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Associations of Behavioral Profiles with Social and Vocal Behavior in the Carolina Chickadee (Poecile carolinensis)

Ellen H. Williams

University of Tennessee - Knoxville

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To the Graduate Council:

I am submitting herewith a dissertation written by Ellen H. Williams entitled "Associations of Behavioral Profiles with Social and Vocal Behavior in the Carolina Chickadee (Poecile carolinensis)." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Psychology.

Todd M. Freeberg, Major Professor

We have read this dissertation and recommend its acceptance:

Gordon M. Burghardt, Neil Greenberg, Wesley G. Morgan

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Carolyn R. Hodges

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ASSOCIATIONS OF BEHAVIORAL PROFILES WITH SOCIAL AND VOCAL BEHAVIOR IN THE CAROLINA CHICKADEE (*POECILE CAROLINENSIS*)

A Dissertation Presented for the
Doctor of Philosophy Degree
The University of Tennessee, Knoxville

Ellen H. Williams

August 2009

Dedicated to Ginger, the most loyal and
and loving best friend, who stood by my side for the past
fifteen years, and who will never be forgotten.
March 1993 – October 2008

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ABSTRACT

The research described here tested for relationships among behavioral consistency, personality traits, and communicative behavior in a socially and vocally complex avian species, the Carolina chickadee (*Poecile carolinensis*). First, I tested for the existence of behavioral profiles, also known as non-human animal personality, across varying contexts (presence of predator, foraging within a novel object, and novel conspecific) in the laboratory. I found evidence for behavioral profiles encompassing behavioral patterns such as activity, affiliation, aggression, and boldness. Second, I incorporated a larger social component to these studies by testing birds housed in social groups in semi-naturalistic aviary settings. In the aviaries, I tested for behavioral profiles in more complex social environments, and also tested for relationships between personality-like influences and the chick-a-dee call, the key vocalization of this species used in social organization. There has been very little work devoted to testing relationships between personality-like traits and communicative behavior. As in the laboratory study, I found evidence for behavioral profiles in the more complex social setting of the aviaries. I found aggression and boldness to be strongly, positively correlated with chick-a-dee call rate. Additionally, I found particular note types within the chick-a-dee call to be indicative of both aggressive behavior and avian predator presence. Taken together, findings from these studies indicate that personality-like influences in chickadees may play an important role in constraining variation in individual, social, and communicative behavior.

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INTRODUCTION

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Background: the behavioral plasticity / consistency debate

Individual behavioral differences are familiar to all of us. From personal experiences we would all most likely agree that there is great variation in personality among individuals (Gosling & John, 1999; Buss, 2008). For example, we find that some individuals tend to be more aggressive while others tend to be more submissive (Huntingford, 1976; Riechert & Hedrick, 1993). Likewise, we find that some individuals thrive on risky, relatively dangerous experiences, while others exhibit shyer behavioral tendencies. This latter phenomenon is referred to as the "shy-bold" continuum, a "fundamental axis of [human] behavioral variation" (Wilson, Clark, Coleman, & Dearstyne, 1994, page 250). Furthermore, within an individual, we find that personality traits are relatively stable and repeatable (Armitage & Van Vuren, 2003). Traditionally, however, researchers were hesitant to make this and similar claims with regard to non-human animals.

Individual variation in behavioral responses and between-individual differences in non-human animals were largely ignored and oftentimes considered as measurement error of, or nonadaptive variation in, behavior (Burghardt, 1975; Coleman & Wilson, 1998; Dall, Houston, & McNamara, 2004). It was assumed that individuals within a species responded similarly in different situations. Individuals can experience a very wide range of possible environments and stimuli, and one type of behavioral response (or a single variant of a behavioral phenotype) will not always be adaptive across different situations. Therefore, it seems that the most adaptive, optimal behavior for any individual animal would be to exhibit plasticity in responding to new environmental situations. Humans, on the other hand, are often believed to respond to new environments largely based on personality traits. Why this discrepancy?

For many years, behavioral ecologists have studied multiple behavior systems of species, assuming that individuals of each species, or population, behave in adaptive ways to solve problems they face. Animals are viewed to exhibit behavioral plasticity – a flexible ability to modify behavior depending on the environment and the conditions of that moment (West-Eberhard, 1989). Such flexibility to changing environments is often viewed as an advantageous behavioral strategy (Wilson, 1998; Fairbanks, et al., 2004). On the other hand, if we apply a personality framework to non-human animals, it raises notions of limited behavioral plasticity for different environmental contexts.

More recently, researchers have begun to apply such a personality framework, finding that non-human animals exhibit great variation across individuals and often show consistency of behavior in different contexts. Thus, two major hypotheses emerged regarding animal behavior patterns in different contexts: the adaptive behavioral plasticity hypothesis and the behavioral syndromes hypothesis. First, the adaptive behavioral plasticity hypothesis states that variation across individuals of a species is context dependent (Wilson, Clark, Coleman, & Dearstyne, 1994; Coleman & Wilson, 1998; Neff & Sherman, 2004). Context sensitivity occurs when individual traits vary with contextual changes. In adopting this framework, emphasis is centered around high levels of behavioral plasticity and individuals responding in optimal ways depending on the current situation, as described above. If an individual can modify its behavioral responses to match a very wide range of environmental situations, it seems that this would be highly adaptive.

On the other hand, the behavioral syndromes hypothesis (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004) assumes limited behavioral plasticity, suggesting that individuals are constrained in regards to behavioral strategies due to behavioral syndromes (Gosling, 2001; Sih, Bell, & Johnson, 2004; Dingemanse & Reale, 2005). The behavioral syndromes hypothesis states that individuals exhibit stability in behavioral responses across multiple contexts (Sih, Bell, Johnson, and Ziemba, 2004). A clear prediction of the behavioral syndromes hypothesis is that observing an individual's behavior in one context should reliably predict how it would behave in another context (Sih, Bell, & Johnson, 2004). A behavioral syndromes framework acknowledges that there may be slight variations in behavior within individuals across situations, but those individuals that tend to be more aggressive or bolder, will consistently be more aggressive or bolder (maintaining rank order). It has been proposed that an increased understanding of behavioral syndromes is fundamental to the study of behavior because they can limit behavioral plasticity, work to explain non-optimal behavior, and contribute to the maintenance of individual variation in behavior (Sih, Bell, & Johnson, 2004).

There are limits or constraints on the extent of behavioral plasticity (Futuyma & Moreno, 1988). A couple of the potential costs of behavioral plasticity include information costs and production costs (DeWitt, Sih, and Wilson, 1998). An information cost occurs when the individual is gathering information about the surrounding environment. For example, in a predator-rich environment, an individual needs to gather information about the predator, possibly by approaching the predator, engaging in predator inspection behavior, producing alarm calls, or some other means of detection, and oftentimes this can be very risky. Furthermore, in situations such as this, 'noise' is inevitable and detection errors may be common (McElreath & Strimling, 2006). Additionally, there are energetic costs associated with gathering information or making an error regarding the immediate environment (DeWitt, 1998). Production costs of a plastic strategy would include the energy and resources required by the individual to produce multiple behavioral patterns and responses (DeWitt, Sih, and Wilson, 1998). The costs associated with the ability to produce various phenotypes likely are greater than any potential production cost associated with producing a fixed, stable phenotype (DeWitt, Sih, & Wilson, 1998).

However, similar to phenotypic plasticity, behavioral stability (also referred to as phenotypic stability), can be maladaptive in some environments. For example, one of the worst scenarios for an individual who exhibits behavioral stability would be to find itself in a contrasting environment – this is an example of a mis-matched phenotype (DeWitt, Sih, & Wilson, 1998). Such mis-matches, or mistakes, can occur in both phenotypically plastic and phenotypically stable individuals (DeWitt, Sih, & Wilson, 1998), but clearly the plastic strategy should typically result in lower levels of mis-matching than the behavioral syndromes strategy.

A behavioral syndromes framework asserts that an individual that is aggressive in a territorial / intruder context will be expected to exhibit similar aggressive tendencies in other contexts, such as foraging, predatory, or mating contexts. However, this does not make perfect sense from an evolutionary perspective. For example, although an aggressive response may be adaptive in the presence of an intruder, it is most likely maladaptive in a courtship or mating context. Therefore, some animals will do well in one context and not in another, while for others, the reverse may be true – this likely is responsible for the maintenance of individual variation (Sih, Bell, Johnson, & Ziemba, 2004). Each context that is encountered has its own specific characteristics and potentially requires a different response, especially those contexts that are directly related to survival or reproduction (Coleman & Wilson, 1998). However, animals do seem to exhibit stable behavioral tendencies across contexts. Thus, work is needed to address this puzzle by testing context-specificity of behavior versus generalized behavior across contexts.

A series of studies performed on pumpkinseed sunfish (*Lepomis gibbosus*) tested the adaptive behavioral plasticity and behavioral syndromes hypotheses. Wilson, Coleman, Clark, and Biederman (1993) trapped fish using two methods, a minnow trap and a seine (a fish net). It was assumed that the fish that voluntarily entered the trap were bolder than those that were trapped via the net. These two groups were then assessed using a "shy-bold" continuum dimension and it was found that the trapped "bold" fish habituated to captivity quicker and tended to forage further from the shore; that is to say, they were more likely to forage in open-water compared to the seined "shy" fish. Additionally, Wilson, Coleman, Clark, and Biederman (1993) conducted a gut analysis and discovered that the trapped "bold" group had ingested much more open-water prey than the seined "shy" individuals, suggesting that this "shy-bold" dimension may predict environmental exploration and the ability to exploit a greater diversity of food resources. This experiment demonstrates that, in this species, a "shy-bold" continuum exists and that the behavioral traits of shyness and boldness are applicable across multiple contexts, offering support for the behavioral syndrome hypothesis. The second study was a semi-naturalistic study in which the fish were presented with a threatening stimulus (red-tipped meter stick to mimic a natural predator) and a novel food item (Coleman & Wilson, 1998). Results of this study indicated that individual behavior within each context was highly repeatable; however, behavioral responses did not correlate across the two contexts. In other words, individual behavioral responses were context-specific. Fish that exhibited boldness by approaching the meter stick were no more likely to approach the novel food item than those fish classified as shy during the meter stick presentation. Findings from this experiment support the adaptive behavioral plasticity hypothesis. With two different data sets supporting each hypothesis, research directions are now aimed at testing these ideas across multiple species, as well as within and across various contexts.

Terminology and the origin of *behavioral profiles*

Numerous terms have been used to reference personality-like influences, most frequently described as behavioral syndromes, personality, behavioral profiles, temperament, behavioral polymorphisms, and coping strategies (Burghardt, 1975; Gold & Maple, 1994; Boissy, 1995; Sih, Bell, & Johnson, 2004; Groothius & Carere, 2005; Gosling, 2008). In collapsing the many definitions of non-human animal personality into a simple definition, personality-like influences can be described as intrinsic characteristics of an individual that can influence, or constrain, its behavioral responses spanning across multiple contexts. In discussing my program of research, I have chosen the term *behavioral profiles* to refer to non-human animal personality or behavioral syndromes. Specifically, I define a behavioral profile as the core behavioral patterns that an individual typically exhibits, regardless of specific contextual and social factors. I chose this term because my research interests overlap the ideas behind the behavioral syndromes paradigm, yet I am incorporating interesting facets not yet included in the behavioral syndrome literature, described in greater detail below. Furthermore, I find that the term *behavioral profiles* does not carry with it the subjective connotations that the term personality does; as it is a new direction in ethology, it is deserving of its own separate term.

Research in ethology and behavioral ecology is beginning to explore ideas of individual variation by investigating the existence of behavioral profiles and the stability of non-human animal behavioral traits (Sih, Bell, Johnson, & Ziemba, 2004). Although behavioral profiles are a relatively new branch to the field of animal behavior (Gosling, 1998; Dall, Houston, & McNamara, 2004; Sih, Bell, Johnson, & Ziemba, 2004), these ideas have deep historical roots in human personality theory (Gosling & John, 1999), as well as ethology and comparative psychology (Darwin, 1872; Hebb, 1946; Burghardt, 1975; 1985; Griffin, 1998).

An important distinction in discussing terminology is the difference between a behavioral trait and a behavioral profile. A behavioral trait, also referred to as a behavioral type, is measured using a single dimension or axis and represents repeated and correlated behavioral responses within a single context (Sih, Bell, Johnson, & Ziemba, 2004; Smith & Blumstein, 2008). A behavioral profile represents behavioral correlations across contexts, or context-independent personality (Sih, Bell, Johnson, & Ziemba, 2004; Smith & Blumstein, 2008). Within a behavioral profile, individuals have certain behavioral traits, such as bolder versus less bold or more aggressive versus less aggressive (Sih, Bell, & Johnson, 2004). Many more studies of behavioral traits exist than those that truly assess behavioral profiles. For example, in reference to aggression, when an individual repeatedly responds in an aggressive manner within a single context, that is an example of a behavioral trait. When aggressive behavior 'spills-over' to both foraging and predatory contexts, that demonstrates a behavioral profile (Johnson & Sih, 2005). Behavioral profiles can also encompass more than one behavioral trait. For example, a consistently aggressive individual may also tend to exhibit traits of boldness and higher activity levels.

Oftentimes, behavioral traits are easily captured using behavioral axes, such as the "shy-bold" continuum (Wilson, 1998). Such a continuum allows for relatively easy ranking of individuals, thus allowing for direct comparisons both between and within individuals. Furthermore, the continuum reference helps to clarify how an individual's behavior is to be assessed. In assessing behavioral variations between individuals, there have been three primary approaches to quantifying behavioral traits: (1) behavioral coding, (2) rating of personality traits, and (3) naturalistic observation (Gosling, 2001). Most often, studies implement behavioral coding, in which subjects are tested while manipulating the immediate context, such as presentation of novel stimuli or predator models. This is the approach I have taken in my research. Personality studies using ratings of traits tend to be those studies conducted in captivity, either by owners or, most often, zoo keepers. For example, using the 'Gorilla Behavior Index,' traits such as extraversion, dominance, and fearfulness were assessed in zoo-housed gorillas (Gold & Maple, 1994). Lastly, naturalistic observation studies are frequently utilized when assessing nest defense, mating, and courtship behaviors. For example, in a study of great tits, field observations were conducted in breeding territories of great tits to observe next defense behavior, when a human observer was standing 1 – 2 m from the nestbox (Hollander, Overveld, Tokka, & Matthysen, 2008). Across all three approaches, there have been numerous terms used in the literature to describe behavioral traits – oftentimes there are multiple terms for the same behavior. In a broad comparison, activity level or general exploration, aggression, and fearfulness or timidity, are the three most frequently measured behavioral traits (Gosling, 2001).

Behavioral profiles and vocal communication

Despite the fundamental importance of vocal communication to the lives of many animal species (Hauser, 1996; Bradbury & Vehrencamp, 1998), it is one behavior system that has been relatively neglected across both fields of non-human animal and human personality research. Gosling (2001) conducted a rather thorough review of non-human animal personality covering 187 behavioral studies encompassing 64 species, none of which addressed vocal communication. However, interest is arising in how communicative behavior may be generally linked to behavioral profiles and personality. In responding to stimuli, both human and non-human animals often react and interact using some mode of communication; thus, there should be links between behavioral profiles and communicative behavior.

Oftentimes, individuals respond to environmental stimuli using vocal or non-vocal communicative patterns (Hauser, 1996). For example, in the Bonobo (*Pan paniscus*), one of our closest relatives, multi-model signaling has been shown to be most effective in communicative interactions and in eliciting behavioral responses from the receiver (Pollick & de Waal, 2007). Duncan and Fiske (1977) report that humans communicate using subtle non-vocal cues to indicate when they will start speaking, as well as when a conversation has come to its end. Similar questions have been investigated across a few other primate species, but surprisingly, almost no research has been aimed at understanding personality-like influences on individual differences in communicative behavior.

In humans, modes of non-vocal signaling have been studied in connection with specific behavioral traits. For example, an assertive individual is often perceived to dominate another by exhibiting more direct eye gaze with an upward chin, whereas a shy individual is typically thought of as submissive, interacting with a lowered head and a lowered eye gaze (Hall, Coats, & Smith LeBeau, 2005). It is not known what types of vocal behavior may correlate with these traits. However, the importance of these traits is clear in that these non-vocal patterns of behavior can communicate quite a lot about the individual (Lindblom, 1990).

Communicative behavior is closely linked with social behavior and interactions with another individual. Communication is an interaction between a signaler and a receiver, in which the signaler produces some type of signal and the receiver's behavior is modified or changed (Wilson, 1975; Hailman, 1977; Krebs & Davies, 1993). Communicative behavior can take a multitude of forms: olfactory / chemical cues, visual displays, and tactile, for example. Throughout my research, communicative behavior is studied primarily through the channel of vocalizations. If an individual's vocal behavior communicates something to another, it has the potential to modify another individual's internal state and produce a behavioral reaction (Burghardt, 1977; Patterson, 1983). Patterson (1983) claims that non-vocal human behavior informs the receiver of the signaler's characteristic disposition, and therefore potentially her/his willingness to interact with the receiver, a possible indicator of social affiliativeness. Assessments of communicative behavior may lead to more informative conclusions regarding sociability, as well as vocal behavior's role within a social realm (revisited in this and later chapters).

By the definition of behavioral profiles, communicative behavior in individuals should be largely consistent over time and across varying contexts. Partial support for this claim has been found in humans with regard to non-vocal behavior, specifically eye gaze and physical distance while speaking (Daniell & Lewis, 1972; Patterson, 1983). Likewise, Patterson (1983) showed that additional non-vocal behaviors such as forward lean, body stance, and eye gaze were also consistent over time.

Extraversion and communication

Much of human communication is non-vocal and in order to succeed in communicative interactions it is believed that an individual needs to be competent at perceiving and responding to non-vocal cues. It is generally accepted that extraverts are more socially competent than introverts (Akert & Panter, 1988) and even some of the earlier theoretical frameworks exploring these ideas suggest that extraverted individuals are superior at deciphering non-vocal cues (Allport, 1924; Sapir, 1958; Akert & Panter, 1988; Lieberman and Rosenthal, 2001). Carl Jung (1971) suggested that extraverted individuals are more attentive to the external world and surrounding cues than introverted individuals. Such awareness to external stimuli may be a driving factor for an increased necessity for communicative skills. Communicative interactions between two or more individuals is arousing, stimulating, and possibly rewarding for those involved (Akert & Panter, 1988; McCrae & Costa, 2008). It is possible that such stimulation is more rewarding for extraverted individuals, causing them to engage in such communicative behavior more frequently.

Extraversion is a widely researched personality trait in both the human and non-human personality literature (Gold & Maple, 1994; King & Figueredo, 1997; Gosling & John, 1999; Gosling, 2001). In humans, extraversion is positively correlated with louder speaking and an increased tempo of communicating (Siegman, 1978). In addition, Siegman (1978) found extraversion to be positively correlated with amount of speech – the more extraverted an individual, the more speech delivered. Extraverted individuals also maintain a higher percentage of direct eye contact when interacting with another individual (Kendon & Cook, 1969). Generally speaking, extraverts enjoy involvement and interaction with others, seek social stimulation, and possibly expect or desire increased involvement with others (Akert & Panter, 1988). In comparison, an introverted individual is found to report high social anxiety and to seek less affiliation with others (Sapir, 1958). Introverted individuals are found to stand further away from others, display less touching while speaking, a lower percentage of eye contact, and less speech overall, in comparison to extraverted individuals.

Similar parallels between traits related to extraversion and non-vocal behavior have not yet been investigated in the non-human population, and until very recently, correlates between specific behavioral traits and any dimension of communication, such as type of vocalization produced, had not been studied in any non-human species. One potential link between extraversion and non-vocal behavior reported in non-human animals resembles that found for affiliation and social interactions in humans. In humans, extraverts tend to sit closer to others than do introverts (Pederson, 1973). Freeberg & Harvey (2008) report that captive male chickadees (*Poecile carolinensis*) with higher call rates spend more time in close proximity with a female flockmate, suggesting that vocal production is positively correlated with affiliation.

Beyond research on specific personality characteristics such as extraversion, studies have recently been conducted to examine overarching character dispositions and language skills. In a study of 20-month-old human infants, highest language productivity was found to be positively correlated with positive mood, persistence, and adaptability, and negatively correlated with distractibility (Dixon & Smith, 2000). Thus, for these 20-month-old infants, emotional stability and particular temperamental characteristics (mainly adaptability, mood, and persistence) were good predictors of verbal production and communication skills. As mentioned previously, most of the relatively small amount of research linking personality traits to communicative behavior lies in the human literature. These ideas are just beginning to emerge in the field of animal behavior, and there are many questions that need to be answered.

Behavioral profiles and social settings

Much of the behavioral profile research in non-human animals has been conducted on isolated individuals. Many of the experimental tests of behavioral profiles place the focal animal in a testing chamber or separate it in some way from the group (but see recent work from Sih & Watters, 2005; Kinnally, et al., 2008; Nelson, Wilson, & Evans, 2008; Uher, Asendorpf, & Call, 2008). Such a highly controlled environment allows for careful documentation of personality traits and provides an opportunity to study personality development by repeatedly observing the same individuals over a period of time (Gosling, 1998). Unfortunately, this methodology may hinder our ability to extrapolate to more naturalistic settings (Wilson, Coleman, Clark, & Biederman, 1993). It is important to acknowledge that some traits may not be expressed in their natural form when testing a social organism in a solitary situation, and captive studies may not always accurately replicate behavioral responses in more naturalistic, field studies (Wilson, Coleman, Clark, & Biederman, 1993). Many of the species studied in this line of research are highly social; however, the process of taking an individual out of a social context and placing it in an isolated environment may result in a change of behavior that is largely due to the testing condition, thus limiting validity of the experiments. In order to examine potential effects of the testing situation, studies need to be developed and conducted within rich, social environments. For example, Malloy and colleagues (2005) began to address this by testing for 'partner effects' in mice by observing mice engaging in multiple social interactions with other mice, reporting individual consistency for a variety of behavioral traits within an explicitly social context, specifically a dyadic relationship. However, this study did not test the mice across varying functional contexts and did not observe individuals when alone, an important comparison. Unfortunately, a more complete experimental design, one that incorporates both the social context and a comparative dimension of the animals when alone, is extremely rare, and very little is known regarding how an individual responds in a social setting, compared to when it is alone.

Valuable information can be gained from data collection occurring in both social and nonsocial environments. As mentioned, it is rare to find a study which incorporates both types of environments (Gosling, 1998). Taking this into consideration, my research projects aimed to test for evidence of behavioral profiles both in the laboratory and in more naturalistic settings, while simultaneously looking for an effect of the social environment on vocal and non-vocal behavior. Specifically, I created a laboratory study that tested the same individuals in both social and nonsocial contexts. Next, I expanded this work toward a more naturalistic setting by conducting observations of larger social groups in large outdoor aviaries.

