Examining *chick-a-dee* call characteristics as a novel behavioral syndrome in mixed flocks of tufted titmice (*Baeolophus bicolor*) and Carolina chickadees (*Poecile Carolinensis*)

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ABSTRACT

Animal communication and the study of nonhuman personality (including behavioral syndromes) are popular fields of study. However, few studies have combined the two fields. The majority of the studies that do combine the two fields, moreover, examine communication as a subcomponent of the behavioral type in question, such as boldness or exploration. These results are variable and suggest that while communicative signals are often repeatable, they are not always perfectly correlated with other behavioral syndromes. An alternative possibility is that communication is a standalone behavioral syndrome that correlates with other behavioral types. If communication is a unique behavioral syndrome, this would help explain variation in observed behaviors, including suboptimal behavior such as a lack of communication. This dissertation examines communication as a novel behavioral syndrome in two species of closely related songbirds, Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*). Communicative behaviors in these species were examined in several ways. First, the overall repeatability of call characteristics was calculated after a week of recording calls made by conspecific pairs of birds in non-manipulated contexts. Second, a new set of birds were each recorded in two different social contexts: in conspecific pairs and in small mixed-species groups. The calls were then compared for repeatability and consistency across social conditions. During this study, the birds' behavior was also measured in a variety of behavioral assays, such as the novel environment test, to compare communicative behavior with other behavioral syndromes. Lastly, communicative outputs from the first two studies were combined and compared with each individual's relative dominance status. The results from these three studies suggest that individual chickadees and titmice differ from conspecifics in call rate, note use, call type use, and call complexity. These calls are generally repeatable within an individual across different social contexts. The call characteristics that were investigated in these studies were not related to other behavioral syndromes, and only some characteristics were correlated with relative dominance status. The strong repeatability of these calls and the lack of clear relationship between communication and other behavioral

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CHAPTER ONE
INTRODUCTION

Communication is critical within the animal kingdom. There are several modalities of communication that are often studied including acoustic, visual, vibrational, tactile, chemical, and electrical (Bradbury & Vehrencamp, 1998). Signals from multiple modalities may be used concurrently or sequentially, creating a multimodal signal that has a potentially complex message (Partan & Marler, 1999; Partan & Marler, 2005). Information produced by signalers can be utilized by receivers for decisions on mate choice, social facilitation and cohesion, foraging opportunities, agonistic encounters, and more (Bradbury & Vehrencamp, 1998). Studies across several taxa have found between-individual variation in communication, where signals have individually identifiable characteristics like signal composition, duration of signal bout, frequency, or entropy (e.g., amphibians, Bee et al., 2008; bats, Davidson & Wilkinson, 2002; birds, Thomsen et al., 2013; rodents, Loughry et al., 2019; ungulates, Xie et al., 2024; and perhaps even plants, Karban et al., 2022). In some species, these between-individual differences can also facilitate individual recognition (Soltis et al., 2005; Buhrman-Deever et al., 2008; Pardo et al., 2024). When individuals have differences in the signals that they produce, receivers may discriminate between signalers and selection can occur.

In acoustic communication, the modality of study for this dissertation, within-individual differences in mating signal consistency (e.g., varying call rate) may lead to poorer discrimination between potential mates and weaker overall sexual selection (Tanner & Bee, 2020). Specifically, in treefrogs females prefer males with greater consistency in the call rate and individual inconsistency may prevent females from choosing an optimal mate (Tanner & Bee, 2019). In other social groups, the between-individual characteristics of calling may also impact natural selection. Individuals that use certain types of calls more may have increased survival or reproduction, for example kleptoparasites that exploit alarm calls or species that gain benefits from social recruitment (Krause & Ruxton, 2002; Baigrie et al., 2014). Differences in call amplitude or the amount of calling could make certain individuals more conspicuous to predators and competitors.

Behavioral Syndromes and Personality

It is important to know whether these communication differences are stable over time and across contexts, constituting a personality trait or behavioral syndrome (Sih et al., 2004a). Behavioral syndromes are defined as suites of correlated behaviors that are consistent across two or more observations (Sih et al., 2004a; Sih et al., 2004b). Personality is defined as temporally repeatable patterns of behavior and cognition in response to various stimuli (Gosling, 2008; MacKay & Haskell, 2015; Kelleher et al., 2018). While personality and behavioral syndromes address different aspects of individual variation of behavior, more recent studies integrate the terms to create a holistic image of behavior (MacKay & Haskell, 2015; Rudin et al., 2017; Underhill et al., 2021).

Rather than focusing on communication as a part of personality, a classification fraught with controversy over terminologies and methodologies, the inclusion of a set of behaviors into behavioral syndromes are clearly operationalized (Sih et al., 2004a; Sih & Bell, 2008). Patterns of behavior can still be classified as syndromes if there is a correlation between behaviors across a minimum of two observations (within a single context or across multiple contexts) (Sih & Bell, 2008). Behavioral syndromes can be closely interrelated, with some ecological outcomes, like mating success, depending on the interplay between multiple behavioral syndromes (Sih & Bell, 2008). In these studies, I examine whether aspects of communication, such as call rate and note use, can be classified as a behavioral syndrome across social contexts. I also compare communicative behaviors to other commonly studied phenomena such as activity level, exploration (neophobia), coping strategy, and dominance.

Boldness and exploration. The bold-shy syndrome is one of the most well-studied behavioral syndromes currently proposed (Kerman et al., 2016). Measurements of boldness typically include agonism towards intruders and predators, neophobia, foraging under risk, or time spent in refuge (Ibáñez et al., 2013; Kerman et al., 2016). Exploration is also sometimes included as a boldness behavior (Atwell et al., 2012; Kudo et al., 2021), though other researchers separate it from the bold-shy axis (Huang et al., 2016; Xu

et al., 2021). Exploration is often assayed by placing an individual in a novel environment and measuring how quickly it visits all zones (Beauchamp, 2000).

Animals that are bolder are less neophobic and are more likely to approach food or another resource under risk (Carter et al., 2010). In one study where boldness was defined as a lack of vigilance behaviors, receivers varied their behaviors depending on the signaler's boldness. Receivers were more likely to respond appropriately when bolder, rather than shyer, individuals produced alarm calls (Couchoux et al., 2018).

There is relatively little research into the association of boldness with communicative behaviors. Birds low in exploration sang more songs, shorter songs, and slower songs than fast explorers when presented with a rival male playback (Amy et al., 2010). Birds that were low in boldness/exploration were also more likely to give more alarm calls when predators were present (Kerman et al., 2016). This finding is not consistent across taxa. One study in song sparrows describes how bolder, more aggressive individuals are also more likely to produce alarm calls in response to a heterospecific alarm call (Hyman et al., 2013). Another focusing on bats found that bolder, more exploratory, bats produced more social calls in risky contexts (Schabacker et al., 2024). These discrepancies may be due to researchers using different behavioral assays and describing them as the same output behavior (i.e., boldness) (Carter et al., 2012; Kerman et al., 2016).

Activity. Researchers typically use similar behavioral assays for exploration and activity, but where exploration is a latency measure, activity is the total number of movements made during the sampling interval and can occur in either novel or familiar environments (Beauchamp, 2000; Kelleher et al., 2018; Lundgren et al., 2021). Activity is more likely to be correlated with exploration when testing an animal with a novel environment compared to a novel object (Garamszegi et al., 2013). Activity is also sometimes correlated with boldness and aggression, and may fluctuate due to environmental and physiological factors throughout the lifespan (Herde & Eccard, 2013; Santostefano et al., 2016). Due to the relative lack of focus on activity syndromes, there are no studies examining the correlation between activity level and communication.

