large amount of variation in pre-treatment periods across treatments (Figure 3-1) within most component behaviors reflects the high intraspecific variation in cardinal exploratory behavior, relative to other species, that I detected in Chapter 2 (Table 2-1). The exception to this high variation lies in the active scanning measures – number and time (Figure 31 E, F). The overall measures during the pre-broadcast period were very consistent, suggesting that changes in these behaviors are very precise measures of perceived predation risk. This relates to other findings for changes in vigilance with perceived risk (e.g. Beauchamp, 2003; Jones and Whittingham, 2008; Newey, 2007), and emphasizes the importance of scanning in exploration of individuals' immediate environments; a measure of exploratory behavior that is largely overlooked in recent studies characterizing it in novel environments.

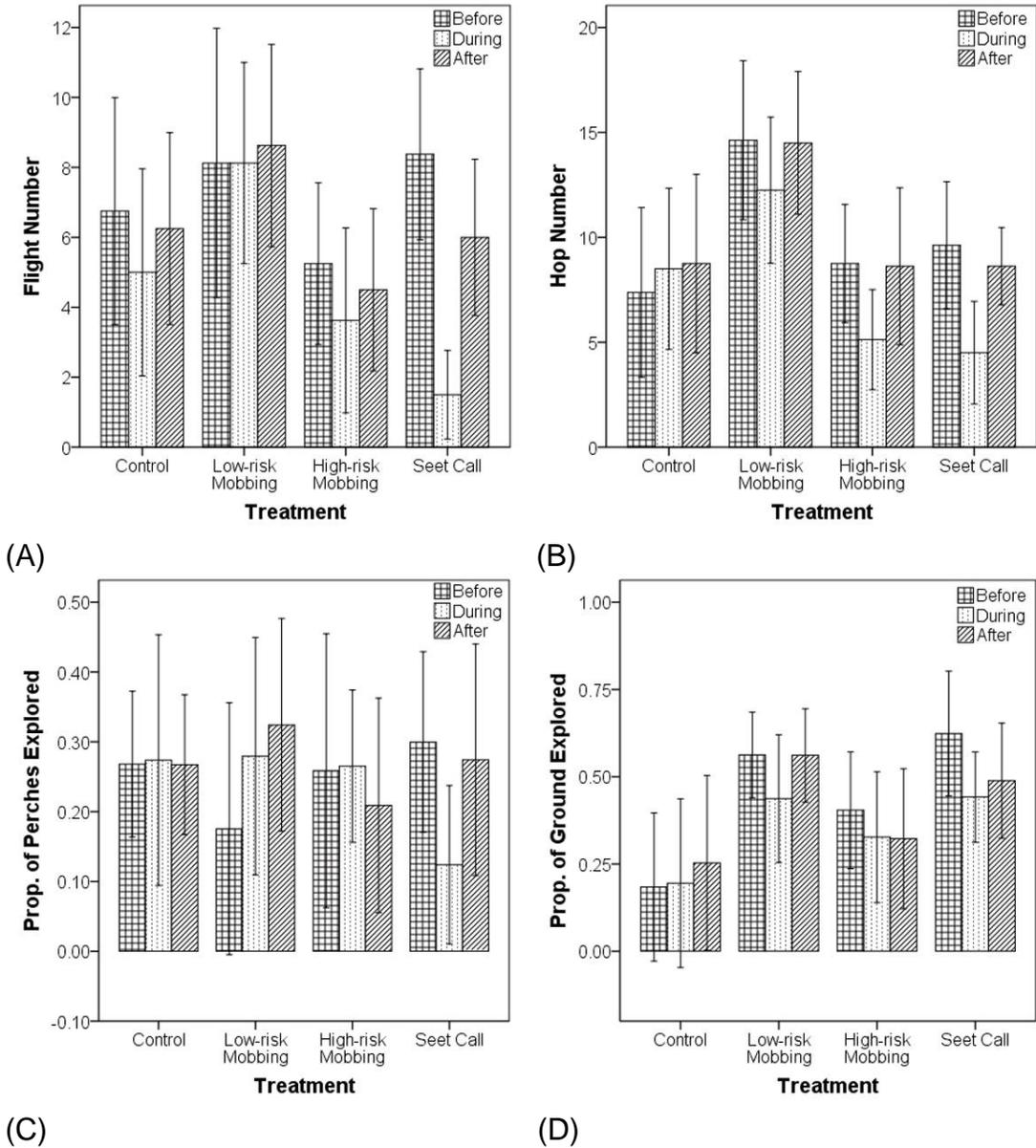
Information, Spatial Behavior and Future Implications