Behavioral profile work in the great tit

Considerable research on behavioral stability, behavioral traits, and behavioral profiles has been conducted in the great tit (*Parus major*), a species closely related to my study species, the Carolina chickadee. Interestingly, some great tit studies support behavioral stability and behavioral profiles (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005), while others offer support for context-sensitivity and context-dependency (Dingemanse & de Goede, 2004). These great tit studies mainly address specific variants of exploration (slow versus fast explorers of new environments) and potential correlates with both reproductive success and nest success (for example, fledging size and brood number: Hollander, Overveld, Tokka, & Matthysen, 2008; Both, Dingemanse, Drent, & Tinbergen, 2005). In great tits, individuals vary in exploratory behavior of novel environments or situations (Verbeek, Drent, & Wiepkema, 1994) and the behavioral traits of exploration and aggression appear to co-vary within individuals (Verbeek, Boon, & Drent, 1996). Fast explorers, in this case, arrive at mating grounds earlier, therefore acquiring territories of higher quality. Additionally, individuals described as fast explorers (that also exhibit high levels of aggressive behaviors) appear to have advantages over slower explorers that are less aggressive. Individuals adopting a slow exploration phenotype are more sensitive to changes in the environment (Verbeek, Drent, & Wiepkema, 1994). Slow explorers tend to be better parents and are more adept at foraging in changing conditions because they are more aware of, and more sensitive to, environmental changes. Thus, presumably, slow explorers are better at responding to novel stimuli. Intriguing results involving fitness and nest success were found in relation to behavioral traits of the parents. Larger, more successful young were found to be the offspring of pairs in which either both mother and father were fast explorers or both were slow explorers (Both, Dingemanse, Drent, & Tinbergen, 2005). These findings support the existence of behavioral profiles within this species.

As mentioned above, other studies involving great tits found evidence of context-sensitivity. Great tits have linear, sex-specific dominance hierarchies, where males are most often the more dominant sex (Dingemanse & de Goede, 2004). Fast explorers had higher dominance ranks for territorial males, but this finding did not hold for non-territorial males (Dingemanse & de Goede, 2004). Territorial birds were more dominant when closer to their territory than when further away, and dominance was negatively correlated to distance (the further an individual was from its territory, the lower the dominance rank). Additionally, Dingemanse & de Goede (2004) report that when males lose an aggressive interaction, fast explorers have a more difficult time coping with the loss and tend to rapidly lose dominance status. They conclude that the relationship between dominance and exploratory behavior is context dependent and is a function of both the individual and the immediate social environment.

Many factors can influence dominance rank and the development of dominance hierarchies. In the great tit, size, age, territory, previous interactions (winning versus losing), exploratory behavior, and aggressive tendencies all impact dominance. Also in this species, dominance hierarchies do not develop quickly; there appears to be a dynamic period in which individual ranks repeatedly shift, until settling and then establishing rank order (Verbeek, de Goede, Drent, & Wiepkema, 1999). In an aviary study involving great tits, this dynamic period peaked at three days and dominance hierarchies began to stabilize at that point (Verbeek, de Goede, Drent, & Wiepkema, 1999).

Using a closely related species to the great tit, the Carolina chickadee (*Poecile carolinensis*), I tested similar ideas to begin to investigate behavioral profiles in this new species. These two species have fairly similar social structures; although chickadees are more territorial, explained in greater detail below (Smith, 1972; Smith, 1976; Hogstad, 1989). The studies described above involving great tits build a strong foundation for my dissertation research, allowing me to broaden and expand further investigation of behavioral profiles and possible links to communication.

Carolina chickadees: a model study species

To address the missing links of sociality and communicative behavior, I chose Carolina chickadees, *Poecile carolinensis*, as my study subject - a socially and vocally complex avian species. The complex group organization of chickadees allows for individuals to have multiple interactions with others. During the spring and summer months, chickadees live in mated pairs and maintain these female-male bonds throughout the breeding season. During the early fall months, female-male pairs of chickadees will join territorial groups, maintaining these cohesive, stable groups throughout the winter until the breeding season the following spring (Smith, 1972; Ekman, 1989; Mostrum, Curry, & Lohr, 2002). This territorial flock structure results in individuals primarily interacting with members of their immediate social group (flockmates).

In addition, chickadees are a highly vocal species with a complex vocal system (Hailman, 1989; Lucas & Freeberg, 2007), and therefore are excellent subjects to address potential correlates between communication and behavioral profiles. Chickadees possess large, diverse repertories of recordable vocal and non-vocal behavior linked to social contexts, providing a rich variety of behavioral measures to test multiple hypotheses. For example, the chick-a-dee call, the most frequent vocalization in the chickadee repertoire, is a communicative tool between individuals for maintaining social cohesion (Smith, 1972; Ficken, Ficken, & Witkin, 1978; Hailman, 1989), as well as a recruitment call and an indicator of predator detection (Templeton, Greene, & Davis, 2005). The chick-a-dee call is composed of a small number of distinct note types (Bloomfield, Phillmore, Weisman, & Sturdy, 2005) and recent research indicates that variation in these note types can transmit diverse messages (Hailman, Ficken, & Ficken, 1985; Hailman & Ficken, 1986; Lucas & Freeberg, 2007). Due to their complex social structure (Ekman, 1989; Mostrum, Curry, & Lohr, 2002) and complex vocal communication system (Hailman, 1989; Lucas & Freeberg, 2007), chickadees are ideal for asking questions regarding how behavioral profiles and social contexts may influence the expression of both vocal and non-vocal behavioral traits.

Behavioral stability in the Carolina chickadee

As a preliminary approach to this line of research, I conducted a laboratory study asking if phenotypic stability in chickadees would exist if the immediate social context was altered (Harvey & Freeberg, 2007). This research project questioned whether an individual would exhibit behavioral plasticity or behavioral stability across a changing social context. To test this, I captured twenty-eight Carolina chickadees (fourteen female-male pairs) from two locations in east Tennessee, Oak Ridge and Knoxville, separated from one another by roughly 40 km. Chickadees are a non-migratory species, and the two locations represent two distinct groups of individuals. The female and male of each pair were from the same flock, and thus presumably had had substantial previous interactions with one another; pairs trapped from different trapping sites were from different flocks. Therefore, members of a single pair were familiar with one another, but individuals across pairs had no prior experience with one another.

During the first month in captivity, pairs were housed in chambers vocally and visually isolated from all other pairs, and baseline observations were taken to assess individual behavior in the presence of one's familiar flockmate. During the second month of captivity, the social context was manipulated by introducing a novel opposite-sexed conspecific (Harvey & Freeberg, 2007). Several vocal and non-vocal behaviors were measured prior to and following the shift in social context. Behavioral measures collected included physical activity level, vocal production, affiliation or close proximity, and a range of aggressive behaviors. Results revealed strong behavioral stability despite the major shift in social context. Baseline measurements of behavioral traits such as activity, call rate, and aggression were found to be strong predictors of how an individual behaved when housed with the unfamiliar opposite-sexed conspecific. For example, a male from Knoxville that was relatively aggressive when in the presence of its female flockmate, was also relatively aggressive when housed with a novel female from Oak Ridge.

As a preliminary test for potential links between association or affiliation and communicative behavior, we extended the behavioral data described above and examined potential correlates between the amount of time each male spent in close proximity with its flockmate and the number of chick-a-dee calls that male produced. Our assessment of affiliation was frequency of the two flockmates being perched within 15 cm of one another for two or more seconds. There was a significant positive relationship between rates of affiliation and rates of call production; specifically, the more time individuals spent in close proximity, the more calls the male produced (Freeberg & Harvey, 2008). Although these results reveal that the social context can be associated with call rate, this study lacked information regarding how call composition or the structure of the call may be associated with individual traits. Furthermore, this study only assessed behavioral traits across a strictly social context, and not functionally distinct contexts like the presence of novel stimuli or predator stimuli. These are questions addressed in my dissertation research, aimed at investigating how call complexity and communicative behavior may relate to behavioral profiles.

General overview

The overarching aim of my dissertation was to explore the behavioral profiles paradigm in studying individual variation in vocal and non-vocal behavior. Virtually nothing is known about how behavioral profiles correlate with communication patterns in animals. Although there is a large and growing literature on behavioral profiles in non-human animals, the majority of this research has been conducted on isolated, individually-tested subjects; therefore, little data are available to answer whether behavioral profiles exist in more natural and socially-complex settings. In Chapter 2, I describe a study that tested for the existence of behavioral stability across varying contexts in female-male pairs of Carolina chickadees in controlled, laboratory settings. Chapter 3 details a study of behavioral profiles in social behavior and vocal production of chickadees housed in groups in large outdoor aviaries. In Chapter 4, I describe a study, which is an extension of the aviary study described in Chapter 3, assessing potential links between behavioral profiles and chick-a-dee call structure and use in flock-sized groups. In Chapter 5, I discuss some implications of my findings for further understanding and study of behavioral profiles and possible links to communication.

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CHAPTER 2

DOES THE SOCIAL CONTEXT INFLUENCE BEHAVIORAL PROFILES?

ABSTRACT

This study assessed behavioral profiles, or non-human animal personality, in a socially and vocally complex avian species, Carolina chickadees (*Poecile carolinensis*). The aim was to test for behavioral consistency in individuals across a variety of contexts while manipulating the immediate social environment. Sixteen female-male pairs of chickadees were tested both together and alone across multiple contexts, including the presence of a predator stimulus, a novel food apparatus, and a novel female conspecific. Dependent measures collected on each individual included activity, agonistic behavior, frequency and type of vocalizations produced, and latency to move or eat following presentation of stimuli. Analyses reveal strong individual behavioral consistency across multiple contexts when the birds were tested both by themselves as well as in the social condition, offering support for the existence of behavioral profiles. Thus, personality-like influences may underlie chickadee behavior in more complex social settings. However, behavioral consistency was not as obvious when comparing across the alone and social conditions. It may therefore be important to take caution when extrapolating from alone testing conditions (the typical testing condition for most behavioral profile research) to social testing conditions.

CHAPTER 2

DOES THE SOCIAL CONTEXT INFLUENCE BEHAVIORAL PROFILES?

Research from a wide variety of species indicates that individuals differ from one another in behavioral responses. Furthermore, these individual differences appear to be consistent across very different contexts (Gosling & John, 1999; Gosling, 2001). Behavior of an individual in one context tends to "spill-over" and match the individual's behavior in another context (Johnson & Sih, 2005). Behavioral variation among individuals and behavioral consistency within individuals have been referred to as animal personality (Gosling, 2001), behavioral syndromes (Sih, Bell, & Johnson, 2004), temperament (Reale, et al., 2007), and behavioral profiles (Boissy, 1995). In the present study, I use the term behavioral profiles to represent the core behavioral patterns typically exhibited by an individual, despite powerful contextual and social influences.

Research is beginning to incorporate a multitude of behavioral patterns in this field of non-human animal personality. For example, the study of individual differences has included activity levels, exploration, dominance, aggressive behavior, courtship, anti-predator behavior, and fecundity (Mori & Burghardt, 2001; Dingemanse, et al., 2003; Dingemanse, Both, Drent, & Tinbergen, 2004; Carere, et al., 2005; Sih & Watters, 2005; Fox, Ladage, Roth, & Pravosudov, 2009). Recently, research has shifted toward investigating suites of behavior in which there are positive correlations between specific behavioral patterns, across diverse contexts (Dingemanse, et al., 2007). For example, water striders that are highly aggressive also tend to exhibit higher levels of general activity (Sih & Watters, 2005) and in great tits, individuals that are more exploratory show greater dispersal (Dingemanse, et al., 2003). Furthermore, personality research in both the human and non-human animal literature suggests that broad dispositions (such as extraversion versus introversion) may be responsible for cross-situational consistency (Epstein & O'Brien, 1985; Gosling & John, 1999).

Little research has been conducted on potential associations between behavioral profiles and communication. Early research in humans tested for relationships between verbal and nonverbal communication and personality, finding that behavior such as tone of voice, body distance, and eye gaze appear to be indicative of particular traits belonging to the signaler (Mehrabian & Weiner, 1967; Patterson, 1983). However, in-depth information linking communication and personality type is lacking from the non-human animal literature (Gosling & John, 1999; Gosling, 2001; Sih, Bell, Johnson, & Ziemba, 2004). Moreover, much of the behavioral profile research has been conducted on isolated individuals – comparing trait consistency in one individual across differing contexts – despite the fact that many of the species studied in this work are highly gregarious (but see Malloy, Barcelos, Arruda, DeRosa, & Fonseca, 2005; van Oers, Klunder, & Drent, 2005; Nelson, Wilson, & Evans, 2008; Uher, Asendorpf, & Call, 2008). Some of these experimental testing situations place the focal animal in a testing chamber and/or separate it in some way from the familiar social environment (Gosling, 2001). Thus, the process of taking an individual out of a familiar social context and placing it in an isolated environment may be partially responsible for observed behavioral consistency or behavioral shifts (see van Oers, Klunder, & Drent, 2005). Therefore, it is important for researchers to be aware that some traits may not be expressed in their natural form when testing a social organism in a solitary situation or when placing that animal in a strictly unnatural captive environment (Wilson, Coleman, Clark, & Biederman, 1993). Taking this into consideration, the current study aimed to test for behavioral profiles and communicative behavior of individuals in two socially distinct conditions: when alone and when with a familiar flockmate (explained in more detail below).

In efforts to incorporate communicative behavior and to test for potential influences of the social context, the Carolina chickadee, *Poecile carolinensis*, is an ideal subject. The chickadee is an avian species possessing a highly complex vocal communication system (Hailman & Ficken, 1986). One of the main vocalizations in chickadees, the chick-a-dee call, is important for maintaining group structure and organization (Lucas & Freeberg, 2007). This call is frequently produced by both sexes year round and appears to be strongly associated both with the complexity of the social environment (Freeberg, 2006) and with affiliative behavior between female – male pairs (Freeberg & Harvey, 2008). In addition to being a vocally complex species, the chickadee has a highly complex social system (Ekman, 1989). Chickadees, a territorial, non-migratory passerine species, reside in female-male pairs during the breeding season and these pairs join territorial groups during the fall months. These territorial, cohesive groups are then maintained throughout the winter

(Smith, 1972; Ekman, 1989; Smith, 1991). As a result, throughout a lifetime, individuals live in both exclusive pairs as well as in stable multi-pair groups (Smith, 1972; Smith, 1991). In using a socially complex species, we are able to extend our research questions beyond individual behavioral consistency into the social realm, testing for an effect of a familiar conspecific on a focal individual's behavior. An earlier study with female-male pairs of Carolina chickadees found strong evidence of behavioral consistency, across a range of behavior, when the social context alone was altered (Harvey & Freeberg, 2007). This earlier study did not test for behavioral consistency across multiple contexts, however.

The present study incorporates both vocal communication and sociality to test for behavioral profiles across various contexts (presence of predator, foraging within a novel object, and novel conspecific) in a controlled laboratory setting. Behavioral patterns recorded include: activity, vocalizations, foraging, neophobia versus neophilia, behavior in the presence of a perched predator, aggression, and affiliation. Throughout the present study, the context (presence of predator, novel food apparatus, and novel conspecific) varied, as well as the social condition (with familiar flockmate versus alone). Hereafter, the term *context* refers to stimulus presentation and the term *condition* refers to alone or social testing. This study sought to address three points: (1) consistency of distinct behavioral traits across the three experimental contexts; (2) consistency of behavioral traits across social and alone testing conditions; and (3) clusters of correlated behavior within each of the three experimental contexts.

METHODS

Subjects and housing

The present study included 32 wild-caught chickadees (16 female-male pairs). All subjects in this study were captured from the University of Tennessee Forestry Resources, Research, and Education Center in Oak Ridge, Tennessee using treadle (potter) traps and mist nets. Stimulus birds (described below) were captured from a site over 30 km away, to ensure that stimulus birds and subjects were unfamiliar with one another. Chickadees are a monomorphic species, but males are slightly larger than females. To sex the individuals, wing chord measurements were taken at the time of capture. Males were classified as having wing chord measurements equal to or greater than 62 mm and females were classified as having wing chord measurements less than or equal to 60 mm (Thirakhupt, 1985). Using this technique for sexing individuals, Williams & Freeberg (unpublished data) paired male and female chickadees in outdoor aviaries and found that six out of seven pairs successfully laid viable eggs. Additionally, when re-trapping during the late spring months, six individuals were re-captured that had been sexed via wing chord measurements. Two of these chickadees, judged earlier to be males by wind chord measurements, had cloacal protuberances and the remaining four chickadees, classified as females, had brood patches, lending support to this sexing method. At capture, individuals were banded with colored, plastic leg bands on the right and left legs, allowing for individual identification. Average body mass at capture for all individuals was 9.22 g (M_{females} = 8.88 g, SD = 0.36; M_{males} = 9.54

g, *SD* = 0.57). Average wing chord measurement for females was 59.41 mm, *SD* = 0.64, and for males, the average wing chord measurement was 62.81 mm, *SD* = 0.66.

Subject pairs were trapped from overwintering flocks to increase the certainty that female-male pairs in this study were familiar with one another and had had previous interactions. The female and male of each pair were captured at the same capture site on the same day and within 60 min of each other, to ensure they were from the same flock. Data collection took place during late fall and winter months to prevent potential influences of courtship behavior, which occurs during the spring and early summer months. The first eight female-male pairs were captured and tested between January and March 2007. The remaining eight pairs were captured and tested between October 2007 and February 2008.

In the laboratory, pairs were housed in cages (0.5 x 0.5 x 1 m) inside MED-Associates Large Monkey Cubicles; pairs in different cubicles were both vocally and visually isolated from one another. Birds had access to three natural, wooden perches within the home cage and were provided with *ad libitum* food and vitaminized water. Food comprised a 1:1 mix of black oil sunflower seed and safflower seed, crumbled suet, crushed oyster shell, and grit. Subjects also received Bronx Zoo diet for omnivorous birds mixed with sprouted seed, chopped fresh fruit and vegetables daily. Each day during the two-week acclimation period, pairs were given two to four mealworms, a highly preferred food item. During this two-week period, all individuals were readily consuming mealworms. In efforts to standardize hunger levels and to maximize motivation for a desired food source during the experimental period, subjects were no longer given mealworms during daily feeding procedures – subjects only received mealworms during the novel object test of behavioral profile testing (additional explanation below). All cubicles were maintained on a light:dark cycle adjusted weekly to match the natural environment. Subjects were given a minimum of two weeks to acclimate to captivity and the housing environment prior to any behavioral testing.

To avoid stress and disturbance, chickadees were tested in their home cages. Bowls of water and seed were left in the home cages during testing. In additional efforts to minimize stress, home cages were covered and carried into the testing room the morning of testing. Pairs were acclimated to this procedure and the testing room one to two weeks prior to the start of the study. Specifically, for one pair at a time, home cages were covered, quietly carried into the testing room, uncovered, and left for up to 60 minutes. No exposure to test stimuli occurred during this process. All pairs spent approximately two hours in the testing room during acclimation. These hours were split into two 30 min and one 60 min time blocks.

Design and procedure

Behavioral tests

Behavioral test procedures were conducted in two socially distinct experimental conditions: each individual was tested (1) alone, and (2) with their opposite-sexed flockmate, with orders of test condition counter-balanced across subjects. No individual was tested a second time within 48 hours of the first experimental test condition. Behavior and vocalizations were recorded using two digital video camcorders (Canon GL2 mini DV), one directed toward the top half of the cage and one positioned toward the bottom half of the cage. In efforts to maintain novelty of the stimuli presented, each individual was tested in the social condition only once.

Dimensions of the testing room were 2.4 x 1.7 x 2.4 m. Prior to testing, subjects were left in the testing room for approximately 15 min. The experimenter then entered the room, turned on the two cameras, left the room, and testing began with a 30 min baseline period. Following baseline, the experimenter entered the testing room to present one of three stimuli, then immediately left the testing room; no person was in the room during testing. Each stimulus was presented for 30 min, separated by a 30 min inter-trial interval. In efforts to avoid order effects due to sequence of testing, stimulus order was randomly assigned at the start of each testing period. Additionally, to minimize stress of the individuals, and to minimize handling of these wild-caught animals, the three stimulus presentations, within each of the two testing conditions, were conducted on the same day. Beginning with the 30 min baseline period, including all three stimulus presentations and inter-trial intervals, there were 144 hours of testing (96 hours of alone testing and 48 hours of social testing). Of these 144 hours, video recording (minus the inter-trial intervals) lasted 96 hours (64 hours of alone recording and 32 hours of social recording). Due to equipment malfunction, data reported are missing the alone testing condition for one subject. All testing was conducted between 0800 and 1500 hours.

Novel object test

A multi-colored square Duplo ® block tower was constructed to encompass a small ceramic bowl (8.9 cm diameter) containing mealworms. The novel object was placed on the floor of the subject's cage. All subjects were readily consuming mealworms from an identical ceramic bowl prior to testing. The novel object was rebuilt, changing the color and placement of individual blocks, prior to each presentation. The novel object did not change in overall size, maintaining dimensions of approximately 19 x 19 x 8 cm throughout the study.

Novel conspecific test

An identical home cage containing one female conspecific (stimulus bird) was covered, carried into the testing room, and placed against the subject's cage. At the start of each trial, the cover was removed. Four conspecifics served as stimulus birds for the subjects in this study (two conspecifics for the first eight subject pairs and two for the remaining eight pairs). Each subject was exposed to a different and novel conspecific, regardless of whether alone or social testing occurred first. Females were used as stimulus birds in efforts to maintain control of potential differences due to using to two different sexes for the stimulus bird.

Predator/threat test

This test represented a threat context and utilized a taxidermy model of a sharp-shinned hawk (*Accipiter striatus*) paired with a 22 sec vocal recording of a sharp-shinned hawk's call (Elliot, Stokes, & Stokes, 1997, Disc 1, Track 40). The model, mounted on a tree limb, was placed 1.4 m from the testing cage in the upper corner of the testing room. The speaker was hidden behind the model draped with a black cloth. From outside the testing room, the experimenter revealed the predator model using a pulley system while simultaneously using a laptop to play the predator recording twice (44 sec call duration).

Video coding and data scoring

The first 15 min of each 30 min stimulus presentation and the last 15 min of each baseline session were assessed for behavioral and vocal data. Therefore, there were 128 hours of video coding (64 hours of alone data and 64 hours of social data). Dependent measures in the alone condition included: activity level, vocalizations produced (chick-a-dee call and gargle), eating or taking a seed, and latency to approach a novel object or to move following the presentation of an experimental stimulus (see Table I for behavioral descriptions). Data collected during the social condition included the behavior described above as well as supplants (an aggressive behavior) and instances of perching close to mate (see Table I). A trained observer independently scored a subset (approximately 8%) of the total data and inter-observer reliability was high (average Spearman's correlation: 0.92, range: 0.85 - 0.96).

Repeatability of behavior

When studying behavioral consistency and stability, a concern that is often raised is the importance of addressing the repeatability of behavioral traits (see also Bell, Hankison, & Laskowski, 2009). A potential concern of the current study is that each of the three stimuli was presented on the same day. Secondly, in regards to the novel object context, there is the potential for motivational confounds involved with the presentation of the mealworm and novel object. Although these are important issues to keep in mind, in designing the present study I had greater concern for the welfare of the animals and believed it more important to minimize the total time that these wild-caught birds were exposed to the stimuli and the total amount of time that they were in captivity.