Coping strategy. This is sometimes included within the umbrella of the proactive-reactive behavioral syndrome (Sih, 2011). Proactive individuals have higher levels of boldness, exploration, and aggressiveness (Sih, 2011; Blight et al., 2016). While coping behaviors, such as response to handling stress during capture, have not explicitly been classified as a unique behavioral syndrome, Koolhaus et al. (2010) links the two together. In support of this connection, several studies have found that coping behaviors are repeatable within individual (Réale et al., 2000; David et al., 2012; Kluen et al., 2014; Qu et al., 2018). Coping strategy is often examined through both behavior and physiological measurements like respiration rate, heart rate, and endocrine responses (Wechsler, 1995; Koolhaus et al., 1999). Common behavioral measurements for coping strategy include docility during handling, defensive behavior, and aggressive behavior (Morrison et al., 2012; Young et al., 2014; Cooper et al., 2015; Whitten et al., 2025).

Another behavioral coping strategy is increasing the number of vocalizations produced (Lehner et al., 2006). These vocalizations may be repeatable in individuals across contexts (Branch & Freeberg, 2012). Individuals that vocalize more during stressors are believed to be more resistant to stress (Lehner et al., 2006; Melotti et al., 2011; van Zeeland et al., 2013). Less is known about the connection between coping strategy and the types of calls or note types used, however mobbing calls have been considered to be part of an active coping strategy rather than a more passive coping strategy (Quah et al., 2020). Likewise, few studies have examined the acoustic fine structure of the calls made under stress to compare with coping strategy. For example, a study on lab rats (*Rattus norvegicus*) found that they produce long pure-tone calls in response to handling stress (Brudzynski & Ociepa, 1992) and piglets (*Sus domesticus*) utilize lower frequency scream calls when severely stressed (Moura et al., 2008).

Dominance

In addition to personality and behavioral syndromes, researchers often examine relative dominance status within a group as a major factor in behavioral diversity. Drews (1993) defined dominance as an attribute of the pattern of repeated agonistic encounters between two individuals where one individual wins more often than the other. An individual's status can affect access to food, mates, territories, and other resources.

Perceived status can determine the types of interactions that occur between individuals, and experimental manipulations on badges of dominance status (e.g., altering vibrancy, darkness, lightness, etc.) in several bird species changes the outcome of challenges (Grasso et al., 1996; Gonzalez et al., 2002; Chaine et al., 2018). Status is also often communicated through type and timing of vocalizations. For example, challengers may overlap their vocalizations with those of a rival (Kroodsma, 2005), dominants may suppress subordinate calls (Pasch et al., 2013), certain vocalizations indicate submission or dominance (Bradbury & Vehrencamp, 1998), and the rate and type of vocalizations used may be correlated with dominance style within the group (Kavanagh et al., 2021; Fichtel et al., 2024). Given the variety of ways that dominance status can affect the production and use of vocalizations, status is a critical factor to consider when examining repeatability within communicative behaviors.

It is well documented that dominance status often determines what types of calls an individual commonly uses, such as appeasement, reassurance, or aggressive displays (Bradbury & Vehrencamp, 1998; Preuschoft & van Schaik, 2000), but there is relatively less known about the effects of dominance on communicative behaviors like calling rate and individual note type usage. Interruptions and overlapping are often aggressive challenges of dominance status (Kroodsma, 2005). Dominant individuals within a group typically have higher calling rates than subordinates (Krams, 2000; Bolt, 2013). In mixed-species groups and at species boundaries, subordinate species suppress vocalizations in the presence of dominant heterospecifics (Pasch et al., 2013; Coppinger et al., 2020). In a large comparative study of primates, despotic species tend to have richer repertoires of hierarchy-related calls, but tolerant species have higher calling rates (Kavanagh et al., 2021). Similarly, an increase in vocalization rate leads to an increase in social attraction in humans (Massey-Abernathy & Haseltine, 2019). In some corvid species, dominant individuals use more sequential note types in their calls than subordinate individuals, but there is no status difference in contact call usage (Kondo & Hiraiwa-Hasegawa, 2015). Overall, prior research appears to suggest that highest-calling individuals should also be the most dominant and differences in dominance style may affect repertoire use.

The focus of this dissertation is not to examine the relationship between dominance and other behavioral syndromes, but it is valuable to understand how dominance is expressed in other contexts. Depending on the species being studied, correlations have been found among dominance, boldness, and/or activity (field crickets, *Gryllus integer*, Kortet & Hedrick, 2007; zebrafish, *Danio rerio*, Dahlbom et al., 2011; great tits, *Parus major*, Snijders et al., 2017). Conversely, sometimes little or no correlation has been found (rooks, *Corvus frugilegus*, Jolles et al., 2013; black-capped chickadees, *Poecile atricapillus*, Devost et al., 2016; homing pigeons, *Columba livia*, Portugal et al., 2017). Dominance may affect how behavioral syndromes are expressed, and changes in dominance status within a social group could cause shifts in behavior within an individual (Rudin et al., 2017). For example, in a primate study, individuals that gain status may become bolder and those that lose status become less bold (Kohn et al., 2016). Overall, the relationship between dominance and personality traits appears to be dependent on the methodologies chosen for measuring behavior and on the species.

Social and Comparative Complexity

Social complexity arises in groups where individuals frequently interact in several contexts with many different individuals (Freeberg et al., 2012). Communities that are socially complex typically also have a variety of social roles (Boucherie et al., 2019; Kappeler et al., 2019). Larger groups in general tend to innovate and problem solve more rapidly than smaller groups (Cantor et al., 2020), but greater diversity of social roles often has a positive outcome on the functionality of the group. For example, groups that contain a diverse array of personality types are less affected by stress (Vágási et al., 2021), and mixed-species groups with a more diverse composition of species are able to solve challenges more rapidly (Freeberg et al., 2017). Another common outcome from an increase in social complexity is the co-occurrence of an increase in communicative complexity (Freeberg et al., 2012).

A complex system of communication is defined as one that contain large repertoires composed of structurally and functionally distinct elements or many bits of information (Freeberg et al., 2012). Social complexity has been found to be linked to communicative complexity across several taxa (rodents, Blumstein & Armitage, 1997;

parids, Krams et al., 2012; non-human primates, Bouchet et al., 2013; bats, Knörnschild et al., 2020). Larger groups, denser groups, groups with more social roles, and egalitarian groups are expected to have greater communicative complexity (Freeberg et al., 2012). The strength of these effects may not be equally distributed throughout a group. For example, within both conspecific and mixed-species groups, individuals or whole species that occupy a leadership role have higher calling rates and greater diversity in call types than compared to those in follower or satellite roles (Pagani-Núñez et al., 2018; Gustison et al., 2019). Some individuals within a group may act as keystones that disproportionally influence information flow within a group (Snijders & Naguib, 2017). Likewise, there are certain species that are considered community informants, a role that is highly vocal and serves to alert surrounding species, regardless of taxa, to the presence of food and predation risk (Carlson et al., 2020). Closely related species can also differ in their communicative complexity, perhaps due to differences in sociality and other ecological constraints (Brooks & Freeberg, In press).