Every species, as Danchin et al. (2008) point out, at some point in their lives, have to answer the following question: “Do I have all that I need here and now?” Then the animal has to choose when, where, and whether to move. Animals use information to decide where to go, where to forage, where to breed, and where to live. Therefore the study of behavior can actually be viewed as the study of decision-making (Danchin et al., 2004). In turn, spatial behavior is, in many ways, the defining feature of non-sessile animals, and its analysis addresses fundamental aspects of animal decision-making processes.

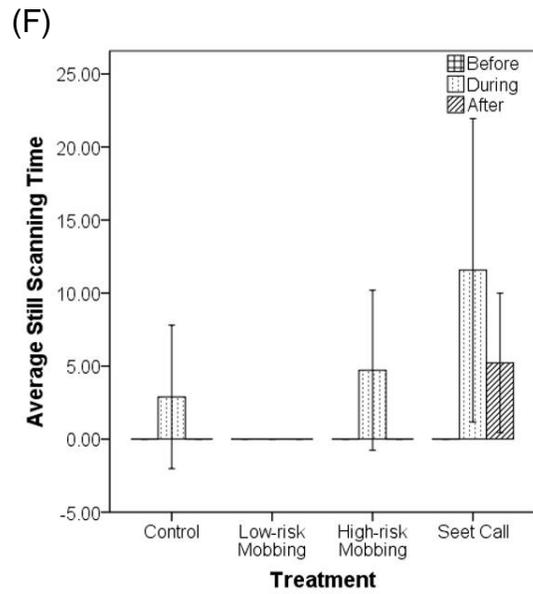
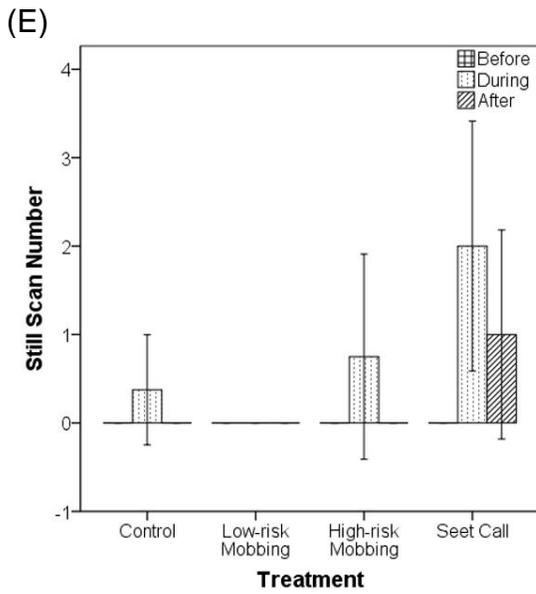
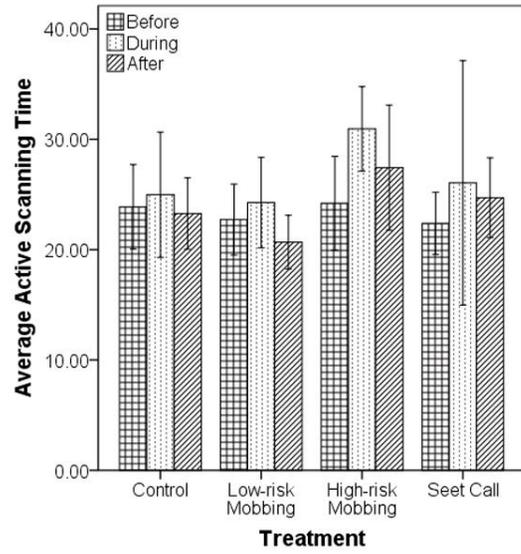
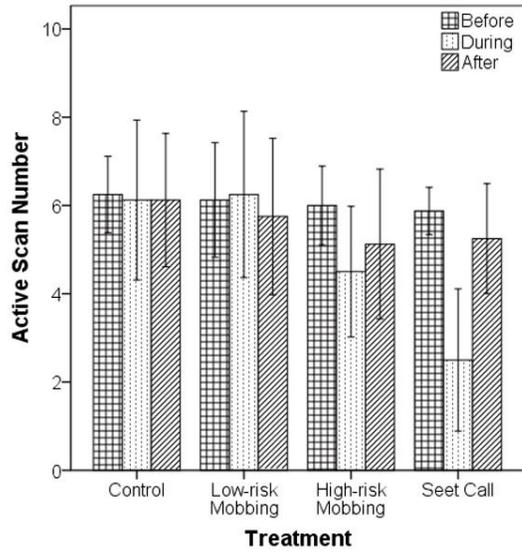
Information plays a critical role in decision-making. Successfully adaptive responses to the environment depend on the accurate estimation of relevant ecological parameters in order to adjust behaviors (Dall et al., 2005). Even though one cannot see it, a “landscape of information” exists and produces strong influences on animal behavior (Plotnick et al., 2010). Social information about predation threats (location, type, etc.) is an important and widely produced and used class of signals and cues that, collectively, define what has been called the ‘landscape of fear’ (e.g. Apfelbach et al., 2005; Dall et al., 2005; Valeix et al., 2009; Willems and Hill, 2009). Use of anti-predator information can profoundly influence a species use of space, interactions, population, and community dynamics (Cresswell, 2008); responses collectively identified as non-lethal effects of predation (Lima and Zollner, 1996). Evidence is accruing that the alarm calls of titmice and other Paridae may define a landscape of fear for a large number of species that share predators with them (Langham et al., 2006; Templeton and Greene, 2007; Schmidt et al., 2008). One important consequence with potentially far-reaching conservation implications is how parid information may influence small and large-scale movements in complex landscapes, or functional connectivity for north-temperate forest birds (e.g., Sieving et al., 2004).