A previous study conducted in our laboratory housed subjects with an opposite-sexed flockmate in our laboratory chambers (Harvey & Freeberg, 2007). This previous study allowed me to measure behavioral consistency and to address the potential concern of repeatability for the present study. During the aforementioned laboratory study, I collected eight 15-min focal samples each from 28 chickadees spanning a two week period (see Harvey & Freeberg, 2007 for more information). During these focal sample periods, behavioral measures such as activity level, chick-a-dee call rate, supplants, gargles, and eating behavior were collected from each individual.

Statistical analyses

Statistical tests were performed using SPSS, versions 16.0 and 17.0, for Windows. Analyses were conducted using Spearman's Rank correlations to assess consistency of behavioral patterns across baseline and three experimental contexts. A concern with the present study, and other studies of this type, is assessing behavioral profiles with a large number of correlations. Computing multiple correlations may lead to detection of some statistically significant correlations purely by chance. In efforts to minimize this possibility, I implemented sequential Bonferroni correction (also known as Holm’s procedure) within each set of comparisons and used adjusted alpha levels for detection of significance (Holm, 1979; Rice, 1989). Friedman tests were used to assess overall context effects on behavior, followed by pairwise comparisons using Wilcoxon Signed-Ranks tests. Mann-Whitney *U* tests were used to assess differences by sex, as well as for comparisons on latency measures.

Spearman's Rank correlation coefficients were used to assess repeatability of behavior in chickadees housed in our laboratory. Only non-parametric statistics were used, due to the non-normality of many of the data sets presented here.

RESULTS

Overall effects of context

Alone condition

There was an overall effect of context on some behavioral measures when tested in the alone condition (Fig. 1). Latency to resume activity following the stimulus presentation was longest in the predator context (Fig. 1d; Friedman's ANOVA: $\chi^2 = 27.05$, df = 2, $p < 0.001$, adjusted alpha = 0.01). Chick-a-dee call rate varied significantly by context (Fig. 1b; Friedman's ANOVA: $\chi^2 = 15.110$, df = 3, $p = 0.002$, adjusted alpha = 0.0125), with more chick-a-dee calls produced during the novel conspecific context than any other context. Likewise, aggressive behavior, specifically gargling behavior, differed by context (Fig. 1c; Friedman's ANOVA: $\chi^2 = 12.030$, df = 3, $p = 0.007$, adjusted alpha = 0.0167) and was highest in the novel conspecific context. There was no overall effect on activity or eating behavior (Friedman's ANOVA: $\chi^2 = 4.280$, df = 3, $p < 0.233$, adjusted alpha = 0.025 and $\chi^2 = 2.502$, df = 3, $p = 0.475$).

Social condition

Aggressive behaviors, specifically gargles and supplants, differed significantly by context (Fig. 1c and 1e; Friedman's ANOVA: $\chi^2 = 29.509$, df = 3, $p < 0.001$, adjusted alpha

= 0.007 and $\chi^2 = 11.314$, df = 3, $p = 0.010$, adjusted alpha = 0.0167, respectively). Again, gargles were observed more in the novel conspecific context than any other. Instances of the females and males being perched close to one another differed significantly by context (Fig. 1f; Friedman's ANOVA: $\chi^2 = 19.618$, df = 3, $p < 0.001$, adjusted alpha = 0.008), with higher frequency of being close together during the predator presentation. Similar to the alone condition, chick-a-dee call rate differed by context (Fig. 1b; Friedman's ANOVA: $\chi^2 = 24.493$, df = 3, $p < 0.001$, adjusted alpha = 0.01), with higher call rates during the novel conspecific context. There was also an overall effect on latency to resume activity following stimulus presentation (Fig. 1d; Friedman's ANOVA: $\chi^2 = 23.302$, df = 2, $p < 0.001$, adjusted alpha = 0.0125), with longest latency following the predator presentation. There was an overall effect of context in the social condition on activity (Fig. 1a; Friedman's ANOVA: $\chi^2 = 9.639$, df = 3, $p = 0.022$, adjusted alpha = 0.025). There was no overall effect on eating (Friedman's ANOVA: $\chi^2 = 5.358$, df = 3, $p = 0.147$).

Female-male behavioral differences

There was only one significant difference between males and females in the alone and social testing conditions after correcting for multiple comparisons. During the social testing condition, males performed more supplanting behavior than females during the novel conspecific context (Mann-Whitney U: $Z = -2.786$, all $N_1 = N_2 = 16$, $p = 0.005$, adjusted alpha = 0.008). In the alone testing condition, there was a trend in latency to resume activity following presentation of the novel female conspecific (Mann-Whitney U: Z

= -2.629, $p = 0.009$, adjusted alpha = 0.008). In this case, males tended to have shorter latencies than females.

Consistency across contexts

Overall, analyses reveal strong individual behavioral consistency comparing baseline measurements to the three experimental contexts (Table II). Individual behavioral profiles emerge despite changing environmental stimuli such as the presentation of a novel female conspecific or a predator model. In the alone condition, strong consistency was particularly seen in activity and gargling behavior. In the social condition, strongest consistency was observed for instances of gargles, supplants, and perched close.

Consistency across social and alone conditions

When comparing behavioral traits across the social and alone testing conditions, activity was the only highly predictable behavioral traits across contexts (see Table III). Within context, there appears to be slight predictability for communicative behavior across the alone and social conditions in the predator and novel conspecific contexts (Table III). Eating behavior showed some predictability comparing the alone and social testing conditions, but this correlation is likely explained in part by the nature of the measure, described in more detail next.

Latency to approach novel object

Eight of the 32 individuals (six males and two females) approached the novel object during the alone testing condition. Eight individuals (four males and four females) approached the object during the social testing condition. Six of these individuals approached the object and made contact during both conditions. Thus, the individuals that approached the novel object when alone were highly likely to contact the object when tested with their familiar flockmates (Fisher's Exact Test: $p = 0.0005$). In other words, neophilic individuals, those that approached and were quicker to contact the object, exhibited similar behavior when tested alone and in the social testing condition. In comparing between those that approached the object and those that did not, the only behavioral differences found were activity levels and eating. During both the alone and social conditions, individuals that approached and contacted the novel object had lower levels of activity (alone condition: Mann-Whitney U: $Z = -2.219$, all $N_1 = 8$, $N_2 = 24$, $p = 0.026$; social condition: $Z = -2.024$, $p = 0.041$) and ate more (alone condition: $Z = -4.693$, $p < 0.001$; social condition: $Z = -4.576$, $p < 0.001$) than the individuals that did not approach and contact the novel object (see Fig. 2). It is possible that the individuals who approached the object had higher counts of eating because of the mealworm that was often picked up as a result of contacting the object. Additionally, activity levels during this context may be lower due to increased bouts of eating.

Interestingly, the individuals that did not approach the novel object did not even go to the bottom portion of the cage, where the novel object and mealworm were placed, and also where the water and seed bowls were located. Among the individuals that contacted the object, there were no differences between the alone and social testing conditions in latency, activity level, or eating behavior (latency: Wilcoxon Signed-Ranks test: $Z = -0.70$, all $N_1 = N_2 = 8$, $p = 0.484$; activity: $Z = -0.35$, $p = 0.726$; eating: $Z = -1.380$, $p = 0.168$). Similarly, the individuals that did not contact the object did not differ in activity or eating between the alone and social conditions (activity: Wilcoxon Signed-Ranks test: $Z = -0.543$, all $N_1 = N_2 = 24$, $p = 0.587$; eating: $Z = -0.271$, $p = 0.786$).

Latency to resume activity following predator presentation

Longer latency to resume activity during the predator context was inversely correlated with activity, chick-a-dee call rate, and eating behavior during the predator presentation. Thus, individuals with relatively longer latencies exhibited lower activity levels, produced fewer chick-a-dee calls, and ate less in the alone testing condition (Spearman's Rank correlation: $r_s = -0.853$, $N = 31$, $p < 0.001$; $r_s = -0.536$, $N = 31$, $p = 0.002$; $r_s = -0.360$, $N = 31$, $p = 0.047$, respectively). These individuals also had lower activity levels in the social testing condition (Spearman's Rank correlation: $r_s = -0.420$, $N = 32$, $p = 0.017$).

In addition to testing for behavioral predictability by way of latency to approach a novel object or to resume activity following a presentation of a predator, latencies to resume activity across all contexts were relatively similar (Table IV). Thus, individuals that were slower to resume activity in one context also tended to be slower to resume activity in the other two contexts, particularly when comparing the predator and novel object contexts (Table IV). Data also reveal strong predictability of latency to resume activity comparing across the alone and social testing conditions (Table III), demonstrating that individuals with longer latencies to resume activity when alone, performed similarly when their flockmate was present.

Correlated behaviors within contexts

Chick-a-dee call rate and gargling were positively correlated during baseline (Spearman's Rank correlation: $r_s = 0.581$, all $N = 32$, $p < 0.001$, adjusted alpha = 0.008) and during presentation of the novel conspecific (Spearman's Rank correlation: $r_s = 0.497$, $p = 0.004$, adjusted alpha = 0.01). When subjects were in the alone testing condition, activity levels and chick-a-dee call rates were positively correlated in the novel conspecific context (Spearman's Rank correlation: $r_s = 0.491$, $p = 0.004$, adjusted alpha = 0.0125) and during the predator context ($r_s = 0.392$, $p = 0.029$, adjusted alpha = 0.05). Interestingly, activity level and eating behavior varied between baseline and presentation of the novel conspecific. When the novel conspecific was present, data suggest that activity and eating behavior were inversely related (Spearman's Rank correlation: $r_s = -0.453$, $p = 0.009$, adjusted alpha = 0.0167). However, during baseline, data demonstrate that the most active individuals were the ones who ate more (Spearman's Rank correlation: $r_s = 0.405$, $p = 0.021$, adjusted alpha = 0.025).

Similar relationships were found with the social testing data, suggesting that the most aggressive birds, those with the highest number of supplants, have increased activity levels, decreased latency to resume activity, and increased chick-a-dee call rate. Those individuals with the highest activity levels also had shorter latencies in the novel object (Spearman's Rank correlation: $r_s = -0.555$, all $N = 32$, $p = 0.001$, adjusted alpha = 0.008) and predator (Spearman's Rank correlation: $r_s = -0.420$, $p = 0.017$, adjusted alpha = 0.0125) contexts. Interestingly, those individuals who were relatively active were also relatively aggressive in the novel object context (Spearman's Rank correlation: $r_s = 0.474$, $p = 0.006$, adjusted alpha = 0.01), with a trend for this relationship in predator context (Spearman's Rank correlation: $r_s = 0.378$, $p = 0.033$, adjusted alpha = 0.025). In the novel object context, there is a trend suggesting that the most aggressive individuals had shorter latencies (Spearman's Rank correlation: $r_s = -0.397$, $p = 0.024$, adjusted alpha = 0.0167). Additionally, social data suggest that activity levels may be positively correlated with chick-a-dee call rate during presentation of a predator (Spearman's Rank correlation: $r_s = 0.340$, $p = 0.057$).

Repeatability of behavior

Figure 3a illustrates the stability of behavior observed via Spearman’s Rank correlation coefficients assessing the repeatability of behavior across the eight focal samples.

In addition, I found strong, positive relationships when comparing the average responses of the first three focal samples to data collected during the final three focal sample periods (focal samples 6, 7, and 8): was supplanted (Spearman's Rank correlation: $r_s = 0.711$, $p < 0.001$), activity (Fig. 3b; $r_s = 0.568$, $p = 0.002$), eating behavior ($r_s = 0.541$, $p = 0.003$), supplants ($r_s = 0.502$, $p = 0.006$), chick-a-dee call rate ($r_s = 0.442$, $p = 0.018$), and gargles ($r_s = 0.304$, $p = 0.116$).

DISCUSSION

Overall findings support the existence of individual behavioral profiles and behavioral consistency across distinct contexts, specifically social interaction, foraging, and a threatening or predatory context. The most aggressive and active individuals in one context tended to be the most aggressive and active in another context – suggesting that individuals respond to stimuli similarly despite fluctuations in the immediate environment.

In the predator context, activity level and chick-a-dee call rate were strongly correlated between the alone and social testing conditions (Table III). Interestingly, Bell and Sih (2007) also report an increase in the strength of behavioral correlations, specifically in regards to boldness and aggression, in threespined sticklebacks (*Gasterosteus aculeatus*) following presentation of predators. Bell and Sih (2007) suggest that predation pressure may be responsible for the behavioral correlations often observed between levels of aggression and boldness (Huntingford, 1976; Riechert & Hedrick, 1990; Johnson & Sih, 2005). Another potential pressure that may help to explain the expression of such behavioral correlations is selection pressure (see Dingemanse & Reale, 2005). For example, Dingemanse, et al. (2007) found that activity, aggression, and exploration were highly correlated with one another in a predator-rich environment, but a similar relationship was not found in predator-free populations. Thus, one potential conclusion is that the presence of a predator may be responsible for the expression of these correlated behaviors. One possibility could be that the presence of the predator constrained behavioral variation in individuals.

For chickadees, when a predator was present, increased activity levels correlated not only with higher call rates, but also decreased latencies to resume activity and increased aggressive behavior. Current findings, combined with Bell & Sih (2007), suggest that a suite of correlated behaviors, referred to as a behavioral syndrome (Sih, Bell, Johnson, & Ziemba, 2004), may occur in some contexts but not in others, such as the novel object or novel conspecific contexts in the present study. Interestingly, in five of the ten behavioral traits observed, highest predictability was found when comparing the baseline and predator contexts – baseline being representative of the lowest stress context and the predator context most likely of highest stress (Table II). More interestingly, however, was that during social testing, there were significantly more instances of perched close or spending time in close proximity, during the baseline and predator contexts. One reason behind these findings may be the stress imposed on an individual due to the immediate context of a potentially threatening stimulus in the environment. For example, in an intense situation of high arousal, such as a predator-rich environment, it may be most adaptive for the individual to resort to a previously defined behavioral profile (such as behavioral patterns exhibited during baseline measures). In a moderately stressful environment, more variable behavior such as exploration may be more likely (Leary, 1957). It is possible that high levels of stress decrease variability of behavior, while mild stress may result in excitation and increasing variability of behavior, allowing the individual to explore and exhibit a variety of behavioral patterns. For example, Leary (1957) has reported that humans may have some behavioral flexibility in undemanding situations, but reveal their predominant behavioral patterns (similar to those displayed during low stress or baseline measures) when in stressful situations.

For some of the behavioral traits observed there was an effect of context, for example in activity levels, call production, and aggressive behaviors. This may suggest that the limited behavioral plasticity assumed of behavioral profiles may be more evident in some contexts versus others. Therefore, predictability of behavior, both across contexts and social conditions, may prove to be greatest when the immediate environment provides the necessary provocation to evoke a specific behavioral trait (Marshall & Brown, 2006). An individual's behavioral profile or behavioral response may not be fully understood or explained without encompassing influences of the situational context. Both predictability of behavior, and factors of the immediate context that are constricting the expression of such specific traits, are important when trying to understand and define behavioral profiles. By studying the stability and consistency of behavior within the constraints or influences of the situation, more in-depth understanding of behavior can be achieved (Marshall & Brown, 2006).

Context specificity does not, however, contradict the idea of behavioral profiles but suggests that contextual factors may influence behavior, while maintaining individual predictability of behavior (Sih, Bell, Johnson, & Ziemba, 2004). For example, imagine that individuals are observed and rank ordered based on level of boldness, specifically feeding behavior, when there are no predators in the environment. Next, predators are placed in the environment and again individuals' feeding behavior is observed and individuals are rank ordered based on an identical measure of boldness. It is expected that there will be an overall decrease in rate of feeding behavior when predators are present; however, it is also probable that individual rank order will be apparent despite the contextual change, supporting a behavioral profiles framework.

The present study suggests that there are strong links between communication and behavioral profiles. Data presented here are the first step toward integrating a complex vocal behavior, specifically the chick-a-dee call, to the study of behavioral profiles. Current results suggest that more active and more aggressive individuals have higher rates of vocal production. Previous research found that males who spent more time in close proximity to their female social companion produced more chick-a-dee calls (Freeberg & Harvey, 2008). What is left to be determined is if the structure of, or variation in, the chick-a-dee call is associated with the individual's behavioral profile. Much more work is needed to understand potential relationships between behavioral traits and communicative behavior. This study is one of the first to provide data linking a complex communicative system with any dimension of personality in a non-human species. Ongoing studies are exploring the chick-a-dee call in greater detail and investigating how call composition and note type may be linked to particular behavioral traits or correlated behavioral patterns.

In trying to understand behavioral profiles, early researchers tended to study individuals in a solitary testing arena (but see Uher, Asendorpf, & Call, 2008; Nelson, Wilson, & Evans, 2008). As results of the present study demonstrate, it may not be safe to extrapolate behavioral profiles in a social setting from data collected in an isolated individual setting. The strength of behavioral profiles differed when comparing the alone and social conditions (also see van Oers, Klunder, & Drent, 2005). Some of the behavioral measures reported exhibited substantial consistency across the alone and social testing conditions, but most measures did not (Table III). We, as researchers, should be cautious in conducting non-human animal personality research involving social species in which subjects are tested as isolated individuals. In social species, it may be important, if not vital, to consider the influences of an individual's immediate social environment when conducting behavioral profile research.

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APPENDICES

APPENDIX A

TABLES

Table I. Definitions of the behavioral traits measured across all contexts

Behavioral Trait	Description
Motor Behavior	
Activity	Relocation in home cage via hopping and/or flying
Eat	Pecks at and consumes seed or other food type
Latency – Novel Object	Latency to make contact with the novel object
Latency – Predator	Latency to resume activity following presentation of predator
Social Behavior	
Perched close	Birds perched within 15cm of one another, most often on same perch
Supplant	Bird moves toward other individual, forcing other to move from perch, and takes other bird's position; typically an aggressive behavior
Vocalization	
Chick-a-dee call	Characteristic vocalization of the chickadee used in a diversity of contexts related to social cohesion
Gargle	Common vocalization, oftentimes made by individuals engaged in an agonistic interaction

Table II. Spearman's Rank correlations comparing baseline measurements to each of three distinct contexts: novel object, novel conspecific, and predator/threat

	r_s	p	r_s	p	r_s	p
Baseline	Novel Object		Novel Conspecific		Predator	
Alone Testing						
Activity	**0.367**	**0.039***	**0.507**	**0.003***	**0.445**	**0.012***
Eat	0.060	0.743	0.149	0.416	-0.009	0.960
Chick-a-dee call	0.273	0.130	0.341	0.056	**0.478**	**0.006***
Gargle	**0.621**	**< 0.001***	**0.461**	**0.008***	**0.483**	**0.006***
Social Testing						
Activity	-0.004	0.984	0.185	0.312	**0.623**	**< 0.001***
Eat	0.070	0.705	0.008	0.967	0.090	0.623
Chick-a-dee call	0.336	0.060	0.019	0.920	**0.485**	**0.005***
Gargle	**0.434**	**0.013***	**0.456**	**0.009***	0.287	0.112
Social Measures						
Supplant	**0.407**	**0.021***	**0.776**	**< 0.001***	**0.751**	**< 0.001***
Perched Close	0.109	0.552	**0.657**	**< 0.001***	**0.693**	**< 0.001***

Significant correlations, after implementing sequential Bonferroni adjustments for each behavioral comparison, are indicated with bold font and an asterisk.

Table III. Spearman's Rank correlations comparing behavioral measures of chickadees facing different stimulus contexts in the alone relative to the social testing condition

	Alone versus Social Comparison for Each Context							
	r_s	p	r_s	p	r_s	p	r_s	p
	Baseline		Novel Object		Novel Conspecific		Predator	
Measure								
Activity	**0.506**	**0.003***	**0.561**	**0.001***	0.303	0.092	**0.661**	**< 0.001***
Eat	0.109	0.552	**0.491**	**0.004***	0.255	0.159	0.183	0.324
Chick-a-dee call	0.312	0.082	0.104	0.572	0.318	0.076	**0.504**	**0.004***
Gargle	0.168	0.357	0.109	0.552	**0.553**	**0.001***	0.315	0.084
Latency	-	-	**0.447**	**0.010***	**0.378**	**0.033**	0.344	0.058

Significant correlations, after implementing sequential Bonferroni adjustments, are indicated with bold font and an asterisk; correlations in bold without an asterisk indicate statistical trends after correction for multiple comparisons. The measure latency denotes latency to resume activity following stimulus presentation, which did not occur in the baseline context.

Table IV. Spearman's Rank correlations comparing individuals' latencies to resume activity across three distinct contexts: novel object, novel conspecific, and predator, when tested alone and with a familiar flockmate

	r_s	p	r_s	p
	Novel Object		Predator	
Alone Testing				
Novel Conspecific	**0.355**	**0.046**	**0.380**	**0.035**
Novel Object			**0.526**	**0.002***
Social Testing				
Novel Conspecific	**0.370**	**0.037**	0.066	0.718
Novel Object			**0.398**	**0.024**

P-values < .05 are highlighted in bold font and significant correlations, after Bonferroni adjustments (alpha = 0.016 for 3 comparisons for each latency measure in each condition), are indicated with an asterisk; correlations in bold without an asterisk indicate statistical trends after correction for multiple comparisons.

APPENDIX B

FIGURES

Figure 1. Behavioral differences (average number per 15 min observation period) across four distinct contexts: baseline (grey box), predator (white box), novel object (diagonal box), and novel conspecific (dotted box), comparing across two testing conditions: alone and social. Baseline is omitted from the latency plot due to no latency measure during this context.