A related phenomenon that occurs within social groups is the presence of audience effects, where individuals alter their behavior based on the composition of the surrounding audience. The presence of an observer can increase or decrease signal production and can lead to changes in signal rate, call type, or acoustic fine structure of the calls (Coppinger et al., 2017). For example, lower-ranking primates increase note frequencies and duration, and decrease the rate of their calls, when attacked in the presence of a high-ranking individual (Slocombe & Zuberbühler, 2007). The presence or absence of a specific audience can also lead to the production of specific call types, such as recruitment calls (Mahurin & Freeberg, 2008; Suzuki, 2012) and deceptive calls (Slocombe & Zuberbühler, 2007; Baigrie et al., 2014). The relationship between partners is also important to understand any potential audience effects. For example, animals that are affiliative and regularly play together may have a different repertoire of communicative signals than animals that only have aggressive interactions (Pellis & Pellis, 1998; Brooks & Burghardt, 2023). While most research on audience effects focuses on the characteristics of the audience, it is also important to consider the

influence of environment on audience effects, where presence of desired resources may induce behaviors that are not seen under other contexts (Dzieweczynski et al., 2005).

Taking all of the above into consideration, we may expect to see changes in an individual's communication style that are dependent on the other behavioral characteristics of the individual, the social complexity of the group, and the relative dominance status of the other group members. These complex interactions must be carefully teased apart through a series of studies to best understand whether communicative behaviors constitute a novel behavioral syndrome.

Study Species

The two species used in the studies to follow are Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*). These birds are common backyard residents throughout Southeastern North America where they form fairly stable mixed-species flocks over the winter, along with nuthatches (*Sittidea*), kinglets (*Regulidae*), woodpeckers (*Picidae)*, and occasionally other species like Carolina wrens (*Thryothorus ludovicianus*) and northern cardinals (*Cardinalis cardinalis*) (Morse, 1970; Ekman, 1989). Chickadees and titmice are nuclear species within these groups, meaning they are the species that drive the formation and maintenance of the flock throughout the season (Moynihan, 1962; Morse, 1970; Contreras & Sieving, 2011). Titmice typically also take on the role of community informant, influencing the behavior of birds across North American forests (Hetrick & Sieving, 2012). Chickadees are also very vocal but are smaller in body size compared with titmice and may be less vocal in the presence of the larger, more dominant heterospecifics (Coppinger et al., 2020).

Both parid species in this study use structurally complex acoustic signals that encode a wide range of information (Freeberg & Lucas, 2002; Freeberg, 2008; Soard & Ritchison, 2009; Courter & Ritchison, 2010; Sieving et al., 2010; Freeberg et al., 2014). One of the most well-studied types of parid calls is the *chick-a-dee* call, common to both species used in this study (Mahurin & Freeberg, 2008). The *chick-a-dee* call typically consists of one or more introductory whistle notes followed by a string of broad-frequency *D* notes (Owens & Freeberg, 2007; Freeberg & Lucas, 2012). Depending on the number and quantity of the introductory notes and *D* notes, the calls can alert flock

members to foraging opportunities, indicate the level of perceived risk from perceived predators, and can also provide individual identification within a flock (Mammen & Nowiki, 1981; Krams et al., 2012). The flexibility of *chick-a-dee* calls makes them a popular focus for bioacoustics research. In addition, there are several *chick-a-dee* subtype calls that are used frequently within these groups and should also be considered when examining social relationships. Examples of other call subtypes within the *chick-a-dee* call system include *seet* calls (freeze alarm calls; Hetrick & Sieving, 2012), *flight* calls (signaling movement; Freeberg, 2008; Zachau & Freeberg, 2012), and *tseet* calls (to maintain spatial proximity to flock mates; Dooling & Blumenrath, 2013). Another important call in the parid system is the *gargle* call, which is used in dominance interactions (Baker & Gammon, 2007).

In many species, dominance status is often related to body size, resource-holding ability, age, sex, residency status, and/or fighting ability (Bradbury & Vehrencamp, 1998), and parids are no different. Dominance across wild North American bird species is closely related to relative body mass (Miller et al., 2017). At an average body mass of 20.5g, tufted titmice are often socially dominant towards the diminutive Carolina chickadees, which weigh around 10g on average (Mostrom et al., 2020; Ritchison et al., 2020). Within parid species, males tend to dominate females, and older birds dominate juveniles (Hogstad, 1989; Krams et al., 2020). In conspecific groups, dominant titmice tend to wait longer to move after a high-risk alarm call presentation than subordinates (Waite & Grubb Jr., 1987). This phenomenon is often attributed to dominant individuals excluding subordinate animals from accessing food, leading to lower-ranking individuals taking more risks while foraging (Waite & Grubb Jr., 1987). Subordinate individuals frequently increase their body reserves to compensate for reduced access to food, but the costs of this tactic are reduced agility and increased predation risk (Pravosudov et al., 2003; Ratcliffe et al., 2007; Krams et al., 2020).

The combination of social status and environmental context alters the calling behavior of parids. During lower-risk foraging, subordinate species in mixed-species parid groups must optimize the risk for two potential costs, risk of injury from predators and risk of kleptoparasitism from dominant species. Low-ranking parids that reach a

novel foraging patch first produce recruitment calls if they forage in one spot but stay silent if they cache the seed away from more dominant individuals (Suzuki & Kutsukake, 2017). In higher-risk contexts, such as during mobbing events, chickadees and nuthatches are more active mobbers and vocalize more whereas titmice tend to stay farther away and vocalize less (Nolan & Lucas, 2009). These species may mob more due to increased species-specific predation risk as smaller, more subordinate, individuals (chickadees) or due to foraging position and visual perception (nuthatches) (Nolan & Lucas, 2009). Other closely related parids alter their calling rate depending on the proximity of the predator, with increased rates under higher risk (Baker & Becker, 2002; Bartmess-LeVasseur et al., 2010) In the highest-risk context, like a predator actively hunting, a few birds emit high frequency calls and all others stay silent, cease moving, and/or move to safety if necessary (Morse, 1973; Hetrick & Sieving, 2012).

All birds typically decrease their foraging behaviors while a predator is present and attentive (Kyle, 2021), but bolder birds may be more likely to approach a feeder under potential predation risk (Dykstra et al., 2021). Bolder, more active birds are also more likely to have the highest rates of chick-a-dee calls during a predation event (Williams, 2009). The complex interactions between individual variation in behavior, dominance status, environmental context, social structure, and their variable calls make these two parid species especially interesting for studying communicative behaviors at an individual level.

Field Site Information

I sampled birds from natural flocks at the University of Tennessee Forest Resources AgResearch and Education Center (UTFRREC) in East Tennessee. This field site consists of 2,204 acres of land in the Oak Ridge Forest, separated into two sections by an active road. It is a mixed-use forest, with 250 acres serving as an Arboretum open to the public, and oak-chestnut forests throughout, populated with species like oaks (*Quercus spp.*), pines (*Pinus spp*.), and tulip poplar (*Liriodendron tulipifera*). The sites vary from open to dense understory, regular human presence to secluded, and low traffic noise to high traffic noise. There is an active quarry between the two sections of UTFRREC which can also contribute significant noise to the environment.

There are 36 artificial feeding platforms at UTFRREC (**Figure A-1**). Sites are spaced 375 m from one another at minimum to ensure that flocks are independent and there is little overlap between the individuals frequenting neighboring feeders (Bartmess-LeVasseur et al., 2010). Each natural mixed-species flock typically consists of two to eleven birds, and they maintain a small home range (Freeberg et al., 2017; Brooks & Freeberg, 2024). These feeding platforms are stocked with safflower and black oil sunflower seeds throughout the winter to maintain bird presence. For these studies, I captured flocks of two or four birds using treadle traps at these feeding stations at UTFRREC. Flocks of two were size-matched conspecific pairs and flocks of four consisted of one conspecific pair per focal species (roughly size-matched within pair). The traps were baited with birdseed for several days prior to capture. Once caught, the birds were placed in one of six naturalistic aviaries at UTFRREC that measure approximately 6 m x 9 m x 3.5 m (**Figure A-2)**. After capture, the birds were given the remainder of the handling day as well as an additional three days to acclimate to the aviaries, their new social environment, and to human presence.