Landscape connectivity refers to the functional relationship among habitats, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure (Taylor et al., 1993; With et al., 1997). Functional connectivity has been defined to express an organism-centered view of movement responses that are not solely determined by landscape structure

(Crooks and Sanjayan, 2006; Wiens, 1989). By including explicitly behavioral motivations and constraints in models of animal movement for complex landscapes (Zollner and Lima, 1998), the predictive power of spatial models used in conservation planning can be enhanced (Belisle, 2005; Castellón and Sieving, 2007). My work can inform future efforts to understand how behavioral (functional) connectivity varies in time and space. For example, the finely tuned predation-communication 'code' of the Paridae has been extensively detailed (see Sieving et al., 2010). Titmice and other Paridae are widespread and abundant in the Holarctic, and most species are highly vocal (Olsen and Grubb, 2007). A dynamic map of Parid anti-predators calls would represent a landscape of fear that likely influences many species' small and large scale movements (Mönkkönen and Forsman, 2002; Sieving et al., 2004) and foraging (Dolby and Grubb, 2000) and breeding success (Hogstad, 1995). Directed studies of dispersal behavior in complex landscapes, by species that participate in the parid communication network, could be an effective way to test for the influence of information on connectivity, and its relevance to conservation. Since exploratory behavior is highly correlated with the dispersal ability of birds (Dingemanse et al., 2003), my work strongly suggests that dispersal (timing, distance, path) could be influenced by titmouse anti-predator information. In turn, the connectivity of landscapes for animals privy to titmouse information would be influenced in ways not visible on an aerial photograph (Figure 3-2).



(C) (D)
 Figure 3-1. Bar graphs showing changes in 8 components of exploratory behaviors over the three trial periods (before, during and after broadcasting) for each treatment (control, low-risk mobbing, high-risk mobbing, and seet call): (A) flight number, (B) hop number, (C) prop. of perches explored, (D) prop. of ground explored, (E) active scan number, (F) average active scanning time, (G) still scan number, and (H) average still scanning time. Bars show mean values with 95% confidence intervals.



(G) Figure 3-1. Continued.