Figure 1

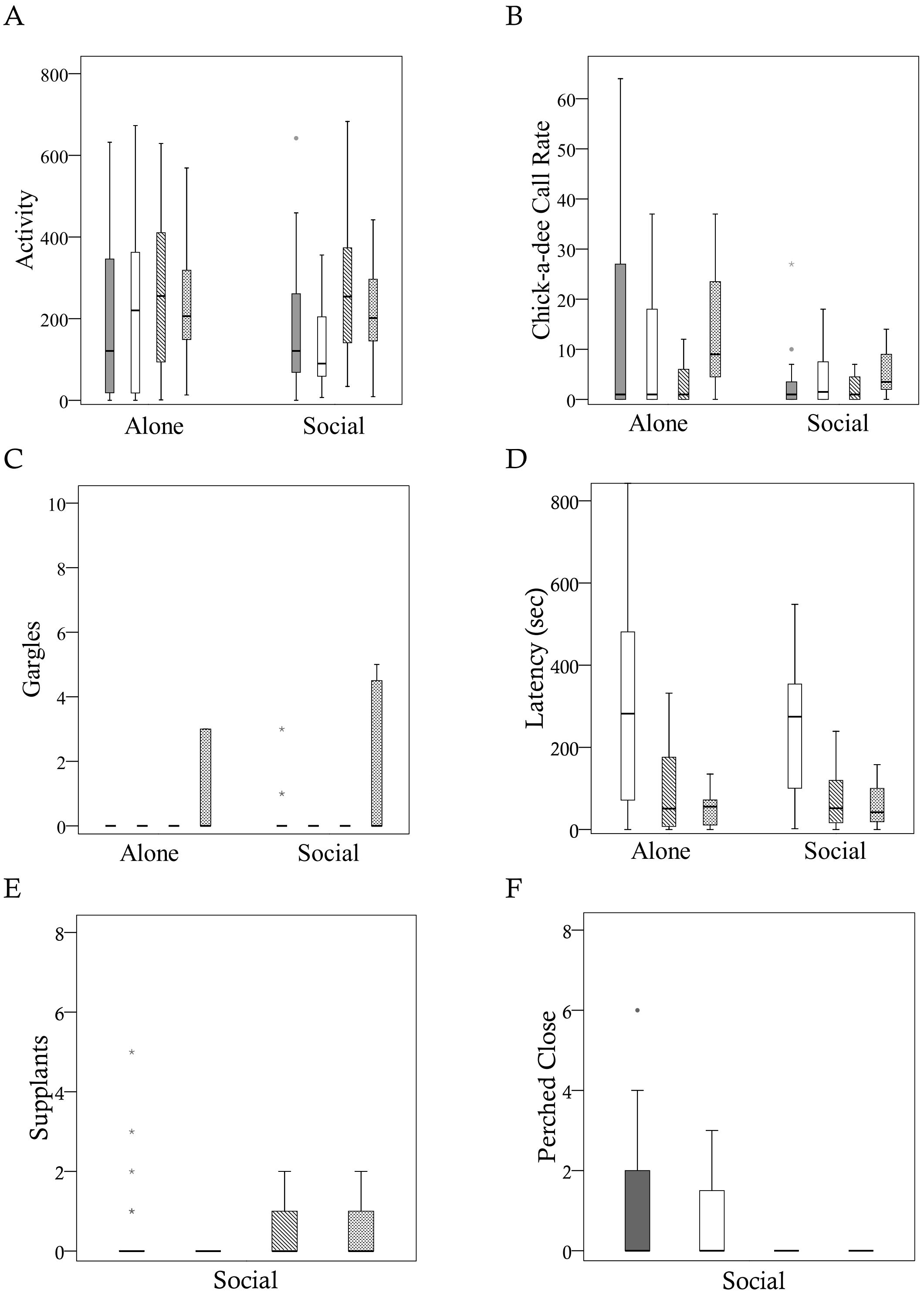

A
B
C
D
E
F
Activity
0
200
400
600
800
Alone
Social
Chick-a-dee Call Rate
0
10
20
30
40
50
60
Alone
Social
Gargles
0
2
4
6
8
10
Alone
Social
Latency (sec)
0
200
400
600
800
Alone
Social
Supplants
0
2
4
6
8
Social
Perched Close
0
2
4
6
8
Social

Figure 2. Boxplot diagrams depicting activity level (number of flights and hops per 15 min observation period) and frequency of eating behavior across individuals that contacted the novel object and those that did not contact the novel object, independent of alone or social testing condition.

Figure 2

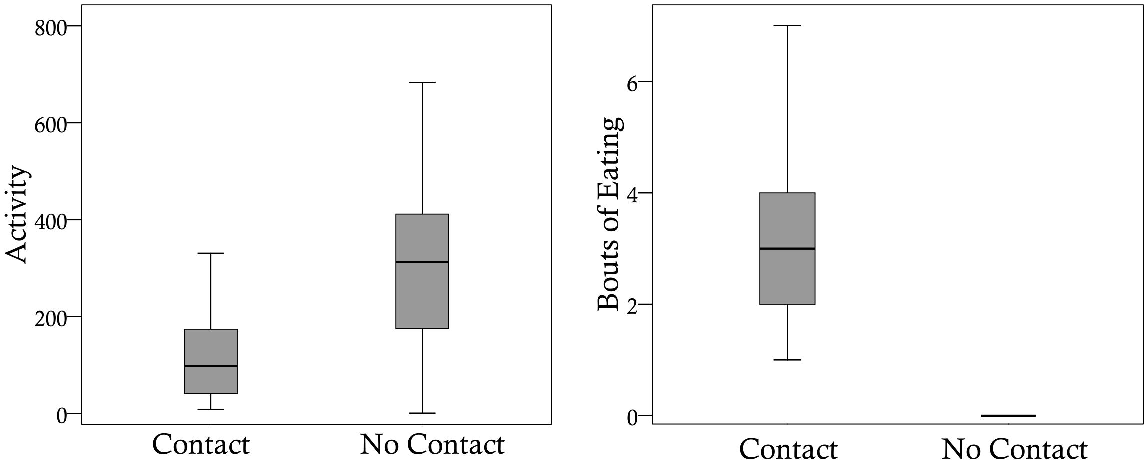
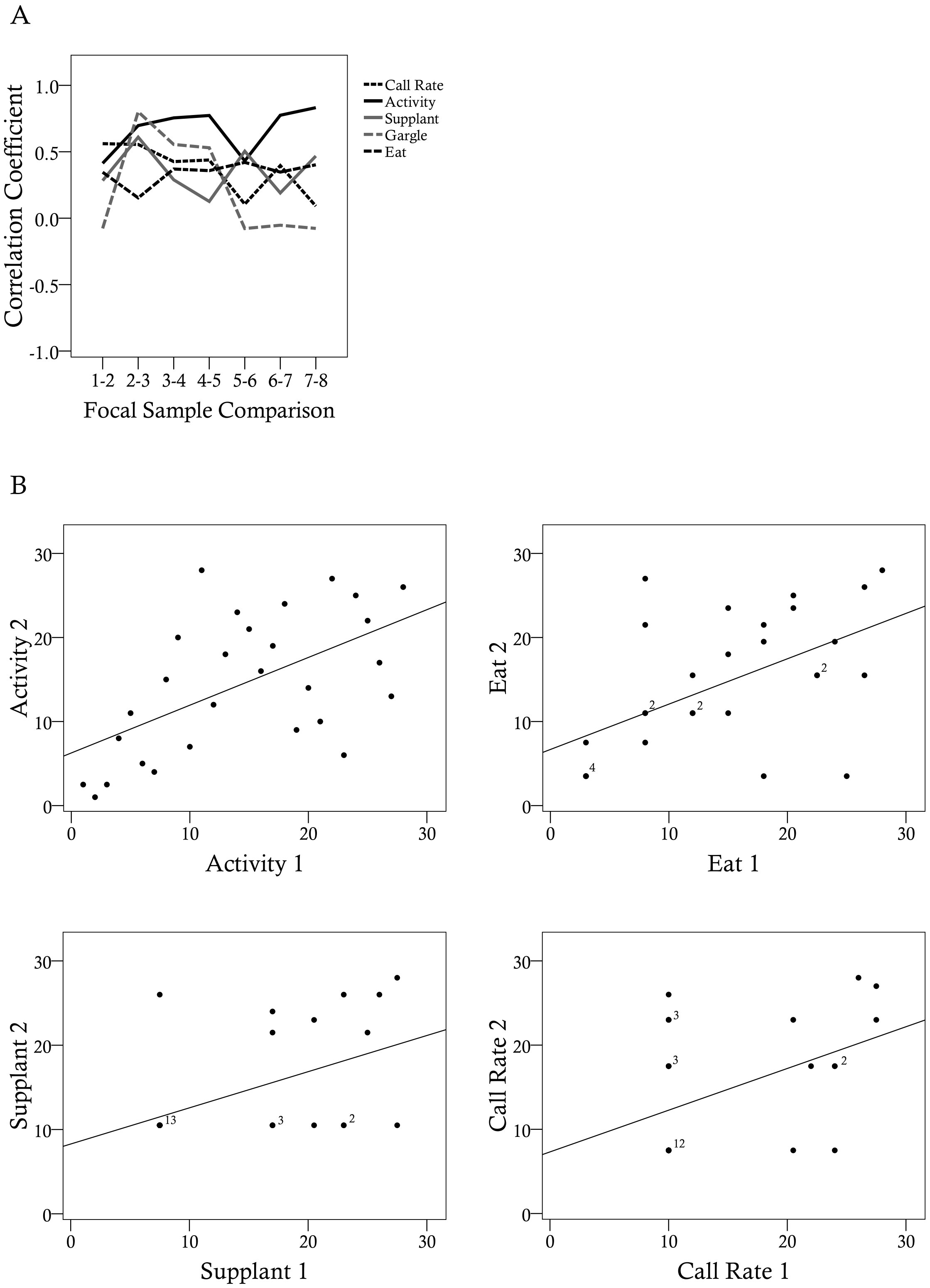

800
600
400
200
0
Activity
Contact
No Contact
6
4
2
0
Bouts of Eating
Contact
No Contact

Figure 3. (A) Spearman's Rank correlation coefficients assessing the repeatability of multiple behavioral measures for 28 individuals across eight 15-min focal sample periods, spanning a period of approximately 14 days. (B) Individuals were ranked from 1 to 28 according to average behavioral responses during the first three (x-axis) and last three focal sample periods (y-axis).

Figure 3


A
Correlation Coefficient
1.0
0.5
0.0
-0.5
-1.0
1-2
2-3
3-4
4-5
5-6
6-7
7-8
Focal Sample Comparison
Call Rate
Activity
Supplant
Gargle
Eat
B
Activity 2
Activity 1
Eat 2
Eat 1
2
2
2
4
Supplant 2
Supplant 1
13
3
2
Call Rate 2
Call Rate 1
3
3
2
12
0
10
20
30

CHAPTER 3

BEHAVIORAL PROFILES IN A COMPLEX SOCIAL SETTING

ABSTRACT

The study of individual differences and personality-like influences on behavior (hereafter 'behavioral profiles') has become an eminent area of investigation. Within the realm of behavioral profiles, numerous species have been studied across an array of behavioral traits, such as aggression, boldness, exploration, and general activity. Surprisingly, this field has been largely void of a key research focus in animal behavior – communicative behavior. Furthermore, very little work in behavioral profiles has been done with subjects in social groups, despite the fact that most species tested to date for these questions are social species. The current study is directed toward filling these gaps by testing behavioral profiles in a species with a highly complex vocal system, the Carolina chickadee (*Poecile carolinensis*), in complex social settings. Thirty-six Carolina chickadees were housed in large outdoor aviaries in six independent groups, mimicking normal flock sizes for this species. There were three independent contexts in which recording occurred: baseline, predator present, and treadle trap present. Behavioral measures recorded included activity level, aggression, frequency of eating, latency to approach unfamiliar stimuli, and vocal production. Data indicate that the most aggressive individuals were also the boldest individuals, and they produced the highest rates of chick-a-dee call production. Results suggest that not only do behavioral traits co-vary with one another, but there is an important link between communicative behavior and behavioral profiles. Finally, this work indicates that behavioral profiles can manifest themselves even in complex social groups housed in semi-naturalistic environments.

CHAPTER 3

BEHAVIORAL PROFILES IN A COMPLEX SOCIAL SETTING

Individual differences in behavior within a species have been found to exist across a variety of contexts and situations (Gosling & John, 1999; Gosling, 2001). Despite changes in the immediate context, behavioral patterns within an individual often tend to stay relatively stable and consistent (Armitage & Van Vuren, 2003; Sih, Bell, Johnson, & Ziemba, 2004). Many terms have been used to describe this phenomenon, such as temperament, behavioral syndromes, personality, behavioral profiles, and even coping strategies (Sih, Bell, & Johnson, 2004; Boissy, 1995; Gosling, 2008). Evidence for such behavioral stability exists across a vast array of traits, including shyness and boldness (Wilson, Clark, Coleman, & Dearstyne, 1994), exploration (Verbeek, Drent, & Wiepkema, 1994; Dingemanse, et al., 2002), aggression (Johnson & Sih, 2005; Uher, Asendorpf, & Call, 2008), and even introversion and extraversion (Gosling & John, 1999). Recent research has documented that aggressive individuals also tend to be more active (Johnson & Sih, 2005; Sih & Watters, 2005; Williams, In preparation). Despite the great research effort that has been done on non-human animal personality, only 4% of the documented studies focus on avian species (Gosling, 2008). Surprisingly, even fewer studies in the personality literature have incorporated any dimension of communicative behavior and addressed potential correlates between non-human animal personality and communication (but see Nelson, Wilson, & Evans, 2008; Williams, In preparation). This paucity of data is problematic because of the fact that communicative behavior is fundamental to individual survival and reproductive success (Hauser, 1996). The present study aimed to address this missing link by analyzing non-human animal personality, or behavioral profiles, in a species that is highly social and possesses a highly complex communication system, the Carolina chickadee (*Poecile carolinensis*).

The social organization of Carolina chickadees is complex – a chickadee will experience both pair bonding and flock living over the course of a year (Ekman, 1989; Mostrum, Curry, & Lohr, 2002; Smith, 1991). Specifically, chickadees are in female-male pair bonds during the breeding season and maintain these bonds throughout the summer months. During the late summer through early fall months, after the young have fledged, unrelated chickadee pairs will form cohesive flocks. These flocks jointly defend their territories during the overwintering months. The following spring, this cycle is then repeated in association with the new breeding season. Perhaps related to the complexity of their social system is the complexity of the chick-a-dee call system. The call system of this species has elicited a great deal of investigation for many years (Hailman, Ficken, & Ficken, 1985; Lucas & Freeberg, 2007). However, little work has been done to investigate individual variation of call use across changing contexts and the potential for call rate to co-vary with other behavioral measures. Therefore, I manipulated immediate contextual factors of groups of individuals by placing a highly desirable food source in the presence of various stimuli, such as a model of a natural avian predator and a treadle (potter) trap. These manipulations tested if chickadees modify production of their vocal signals to reflect the presence of a new stimulus, and allowed me to test for relationships between behavioral profiles and chick-a-dee call production in individuals.

Since previous research in chickadees has documented that vocal complexity increases as group size increases (Freeberg, 2006), the present study aimed to extend recent research on behavioral profiles by recording groups of chickadees in experimental flock sizes, simulating their natural, relatively complex social structure. In much of the behavioral profile literature individuals are tested alone. Although solitary testing is an established methodology for assessing some particular behaviors, many of the study species in the animal personality literature are social (Gosling, 2001; Sinn, Gosling, & Moltschaniwskyj, 2008; Uher, Asendorpf, & Call, 2008). There could be serious problems with testing individuals of a highly social species as isolated subjects in individualized testing arenas (Wilson, Coleman, Clark, & Biederman, 1993; Williams, In preparation). Recent approaches to studying behavioral profiles examine female-male pairs (Carere, et al., 2005; Harvey & Freeberg, 2007; Hollander, Overveld, Tokka, & Matthysen, 2008), but even fewer adopt a group level approach that is representative of the natural social environment and group structure of the study species (one recent exception is Nelson, Wilson, & Evans, 2008).

For this study, I collected both vocal and non-vocal behavioral data across three contexts in captive chickadees. To assess if specific behavioral traits were associated with vocal production, I tested for correlates between vocal and non-vocal behavior in flock-sized groups of female and male chickadees. This is one of the first studies to incorporate a highly complex vocal behavior into the field of behavioral profiles.

METHODS

Subjects and housing

The present study included 36 wild-caught chickadees (18 female-male pairs). Birds were captured from established trapping sites in east Tennessee, including the University of Tennessee Forestry Resources, Research, and Education Center in Oak Ridge, Tennessee; Ijams Nature Center in Knoxville, Tennessee; and three residential sites, all located in Knoxville, Tennessee. Trapping sites were far enough away from one another to ensure that the birds visiting each site were from independent flocks. To ensure that the female and male of each pair were familiar with one another and members of the same flock, members of each pair were trapped from the same trapping site, on the same day, and at roughly the same time (captured no more than 90 min apart). Three female-male pairs were grouped together to form aviary flocks (explained in more detail below). At the time of capture, all individuals were weighed, sexed via wing chord measurements (females' wing chords measured 60 mm or less and males' wing chord measurements were equal to or greater than 62 mm, after Thirakhupt, 1985), and individually marked with colored plastic bands. Previous work in our laboratory supports the validity of this wing chord length sexing technique for chickadees (see Chapter 2).

On the day of capture, pairs were placed in large outdoor aviaries (6 x 9 x 3.5 m). Pairs of each aviary flock were put into the aviary on different days in efforts to establish a residency effect for the first pair introduced (see below). Aviaries included hanging perches made from tree branches, natural trees, as well as an enclosed shelter adjacent to the aviary. Aviary birds were checked daily and provided with *ad libitum* food and fresh vitaminized water. Bowls, located on the feeding stand within each aviary, contained a 1:1 mix of black oil sunflower seed and safflower seed, wild bird seed, crumbled suet, crushed oyster shell, and grit. Made fresh daily, birds were given Bronx Zoo diet for omnivorous birds mixed with sprouted seed and 12-18 waxworms and mealworms.

Design and procedure

Three female-male pairs (six individuals) composed one aviary group. The present study consisted of six independent groups. Once the third pair was placed in the aviary, groups were given a two-week acclimation period to adjust to their new social and physical environments. Specifically, this period allowed them to acclimate to captivity, to familiarize with group members, and to habituate to humans. At the end of this two-week period, I conducted an average of ten 10 min focal samples per individual (*range* 4 – 14). During the final four days of recording, two different stimuli were presented to assess potential changes in chick-a-dee call rate and other non-vocal behavior (see description below). These presentations were conducted at the end of the subjects' recording periods and no more than once per day. The first group began in September 2008 and the study ran continuously through March 2009. All recording sessions occurred between 0830 and 1500 hours. Once recording was completed for each experimental flock, pairs were released at their capture sites.

Behavioral observations

Vocal and non-vocal behavior was recorded during the baseline period (when no stimuli were presented) via focal sampling (Martin & Bateson, 1986). Behavioral measures observed included frequency of vocal production (the chick-a-dee call and the gargle, an agonistic vocalization; Hailman, 1989), eating, physical activity (flights and hops), and social and aggressive behavior (including supplanting and chasing another individual). Four individuals died during the duration of this study, resulting in fewer than ten focal samples for these individuals (one individual had four focal samples; two individuals had five samples, and one with six focal samples). These individuals were included in baseline data analyses (adjusted for the number of focal samples obtained), but were not included in analyses involving the two stimulus presentations. I conducted a total of 370, 10 min focal samples.

Predator and treadle (potter) trap presentations

Groups were presented with a predator model and a treadle (potter) trap (36 x 18.5 x 18.5 cm) during the final days of recording. The hawk model (Dalen Products, Inc. by wildlife artist Pamela Rickman) was designed to mimic a natural predator for this species, the Cooper's hawk (*Accipiter cooperii*). Each stimulus was presented twice and stimulus presentations occurred over a 4 day period. Stimuli were placed directly on the feeding stand, where all food bowls were located. Simultaneously with presenting the stimuli, live mealworms were placed on the feeding stand, in the same bowl that the birds received live mealworms daily. For the predator model presentation, the bowl was located next to the base of the predator model. During the treadle trap presentation, the bowl was inside the locked-open trap; therefore, in order to retrieve a mealworm, the birds had to enter the trap.

Each stimulus presentation lasted for 20 min. During this recording period, I aimed to individually identify each chick-a-dee call produced. Additionally, I noted latency for each individual to fly toward the stimulus or feeding stand, land on the feeding stand, and pick up a mealworm. At the end of this 20 min recording period, I walked up to the stand, removed the stimulus and then recorded a 5 min post-stimulus period. During this 5 min recording period, I again aimed to individually identify chick-a-dee calls produced, as well as to record latency for each individual to fly toward, land on, or to pick up a mealworm from the feeding stand.

Statistical analyses

All statistical tests were performed using SPSS, Versions 16.0 and 17.0 for Windows. Due to the non-normality of many of the data sets, non-parametric statistical tests were used. Friedman's ANOVA was used to test for an overall effect of context on chick-a-dee call rate, followed by Wilcoxon Signed-Ranks pairwise comparison tests. Spearman's Rank correlation coefficients were used to test for correlated behavioral responses across the three independent contexts, as well as to test for correlated behavioral measures. In testing for group level differences, I began with a Kruskal-Wallis test and, if a significant overall effect was found, I carried out pairwise Mann-Whitney U tests. Mann-Whitney U tests were also used to compare latency measures across individuals. Spearman’s Rank correlation coefficients were used to assess repeatability of behavior across multiple focal samples. Additionally, I conducted an exploratory Factor Analysis with Varimax Rotation and Kaiser Normalization, in efforts to uncover potential behavioral traits among the primary behavioral measures observed. In cases of multiple tests, I implemented a sequential Bonferroni adjustment, or Holm’s procedure (Holm, 1979; Rice, 1989). The adjusted alpha level in these cases is reported along with each statistical test.

RESULTS

Baseline behavior

Individuals that exhibited a high frequency of supplants (an aggressive behavior) during baseline were also more likely to gargle (an agonistic vocalization) and to chase other individuals during baseline (Table I). Aggressive behavior also tended to be correlated with rates of chick-a-dee calling during baseline recordings. The most aggressive, highest calling individuals, also ate the most food during baseline (see Table I).

Behavioral consistency across contexts

Chick-a-dee call rate was consistent and individual rank order was maintained across all three contexts (see Fig. 1). In other words, those individuals who produced more calls during baseline also had higher call rates when the predator was presented.

There was a significant effect of context on chick-a-dee call rate (Friedman's ANOVA: $\chi^2 = 10.429$, df = 2, $p = 0.005$). More chick-a-dee calls were produced during the predator context than during either baseline (Wilcoxon Signed-Ranks: $Z = -3.890$, $p < 0.001$, adjusted alpha = 0.0167) or the trap ($Z = -2.755$, $p = 0.006$, adjusted alpha = 0.025) context (Fig. 2). There was no difference in call rate between baseline and presentation of the treadle trap (Wilcoxon Signed-Ranks: $Z = -0.832$, $p = 0.405$; Fig. 2).

Predator presentation

Of the 32 birds, only seven (four females and three males) landed on the feeding stand while the predator was on the stand. Only one individual out of those seven picked up a food item during the predator presentation. These seven individuals did not differ from the other 25 birds in activity level (Mann-Whitney U: $Z = -0.160$, all $N_1 = 7$, $N_2 = 25$, $p = 0.873$), vocal production (chick-a-dee call: $Z = -0.752$, $p = 0.452$; gargle: $Z = -0.157$, $p = 0.875$); aggressive behavior (supplant: $Z = -0.429$, $p = 0.668$; chase: $Z = -0.166$, $p = 0.868$), or eating behavior ($Z = 0.00$, $p = 1.00$). Out of the seven individuals that approached the predator model, four also entered the treadle trap during the trap presentation (Fisher's Exact Test: $p = 0.576$); thus, it does not appear that behavior in one of these experimental contexts was contingent on the other.