Dissertation Outline

In chapter one, I have briefly reviewed the current literature on social and communicative complexity and behavioral phenomena, such as exploration/boldness, activity, coping strategy, and dominance. I explored what is known about the relationships between these syndromes and communicative behavior. I described how an individual's social environment may affect their communicative behavior.

In chapter two, I conducted an observational study to examine if birds differ from one another in their communication patterns (such as call rate and note use) during non-experimental conditions, and whether these patterns are repeatable within an individual. I captured conspecific pairs of chickadees and titmice and placed them in naturalistic aviaries. I recorded each flock for 35 minutes every day for a total of five days of sampling (175 minutes total per flock). In this study, I hypothesized that if communicative behavior is repeatable, then birds will tend to have the same communicative patterns across sampling periods (e.g., the birds will be calling roughly the same amount each time).

In chapter three, I follow up the first observational study with a study that tests whether these communicative patterns remain consistent across social contexts. In this study, I manipulated the social environment of the birds by testing the same individuals in both mixed-species flocks and conspecific pairs. In this study birds were sampled in conspecific flocks for five days and mixed-species flocks for five days (625 minutes of sampling per flock). If communicative behavior is repeatable, then the birds should have similar call rates and/or note use across social contexts. This study starts to examine whether communicative behaviors could be a novel behavioral syndrome. I also compare the birds' communication patterns to other behavioral syndromes and phenomena such as their coping style when handled and their activity and exploration behavior.

In chapter four, I analyzed video recordings of dominance interactions from each flock taken during the first two studies. This study examines whether the communication patterns found in the earlier two studies were related to the relative dominance status of the birds in the flocks. After the audio sampling from the first studies were completed, I presented the flocks with a limited amount of high-quality food source (mealworms) and placed a camera nearby to record any supplants or other antagonistic interactions. I also recorded the order of approach to the food source as dominance status also affects access to resources. Birds in the first study were recorded for a minimum of 30 minutes each day for five days (150 minutes per flock) and birds in the second study were recorded for a minimum of 30 minutes for five days in both social conditions (450 minutes per flock). I hypothesize that if dominance status affects calling behavior, then more dominant individuals should call more than less dominant individuals, and more dominant species should call more than less dominant individuals. Note use is also expected to differ between relative rankings if dominance status is important.

In chapter five, I summarize the findings from my three empirical studies and describe whether communication is repeatable within individual and whether it potentially constitutes a novel behavioral syndrome. I also discuss the importance of understanding communicative behaviors at the individual level and suggest future research that would be valuable for exploration this phenomenon.

Significance and broader implications

Recent work on frogs has supported these predictions, suggesting that call rate and spectral qualities of the calls may be relatively repeatable within an individual across different days (Moreno-Gómez et al., 2024). This repeatability may be useful for individual discrimination or species discrimination within mixed-species choruses (Bee et al., 2008). Similar work has been done to look at the repeatability of call characteristics in other species like crickets (Nandi & Balakrishnan, 2013); birds (Zsebők et al., 2017); and bats (Chaverri & Gillam, 2015). No other studies have examined communication as a potential behavioral syndrome, however the closest analogue to date may be in the study of human personality traits.

Human personality research has changed frequently over the decades, and a measurement called the Big Five is one of the most popular methods of categorization today (Bainbridge et al., 2022). The Big Five describes human personality with five traits (openness, conscientiousness, extraversion, agreeableness, and neuroticism)(Goldberg, 1990). Individuals may present as high or low on the scale for that trait. Furthermore, each trait is further broken down with the inclusion of descriptive adjectives, and "talkative" is often included at the high end of extraversion (Goldberg, 1990; Roccas et al., 2002). In the communication literature, extraversion has been linked to increased speech tempos (Feldstein & Sloan, 1984) and dominance (Massey-Abernathy & Hasseltine, 2019), whereas individuals with high levels of neuroticism have more verbal aggressiveness and emotionality (Ahmed & Naqvi, 2015). In workplace settings, extraversion is related to faster paced communication, lower pitches, more variation in pitches and amplitude, and fewer pauses (DeGroot & Kluemper, 2007). These findings in the human personality literature parallel results found in nonhuman animal systems, suggesting that individual differences in communicative behavior are repeatable, found across many species, and potentially indicate the presence of a behavioral syndrome.

If the findings of these studies support a behavioral syndrome, this syndrome would be an exciting and novel way to interpret communicative behaviors. Researchers often predict that animals will call in optimal ways, with the correct responses to each possible context (Proppe et al., 2011). However, research has shown that this may not be

the case, including animals that cannot call at the optimal rate or frequency for long bouts (Tanner & Bee, 2019). Classification as a behavioral syndrome would suggest instead that animals may be constrained in their behavior by these individual differences and may demonstrate suboptimal behavior in certain contexts (Sih et al., 2004a). For example, some individuals within a population would vocalize too much and potentially be at greater risk of predation, and other individuals may not vocalize enough and have greater difficulty maintaining social affiliations. It may even be the case where some individuals do not vocalize at all even though they have the physical capacity to do so, which would be unexpected in the current communication framework.

There are many reasons why an animal may choose to communicate, including social affiliation, mate attraction, and predator detection and deterrence (Bradbury & Vehrencamp, 1998). Likewise, individuals may decide not to signal, including contexts such as audience effects from more dominant individuals, large risk from predators, or a higher threshold to signal (Rose & Brenowitz, 2002; Dapper et al., 2010; Coppinger et al., 2020). For example, in Hawaiian Pacific field crickets (*Teleogryllus oceanicus*), researchers have been documenting males that choose to be silent and the rapid evolution of a silent male morph due to excessive predation from parasitoid flies (Zuk et al., 1993; Heinen-Kay et al., 2019). These individuals may be behaving appropriately when predators or potential aggressors are present, but suppress their signals too much when not in these contexts. These silent male crickets employ alternative mating methods such as staying close to a calling male to gain access to a female (Heinen-Kay et al., 2019). While currently unknown, if individual crickets varied in their proclivity to call or not call (depending on the population), there would be different selection pressures acting on each subpopulation due to their communicative behavior choices. Elucidating which individuals are calling, how often, and what they are signaling would open the door for further questions about how natural and sexual selection act differently on individuals within a population.

Logical next steps for this work are to continue to explore potential differences in acoustic communication as a behavioral syndrome within different species, especially given the growing literature looking at acoustic communication as a repeatable trait.

However, the other modalities of communication are also important to understand because not all species use acoustic signals. In one example, the push-up visual display by some lizards may be individually repeatable (Martins, 1991). Similar results can be found in the vibrational communication of treehoppers (Sattman & Cocroft, 2003). Yet, to date only a few studies have examined individual differences in communication within different signaling modalities. Future studies should be done to investigate the results of this dissertation within other modalities to remedy this problem.