(H)

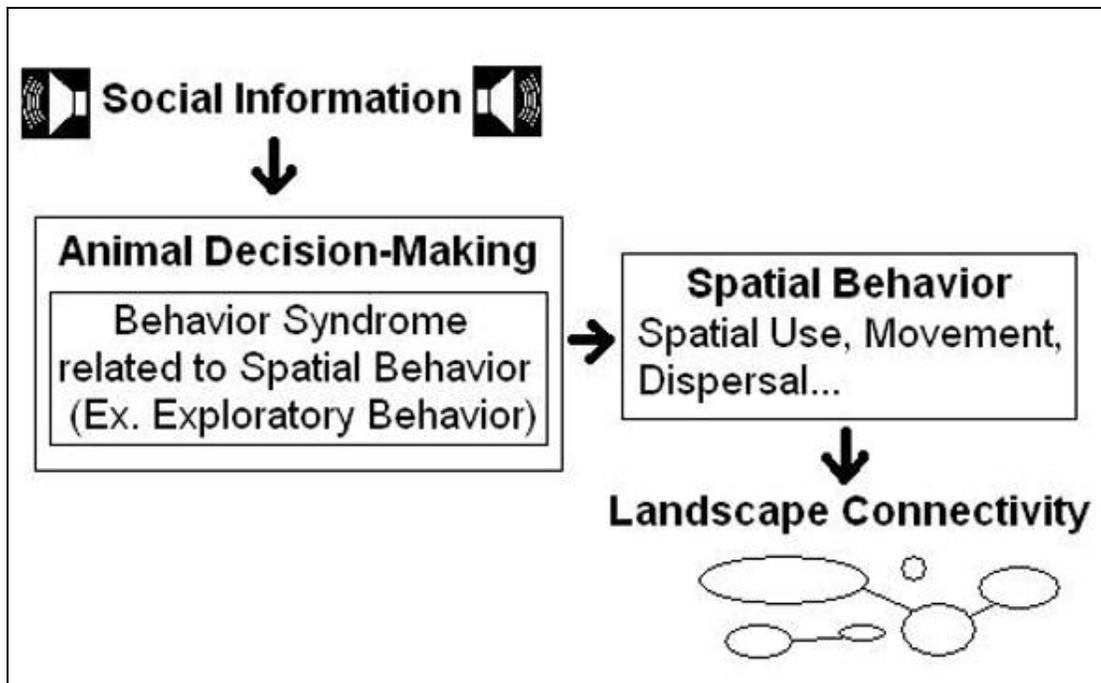


Figure 3-2. The relationship among social information, animal behavioral ecology, and functional connectivity.

Table 3-1. Prediction of influence of 4 different vocalization trials through time. Sign → means no changes at all, ↓ means decreasing, and ↑ means increasing. The number of signs indicates the strength of the influence.

Treatment	Time	Flight Number	Hop Number	Prop. of Perches Explored	Prop. of Ground Explored	Active Scan Number	Average Active Scanning Time	Still Scan Number	Average Still Scanning Time
Control	Before vs. During	→	→	→	→	→	→	→	→
	During vs. After	→	→	→	→	→	→	→	→
	Before vs. After	→	→	→	→	→	→	→	→
Low-risk Mobbing	Before vs. During	↓	↓	↓	↓	↑	↑	→	→
	During vs. After	↑ ↑	↑ ↑	↑ ↑	↑ ↑	↓	↓	→	→
	Before vs. After	↑	↑	↑	↑	→	→	→	→
High-risk Mobbing	Before vs. During	↓ ↓ ↓	↓ ↓ ↓	↓ ↓ ↓	↓ ↓ ↓	↑	↑	↑	↑
	During vs. After	↑ ↑	↑ ↑	↑ ↑	↑ ↑	↑	↑	↓	↓
	Before vs. After	↓	↓	↓	↓	↑	↑	→	→
Seet Call	Before vs. During	↓ ↓ ↓	↓ ↓ ↓	↓ ↓ ↓	↓ ↓ ↓	↓ ↓ ↓	↓ ↓ ↓	↑ ↑	↑ ↑
	During vs. After	↑	↑	↑	↑	↑	↑	↓	↓
	Before vs. After	↓ ↓	↓ ↓	↓ ↓	↓ ↓	↓ ↓	↓ ↓	↑	↑

Table 3-2. Factor loadings of the 8 component behaviors on the 3 principal components after varimax rotation. Eigenvalues and amount of variance explained by the respective components are given at the bottom. MANOVA results from these three principal components for different comparisons are shown in the bottom panel.