To measure latency during the predator presentation for those individuals that did not approach the stand, latency to approach the stand during the 5 min post presentation period was used. For example, if an individual landed on the feeding stand 60 sec following predator presentation, its latency measure would be 1260 sec (the 20 min period that the predator was present plus the additional 60 sec latency). Strong behavioral consistency, or repeatability, was found when comparing individuals' latency to approach the feeding stand in the presence of the predator model during both the first and second presentations ($r_s = 0.683$, $N = 32$, $p < 0.001$). Latency, when the predator was presented for the first time, was inversely correlated with both chasing behavior (Spearman's Rank correlation: $r_s = -0.442$, N

= 32, $p = 0.011$, adjusted alpha = 0.007) and chick-a-dee call rate ($r_s = -0.436$, N = 32, $p = 0.013$, adjusted alpha = 0.008) during baseline. This suggests a tendency for bolder individuals, those with the shorter latency times, to produce more chick-a-dee calls and to show more aggression by chasing others. As mentioned, seven out of the 32 birds landed on the feeding stand during the predator presentation. Twenty-four individuals, out of the remaining 25, landed on the feeding stand within five minutes of the avian predator being removed. Such a drastic change in behavior immediately following the removal of the predator offers strong support that the stimulus was successful in simulating predator presence.

Treadle trap presentation

Strong behavioral consistency (repeatability) was found when comparing individuals' latency to approach the treadle trap during the first and second stimulus presentations ($r_s = 0.813$, $N = 32$, $p < 0.001$). In considering only those individuals that approached and entered the trap, latency was significantly shorter for the second presentation (Wilcoxon Signed-Ranks: $Z = -2.844$, $N = 17$, $p = 0.004$). For this reason, analyses were conducted using latency times from the first trap presentation.

Individuals with the shortest latency to enter the trap had higher rates of eating (Spearman's Rank correlation: $r_s = -0.667$, $N = 32$, $p < 0.001$, adjusted alpha = 0.01) and produced more chick-a-dee calls ($r_s = -0.437$, $N = 32$, $p = 0.012$, adjusted alpha = 0.0125) during baseline observations. Of the total 32 birds, 16 approached, contacted, and entered the treadle trap during the first trap presentation. These 16 individuals exhibited higher rates of eating behavior (Mann-Whitney U: $Z = -3.508$, all $N_1 = 16$, $N_2 = 16$, $p < 0.001$, adjusted alpha = 0.01) and produced more chick-a-dee calls ($Z = -2.789$, $p = 0.005$, adjusted alpha = 0.0125) during baseline recordings (Fig. 3).

Repeatability of behavior across focal sampling

Figure 4a depicts the stability, or repeatability, for several of the described behavioral traits across the first nine focal samples conducted per individual, spanning two weeks. In addition, there was relatively high predictability between the average responses of the first three focal samples to data collected during three of the final focal sample periods, approximately one week later, for the primary behavioral measures observed: chick-a-dee call rate (Fig. 4b; Spearman's Rank correlation: $r_s = 0.687$, $p < 0.001$), gargle ($r_s = 0.504$, $p = 0.003$), chasing behavior ($r_s = 0.461$, $p = 0.008$), eating behavior ($r_s = 0.399$, $p = 0.024$), supplant ($r_s = 0.389$, $p = 0.028$), and activity ($r_s = 0.351$, $p = 0.049$).

Factor analysis

An exploratory factor analysis identified three primary factors, accounting for 68.97% of the total variance (Table II). Factor 1 represents agonistic or aggressive behavior. Factor 2 signifies that interest in novelty or boldness in regards to approaching a novel stimulus may also be associated with eating behavior and locating new food sources, in that those birds that contacted the trap, thus likely picking up a mealworm, also ate more during baseline recordings. Lastly, Factor 3 indicates that vocal production, specifically chick-a-dee call production, may be associated with boldness in the predator context or increased riskiness (those with the shorter latencies during the predator context had higher call rates during baseline recordings). Factor loadings, as well as the total variance explained by each of the three factors, can be found in Table II. Activity did not load onto any factor at the 0.600 loading criterion; it loaded most heavily on Factor 1, but was not included due to a factor score of -0.477.

Differences by sex

As is typical of this species, males supplanted others more than females (Mann-Whitney U: $Z = -3.262$, all $N_1 = N_2 = 18$, $p = 0.001$, adjusted alpha = 0.008). There was a non-significant tendency for males to chase others more ($Z = -2.324$, $p = 0.020$, adjusted alpha = 0.01) and to produce more gargles ($Z = -2.060$, $p = 0.039$, adjusted alpha = 0.0125). Activity levels (Mann-Whitney U: $Z = -1.297$, $p = 0.195$), eating behavior ($Z = -0.918$, $p = 0.358$) and chick-a-dee call rates ($Z = -0.127$, $p = 0.899$) were not found to differ between males and females.

Differences by aviary

There were no differences across behavioral traits based on group, or aviary. Although there were tendencies for an "aviary effect" on behavioral rates, after corrections for multiple comparisons there were no aviary effects for chasing behavior (Kruskal Wallis: $\chi^2 = 15.464$, df = 5, $p = 0.009$, adjusted alpha = 0.007), bouts of eating ($\chi^2 = 15.085$, df = 5, $p = 0.01$), gargling ($\chi^2 = 8.390$, df = 5, $p = 0.136$), activity level ($\chi^2 = 8.264$, df = 5, $p = 0.142$), chick-a-dee call rate ($\chi^2 = 5.021$, df = 5, $p = 0.413$), or supplanting behavior ($\chi^2 = 2.635$, df = 5, $p = 0.756$).

Differences by order introduced into aviary

As mentioned, no two pairs were introduced into the same aviary on the same date. Aggressive behaviors did not differ depending upon date of entry into the aviary (Kruskal Wallis: supplant: $\chi^2 = 1.093$, df = 2, $p = 0.579$; gargle: $\chi^2 = 2.508$, df = 2, $p = 0.285$; chase: $\chi^2 = 0.316$, df = 2, $p = 0.854$). Call rate (Kruskal Wallis: $\chi^2 = 4.383$, df = 2, $p = 0.112$), activity ($\chi^2 = 0.515$, df = 2, $p = 0.773$), and eating behaviors ($\chi^2 = 3.540$, df = 2, $p = 0.170$) also did not vary depending upon which pair had been housed in the aviary for a longer period of time.

Differences by trapping location

In grouping together those birds trapped at the University of Tennessee Forestry Resources Research and Education Center with those caught at Ijams Nature Center, there were 26 individuals trapped at natural, non-residential sites. There were a total of 10 individuals trapped at residential sites. No behavioral differences were found based on location, comparing non-residential to residential sites: activity (Mann-Whitney U: $Z = -1.801$, $p = 0.072$), gargle ($Z = -1.684$, $p = 0.092$), eating behavior ($Z = -1.485$, $p = 0.138$), supplants ($Z = -0.803$, $p = 0.422$), chasing ($Z = -0.626$, $p = 0.531$), latency to approach the treadle trap ($Z = -0.213$, $p = 0.831$) or predator ($Z = -0.189$, $p = 0.850$); and lastly, there were no differences in chick-a-dee call rate ($Z = -0.035$, $p = 0.972$).

DISCUSSION

The current study investigated behavioral traits within captive, flock-sized groups of Carolina chickadees and examined individual vocal patterns based on changes in contextual variables. The present study examined the expression of behavioral traits and behavioral profiles within a dynamic group of six individuals, thus testing individuals in a highly social context. There was variation in vocal production across individuals, but consistency and stability across contexts were generally maintained within individuals.

Previous studies have assessed individual behavior in the presence of a predator and used activity level, call rate, and even latency as measures of boldness (Hollander, Overveld, Tokka, & Matthysen, 2008; Williams, In preparation). High levels of activity when a predator is in close proximity could be considered as bold behavior; because movement may increase the likelihood of being seen and captured by the predator. An earlier study with Carolina chickadees reported that bolder individuals, with a shorter latency to resume activity when a predator model was presented, exhibited higher activity levels than individuals with longer latency periods (Williams, In preparation). One possibility is that increased activity and movement result in the individual gathering more information on the predator (Curio & Regelmann, 1985). Results from the present study found that very few individuals approached the predator model by flying toward it. Only seven individuals landed on the feeding stand, placing themselves within close proximity of the predator model. Those individuals that did approach tended to produce higher rates of calling.

Therefore, it appears that the bolder individuals tend to call more, even in the presence of a predator. If an individual produces chick-a-dee calls, both informing flock members of the predator's presence and potentially recruiting them for aid in mobbing-like behavior, the likelihood of being captured may be decreased (Templeton, Greene, & Davis, 2005). It is important to note, however, that across all individuals in the aviary, not just those that approached, modifications of call rate were observed as a result of the predator model, when compared to baseline call rates.

Additionally, the present study found that bolder individuals exhibited higher levels of aggressive behavior (also observed in rhesus macaques, *Macaca mulatta*: Kinnally, et al., 2008). Only seven individuals approached the feeding stand in the predator context, but out of those that did, they were also those that had the shortest latencies during the treadle trap presentation. Furthermore, in the present study, the most aggressive individuals were observed eating the most during baseline recordings (also observed in rhesus macaques: Kinnally, et al., 2008). Explained in more detail in the next chapter, the five most aggressive individuals (representing three of the six aviary groups) significantly differed from the rest of the birds in chick-a-dee call composition (producing calls with varying rates of distinct notes types). These individuals frequently supplanted others, gargled (an agonistic vocalizations), and chased flockmates during baseline observations. Further investigation of behavioral traits for this subset of individuals will begin in this chapter and continue in the next chapter. For our purposes here, these five highly aggressive individuals were the first individuals within their aviary to approach the feeding stand and pick up a mealworm during group sampling recordings. As stated, these aggressive, bold individuals produced the most chick-a-dee calls; however, they did not differ from the other individuals in the study across any other behavioral dimension. This begs the question of how these five individuals may differ from others within their experimental aviary flocks.

Flocks in the black-capped chickadee (*Parus atricapillus*) have been shown to form relatively stable dominance hierarchies where one individual, sometimes one pair within a flock, assumes the dominant position and will repeatedly aggress toward others (Smith, 1976; Ekman, 1989; Hogstad, 1989). One possibility is that these five individuals represent the dominant individuals within their aviary flock. Across various species, the most dominant individuals tend to be those who are rarely aggressed upon. These individuals tend to supplant others, but tend not to be the recipients of supplants (Ekman, 1989; Hogstad, 1989). In looking closely at the five most aggressive individuals, four of these individuals were never supplanted by another individual during focal sampling. Interestingly, three of these five birds came from one aviary flock, suggesting that something else was driving behavior, possibly in conjunction with a linear dominance hierarchy. In the closely related mountain chickadee (*Poecile gambeli*), which exhibits stable dominance hierarchies, behavioral profiles predicted dominance status, such that dominants and subordinates likely differ from one another prior to establishing dominance rank (Fox, Ladage, Roth, & Pravosudov, 2009). Present findings, taken with recent reports in the mountain chickadee, suggest that a specific behavioral type, or behavioral trait, could be one of the driving factors in the development of social rank and the acquisition of dominance. If such aggression were the result of a linear dominance hierarchy, we likely would have seen such clear aggressive differences equally across all six aviaries, with only one or two individuals assuming the most dominant rank. This was not the case. In many *Parus/Poecile* species (including the Carolina chickadee), males are, on average, larger in size than females and dominance rank is believed to be positively correlated with size (Verbeek, de Goede, Drent, & Wiepkema, 1999), with males typically dominating females (Hogstad, 1989; Dingemanse & de Goede, 2004). In looking at the subset of the five most aggressive individuals from the present study, four of the five were males. Surprisingly, though, these males were not statistically larger than the other males in the study based on wing chord measurements. Additionally, as mentioned earlier, the individuals that were placed in the aviary first were no more likely to exhibit aggressive behavior. Actually, two of the males in this subset were in pairs that were introduced last to their aviaries. Data suggest that "aggressiveness" may in fact be a powerful and significant behavioral trait.

Results from the present study add support to prior research in behavioral profiles, while contributing a new dimension, communicative behavior. In this study, results indicate that chick-a-dee call production was positively correlated with aggressive behavior, as well as eating behavior, which may be an indicator of boldness. The most aggressive individuals were the ones most likely to approach the feeding stand, pick up a food item, and eat. Those individuals that approached and contacted the treadle trap had higher rates of call production. Further studies investigating exploratory behavior would offer additional insight into how novelty and individuals' willingness to approach novel stimuli might be associated with chick-a-dee call rates. The best approach for studying behavioral traits and animal personality is to design a research project that incorporates repeated observations of a variety of behavioral traits across varying contexts, collected repetitively over a period of time. A single snapshot of data collection per individual is not adequate for truly assessing behavioral variations (Sih, Bell, Johnson, & Ziemba, 2004; Uher, Asendorpf, & Call, 2008). Taking this type of systematic approach, the present study collapsed multiple days and weeks of data collection, aggregating potential fluctuations in individual behavior. This approach offers a more holistic understanding of trait-related behavior and how personality and behavioral profiles play an influential role in the manifestation of the complex social system and call system of the chickadee.

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APPENDICES

APPENDIX A

TABLES

Table I. Spearman's Rank correlations between behavioral measures observed during 10-min focal sampling periods

Traits	r_s	p	adjusted α
Supplant – Gargle	**0.533**	**0.001***	**0.0033**
Eat – Supplant	**0.490**	**0.002***	**0.0036**
Gargle – Chase	**0.481**	**0.003***	**0.0039**
Chick-a-dee – Chase	**0.473**	**0.004***	**0.0042**
Eat – Gargle	**0.463**	**0.004***	**0.0046**
Supplant – Chase	**0.460**	**0.005***	**0.0050**
Eat – Chase	**0.421**	**0.010**	**0.0056**
Chick-a-dee – Eat	**0.420**	**0.011**	**0.0063**
Chick-a-dee – Supplant	**0.398**	**0.016**	**0.0071**
Chick-a-dee – Gargle	**0.354**	**0.034**	**0.0083**
Activity – Chase	-0.295	0.081	0.0100
Activity – Supplant	-0.245	0.151	0.0125
Activity – Chick-a-dee	-0.112	0.517	0.0167
Activity – Gargle	-0.111	0.518	0.0250
Activity – Eat	-0.089	0.607	0.0500

Correlations with a $p < .05$ are indicated with bold font. Significant correlations after Bonferroni adjustment (smallest p value of $0.05 / 15 = 0.0033$) are denoted with bold font and an asterisk.

Table II. Behavioral measures, factor loadings, and variance explained

Behavior	Factor 1	Factor 2	Factor 3
Chase	**0.866**	0.110	-0.006
Gargle	**0.857**	0.002	-0.001
Supplant	**0.643**	0.539	-0.015
Eat	0.176	**0.902**	-0.024
Trap latency	0.001	**-0.829**	0.197
Predator latency	0.064	0.046	**0.868**
Call rate	0.167	0.310	**-0.713**
Eigenvalue	2.900	1.461	1.158
Variance	36.247	18.257	14.471
Cumulative	36.247	54.504	68.974

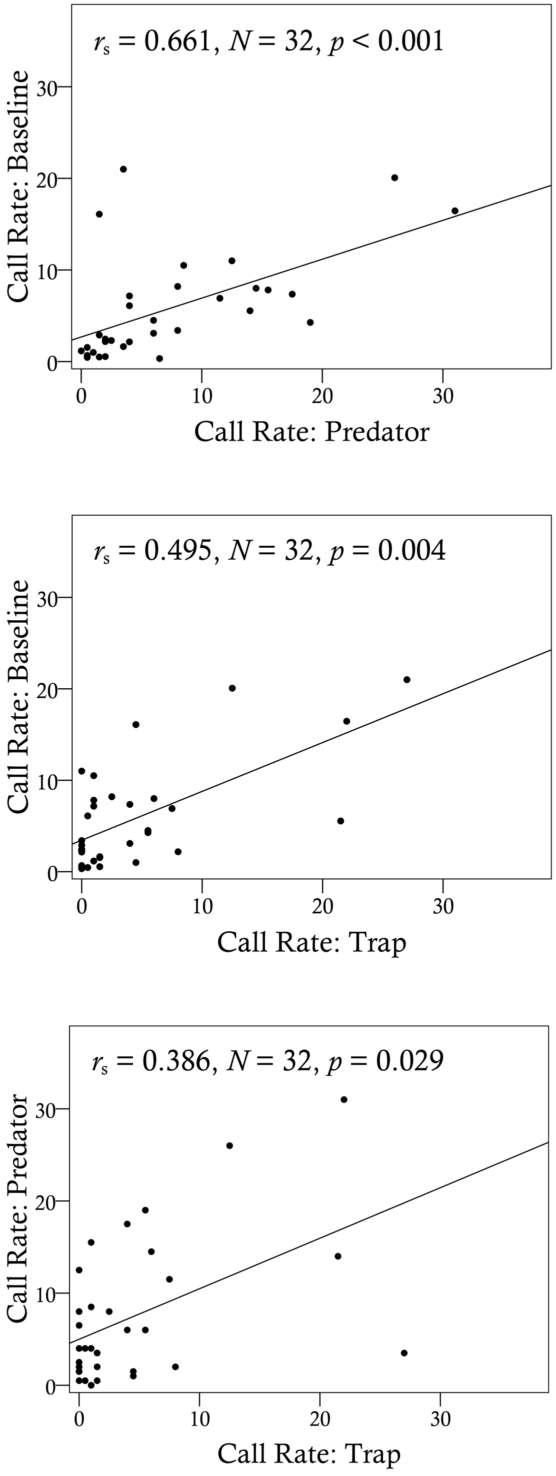
One behavioral measure, activity, did not reach the loading criterion of 0.600.

APPENDIX B

FIGURES

Figure 1. Spearman's Rank correlation coefficients comparing chick-a-dee call rates (average number per 10-min focal sample) of 32 Carolina chickadees across three experimental contexts: baseline, predatory context (presence of predator model), and trap (treadle trap presentation).

Figure 1



$r_s = 0.661$, $N = 32$, $p < 0.001$
Call Rate: Baseline
0
10
20
30
0
10
20
30
Call Rate: Predator
$r_s = 0.495$, $N = 32$, $p = 0.004$
Call Rate: Baseline
0
10
20
30
0
10
20
30
Call Rate: Trap
$r_s = 0.386$, $N = 32$, $p = 0.029$
Call Rate: Predator
0
10
20
30
0
10
20
30
Call Rate: Trap

Figure 2. Boxplot diagram illustrating chick-a-dee call rate across three different contexts: baseline, presentation of a treadle trap, and presentation of an avian predator. Different letters above boxes designate contexts in which call rate was significantly different.

Figure 2

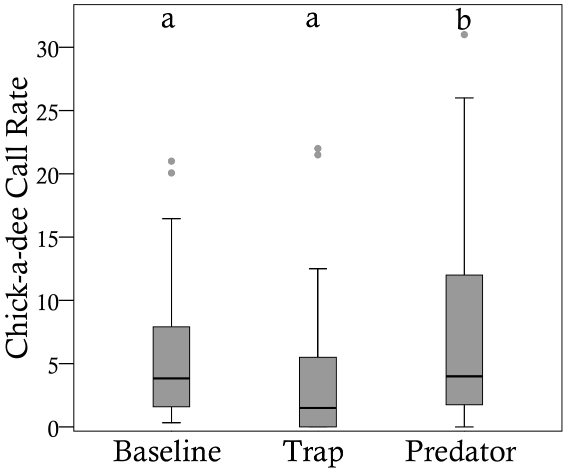

a
a
b
30
25
20
15
10
5
0
Chick-a-dee Call Rate
Baseline
Trap
Predator

Figure 3. Boxplot diagrams depicting frequency of eating behavior (average bouts per 10-min focal sample) and chick-a-dee call rate (average number per 10-min focal sample) across 32 Carolina chickadees that entered the treadle trap compared to those that did not enter the trap during a 20-min stimulus presentation period.

Figure 3

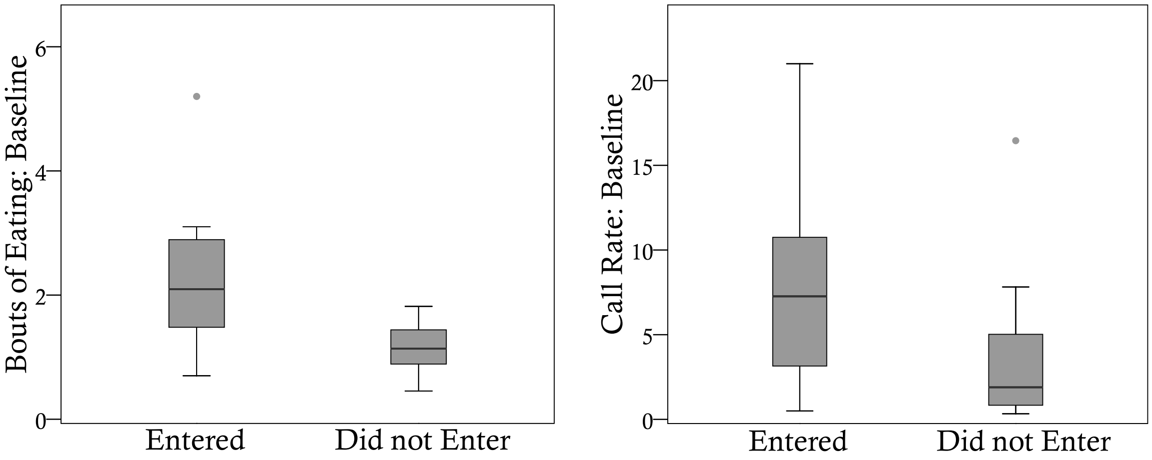
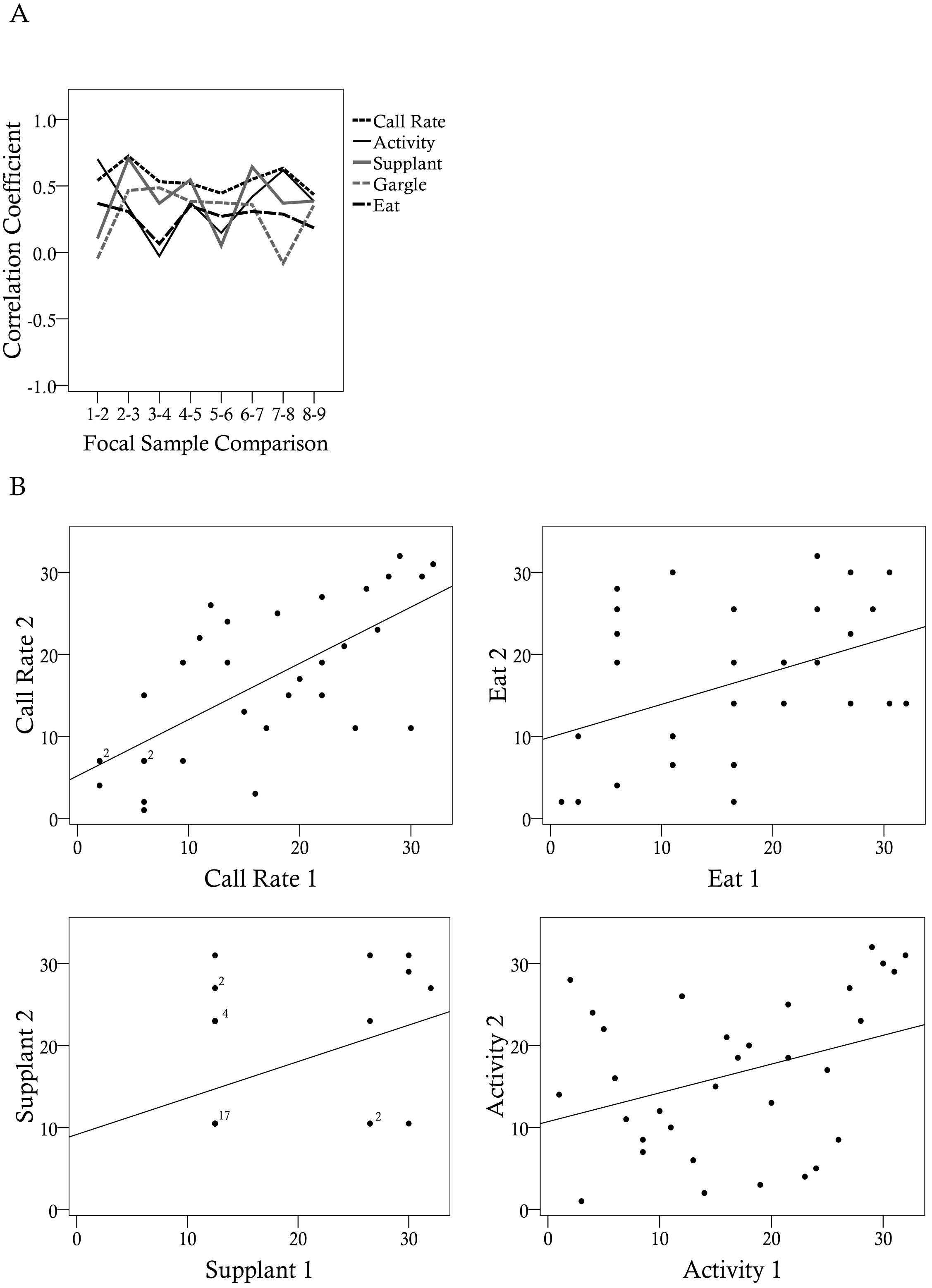

Bouts of Eating: Baseline
0
2
4
6
Entered
Did not Enter
Call Rate: Baseline
0
5
10
15
20
Entered
Did not Enter

Figure 4. (A) Spearman's Rank correlation coefficients comparing consistency of behavior between nine different focal samples for 32 individuals, spanning a period of approximately 15-days. (B) Individuals were ranked from 1 to 32 according to average behavioral responses during the first three (x-axis) and last three focal sample periods (y-axis).