CHAPTER TWO
COMMUNICATIVE REPEATABILITY DURING NON-EXPERIMENTAL CONDITIONS

Abstract

In communication, redundancy is a common strategy used by nonhuman animals to ensure that their signals are received. Until recently, little focus has been given to whether redundancy could be related to a personality trait or behavioral syndrome. Both personality and behavioral syndromes require behavioral traits to remain consistent across contexts. This study takes the first step towards understanding whether communicative behaviors of Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) are repeatable within individual callers and if these characteristics differ between individuals. To do this, I captured conspecific pairs of chickadees and titmice and placed these pairs into naturalistic aviaries. I recorded five days of non-manipulated vocalizations for each of the birds and measured the output in a variety of ways, including call rate, note type, call type, note transition probabilities, and call complexity. I calculated the repeatability estimate, *R* or *ICC* (intraclass correlation coefficient), for each variable. I also used principal components analysis (PCA) to find the variables influencing calling behavior for each species and if those variables covary with one another. This analysis reduces the number of variables needed for future studies. Lastly, I used an ANOVA to understand whether these PC scores were related to the size of bird. Many, but not all, call characteristics were very repeatable within each species. Call type, note use, zero-order call uncertainty (a complexity measure), and call rate were the primary variables in the PCA. Prior to this study, it was expected that birds would be flexible in their call use, especially over several days of vocal output. However, it appears that birds may prefer to use certain call and note types and that these preferences are not the same throughout the species. The variables found in this study can be used in future studies examining calling behavior, especially in studies working to understand whether these behaviors are consistent within an individual across various contexts.

Introduction

Animals in noisy environments need to ensure that their signals are being received, and they may employ one or more strategies to cope with the degradation or masking of their signals. In acoustic communication, these strategies may include increasing the amplitude (loudness) of the signal, decreasing the distance between

individuals, or increasing the redundancy of the signal (Bradbury & Vehrencamp, 1998; Brumm & Slabbekoorn, 2005). To increase the redundancy, animals may repeat entire signals (Mowles & Ord, 2012), particular phrases or syllables within the signal (Kawaji et al., 2024), or other characteristics of the signal such as dominant frequency or duration (Moreno-Gómez et al., 2024). Using these strategies increases the chance that the signal will reach a reciever. However, there may be between-individual differences in which strategies are preferred and utilized (Botero et al., 2010).

Animals may also be flexible in which strategies to use and when to use them. For example, male Cope's gray treefrogs (*Dryophytes chrysoscelis*) produce advertisement calls at an inconsistent rate but females prefer consistency (Tanner & Bee, 2020). Less consistent males may use short bouts of higher-quality signaling to exploit female assessment in noisy and dynamic environments (Tanner & Bee, 2020). Likewise, male great tits (*Parus major*) use different strategies to tailor their songs to the constraints of their territories, often singing at higher frequencies (Hz) in noisy environments (Slabbekoorn & Peet, 2003). These changes are not merely a permanent trait of urban birds but are often plastic responses to the environment. This was clearly demonstrated during the COVID-19 lockdowns when white-crowned sparrows in San Francisco rapidly optimized their signals to the new soundscape by lowering the frequencies of their songs (Derryberry et al., 2020). This plasticity in communicative behavior is seen across many species and can lead to observable differences between individuals. When these differences are repeatable across contexts they are sometimes called personality traits.

Traditional personality research focuses on differences between individuals, but only occasionally includes communication and signaling in the categorization of nonhuman animals. The Big Five categorization scheme (Openness, Conscientiousness, Extraversion, Agreeableness, and Neuroticism) is a common method of measuring human personality, but it has also been used in other primate species (*Callithrix jacchus*, Iwanicki & Lehmann, 2015; *Gorilla Beringei*, Eckardt et al., 2014; *Gorilla gorilla,* Schaefer & Sterklis, 2014; *Pan troglodytes*, King & Figueredo, 1997) and in some other captive species that interact closely with humans (e.g., pets, Gosling & Bonnenburg, 2015; zoo animals, Bullock et al., 2021). The Big Five is most often presented as

dichotomies where individuals are listed at high or low levels for each trait (Goldberg, 1990). Each trait is further broken down with the inclusion of descriptive adjectives. For example, individuals high on extraversion may be described as sociable, assertive, and active (Roccas et al., 2002) or spontaneous, vain, brave, and talkative (Goldberg, 1990).

Talkative is a common descriptive adjective for extraversion used in the Big Five classification (Goldberg, 1990; Roccas et al., 2002). Talkative usually refers to the vocalization rate, where talkative individuals vocalize more often, and quiet individuals vocalize less. Talkativeness is a trait that may be repeatable within felids (Bullock et al., 2021). Cheetahs (*Acinonyx jubatus*) that were more vocal were also excitable, playful, and smart (Wielebnowski, 1999). Some breeds of housecat (*Felis catus*), such as Siamese cats, are known for their unusual talkativeness (Turner, 2000). Being vocal is also a highly prized trait for other pets, including various avian species. Parrots, and other species known for their mimicry and mastery of human language, are popular pets and some research has been done into individual differences in their communication. For example, grey parrot (*Psittacus erithacus*) individuals have differing capacities to acquire human language (Pepperberg, 2007). During puzzle feeder tasks, the parrots that had better language skills were more likely to attempt to solve the puzzle through vocalizations (i.e., asking the researcher to solve the puzzle for them), when compared to the birds with poorer language skills that attempted to solve the puzzle through physical manipulation (Pepperberg, 2007). However, beyond case studies in captive populations, there have been few studies examining individual differences in communicative behavior, and these studies typically are focused on fine acoustic characteristics of the signals like amplitude and dominant frequencies (Sanvito & Galimberti, 2003; Cocroft et al., 2006). Another common issue with studies examining individual differences is that researchers may only compare behaviors from two testing periods (Niemelä & Dingemanse, 2018). This can be problematic because short timeframes may overestimate the repeatability of these outputs (Ellis, 2008).

I address these gaps by examining whether Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) differ among individuals in their call characteristics, such as call rate or note use, and if those differences are repeatable

during non-experimental conditions over the span of five days. Birds in the family Paridae are appropriate study species to answer these questions because there is a wealth of knowledge about their communication systems spanning almost 60 years and multiple continents (Thielcke, 1968; Hailman, 1989). Chickadees and titmice have relatively high communicative complexity (Freeberg et al., 2012), indicating that they may be signaling more complicated messages than other, less communicatively complex species in their environments. Contributing to this higher level of complexity, these birds can vary the type and number of notes within their calls according to their social and environmental context (Templeton et al. 2005; Soard and Ritchison 2009; Suzuki 2014; Kalb et al. 2019). Indeed, a common perspective on the *chick-a-dee* call system is that it is completely flexible and open-ended, with near infinite possibilities (Bloomfield et al., 2005; Freeberg, 2008; Jung & Freeberg, 2017). Parid calls generally have note ordering rules (a simple syntax), but these call systems can also include reversals in the syntax that appear meaningful (Hailman & Ficken, 1986; Clucas et al., 2004; Selman & Freeberg, 2025). Much work has been done on the overall message encoded in *chick-a-dee* calls but there has been less focus on the use of calls at an individual level.

It is important to understand more about which individuals are calling and how they are doing so. Chickadees and titmice are very important ecologically because they act as informants for entire forest communities (Hetrick & Sieving, 2012; Carlson et al., 2020). Many species eavesdrop on Parid signals to make decisions about the environment, and some species rely so heavily on this information that even the mere presence of Parids is enough to alter the community species composition (Monkkonen & Forsman, 2002; Szymkowiak, 2013). If individuals are consistent in the types of signals they produce and their rate of production, this may have downstream implications for flock formation and cohesion.