Factor loadings						
Parameter	PC1		PC2		PC3	
1 Flight Number	0.81		-0.23		0.22	
2 Hop Number	0.38		-0.24		0.79	
3 Prop. of Perches Explored	0.57		-0.21		-0.62	
4 Prop. of Ground Explored	0.16		-0.07		0.80	
5 Active Scan Number	0.75		-0.41		0.09	
6 Average Active Scanning Time	-0.69		-0.40		-0.37	
7 Still Scan Number	-0.17		0.92		-0.07	
8 Average Still Scanning Time	-0.14		0.92		-0.09	
Eigenvalues	3.19		1.80		1.29	
% of Variance	39.88%		22.45%		16.10%	
MANOVA results						
	PC1		PC2		PC3	
	F _{df}	p-value	F _{df}	p-value	F _{df}	p-value
Treatments (During-Before Diff.)	8.46 _{3,31}	≤ 0.01	3.83 _{3,31}	0.02	6.00 _{3,31}	≤ 0.01
Treatments (After-Before Diff.)	4.34 _{3,31}	0.01	4.01 _{3,31}	0.02	1.72 _{3,31}	0.19

CHAPTER 4 CONCLUSION

Exploratory behavior exhibits great intraspecific variation; sex, age, social status, environmental conditions, and experience of the individual can all cause variance in exploratory behavior within species (e. g. Arakawa, 2005; Lodewijckx, 1984). Exploratory behavior is highly correlated with other behaviors (e.g., dispersal) and is a reliable indicator of animal personality, or behavior syndromes (Dingemanse et al., 2003; Sih et al., 2004). Neophobia, one trait that has been linked to different life-histories and habitat associations (Greenberg, 2003), together with exploration, represent two distinct spatial responses. The former is a spatially negative or avoidance behavior, and the latter is a spatially positive, or attraction behavior, with respect to environmental cues. When the two interact in an individual, spatially (or decisively) ambivalent responses can result (Greenberg and Mettke-Hoffman, 2001). The environment is full of dangers and critical resources for every species at all scales and times, and spatial decision-making (navigation of landscapes) must be continuously responsive to relevant information (navigation to information-scapes) to maximize gain and minimize risks in survival and reproduction (Danchin et al., 2008). To enhance understanding of animal spatial ecology, measures of spatial behavior in response to stimuli must encompass the range of spatial stimulus-response dynamics, from avoidance and escape to attraction. And measures of utility in landscape ecology and conservation should be useful in comparative studies among taxa of animals. Exploratory behavior as I have described it in Chapter 2 is a step in this direction.

Neophobia has been to show significant interspecific variation in avoidance behaviors that are correlated widely with species traits linked to extinction-sensitivity

(Greenberg, 1983; 2003; Mettke-Hofmann et al., 2002; 2005; 2006). Work on animal personalities and behavioral syndromes are opening up our understanding of the mechanisms underlying ecological variation of importance to animal conservation (e.g., dispersal, reproduction). However, investigation of behavior complexes linked to spatial exploration has been focused primarily within species. Therefore, the strong links that have been established between exploratory behavior and its diverse correlates in personality (Sih et al., 2004), reproduction (Dingemanse and Réale, 2005), and movement (Dingemanse et al., 2003), do not allow interspecific comparisons.