Figure 4


A
Correlation Coefficient
1.0
0.5
0.0
-0.5
-1.0
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
Focal Sample Comparison
Call Rate
Activity
Supplant
Gargle
Eat
B
Call Rate 2
Call Rate 1
Eat 2
Eat 1
Supplant 2
Supplant 1
Activity 2
Activity 1
0
10
20
30
2
2
2
4
17
2

CHAPTER 4

BEHAVIORAL PROFILES AND THE CHICK-A-DEE CALL

ABSTRACT

There has been a surge of interest in investigating individual variation and stability of traits across a wide variety of species and across a range of contexts and situational influences. This rapidly growing field works to understand why individuals respond to changing contextual factors in a relatively predictable manner. Studies have addressed behavioral traits such as aggression, affiliation, boldness, general activity, and exploration levels. There is one behavior system that has been somewhat neglected in this body of work: communicative behavior. The present study aimed to address this missing link by testing for contextual influences on the production of the 'chick-a-dee' call, a complex call system of chickadees and related species. In the current study, experimental flocks (each composed of three female-male pairs) of Carolina chickadees (*Poecile carolinensis*) were housed in large outdoor aviaries. Birds were recorded during three distinct contexts: baseline, presence of predator model, and presence of treadle trap. The chick-a-dee call of the Carolina chickadee was analyzed for frequency of each note typed produced by context, and individual differences in length of call and rate of each note type produced. Rates of different notes types varied by context, and individual differences were found in the rates of different note types produced, as well as in length of call produced across experimental contexts.

CHAPTER 4

BEHAVIORAL PROFILES AND THE CHICK-A-DEE CALL

The chick-a-dee call of many *Parus* species is a highly complex vocal communication system (Baker & Becker, 2002; Templeton, Greene, & Davis, 2005; Lucas & Freeberg, 2007; Freeberg, 2008). Both male and female chickadees produce the chick-a-dee call throughout the year, when in breeding pairs as well as when in stable flocks (Mostrum, Curry, & Lohr, 2002). This suggests that an important function of this call is for group structure and maintaining group cohesion. Furthermore, variation in the chick-a-dee call and note composition of the call can communicate a variety of messages, including avian predator presence, urgency of threat, and detection of food (Ficken, Hailman, & Hailman, 1994; Baker & Becker, 2002; Templeton, Greene, & Davis, 2005; reviewed in Lucas & Freeberg, 2007).

The chick-a-dee call is composed of distinct note types that may or may not occur within a single call (Ficken, Hailman, and Hailman, 1994; Hailman, 1989). If a note type does occur, it may occur more than once; however, it appears that relatively strict ordering rules are followed and only certain note types follow other note types (Hailman, Ficken, & Ficken, 1985). More specifically, in the Carolina chickadee call, there are seven distinct note types: A, E, B, Ht (high-tee-chick), C, D_h (D hybrid), and D, in which the introductory notes, A, E, and B almost always begin a call, followed by one or more of the following: Ht, C, D_h, or D (Bloomfield, Phillmore, Weisman, & Sturdy, 2005; Freeberg, 2008; see Fig. 1).

Sometimes, however, a chickadee will produce a call that is composed of a single note type, most likely a string of D notes or a string of C notes (Fig. 1). It has been suggested that the note composition of the chick-a-dee call of Carolina chickadees may communicate specific messages to others in the surrounding environment, such as flockmates (Lucas & Freeberg, 2007). Specific contextual information, such as flying behavior, distance off ground, flock location, or presence of an avian predator, may be transmitted between individuals depending on the note type and note composition of the chick-a-dee call produced (Freeberg, 2008). For example, Freeberg (2008) reports that chickadees produce calls with more C notes and fewer D notes per call during flight and calls composed of more A notes when the presence of a flying avian predator is detected.

Experimental approaches have investigated how contextual factors influence production of the chick-a-dee call across flocks; however, very little is known about individual differences in call structure and call rate across varying contexts. For example, do all individuals within a flock modify their call within a changing environment in the same way or are there individual differences in call structure? These questions have yet to be answered in regards to communicative behavior; however, similar questions pertaining to individual variation have been asked in regards to other behavior systems – including aggression (pigs: Erhard, Mendl, & Ashley, 1997; spiders: Johnson & Sih, 2005), sociability (hyenas: Gosling, 1998), dominance (great tits: Dingemanse & de Goede, 2004), curiosity / novelty (bushbabies: Watson & Ward, 1996), and boldness (sunfish: Coleman & Wilson, 1998). Variation across these traits has been studied in a number of species, including snakes (Herzog & Burghardt, 1988), fish (Wilson, Coleman, Clark, & Biederman, 1993), birds (Verbeek, Drent, & Wiepkema, 1994), and primates (Gold & Maple, 1994; King & Figueredo, 1997). This is not an exhaustive list, but hopefully gives an idea of the breadth of individual variation and the applicability of its study to a range of species. Such individual variation is referred to as non-human animal personality, behavioral syndromes, or behavioral profiles (Gosling, 2001; Sih, Bell, & Johnson, 2004; Gosling, 2008). Despite the enormous literature on vocal communication in animals (Hauser, 1996; Bradbury & Vehrencamp, 1998), there has been little research aimed at understanding individual differences in vocal production.

My goal in the present study was to test for behavioral stability across varying contexts in vocal production of the Carolina chickadee (*Poecile carolinensis*) and to assess if vocal production and/or the structure of the chick-a-dee call were correlated with any other behavioral trait. Despite a great deal of study aimed to understand the function of variation in the chick-a-dee call, such variation has yet to be linked to specific behavioral and personality traits. In order to fill this gap in the literature, the present study aimed to test for correlates between the chick-a-dee call and specific behavioral measures.

METHODS

Subjects and housing

Thirty-six Carolina chickadees (*Poecile carolinensis*) were captured from established trapping sites in east Tennessee, including Ijams Nature Center, the University of Tennessee Forestry Resources, Research, and Education Center (UTFRREC), and three residential trapping sites. Birds were housed in outdoor aviaries (6 x 9 x 3.5 m) at UTFRREC. Individuals were grouped together in experimental flocks of six birds during the overwintering months of 2008-2009 (September 2008 – March 2009). Within each experimental flock, there were three female-male pairs. Each pair within a flock was from a different trapping site, with sites far enough apart to ensure pairs were members of different flocks (see Chapter 3 for a more detailed explanation). Therefore, each individual flock member was housed with one familiar individual and four unfamiliar individuals. Once all birds were introduced to an aviary, an acclimation period of two weeks preceded data collection. See Chapter 3 for additional details regarding capture methodology and housing conditions (including both feeding and maintenance protocols).

Design and procedure

I collected an average of ten 10-min focal recording periods from each individual, totaling 3,700 min of focal recording. In addition, I collected 596 min of *ad libitum* group sampling (Martin & Bateson, 1986), used to collect latency data (explained below) and to supplement the total number of calls recorded per individual from focal sampling, hereafter referred to as baseline.

Following baseline recordings, I created two experimental contexts by presenting various stimuli to each aviary: a treadle (potter) trap (36 x 18.5 x 18.5 cm) and a model of a Cooper's hawk (*Accipiter cooperii*), a common predator of this species. Each stimulus presentation occurred on a separate day; thus, no aviary was presented with both stimuli within a 24 hour period. Stimuli were placed on the feeding stand within each aviary. White ceramic bowls containing live mealworms and waxworms were used during stimulus presentations, identical to food bowls already in use for providing live food. For the trap context, the bowl was placed inside the locked-open trap; thus, birds had to enter the trap in order to pick up a worm. During the predator context, the white bowl was placed next to the hawk model. Each stimulus presentation lasted for 20 min. See Chapter 3 for a more detailed description and methodology of stimulus presentations.

During baseline recordings, behavioral measures collected for each individual included aggressive behavior (supplants, chases, and gargle vocalizations), chick-a-dee calls produced, eating behavior, general activity, and latency measures. During group sampling recordings, when no stimulus was present, live food was placed in the white ceramic bowls and baseline latency for each individual to pick up a worm was recorded. In addition, latency for each individual to pick up a food item during the stimulus presentations was recorded. In addition to analyses of the behavioral data described in Chapter 3, vocal recordings of the chick-a-dee call were analyzed in the laboratory for a detailed assessment of call structure.

Chick-a-dee call recordings

Chick-a-dee calls were recorded with Sennheiser ME-66 microphones using a Marantz PMD-660 digital recorder at a sample rate of 44,100 and 16-bit resolution. Call recordings were collected simultaneously with collection of behavioral data during baseline and during stimulus presentations (see Chapter 3 for more detail). Vocal recordings were then uploaded to a computer for analysis. Using Cool Edit Pro, Version 2.0, individual notes were classified (according to Bloomfield, Phillmore, Weisman, & Sturdy, 2005 and Freeberg, 2008; Fig. 1) by viewing each call on the spectral view window (Blackman-Harris windowing function with a resolution of 256 bands). For this study, I followed the classification of Freeberg (2008), in which the B_1 and B_2 notes of Bloomfield, Phillmore, Weisman, & Sturdy (2005) are combined to form the E note. For the present study, I classified B notes as the inverted U-shape note also indicative of B notes in prior studies with the Carolina chickadee (Lucas & Freeberg, 2007; Freeberg, 2008). Due to the rarity in my sample (less than 1% of total data set), I did not include the D-hybrid or the high-tee-chick notes in additional statistical analyses. Call compositions and note classifications were entered manually into Microsoft Excel and SPSS spreadsheets. Four individuals died before the predator and treadle trap presentation; these individuals were not included in the stimulus presentation analyses below.

Inter-rater reliability

In order to ensure reliable note classification, a trained observer independently scored 433 calls from a random subset of the total sample (11% of the total sample). Inter-rater reliability was high using the Cohen's Kappa statistical test (A notes = 0.848, E notes = 0.850, B notes = 0.863, C notes = 0.975, and D notes = 0.985).

Statistical analyses

Statistical analyses were conducted using SPSS, Version 16.0 for Windows. For the note type and call composition analyses, effect of context (baseline, predator, and trap) was tested using Friedman's ANOVA, followed by pairwise tests using the Wilcoxon Signed-Ranks test. In testing for effect of context by note type, I implemented a sequential Bonferroni adjustment, also known as Holm’s procedure (Holm, 1979; Rice, 1989). The adjusted alpha level is reported along with each statistical test. If no call was recorded for an individual during an experimental context, it was not included in analyses; the corresponding *N* value is reported with each correlation.

RESULTS

Chick-a-dee call scoring

Note type classification

I identified 4,012 chick-a-dee calls. Out of the total sample, it was possible to individually classify note types for 3,896 of the calls, for an average of 108.22 calls per individual (*median* = 74.5). Out of the total 3,896 calls, I classified 26,595 notes (see Table I). There were, on average, 6.83 notes per call (*median* = 6; *range* = 2 – 63).

Note type by context

Out of the total sample, 79.7% of the calls ($N = 3{,}015$) were recorded during baseline, 12.6% of the calls ($N = 478$) were recorded during the predator presentation, and 7.6 % of the calls ($N = 289$) were recorded during the treadle trap presentation (see Table II). For calls produced during baseline recordings, there were 6.49 notes per call on average. During the predator context, there were 8.00 notes per call on average. During the treadle trap presentation there were 8.03 notes per call on average.

Out of the total sample of calls recorded, one note type was significantly associated with context. Specifically, there was a significant effect of context for D notes (Friedman's

ANOVA: $\chi^2 = 12.636$, df = 2, $p = 0.002$, adjusted alpha = 0.01). More D notes were produced per call during the treadle trap (Wilcoxon Signed-Ranks: $Z = -2.829$, $p = 0.005$, adjusted alpha = 0.0167) and predator ($Z = -2.763$, $p = 0.006$, adjusted alpha = 0.025) presentations than during baseline (Fig. 2). The number of D notes per call during the predator and trap presentations did not differ from one another. There was a marginal effect for B notes to differ by context (Friedman's ANOVA: $\chi^2 = 6.500$, df = 2, $p = 0.039$, adjusted alpha = 0.0125), with more B notes in calls produced during the predator stimulus presentation. Likewise, there was a trend for C notes to differ by context (Friedman's ANOVA: $\chi^2 = 6.198$, df = 2, $p = 0.045$, adjusted alpha = 0.0167). The number of A notes and E notes produced per call did not differ by context. See Table II for mean values across all contexts.

Individual consistency of note type across context

Individuals that produced chick-a-dee calls with more C notes or more D notes per call consistently produced calls with a higher frequency of C notes or D notes across all three contexts (see Fig. 3). Therefore, individual differences in both length of call and composition of call were stable across changing contextual factors.

Correlates between note type and behavioral traits

As reported in Chapter 3, the most aggressive individuals, with respect to supplanting, chasing, and gargling behavior, exhibited the highest rates of chick-a-dee call production. The most aggressive individuals during baseline conditions produced higher numbers of D notes per call during the predator context (Fig. 4a-c). Similarly, individuals that produced calls with high rates of C notes per call during the predator presentation exhibited higher rates of supplanting behavior during baseline (Fig. 4d). Likewise, during baseline recordings, birds that produced high rates of C notes per call were also highly aggressive in regard to supplanting behavior (Fig. 4e). Aggressive behavior did not appear to be correlated with any other note type.

Latency to approach the feeding stand during the predator presentation was inversely correlated with both the number of C notes produced per call during the predator context and the rate of C notes produced during baseline recordings (Spearman's Rank correlations: $r_s = -0.473$, $N = 31$, $p = 0.007$ and $r_s = -0.556$, $N = 32$, $p = 0.001$, respectively; see Chapter 3 for more details regarding behavioral measures). Additionally, eating behavior during baseline was positively correlated with the number of C notes per call during baseline (Fig. 5a) and the number of C notes produced per call during the predator context (Fig. 5b).

DISCUSSION

Results reveal existence of individual variation for specific characteristics of the chick-a-dee call, as well as correlates between production of the call and behavioral traits. Calls differed by individual in length (i.e. notes per call), as well as call composition (i.e. note types within each call). In collapsing across all three experimental contexts, more D notes were produced than any other note type (Table II). It may be possible that the D note plays an important role in communication between flockmates, as was suggested by earlier work on this call system (Smith, 1972; Hailman, Ficken, & Ficken, 1985). Potentially, the number of D notes per call may relay more information to flockmates than the other note types of the call.

The number of D notes per call significantly varied depending on contextual factors, with more D notes per call during the predator and trap presentation contexts. These findings were similar to previous research investigating the chick-a-dee call system in the presence of a predator (Templeton, Greene, & Davis, 2005). Additionally, Baker and Becker (2002) report that call rate, in the black-capped chickadee (*P. atricapilla*), was positively correlated to the degree of threat related to an avian predator.

In comparing the average number of note types produced per context (see Table II), the low frequency note type, the D note, was much more likely to be produced in the two stimulus presentation contexts. These increases in D notes are somewhat in agreement with

Morton's (1977) motivation-structural rules. Morton (1977) suggests that harsher, lower frequency sounds in an animal's call system are suggestive of hostile or aggressive contexts, while higher frequency, pure tones are indicative of frightening contexts. One possibility is that instead of reacting with fear to the avian predator and the trap, changes in their call structure may suggest a more hostile, aggressive, and mobbing-like response (e.g. Templeton, Greene, & Davis, 2005). In support of this idea, two of the six experimental flocks exhibited a very different behavioral pattern in response to the predator model than the other four groups. For these two groups, they demonstrated what appeared to be relatively strong anti-predator behavior in which all individuals of the group flocked together in one tree and simultaneously produced great numbers of chick-a-dee calls, so many in fact, that individual identification was impossible. This mobbing-like behavior may be indicative of a more hostile or aggressive response, rather than a fear response to the predator model.

In considering Morton's (1977) motivation-structural rules, the high frequency A note of the chick-a-dee call may serve an alarm function (Ficken, 1990; Freeberg, 2008). Baker & Becker (2002) found that fewer A notes and more B notes were produced per call when a predator was in close proximity (within 1 m), versus 6 m away. Freeberg (2008) reports more A notes and fewer B notes per call in a predatory context, specifically when a live predator flew through the recording area. Findings of the present study, although not statistically significant, found trends for increased numbers of B notes produced per call when a predator model was on the feeding stand of a captive flock. Taken together, these results reveal that (1) more information is needed to understand the complexity of this vocal communication system; and (2) relatively specific messages may be relayed between flockmates via the composition of the chick-a-dee call. In regard to potential messages relayed, across all three of these studies, predator distance varied; thus, discrepancies between call structures (i.e. note composition of the call) may be due to distance between the signaler and the predator. Nonetheless, information regarding predator detection, predator distance, level of risk or danger, and urgency may all be conveyed through call structure (Baker & Becker, 2002; Templeton, Greene, & Davis, 2005; Lucas & Freeberg, 2007).

Despite overall effects of context on call structures, individuals exhibited personality-like differences in call structure across the three experimental contexts. This was particularly evident when assessing call rate (Ch. 3) and length of call (i.e. total number of notes per call). Individual rank-order differences in certain aspects of call structure (particularly C and D notes) were largely maintained across contexts. Such individual stability of note type produced, despite drastic changes in the immediate context, suggests that chick-a-dee call structure is a relatively stable behavioral measure that likely has important implications for the study of behavioral profiles. The next step would be to test if communicative behavior co-varies with other behavioral traits, thereby providing evidence for the existence of behavioral profiles.

Stability of call length persisted when comparing present findings with an earlier study assessing call length, note type, and call function in the chickadee. In regards to length of call, Freeberg (2008) collected over 5,500 calls across 40 recording sites, representative of 40 flocks. In this earlier study, the average number of notes produced per chick-a-dee call was 6.13 (range = 1 – 45), compared to an average of 6.83 notes per call (range = 2 – 63) in the present study, revealing that average call lengths obtained in this captive study are very similar to call lengths obtained in naturalistic observations in field settings.

In testing for a relationship between vocal production and behavioral traits, the present data suggest that more aggressive individuals tend to produce calls with more C and D notes per call in the stimulus presentation contexts. Specifically, individuals exhibiting the highest levels of aggression during baseline measures produced calls with a high number of D notes per call. In crested tits (*Parus cristatus*), dominant individuals produce more calls than subordinates; and males, which are more dominant in this species, produce more calls than females (Krams, 2000). Dominance patterns in relationship to individual behavior, and behavioral profiles, has been investigated in other avian species (great tits, *Parus major*: Dingemanse & de Goede, 2004; mountain chickadees, *Poecile gambeli*: Fox, Ladage, Roth, & Pravosudov, 2009). However, the link between vocal patterns, call structure, and individual behavioral traits had not been investigated prior to the present study.

As depicted by Figure 4, there were five individuals (four males and one female) that exhibited the highest levels of aggression and also produced higher rates of D notes per call. As mentioned earlier, there were other individuals that produced calls with similar numbers of D notes per call, but that exhibited much less aggressive behavior. One hypothesis for this discrepancy is that these five individuals represent 'keystone' individuals (Sih & Watters, 2005). As described by Sih & Watters (2005), 'keystone' individuals have the potential to greatly influence a group's behavior, and are oftentimes the most dominant or aggressive individuals within a group. The high aggression levels and call rates of these five birds likely influenced the behavior of the other members of the flock, thus directly affecting group level dynamics. In further examination of this subset, these individuals represent three of the six groups (so no one aviary was especially aggressive or bold in comparison to the others) and these five individuals were also, most often, the first individuals within their aviary to pick up a live food item during baseline recordings when no stimulus was present. Across many studies in behavioral profiles, the first individual to approach and/or a pick up a food source is rated as highly bold. Therefore, these were not only the most aggressive, but also exhibited characteristics of boldness.

This is the first study to test personality-like influences in a highly complex vocal communication system, offering new research directions to the behavioral profile field. Additional study of individual variation in the structure of social and contact calls needs to be further investigated; however, this is the first approach to understanding how chick-a-dee calls are composed on an individual level. The present study found strong evidence for correlated behavioral traits between aggression, boldness, and call structure. Additionally, individual stability in call structure was demonstrated across functional contexts, revealing important connections with behavioral profiles. Data suggest that by knowing something regarding call rate or note composition, we (or a chickadee receiver) may be able to predict something about the aggressiveness or potentially the boldness of the signaler.