The primary goal of this study is to examine whether various aspects of the Parid communication system differ between individuals and if those differences are consistent over time (i.e., repeatable) under non-experimental conditions. If there are several components that differ between individuals and are repeatable, I also test whether communicative traits are related to one another, such as call rate and call complexity. The

primary goal of these latter analyses was to reduce the dimensionality of the data and to understand which variables may be most important for subsequent studies. To ask these questions, I captured chickadees and titmice and placed them into conspecific pairs. I recorded their vocalizations and measured several components of their calls. I tested whether there are individual differences in calling behavior and if those differences are repeatable within an individual.

H_1: The birds' communicative behavior is repeatable.

Several species have repeatability in at least one component of their communication (Sanvito & Galimberti, 2003; Cocroft et al., 2006; Kershenbaum et al., 2014). Kershenbaum et al. (2014), found that Carolina chickadees use renewal process communication models where they repeat certain elements within their signals until the bird is ready to move on physically or cognitively, however this study focused on species-wide patterns rather than the individual. If this hypothesis was supported, one or more traits of the *chick-a-dee* call would be consistent within an individual over time under non-experimental conditions. For example, if call complexity was repeatable then an individual would have roughly the same level of complexity each testing day.

H_0: There are no patterns in signaling behavior at the individual or species level.

It may be the case that the chick-a-dee call system is fully plastic and open-ended as predicted by previous research (Hailman & Ficken, 1986; Clucas et al., 2004). If so, birds may be extremely variable in their call characteristics, and no repeatability patterns will emerge from the data. Potentially supporting the null hypothesis, the closely related black-capped chickadees (*P. atricapillus*) are individually repeatable in their use of *tseet* calls across baseline and stressful contexts such as mobbing playbacks, but their *chick-a-dee* calls were not significantly repeatable across baseline trials (Guillette & Sturdy, 2011). However, this study tested birds in very different contexts than in the current study (e.g., solitary individuals in small artificial cages in the laboratory) and tested for fewer days overall. Chickadees and titmice are highly social birds and testing them in isolation may impact the ecological validity of the testing (Benson, 2024). Alternatively, poor repeatability estimates may also indicate that birds are all behaving in the same way. To be repeatable, the variance within an individual must be smaller than the variance across

the whole population. If the variance across the population is small, then repeatability will also be poor.

Methods and Materials

Subjects and housing

Conspecific pairs of chickadees and titmice were captured from October 2023 to March 2024 at the University of Tennessee Forest Resources, AgResearch, and Education Center (UTFRREC) in Oak Ridge, Tennessee. All birds were held for approximately one and a half weeks before release. The birds were captured using baited treadle (Potter) traps at permanent feeding platforms. Chickadees and titmice are resident species in East Tennessee and have small home ranges, so the platforms are spaced more than 375 m apart to ensure flock independence between sites (Bartmess-LeVasseur et al., 2010).

Every captured chickadee or titmouse had its wing chord measured to estimate sex and received a unique plastic color band combination on one leg. As in Coppinger (2020), titmice were considered male when their wing chord was greater than or equal to 81 mm and female when the wing chord was less than or equal to 76 mm; chickadees were considered male when their wing chord was greater than 61.5 mm and female when their wing chord was less than 59.5 mm (Coppinger et al., 2020). Birds were labeled as unknown sex when they fell into the middle range where wing chord overlaps between the sexes. Both birds must have been the same sex category to be included in the study. This was due to the inclusion of these individuals in this dissertation's third study that examined the relationship between dominance status and communicative signals. Size matching was utilized to reduce potential confounds between dominance status and bird size or sex. Birds were held for a maximum of 30 minutes before release if an appropriate flockmate was not captured simultaneously. When two untested conspecific birds of the same sex/size class (M-M, F-F, or U-U) were caught within 30 minutes of each other, they were transported to one of four nearby semi-naturalistic, outdoor aviaries that each measure approximately 6m × 9m × 3.5m. Each aviary housed only one conspecific pair at a time.

All aviaries had a covered indoor section that the birds could use as shelter, as well as several natural and naturalistic perches with vegetative cover for the birds. The aviaries were kept stocked with ad libitum black oil and safflower seed, fresh water, and the birds were provided with mealworms approximately every day as a part of a separate study. All birds housed in the aviaries were kept for a minimum of nine days, though some flocks were kept longer if weather conditions delayed data collection. Each flock was given a minimum of four days for acclimation to the aviary. The first day after capture the birds were left alone, and then for three subsequent days I replicated the procedure to acclimate the birds to all components of the observational study (i.e., equipment was set up and I spoke aloud for approximately 35 minutes). After all observations for each flock were completed, the birds were recaptured using baited treadle traps in the aviaries, weighed, and released at their original site of capture.

Procedure

On observation days (capture day five through nine), I entered the aviary between 0800 and 1300 hours (Eastern Standard Time) with the equipment presented during acclimation. I set up the equipment and then sat in a designated corner to observe the birds. A Sennheiser ME-64 electret microphone was placed in a microphone stand located in the middle of each aviary for all recordings. The microphone was connected to a Marantz PMD661 Professional Solid-State Recorder. The sample rate was 22,050 with 16-bit resolution.

Every observation day consisted of ten minutes of focal sampling for each bird in the aviary followed by 15 minutes of all-occurrence sampling. The order of the observations for focal sampling alternated randomly so that each bird was sampled first during a roughly equal number of days. During the focal samples, I visually followed the focal bird with binoculars and state aloud when the focal individual was calling or singing. Other behaviors like taking seed, hammering on vegetation or the aviary, or flight were also recorded when possible. During all-occurrence sampling, I noted calls and songs from both birds in the aviary. Unknown vocalizations and vocalizations from birds outside the aviary were noted. These focal and all-occurrence sampling periods were repeated for five days of observation before the birds were released at the site of

their capture. I was unable to have a second observer collect reliability data for the live data collection procedure. See **Table 2.1** for the study timeline.

Call analysis and note classification

Calls were manually classified within the spectral view window (Blackman-Harris windowing function at a resolution of 256 bands) in CoolEdit Pro, version 2 (Syntrillium Software, Scottsdale, AZ, USA). Both species use a mix of whistle notes and broadband notes in their *chick-a-dee* calls. For titmice, the calls were analyzed using a modified coding scheme from Owens & Freeberg (2007). A histogram of introductory note lengths (in msec) had three roughly equal-sized breaks, so I created note categories to reflect this (**Figure A-3**). We assigned each of the four length clusters as a different introductory note. The four introductory note categories are *A*, *I*, *B*, and *Z*, in order of increasing duration. We defined *A* notes as notes that are less than 75 msec in duration. *I* notes are notes with durations between 75 msec and 144 msec. *B* notes are notes with durations that are between 145 msec and 214 msec. *Z* notes are notes with durations of 215 msec or greater. We also included *D* notes, broad-frequency notes with a harmonic-like structure, and D_h notes, hybrid notes that transition from introductory note to *D* note, in our categorization of the titmouse *chick-a-dee* call (**Figure 2.1**). There was high inter-observer reliability for coding of titmouse note types, with Cohen's Kappas ranging from 0.89 for *I* notes to 1.0 for D_h notes and *D* notes (*Z* notes = 0.93; *B* notes = 0.93; *A* notes = 0.93).