To provide tools and insights for enhancing interspecific analyses of behavior syndromes, my first experiment focused on interspecific comparison of exploratory behavior. I used multivariate approaches to represent exploratory behavior instead of the simplified and traditional exploratory score. The 8 component activities comprising exploratory behavior included multiple measures each of movement, exploratory thoroughness, and scanning exhibited during exploration inside a novel cage environment (Table 2-1). Variation across all 8 components was significant across species, but there were parallel differences that allowed species to be grouped into 'like' explorers (Table 2-2, 2-5, Figure 2-3 A); some component behaviors were more sensitive than the others (Table 2-4). The most appropriate grouping derived from a model that placed species together that either did or did not participate in winter foraging flocks (96.3% correct classification of species into the two groups); higher than a model that used foraging guild (77.8%), or no groupings (species all separate; 72.8%). Flocking species exhibited a higher mean number of flights, and non-flocking species exhibited a larger proportion of ground explored (Figure 2-3 C). Findings confirm that

interspecific groupings of exploratory behavior should reflect interspecific groupings of correlated behavior syndromes (Greenberg, 2003; Mettke-Hofmann et al., 2002). The multivariate approach used here achieves a broader, more complete view of exploration, beyond what previous measures of exploratory or neophobic behaviors could capture. And interspecific comparisons provided insights on how behavior (decision-making) may be shaped by the interaction of an animal's natural history traits and its environment (Figure 4-1, left side).

To explore another aspect of how interspecific interactions can influence exploratory behavior, and the behavioral syndromes related to it, I conducted a second experiment involving provision of social information from the tufted titmouse to Northern cardinals. The anti-predator vocalizations are highly conserved in the Paridae, provide reliable information about predation threats occurring in different contexts in the environment, and those of the tufted titmouse are representative of the family. Titmouse 'chick-a-dee' mobbing calls and seet calls (for attack) have been well-characterized and encode tremendous specificity with respect to predation risk (Sieving et al., 2009; Templeton et al., 2005). Many forest bird species in North America respond appropriately to titmouse anti-predator calls (Hetrick, 2006; Hurd, 1996; Langham et al., 2006; Sieving et al., 2004); including Northern cardinals. Using calls with known different levels of predation threat encoded in them, I broadcasted them to cardinals and was able to set clear expectations about how exploratory behavioral components should change given appropriate anti-predator responses (Table 3-1). Results matched predictions quite well: with increasing threat level encoded in titmouse vocalizations, active movements declined to a greater degree (Figure 3-1 A, B). Measures of

thoroughness of space explored generally followed the same pattern as flights and hops (above; Figure 3-1 D). Scanning behavior, generally held to reflect vigilance levels, were influenced by vocalization treatments as well. Cardinals significantly increased their scanning time with increasing predation risk (Figure 3-1 F) and the rarely-seen still-scanning behavior was induced by the highest risk treatments (Figure 3-1 G, H). Thus, cardinals' spatial decision-making was very finely tuned to, and influenced by, socially-derived information about predation risk (Figure 4-1, right side).

Though I only used one species in this experiment, results from the first experiment strongly suggest that the changes in exploratory behavior with perceived risk (as from social information) will manifest differently across species. Ground, canopy, mid-story, or social versus solitary species, because of the unique combinations of behavioral components in the make-up of their behavioral syndromes, will act out avoidance or attraction or vigilance in different ways. The results of this experiment have generated many ideas about how exploratory behavior, and its correlates, can be affected by heterospecific interaction through social information exchange.

In summary, I established, first, how personal information gathering, expressed as exploratory behavior, varied across species with different and similar natural history traits, and how ecologically relevant social information can affect exploratory behavior at a small scale. Given the profoundly strong correlations established between many aspects of behavioral ecology and exploratory behavior, including large-scale spatial behaviors such as dispersal, future studies of exploratory behavior may provide understanding of functional connectivity of landscapes (Figure 4-1). For so many species, movement among critical habitat patches and regions will be the key to

persistence and continued evolution under the dramatic land cover and climate change scenarios that are being developed for global environments (Virkkala et al., 2008). This analysis provides another potentially useful tool for helping to understand and predict species persistence in a rapidly changing world.