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APPENDICES

APPENDIX A

TABLES

Table I. Distribution of note type and note type usage in the chick-a-dee call of the Carolina chickadee (total sample includes 3,896 chick-a-dee calls and 26,595 notes)

Note Type	Mean ± SD	Range	*N*	Percentage of Total
A	0.26 ± 0.80	0 – 14	1,026	3.9%
E	1.37 ± 1.61	0 – 16	5,344	20.1%
B	0.17 ± 0.38	0 – 3	666	2.5%
Ht	0.01 ± 0.16	0 – 5	2	< 1.0%
C	1.04 ± 1.73	0 – 11	4,044	15.2%
D_h	0.05 ± 0.23	0 – 1	208	< 1.0%
D	3.92 ± 3.84	0 – 62	15,275	57.4%

Table II. Mean, range, and standard deviation of each note type per chick-a-dee call produced (total sample size: 3,782 calls) during three contexts: baseline, presence of avian predator, and treadle trap

	Baseline			Predator			Treadle Trap		
	N = 3015			*N* = 478			*N* = 289		
	x	range	SD	*x*	range	SD	*x*	range	SD
A	0.25	0 – 14	0.771	0.29	0 – 7	0.760	0.36	0 – 13	1.087
E	1.41	0 – 13	1.610	1.18	0 – 16	1.721	1.39	0 – 10	1.551
B	0.15	0 – 2	0.365	0.27	0 – 3	0.464	0.19	0 – 2	0.399
C	1.02	0 – 11	1.698	1.04	0 – 11	1.832	1.10	0 – 8	1.771
D	3.60	0 – 37	3.623	5.13	0 – 30	3.893	4.96	0 – 62	5.220

APPENDIX B

FIGURES

Figure 1. Sound spectrograms for the note type classification system in the chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). The differing notes illustrate the variety of note types and composition within one chick-a-dee call. For the presented spectrograms, time (0 to 1.2 sec) is measured on the X-axis and frequency (0 to 20 kHz) is depicted on the Y-axis.

Figure 1

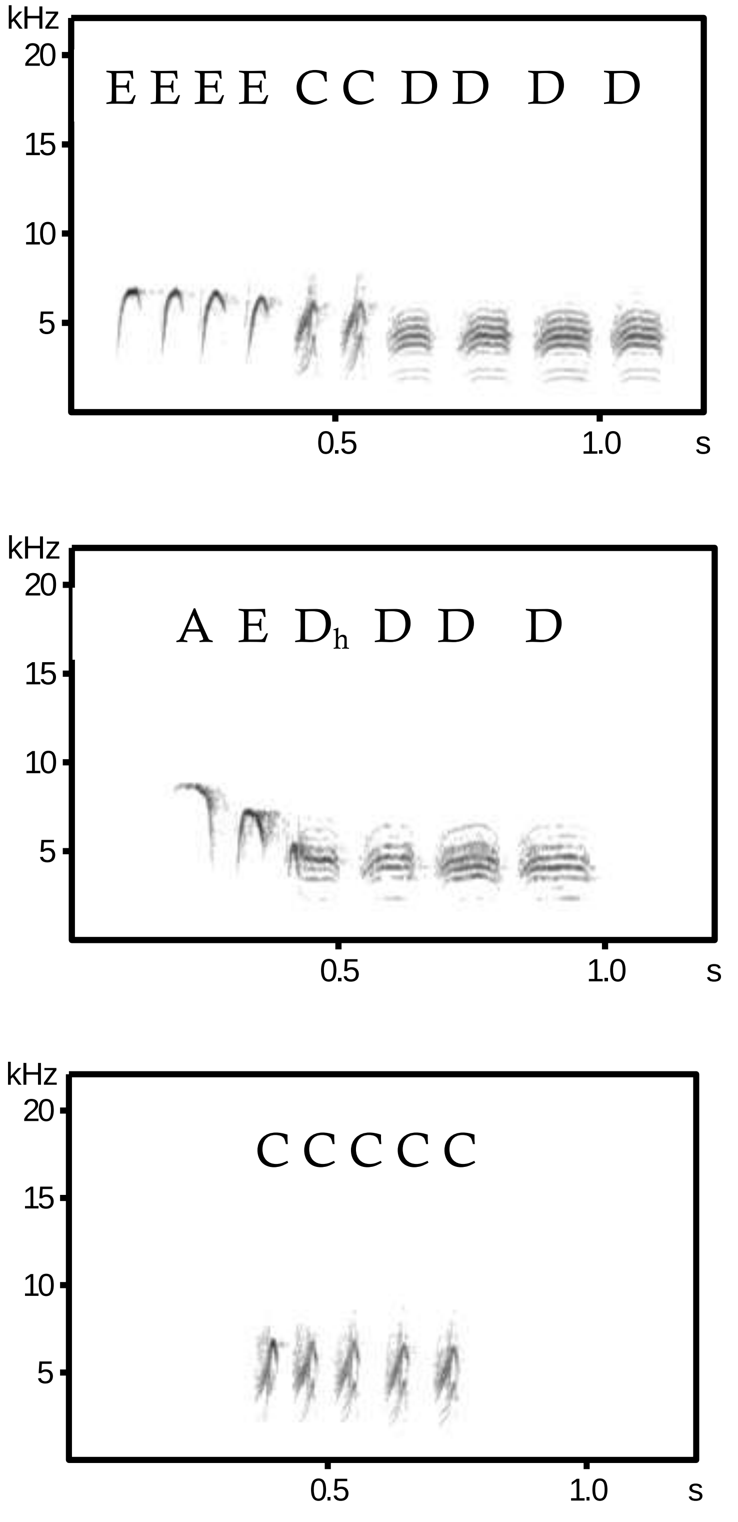

kHz
20
15
10
5
E E E E C C D D D D
0.5
1.0
s
kHz
20
15
10
5
A E D_h D D D
0.5
1.0
s
kHz
20
15
10
5
C C C C C
0.5
1.0
s

Figure 2. Boxplot diagram illustrating contextual differences in production rate per call for the D note type in the chick-a-dee call across three experimental contexts: baseline, treadle trap, and predator, in the Carolina chickadee. Different letters above boxes designate contexts in which the number of D notes per call was significantly different.

Figure 2

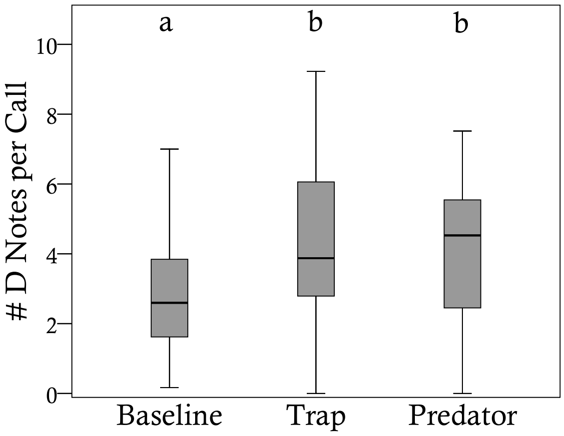


Figure 3. Spearman's Rank correlation coefficients comparing (A) the number of D notes and (B) the number of C notes produced per chick-a-dee call during each of three recording contexts: baseline, treadle trap, and predator.

Figure 3

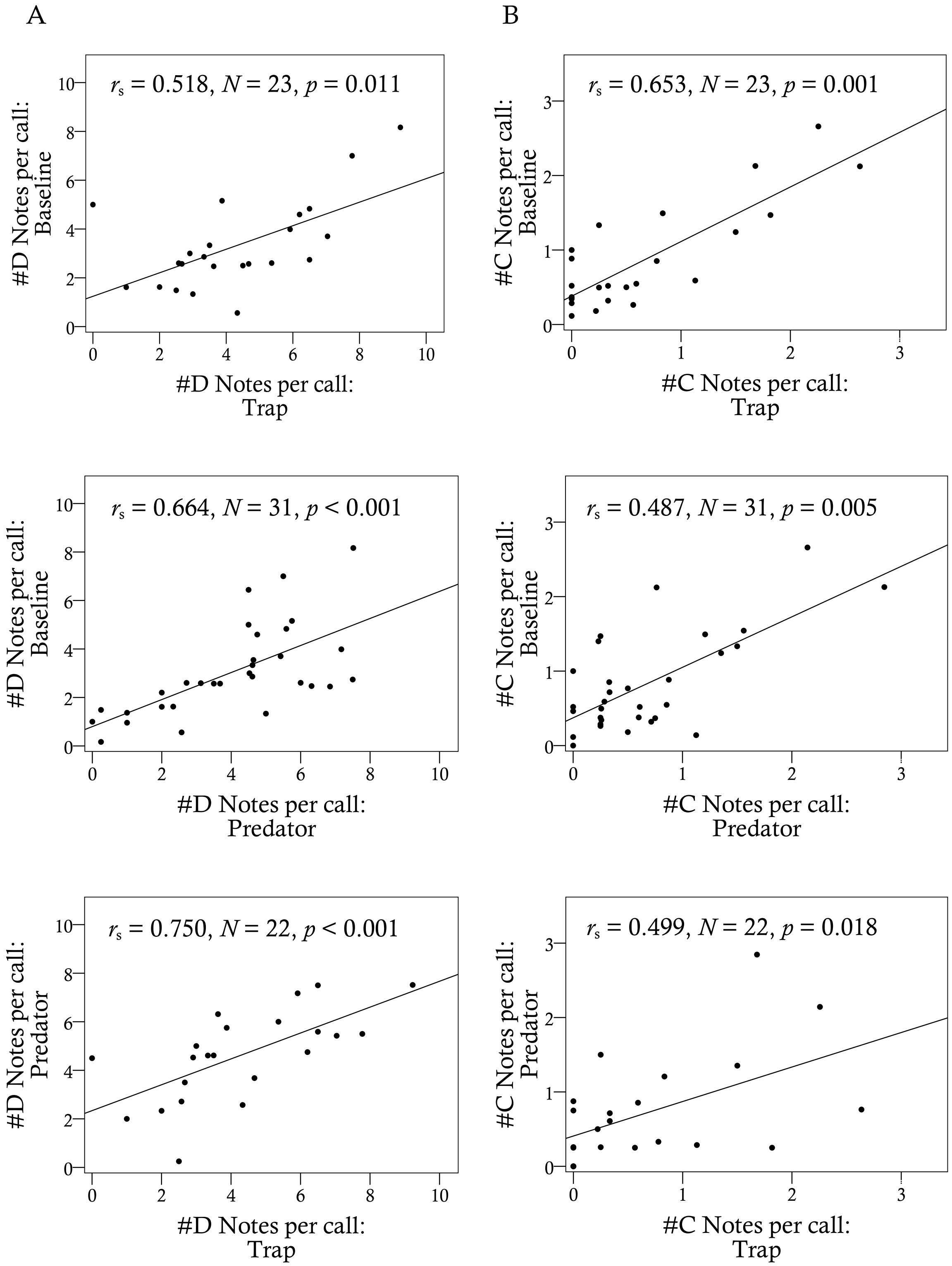

A
B
$r_s = 0.518$, $N = 23$, $p = 0.011$
#D Notes per call: Baseline
#D Notes per call: Trap
$r_s = 0.653$, $N = 23$, $p = 0.001$
#C Notes per call: Baseline
#C Notes per call: Trap
$r_s = 0.664$, $N = 31$, $p < 0.001$
#D Notes per call: Baseline
#D Notes per call: Predator
$r_s = 0.487$, $N = 31$, $p = 0.005$
#C Notes per call: Baseline
#C Notes per call: Predator
$r_s = 0.750$, $N = 22$, $p < 0.001$
#D Notes per call: Predator
#D Notes per call: Trap
$r_s = 0.499$, $N = 22$, $p = 0.018$
#C Notes per call: Predator
#C Notes per call: Trap
0
2
4
6
8
10
0
1
2
3

Figure 4. Spearman's Rank correlation coefficients comparing (A-C) the number of D notes produced per chick-a-dee call during a predatory context with three measures of behavioral aggression: supplant, chase, and gargle, and (D-E) the number of C notes produced during the predator and baseline contexts compared to supplanting behavior during baseline.

Figure 4

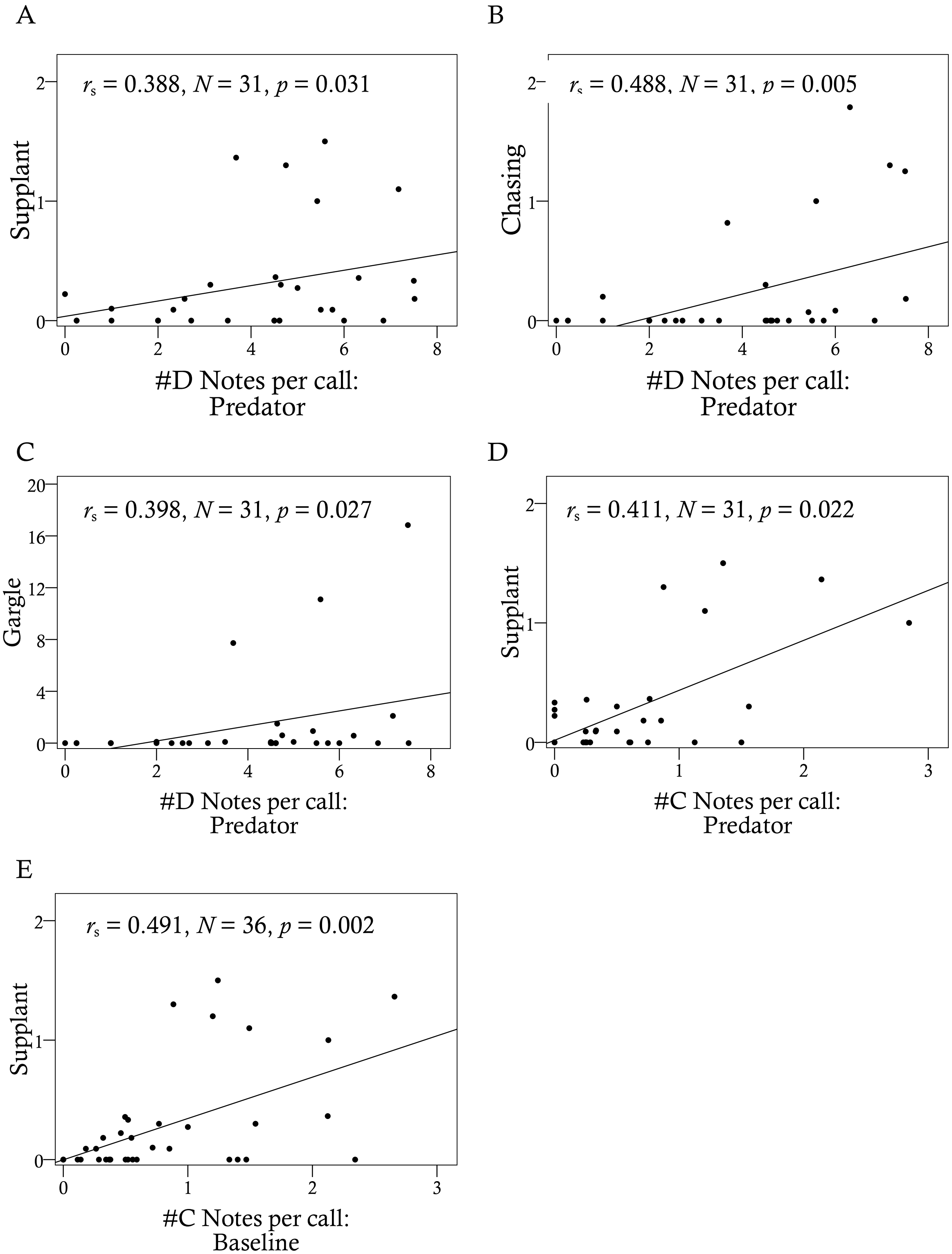
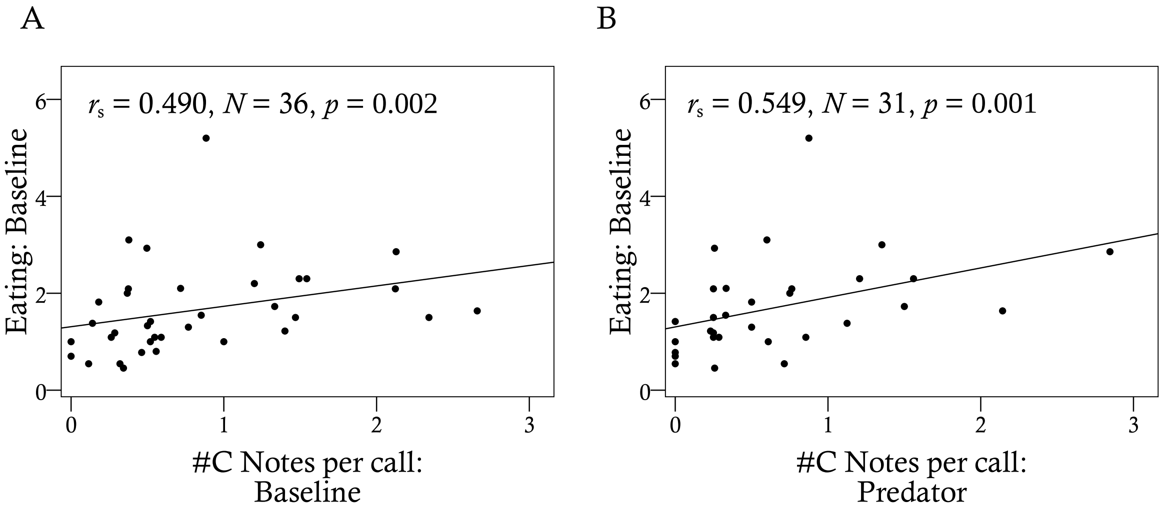

A
$r_s = 0.388, N = 31, p = 0.031$
Supplant
0
1
2
0
2
4
6
8
#D Notes per call:
Predator
B
$r_s = 0.488, N = 31, p = 0.005$
Chasing
0
1
2
0
2
4
6
8
#D Notes per call:
Predator
C
$r_s = 0.398, N = 31, p = 0.027$
Gargle
0
4
8
12
16
20
0
2
4
6
8
#D Notes per call:
Predator
D
$r_s = 0.411, N = 31, p = 0.022$
Supplant
0
1
2
0
1
2
3
#C Notes per call:
Predator
E
$r_s = 0.491, N = 36, p = 0.002$
Supplant
0
1
2
0
1
2
3
#C Notes per call:
Baseline

Figure 5. Spearman's Rank correlation coefficients comparing eating behavior during baseline (average bouts per 10 min focal sample) with the number of C notes produced per chick-a-dee call during (A) baseline recordings and during (B) the predatory context.

Figure 5


A
B
$r_s = 0.490$, $N = 36$, $p = 0.002$
$r_s = 0.549$, $N = 31$, $p = 0.001$
Eating: Baseline
Eating: Baseline
0
2
4
6
0
1
2
3
#C Notes per call: Baseline
#C Notes per call: Predator

CHAPTER 5

CONCLUSIONS AND CONTRIBUTIONS

CHAPTER 5

> However much psychologists may disagree about the best way
> to conceptualize the structure of personality or to define its
> units, on one point – its complexity – there is unanimity.
>
> – MacKinnon (1951)

The study of non-human animal personality is not a new research topic. However, it has grown with fury in the past decade and is rapidly gaining the attention of many current researchers. Researchers are taking old ideas in new directions, applying new approaches to fundamental, historical psychological principles. Research on animal personality has expanded into fields of Comparative Psychology, Behavioral Ecology, and Developmental Psychology. Studies stretch across more than 60 different species (Gosling, 2008) and describe traits such as aggression, curiosity, exploration, nest defense, boldness, and many others.

Over a half century ago, Donald O. Hebb (1946) made an excellent argument for the study of non-human animal personality. He stressed the importance of using descriptive language to further understand animal behavior and to establish order and meaning from an "endless series of specific acts" (page 88). By studying, describing, and objectively labeling specific behavioral traits, such as curiosity, aggression, and boldness, we open up new areas of research and mold the study of personality and temperament into a suitable approach for scientific comparative psychology (Hebb, 1946). As has been documented, multiple behavioral traits do exhibit stability and consistency across varying contexts, allowing for predictability of an individual's behavior.

This chapter will begin by briefly revisiting findings presented in this dissertation and the behavioral profiles paradigm. In discussing the overarching aims of the study of behavioral profiles, I will begin by briefly comparing phenotypic stability and phenotypic flexibility. Our discussion will then move toward the importance of investigating phenotypic stability within a social realm. Next, I will highlight some of the contributions communicative behavior can offer this field of research and potential implications that my dissertation work has for broadening the scope of animal personality. This chapter will conclude with a discussion of the ecological significance and associated costs of behavioral profiles.

A behavioral profiles paradigm

The research presented in this dissertation examines how behavioral profiles impact individual behavior and communicative interactions in social settings. First, in relation to behavioral consistency across varying contexts, behavioral stability was found in both laboratory and semi-naturalistic testing environments. During laboratory testing, activity level, vocal production, and aggressive behavior were all highly correlated when comparing baseline measures to three stimulus contexts: presentation of a novel object, a novel female conspecific, and a predator model (Williams, In preparation; see also Harvey & Freeberg, 2007). These stimulus presentations were conducted in both alone and social testing conditions. Strong within-condition stability was found; however, there was less predictability of behavior when comparing behavioral traits across the two testing conditions. In comparing multiple behavioral traits, activity level, chick-a-dee call rate, and aggression were correlated with one another, such that a more aggressive, active individual had higher rates of vocal production compared to a less active, less aggressive individual (Williams, In preparation).

In expanding my program of research, the next step was to bring my studies of behavioral stability in social contexts into a semi-naturalistic environment. This transition allowed for a more biologically valid examination of behavioral profiles (developed in more detail below). In the aviaries, experimental flocks were established using female-male pairs (different pairs in each flock were unfamiliar), which placed individuals in new physical and social groups. This design presented three possible outcomes: 1) the social context would minimally influence individuals' behavior, thus supporting a behavioral profiles view; 2) the social context would dramatically affect behavior, thus masking the expression of behavioral profiles; or 3) both the social environment and behavioral profiles would together influence behavior.

A behavioral profiles framework emphasizes examining behavior across multiple functional contexts, helping to elucidate the maintenance of individual variation within a species, despite changing environments. The study of behavioral profiles may help to explain why an individual may behave in a maladaptive manner in a particular context. Individuals do not exhibit unlimited behavioral plasticity due to potential carry-over effects. In this case, individuals sometimes appear to exhibit sub-optimal or maladaptive behavior (Sih, Bell, Johnson, & Ziemba, 2004). Currently, research is aimed toward understanding the functional significance of animal personality, its applicability to multiple behavioral patterns, and how these traits may co-vary with one another.

Contextual influences

In his early writings, Mischel (1968) claimed that little empirical evidence existed to support a trait or personality idea. For him, personality had little influence on behavior and he found insufficient evidence to claim that behavior is controlled by underlying motivational states (Mischel, 1984; Funder, 2001). Mischel (1968) believed that researchers could best understand behavior by attending to contextual factors, not limiting themselves to internal or personality psychology. This debate between 'personality' and 'situation' has dominated much of personality and social psychology for decades and has spilled over into many areas of research (Mischel, 1968; Kenrick & Funder, 1988; Funder, 2001; Funder, 2008).