Chickadee calls were analyzed using a condensed coding scheme. Previous work has found between two and seven graded introductory whistle notes with various note subtypes (Freeberg & Lucas, 2002; Bloomfield et al., 2005; Freeberg, 2008). To prevent potential classification errors during coding, I condensed all introductory note categories into a single whistle note category, *I*. For these analyses, I also included structurally complex *C* notes, broad-frequency *D* notes, and D_h hybrid notes that transition from an introductory whistle note to *D* note (**Figure 2.2**). Inter-observer reliability for chickadee note types was good. Cohen's Kappas ranged from 0.88 for *C* notes to 1.0 for D_h notes (*Intro* notes = 0.90; *D* notes = 0.97).

Table 2.1. Study one timeline. The timeframe for a flock that was not held longer due to inclement weather or other events that extended the sampling period.

Day of capture	Activity
1	Capture and banding
2	Acclimation
3	Acclimation
4	Acclimation
5	Audio Sampling
6	Audio Sampling
7	Audio Sampling
8	Audio Sampling
9	Audio Sampling, weighing, and release

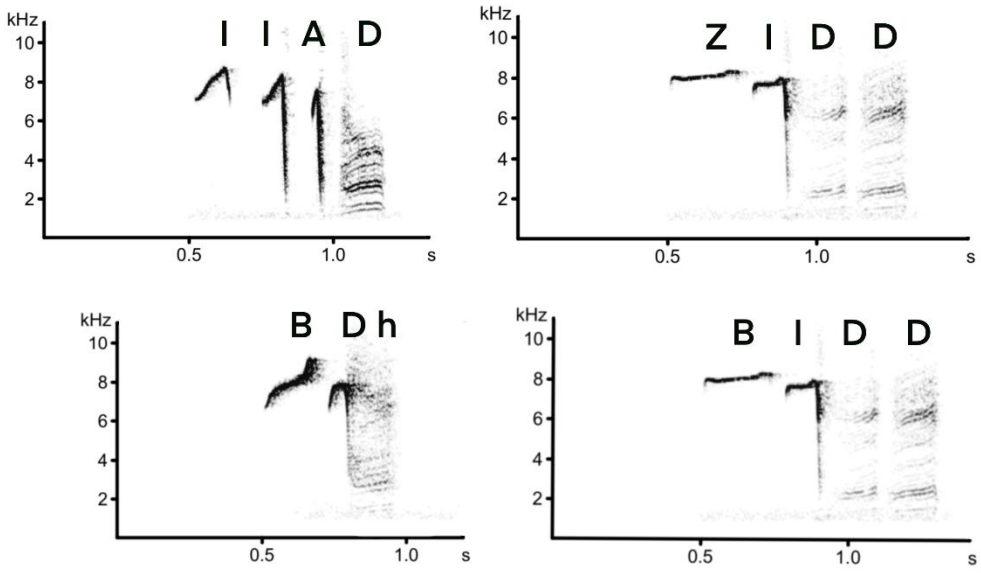

Figure 2.1. Call examples and classifications for tufted titmice. Examples of real tufted titmouse calls from birds used in this study. I used six note classifications for titmice: *Z*, *B*, *I*, *A*, D_h, and *D* notes.

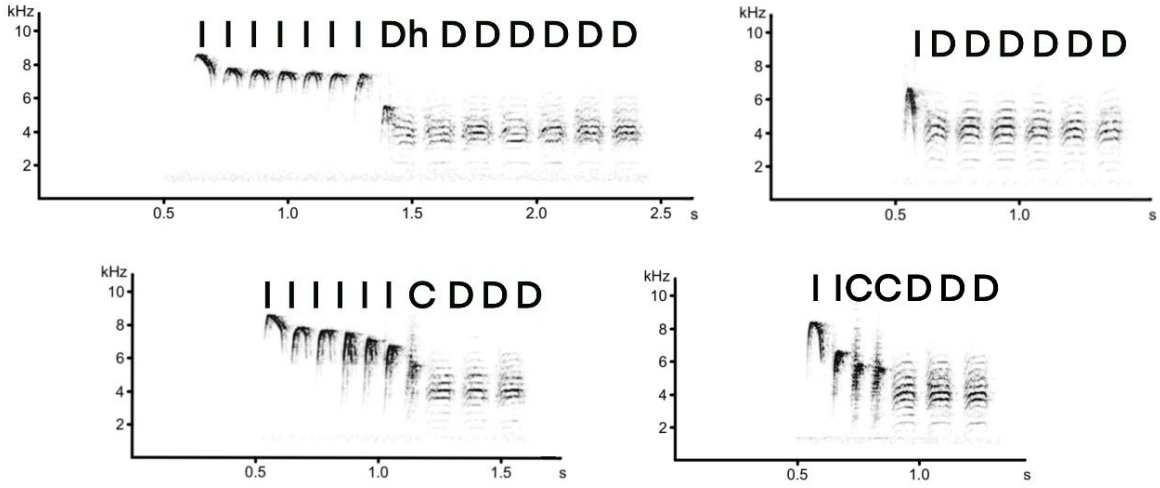

Figure 2.2. Call examples and classifications for Carolina chickadees. Examples of real Carolina chickadee calls from birds used in this study. I used four note classifications for chickadees: *Intro*, *C*, D_h, and *D* notes.

Statistical analyses

All statistical analyses unless otherwise noted were conducted in R (version 4.4.1; R Core Team, 2025). I calculated several characteristics of the calls (call rate, note use, call type, diversity index, zero- and first-order uncertainty, and note transition probabilities) and calculated whether each variable was repeatable within individual. Call rates were calculated for each bird, but birds that called less than five times were excluded from all other analyses (n = 8 titmice). Repeatability was calculated by finding the Intraclass Correlation Coefficient, *ICC*, or with the repeatability estimate, *R*, depending on the type of data. *R* is an *ICC* parameter estimate that is calculated by the commonly used *rptR* stats package (version 0.9.22; Stoffel et al., 2017). Both measurements calculating the amount of variance that is attributable to the measured individual compared to the total population variance (Carrasco, 2010; Stoeffel et al., 2017). In other words, these tests are asking whether individuals behave more like themselves than other individuals in the population. A repeatable result indicates that any given individual within the population is relatively consistent in their behavior across behavioral assays and that each individual's behavior typically differs from other individuals in the full population. For the analyses, I considered repeatability estimates of 0.0–0.3 as not repeatable, 0.3–0.4 as weak repeatability, 0.4–0.5 as moderate repeatability, and 0.5-1.0 as high repeatability. These categories were based on ranges used in other studies of animal personality (Ibáñez et al., 2018; Underhill et al., 2021; Schabacker et al., 2025). Greater repeatability indicates a wider spread in the population data and smaller within-individual variation. Low repeatability suggests either that individuals are very variable in their behavior (large within-individual variation) or the whole population is behaving in the same way (small population variation).

After running repeatability analyses, I selected a subset of characteristics from these variables to include in a principal components analysis (PCA). The variables that were removed were calls types and note transitions that were used infrequently. The top five call types and top ten note transitions were retained for each species. The PC scores from the PCA were then used in a general linear mixed model to examine whether birds

differ from one another and how these differences relate to the birds' demographic information like weight, wing chord length, and site of origin.

Call rate. Calls and songs were filtered by individual ID across focal and all-occurrence sampling periods for each day. Calls made by known individuals during another bird's focal sampling period were not included in these analyses. Likewise, any additional calls that were made after the ten-minute (focal) or fifteen-minute (all-occurrence) sampling periods were not included in the call rate analyses. Call rate was calculated by dividing the total number of vocalizations by 25, for the total observed period per day. I used the median call rate for each bird in the PCA analyses.