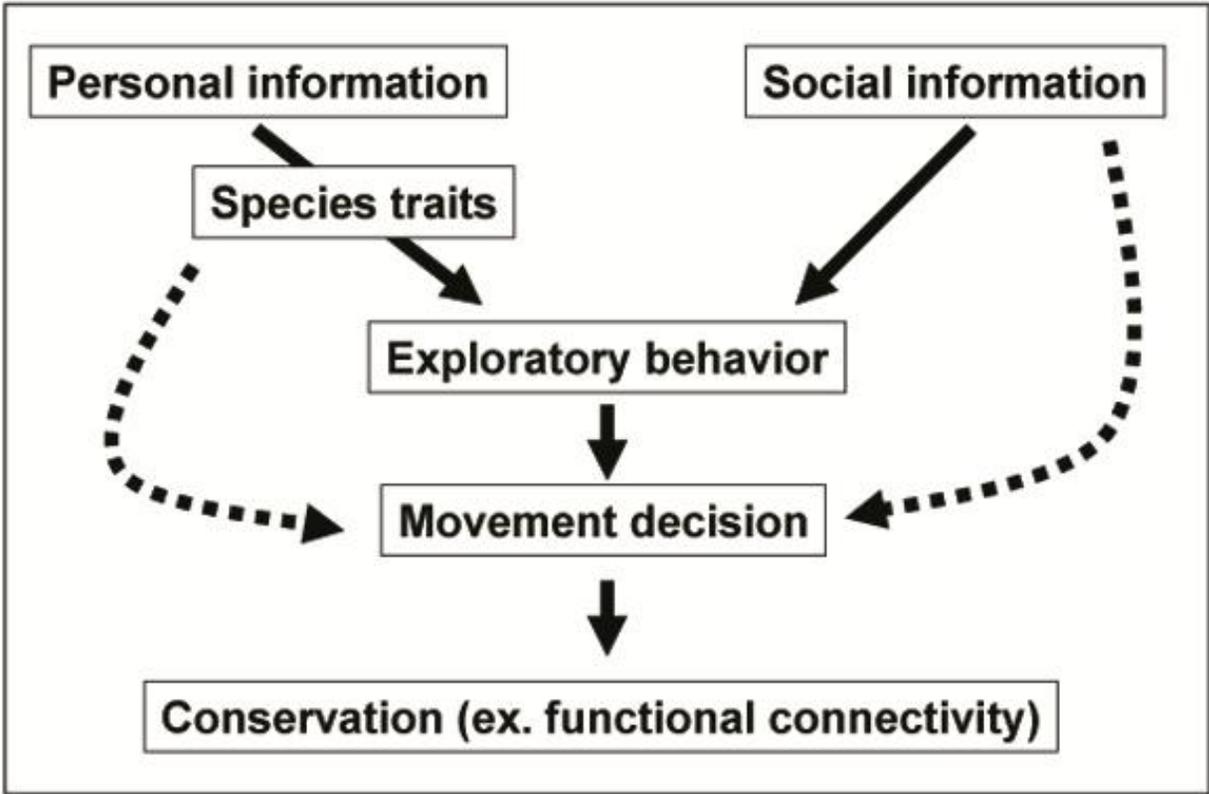


Figure 4-1. Linking knowledge from this study to future researches and application goals.

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BIOGRAPHICAL SKETCH

Ping Huang was born and raised in Taiwan. She is the youngest child and has one older brother. Ping Huang inherited her parents' appreciation of nature. Observing the metamorphosis of caterpillars, watching firebugs flying in front of her grandfather's farm, visiting the wetland preserve of Black-faced Spoonbill in Tainan and other similar outdoor activities were always a part of life in her childhood upbringing. Her interests in animals and natural science rooted on those experiences. Even though diagnosed as a cancer patient at age 16, she never gave up her dream in studying biology and ecology in the future. Actually, the disease taught her to cherish what she has and to own the faith on herself. All the struggles paid off eventually.

Ping Huang later entered Life Science Department in Tunghai University, Taiwan. It was during her years as an undergraduate student there that she learned her life's passion would be behavioral ecology, ornithology and conservation activities. She graduated from Tunghai University with a BS degree in the spring of 2006. After spending times assisting several different field researches, she fortunately got the chance to enter the master's program in Wildlife Ecology and Conservation Department, University of Florida in the fall of 2008. She then chose bird exploratory behavior as her master's study. She just got the Ph D admission from Department of Biology, University of Florida; the higher education will start in the fall semester of 2010. Her long-term career goal is to find a position in a museum, government agency, non-governmental organization concerned with conservation issues, or a university department, where she can conduct basic researches and educate more people about the urgency of our environmental conservation issues as well.