There is diverse literature supporting the importance of environmental and contextual factors across a variety of behavior systems (Ross & Nisbett, 1991; Coleman &

Wilson, 1998; Reale, Gallant, Leblanc, & Festa-Bianchet, 2000; White, King, & West, 2002; van Oers, Klunder, & Drent, 2005; Sinn & Moltschaniwsky, 2005). Moreover, in this collection of literature, traits are believed to be context-specific, mainly because behavior directly related to survival or reproductive success needs to be malleable in order to produce the most adaptive response. For example, a study involving cowbirds (*Molothus ater*) emphasizes the significance of the social context in both species recognition and mating behavior (Freeberg, King, & West, 1995). By varying the immediate social context of male cowbirds, the authors found clear evidence for phenotypic plasticity across multiple behaviors related directly to reproduction, including song production and courtship (Freeberg, King, & West, 1995). Another example deals with bluegill sunfish (*Lepomis macrochirus*) and male parental behavior. Neff (2003) found that male sunfish modify their level of parental care dependent on both the presence of 'sneaker' males (which pose a direct risk to subjects' paternity) and olfactory cues released from newly hatched eggs. These male sunfish adjusted levels of parental care in relation to the degree of genetic relatedness with their young (Neff, 2003); thereby, demonstrating that specific contextual cues can result in behavioral shifts or malleability of behavior.

Interaction between context and behavioral profiles

To demonstrate the interplay between contextual influences and behavioral profiles, I will begin with an example involving rainbow trout (*Oncorhynchus mykiss*). Frost, Winrow-Giffen, Ashley, & Sneddon (2007) report an effect of experience on the level of boldness expressed in captive trout. Bold fish (assessed via latency to approach a novel object or novel prey item) observed another bold individual (a demonstrator) interacting with a novel object. When the demonstrator fish responded boldly, the observer fish maintained its bold tendencies. However, when a bold observer watched a shy fish, who exhibited longer latency to approach a novel object, the bold observer then became shyer, or more cautious, when placed in close proximity to the novel object. Thus, this plasticity in behavior may allow bold fish to respond in the most adaptive way when conspecifics reveal important information regarding the immediate environment and potentially dangerous stimuli. Most interestingly, however, was that shy individuals showed no change of behavior after observing a bold individual approaching the novel stimulus; the shy individuals maintained their cautious behavior independent of what the demonstrator fish did. Data suggest that the bold trait is more plastic, while the shyer tendency is more rigid and stable, and thus more predictable (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007). If these findings endure in wild trout, bold fish may have a more adaptive strategy in their ability to adjust behavior to changing contexts.

Recent research has revealed plasticity of behavior within the scope of behavioral profiles. As mentioned above, some behaviors appear to be influenced by environmental and contextual changes. However, in regards to the existence of behavioral profiles, correlated traits remain correlated (Bell & Stamps, 2004). For example, Bell & Stamps (2004) report that correlated traits can exist without perfect stability throughout ontogeny. For example, aggression and boldness may be strongly correlated with one another, but that does not necessarily mean that a juvenile who displays that combination of traits will exhibit them as an adult (Bell & Stamps, 2004). However, the correlation between these traits will remain consistent across individuals. Thus, an aggressive, bold individual may exhibit low aggressive, shy behavior as an adult while another individual who was shy as a juvenile may exhibit high aggression and boldness as an adult (Bell & Stamps, 2004). This means that ontogenetic plasticity can occur even with the coupling of behavioral traits (Bell & Stamps, 2004).

Thus, personality-like influences and contextual factors are intertwined with one another in the production of behavior, and should not be separated if behavior is to be understood more fully (Marshall & Brown, 2006; Funder, 2008). My thesis work leads me to conclude that the expression of behavioral profiles works in conjunction with demands of the immediate context. In reference back to the discussion on behavioral plasticity versus behavioral stability that began in Chapter 1, my research provides evidence that the behavioral profiles framework is complementary to a behavioral plasticity viewpoint. In efforts to understand and explain behavior patterns in organisms, it is best to acknowledge both frameworks. Data described in this dissertation indicate that behavior is shaped due to the interaction of both individual traits and contextual factors (also see Lewin, 1935; Bowers, 1973; Mischel, 1977; Funder, 2008).

Social and communicative behavior: a missing piece of the behavioral profiles puzzle

The role of the social context in studying variation and stability of behavioral traits has been neglected for many years, despite the fact that most of the study species are highly gregarious (Gosling, 2001; Sinn, Gosling, & Moltschaniwskyj, 2008). Much of the work in this field tests social animals in a solitary testing environment by exposing subjects to a battery of stimuli and observing their behavioral responses. Would such stable behavioral patterns persist when individuals receive the same stimulus presentations in the presence of group members? This question has yet to be fully investigated, but research is beginning to incorporate the sociality of species by testing individuals in either pairs (Carere, et al., 2005; Malloy, Barcelos, Arruda, DeRosa, & Fonseca, 2005; van Oers, Klunder, & Drent, 2005; Harvey & Freeberg, 2007; Hollander, Overveld, Tokka, & Matthysen, 2008; Williams, In preparation) or within more natural social groups (Sih & Watters, 2005; Nelson, Wilson, & Evans, 2008; Uher, Asendorpf, & Call, 2008).

Additionally, the importance of social constraints on the expression of behavioral traits is rapidly surfacing in the animal personality literature (Verbeek, de Goede, Drent, & Wiepkema, 1999; Dingemanse & de Goede, 2004; Sih & Watters, 2005; Cote & Clobert, 2007; Nelson, Wilson, & Evans, 2008). For example, a study with great tits (*Parus major*) reports an effect of social context on an individual's latency to pick up a food item in a novel environment (van Oers, Klunder, & Drent, 2005). Specifically, in this case, the presence of another individual (in an adjacent observation room) decreased a bird's latency to initially pick up a food item, compared to when it was tested alone. The presence of the conspecific had no effect on additional foraging behavior (i.e. return trips to the food bowl).

Behavioral stability is evident when individuals are tested alone as well as within a social testing situation; however, there is less predictability when comparing across an alone and social testing situation (see van Oers, Klunder, & Drent, 2005; Nelson, Wilson, & Evans, 2008; Williams, In preparation). One possibility is that behavioral stability functions for social cohesion and maintaining group membership. Group living is beneficial to members for many reasons, such as increased foraging due to decreased vigilance and predation risk (Elgar, 1989; Grand & Dill, 1999). For this reason, in this particular foraging situation, individuals of a group-living species may be more willing to engage in risky behavior than individuals of a solitary species. In addition to this benefit, there is an associated cost – individuals within a group have increased competition for food and available resources (Grand & Dill, 1999). Consequently, in a foraging context, some individuals may be willing to adopt a riskier strategy, thus risking predation, but increasing their portion of the resource (Grand & Dill, 1999; van Oers, Klunder, & Drent, 2005). If this were the case, personality-like influences, specifically boldness and shyness, should be more prevalent in social species versus solitary species. These ideas are intriguing because the majority of work involving behavioral stability and personality has been done on social species, as stated above.

The other behavior system that is missing from the field of behavioral profiles is communication. Communicative behavior is of fundamental importance for the lives of animals (Hauser, 1996) with implications for mating success (e.g. Freeberg, King, & West, 1995) and survival (e.g. Seyfarth, Cheney, & Marler, 1980). As discussed, non-human animal personality has been investigated across a variety of traits such as extraversion and neuroticism (Gosling & John, 1999), boldness and shyness (Wilson, Clark, Coleman, & Dearstyne, 1994), aggression (Huntingford, 1976; Johnson & Sih, 2005; Uher, Asendorpf, & Call, 2008), and exploration (Verbeek, Drent, & Wiepkema, 1994; Dingemanse, et al., 2003). Communication, however, has been relatively neglected from the study of individual variation and behavioral stability.

A recent study by Nelson, Wilson, & Evans (2008) reveals important aspects of social and communicative behavior to the field of behavioral profiles. The authors report that the vocalizations of fowl (*Gallus gallus*) are not consistent across diverse contexts when taking into account the social context (Nelson, Wilson, & Evans, 2008). The stability of the referential signals used by male fowl across various contexts (predator, courtship, and foraging) was not found when the male was removed from the group and tested in a solitary situation, revealing a lack of consistency across social and alone testing, and suggesting potential concerns of testing social species in solitary testing conditions. Moreover, the context sensitivity of signals reported in this study may be due to the fact that in this species a different signal is used for different functional contexts. Therefore, in assessing behavioral stability in fowl, there is not one call type that is produced across all contexts. Additionally, this signal is produced primarily by males. Contrastingly, aggression or activity, common traits observed in this research domain, can be assessed across multiple contexts and in both females and males of a species.

In comparison, the studies described in this dissertation aimed to fill missing gaps regarding social and vocal behavior by introducing a new species to the field of animal personality. In regards to the social dilemma, research presented in this dissertation tested members of a highly social species in both solitary and social environments. Both within- and between-individual stability was found; however, strongest behavioral stability existed within the alone and social testing conditions – not comparing across the two. Additionally, the chickadee has a highly complex vocal system. Thus, these dissertation studies are among the first to study individual vocal production and call structure in relation to behavioral profiles. Furthermore, both male and female chickadees produce the chick-a-dee call year-round and in a variety of contexts, providing a behavioral trait that is comparable across a variety of contexts.

Consequences of error

In studying communication, it is important to consider the environment in which communicative behavior is employed. Animals must obtain information about their environment for both survival and reproductive successes; however, due to environmental noise, errors are inevitable (Wollerman & Wiley, 2002). In addition to the high likelihood of committing an error, behavioral trade-offs accompany signal detection and the acquiring of information regarding one's environment (explained in more detail below). Thus, it may be beneficial for an individual to adopt the simplest strategy (i.e. behavioral stability) in efforts to minimize the number of errors made (Wollerman & Wiley, 2002). For example, an individual that exhibits shyer tendencies will likely avoid a dangerous situation, such as predation; however, the downside for this individual is the increased possibility of missing stimuli that are potentially beneficial, such as a highly energetic food resource. Thus, there is a trade-off between obtaining the food resource and risking predation (van Oers, Klunder, & Drent, 2005). Individuals must balance potential benefits, such as food and resources, with potential costs, such as predation.

For the present discussion, let us assume that an individual approaches a new territory that is rich in food resources, yet without entering and foraging in the new territory, it is not possible to know if a predator is present. There are two behavioral options for this individual: one, forage in the new territory, unaware of potential predators or aggressive residents; or two, do not approach and return to a more familiar, safer location. In this case, the shyer behavioral response of not foraging in the new environment, one that is potentially predator-rich, may be highly adaptive because this individual is not risking injury or even worse, death (McElreath & Strimling, 2006). An individual that exhibits bold behavior may enter the territory, risk detection by a predator, and forage for new food sources. Unfortunately for this bold individual, while foraging in this new environment, this animal may miss important environmental cues (DeWitt, 1998; DeWitt, Sih, & Wilson, 1998). Information about the surrounding world is 'noisy' (Wollerman & Wiley, 2002; McElreath & Strimling, 2006) and in this case, mistakes will happen more often than not (Wollerman & Wiley, 2002). Therefore, it is highly important that an individual be able to perceive and decode any potentially useful information that is received. Interestingly, it has been reported that as environmental noise increases, female treefrogs (*Hyla ebraccata*) make quicker decisions regarding mate choice (Wollerman & Wiley, 2002). Thus, it may be possible that in situations of high environmental noise, behavioral stability is more likely; and in less noisy conditions, when cues can be better detected and discriminated, more choosy and flexible behavior is exhibited. In great tits (*Parus major*), bolder individuals, who exhibit high exploration levels, exhibit routine-like behavior, which in turn results in a decrease in sensitivity for environmental signals (van Oers, Klunder, & Drent, 2005).

One limitation to this line of thought, however, is that it assumes equality in the ability to detect and perceive environmental cues, specifically cues indicative of the presence of a predator. There are individual differences in the ability to detect and process important environmental cues (McElreath & Strimling, 2006) and individuals rarely have the perfect environment, or the perfect signal, for error-free receiving and decoding of signals (Wollerman & Wiley, 2002). Thus, individuals need to be competent at decoding subtle cues and capable of making behavioral decisions despite environmental noise.

Ecological significance of behavioral profiles

Genetic diversity will likely result when there is great variability of behavioral traits and when individuals on either end of a behavioral continuum (for example a "shy-bold" continuum) exhibit higher fitness than individuals falling somewhere in between (Wilson, Clark, Coleman, & Dearstyne, 1994; MacDonald, 1995; Wilson, 1998; Nettle, 2005; Buss, 2008). In a fluctuating environment, the most advantageous strategy may actually vary depending on current environmental conditions. In such a case, an individual falling on one end of a behavioral continuum may have an advantage in one context, while another individual on the opposite end of the continuum may have an advantage in a different context (similar to disruptive selection). If no one strategy or trait is always the most successful (for example as in directional selection) then variation of the behavioral trait will persist within the population. For example, boldness may be an adaptive foraging strategy in a predator-free population, thus selecting for very bold individuals. However, in a predator-rich context, shy behavior would most likely be favored, with selection shifting toward shyer individuals within the population.

Variation in reproductive success has been shown to be the result of the interaction between behavioral type and a fluctuating environment, such that in particular environments, individuals who exhibit high exploratory behavior are more successful than others within the same population. However, when environmental conditions shift, individuals on the opposite end of the continuum, i.e. low exploration levels, have higher reproductive success (Dingemanse, Both, Drent, & Tinbergen, 2004; Dingemanse & de Goede, 2004; Buss, 2008). One possibility is that behavioral variation continues to exist due to individual variation in overall fitness and reproductive success. Likewise, the fitness of an individual possessing a specific trait may vary depending on the context in which the trait is expressed (as in mating versus predatory contexts: Sih & Watters, 2005).

In reference to fitness levels, overall trends in non-human animals reveal that higher levels of aggression tend to be associated with fitness and reproductive success, more evident in females than males (review by Smith & Blumstein, 2008). Furthermore, boldness is associated with increased reproductive success (more so in males versus females); however, it is paired with the cost of shorter life span (Smith & Blumstein, 2008). Typically, bold behavior means more risky behavior, and therefore an increased chance of death or injury. Thus, specific behavioral traits co-vary with overall fitness advantages and disadvantages. This has been referred to as the 'trade-off' hypothesis (Sih, Bell, Johnson, & Ziemba, 2004). Further study on trade-offs will provide greater understanding of evolutionary processes and the costs and benefits of alternative strategies, thus working to explain stability of individual variation (Nettle, 2006).

Despite its link to reduced survival, bold behavior in the presence of a predator has been shown to have reproductive advantages. For example, female guppies (*Poecilia reticulate*) repeatedly chose male guppies exhibiting higher levels of boldness in the presence of a predator (Godin & Dugatkin, 1996). When boldness was removed as a variable in the mate choice experiment (i.e. females were not able to view the male acting either 'bold' or 'shy'), females' mate choice appeared to be determined by brightness of the male's coloration. Godin & Dugatkin (1996) suggest that boldness may be a more reliable indicator of male fitness although, in the wild, assessments via male coloration are more frequent. This, however, is likely due to the fact that females rarely observe male interactions with predators. One proposition is that shyer guppies, those less likely to approach a predator, would have lower immediate reproductive fitness but would tend to live longer. Therefore, overall fitness levels may in fact balance out between these two behavioral strategies (Smith & Blumstein, 2008).

Additionally, environmental changes can alter overall fitness of varying behavioral traits, such as exploration and nest success in the great tit, *Parus major* (Dingemanse, Both, Drent, & Tinbergen, 2004). In great tits, more exploratory individuals are bolder and more aggressive. In years of abundance, this is highly advantageous to males because more aggressive males tend to find the best territories (and in abundant years there are more individuals fighting for optimal territories). However, in less abundant years, when overall mortality is greater, males need to put more energy into foraging for food than competition over protecting and maintaining territories, thus potentially favoring shyer males. The opposite was found to be true for females of this species. In abundant years, it is more advantageous for females to exhibit traits of lower exploration and lower aggression, due to the lower levels of competition for resources, and focus can be directed toward offspring (Dingemanse, Both, Drent, & Tinbergen, 2004). In poorer years, more aggressive females tend to benefit due to their increased ability to be competitive at obtaining nest sites. For this species, selection for high exploration versus low exploration is directional, depending on current environmental conditions. The maintenance of individual variation and the existence of behavioral consistency could be partially due to fluctuating environmental and selection pressures.

Ideas developing from the trade-off hypothesis have been applied in the human literature as well. For example, a large, muscular individual has advantages over a smaller individual, but those advantages come at a cost (e.g. developmental and metabolic costs). As a personality example, extraversion has been shown to be positively associated with increased mating opportunities and mating success, yet negatively associated with physical injury and parenting skills (Nettle, 2005; 2006). This is a direct benefit, especially to males who exert more energy toward short-term mating and less effort toward parental care (Buss, 2008). Primary disadvantages of extraverted behavior include decreased parenting effort and less time spent ensuring that offspring reach reproductive maturity. If time is allocated toward finding mating opportunities, there is less time and energy remaining for attaining resources and tending to offspring (Trivers, 1972; McGlothlin, Jawor, & Ketterson, 2007; Buss, 2008). Additionally, in humans, extraversion has been shown to be positively related to social dominance, which is also positively associated with increased mating success (Nettle, 2005). This would be an interesting domain for further research in non-human species, possibly investigating the formation of dominance hierarchies in parallel with specific behavioral traits (see Fox, Ladage, Roth, & Pravosudov, 2009).

Another key area of concern regarding the functional significance of behavioral profiles directly deals with conservation biology, such as how a species responds to environmental change. As detailed above, aggressive individuals are likely better at competing for and maintaining resources (Dall, Houston, & McNamara, 2004; Sih, Bell, Johnson, & Ziemba, 2004). Bold individuals are likely more adept at locating new resources if resources become scarce, and as suggested by Frost, Winrow-Griffen, Ashley, & Sneddon (2007), bold individuals may exhibit more plasticity in their behavioral responses. Additionally, bolder individuals have increased reproductive success, but also have increased mortality rates. This associated cost of death may be removed when wild animals are kept in captivity for extended periods of time. Due to repeated generations bred in captivity, offspring of bold individuals may develop even bolder tendencies, without the risk of predation. This does not become of great concern until these animals are released back into the wild, and then the expression of this trait will likely be highly maladaptive (McDougall, Reale, Sol, & Reader, 2005).

These few examples demonstrate the important links between behavioral profiles and fitness. Taking such an evolutionary framework in examining these traits and their associated costs and benefits can be of great value, likely leading to the development and testing of influential ideas for future research (Nettle, 2006).

Additionally, the existence of behavioral profiles has implications for studies involving the selection of subjects in experiments. Researchers should be aware that individuals responding differently to test stimuli or 'shying' away (being behaviorally inhibited) from experimental procedures should not be disregarded from study. Furthermore, when trapping wild animals for study (depending on methods used to capture subjects), or when presenting stimuli to subjects in natural or captive settings, there is a risk that 'shyer' individuals will not be included in data sets, resulting in a sample population that may not be truly representative. One potential limitation to the research described in this dissertation was the method of capturing chickadees. I attempted to capture individuals using both standard, baited treadle traps and mist nets, which are virtually invisible to the birds. One of my primary aims was to capture an equal number of individuals using both trapping methods. In following this methodology, treadle-trapped birds would be classified as ‘bold or neophilic’ and mist-netted individuals as ‘shy or neophobic’ (see Wilson, Coleman, Clark, & Biederman, 1993). Although this appears to be an accurate capture method for establishing ‘bold’ and ‘shy’ experimental groups, there are still potential concerns. A first concern involves the possible mis-categorization of individuals: individuals captured via the mist net method may actually be bold and those individuals that approached and explored the trap, albeit not entering, would be classified as shy. A second concern is that this methodology would likely result in the establishment of two groups consisting of the boldest and shyest individuals, however, this is probably not representative of the entire continuum and the distribution of all phenotypes in natural populations (see Wilson, Coleman, Clark, & Biederman, 1993). Due to uncontrollable environmental conditions, however, I was not able to sufficiently capture enough individuals using the mist net procedure, and so it was not possible to establish two independent groups in this fashion. Future studies should be aware of this limitation when recruiting subjects and work to include both 'shy' and 'bold' individuals in research studies.

Final remarks

Research on behavioral consistency and flexibility has taken two general approaches. One approach is to use a true ‘personality’ framework, working to study non-human animal personality in parallel with human personality. For example, the application of the Five-Factor Model and traits such as extraversion and neuroticism (King & Figueredo, 1997; Gosling, 1998) are becoming more and more common in non-human studies (e.g. Gosling, 1998; Gosling & John, 1999; Gosling, 2008). A second direction is a more behavioral ecology approach in which specific behavioral traits, such as aggression and boldness, are studied in regard to population dynamics and functional significance (e.g. Huntingford, 1976; Dingemanse, Both, Drent, & Tinbergen, 2004; Sih, Bell, & Johnson, 2004; Johnson & Sih, 2005). Interestingly, it has been suggested numerous times that to truly assess behavioral profiles, research should expand beyond one or two behavioral traits, with an objective to study multiple behavioral traits across a variety of contexts. However, the literature tends to focus on boldness and aggression, sometimes addressing activity levels and fitness success. Little research aims to incorporate multiple behavioral traits to test for behavioral profiles. The studies described throughout this dissertation assessed multiple traits, and most importantly, investigated a new behavior system – communicative behavior.

My dissertation research investigated behavioral profiles in chickadees, focusing on communicative and social contextual parameters. My work contributes to the scientific understanding of, and current debate over, the idea of personality-like influences in non-human animals. This research helps to provide answers to social, communicative, and comparative questions of behavior. These dissertation studies intend to offer insight into potential parameters that may be responsible for linking together social and communicative behavior with both behavioral traits and behavioral profiles. Furthermore, this research has implications for future investigations of the function and evolution of vocal signaling, as well as for current work on the evolution of complexity in vocal signaling. Behavioral profiles and the expression of specific behavioral traits may constrain an individual's signaling and/or signal use. My findings indicate that behavioral profiles play an important role in explaining behavioral variation in individual, social, and communicative behavior.

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VITA

Ellen Harvey Williams grew up in Kingsport, Tennessee. She is a graduate of Dobyns-Bennett High school in Kingsport, class of 2000. In 2004, she received her Bachelor of Science degree from Furman University in Greenville, South Carolina. As a Psychology major at Furman, she began her career in Animal Behavior. Under the supervision of Dr. John Batson, she conducted discrimination and learning studies with honeybees (*Apis mellifera*). As an interim between research programs, Ellen attended the University of Edinburgh while working as an instructor at Stevenson College, both in Edinburgh, Scotland. She then went on to begin her graduate studies in Experimental Psychology and Animal Behavior at the University of Tennessee, Knoxville. Under the direction of Dr. Todd Freeberg, she studied vocal and non-vocal behavior of the Carolina chickadee (*Poecile carolinensis*). Ellen will join the Psychology Department at Union College in Barbourville, Kentucky in August 2009.