For the repeatability analyses, I used a zero-inflated negative binomial model in the R stats package *ICCCounts* (version 1.1.2; Carrasco, 2024) to measure the repeatability in the total number of vocalizations summarized across each day. I chose an additive parameter for the extradispersion in both models based on the Akaike information criterion (AIC) scores for chickadees because it had the greater discrepancy in fit. Both models received the same extradispersion parameter for easier comparison. The AIC score for chickadees was lower for the additive model than a proportional model (627.82 and 637.28, respectively), whereas the AIC scores for titmice did not differ between the two models (additive AIC = 674.90; proportional AIC = 669.81). I also used the goodness-of-fit test in *ICCCounts*. I used total vocalizations rather than rate because the repeatability tests in *ICCCounts* do not allow for rate data. *ICCCounts* does not calculate a p-value, so significance is calculated via the confidence interval instead.

Note use. I calculated the maximum likelihood of using each note for every bird that called with a large enough sample size. Once I had maximum likelihood estimates for each bird, I used a chi-square test to examine whether birds should be modeled with their own estimates or if birds are all using the notes in the same ways (i.e., they are all using the same distribution. For the repeatability analyses, I found the number of each note used per day, per bird. I used the *rptR* package in R to find the repeatability estimate, *R*, for each note type. All models were run with the Poisson family, log link, and parametric bootstrapping to calculate the confidence intervals (n = 1000 repetitions). *Z* notes for titmice and D_h notes for chickadees were unable to be modeled in *rptR* due to

zero-inflation, so an ICC score was calculated for these notes with the package *ICCCounts* using a zero-inflated Poisson model.

Call type. When coding the audio files, I recorded the quantity and order of the notes within each call. Individual calls were differentiated when there was 150 msec between notes (rounded from the 147 msec cutoff used Courter & Ritchison, 2010). Call type here refers to the unique ordering of notes without regard to the number of notes in the call. For example, a chickadee call with the notes *IIICCCD* would have the call sequence type [*I*][*C*][*D*], as would a call with the notes *IICDDDDDDDD*. All *chick-a-dee* calls with a known caller were included in these analyses, including any calls with a positive identification that were made during another bird's focal sampling session.

To simplify analyses, I focused on the five most common call types for each species. I calculated the total number of times each of the call types was used per trial day. I used the *rptR* package to calculate the repeatability for each bird. All models were run with the Poisson family, log link, and parametric bootstrapping to calculate the confidence intervals (n = 1000 repetitions). Both chickadee and titmouse [*D*] calls were unable to be modeled in *rptR*, so an ICC score was calculated with the package *ICCCounts* using a zero-inflated Poisson model.

Call uncertainty. The complexity of the calls was estimated by calculating the uncertainty in the calls. Uncertainty refers to the potential bits of information present within the communication system. We calculated two types of uncertainty, zero-order uncertainty (U_0) and first-order uncertainty (U_1) statistics using the UNCERT program written by E.D. Hailman and J.D. Hailman (Hailman *et al*. 1985). Zero-order uncertainty determines how much information is in these calls is due to the proportional use of different note types. The highest U_0 would occur if all note types are equally likely to occur. In Carolina chickadees, for example, this would mean that *I* notes, *C* notes, D_h notes and *D* notes are all equally likely to be used in a call. First-order uncertainty describes the amount of information that is available due to the transition probabilities between note types. The highest U_1 is achieved when all possible pairs of notes are used with equal probability. In tufted titmice, the maximum U_1 would be calculated when each pair of notes (e.g., *Z-B*, *Z-I*, *Z-A*, *Z-*D_h, *Z-D*, and so on) are equally likely to occur. For

both zero- and first-order uncertainty, greater uncertainty indicates greater communicative complexity. I was unable to calculate U_1 for the titmice because the sample size of birds that met the analysis requirements was too small. One U_1 and one U_0 was calculated per individual where possible (i.e., U_1 and U_0 for all chickadees, U_0 for all titmice). I was not able to run repeatability analyses on the call uncertainty because there was only one value per type of uncertainty for each bird. Signal complexity, however, is a valuable measure of calling behavior so it is retained for the PCA analyses.

Diversity index. The Inverse Simpson's diversity index (DI; Simpson, 1949) of the calls was also calculated per individual using SPSS version 27.0 for Windows. The diversity index is determined by the number of note types used out of all possible note types and whether the notes are used in equal amounts. For example, a chickadee call, *IIIID*, would have a lower diversity index score than the call *IICCDD* because the former uses fewer potential note types, and the note types are not used equally. Each bird had one DI score per day and one overall DI score averaging across all days the bird called, weighted towards days with more calls. Thus, each individual has a maximum of five daily DI scores and one overall DI score. Birds that did not call did not have a DI score for that day. I used the daily diversity index scores for repeatability analyses with the *rptR* package in R. For these analyses, I ran the *rptR* models with the Gaussian family and parametric bootstrapping to calculate the confidence intervals (n = 1000 repetitions).

Transition probabilities. An overall note transition probability matrix was calculated for each individual chickadee in UNCERT during the uncertainty analyses described previously. UNCERT was unable to produce transition probabilities for the titmice due to insufficient sample size. I calculated transition probabilities for the titmice with the R package *TraMineR* (version 2.2-11; Gabadinho et al., 2011). The transition matrix calculates the likelihood that a bird will progress from one note to the next. For example, if a titmouse D_h note is almost always followed by a *D* note, this will have a greater probability of occurring than the transition between an *I* note and *B* note when *I* notes are also commonly followed by *A*, and D_h, and *D* notes. These transition matrices were visualized in R with the package *ggplot2* (version 3.5.1; Wickham, 2016) and the ten transitions with the largest transition probabilities were extracted for each individual.

For repeatability, I calculated the daily transition probabilities for each individual with the R package *TraMineR*. I used *rptR* to calculate the repeatability estimates for all repeatability estimates. All models were run with the Gaussian family and parametric bootstrapping to calculate the confidence intervals (n = 1000 repetitions) except for chickadee $D_h \rightarrow D$, which ended up being a binary variable. I used the Binary family, logit link, and parametric bootstrapping for chickadee $D_h \rightarrow D$.

PCA. I used PCAs to examine which call characteristics, if any, are correlated with one another in a principal component to select variables for use in future studies. Chickadees and titmice had different PCA models. For each bird, I included median call rate, mean call rate, zero-order uncertainty, first-order uncertainty (chickadees only), total diversity index of the calls, maximum likelihood estimation for each note, proportion of use for each of the top five call types, and the transition probabilities for the ten most common pair of notes. In the titmouse PCA I only included the birds that called for the other analyses (n = 14). During analyses I centered and standardized calls to compare the variables more effectively. Principal components were calculated with the *prcomp* function in the R *base* package (R Core Team, 2025) and the relative contribution of each variable to the components with the package *factoextra* (version 1.0.7; Kassambara & Mundt, 2020). I chose to limit the number of principal components retained for further analyses by keeping all components that contributed more than 5% to the overall calling variance. Components that contributed less were not included.

Once I had the relevant PC scores, I created GLMs with the R *base* package to understand if the size of the bird is related to the call characteristics. Each individual bird's loading to the component was used at the dependent variable. Weight and wing chord length were used as independent variables. One chickadee did not have a weight, leading to a sample size of 17. I did not have a large enough sample size to include random effects in the models. Thus, the models all followed the same format: PC ~ weight*wc.

Animal use statement

I have adhered to all applicable institutional, national, and international guidelines for the use of animals. This study was conducted under protocols approved by the

University of Tennessee Institutional Animal Care and Use Committee (#1248 and #1326). Birds were collected and banded under US Fish and Wildlife Service scientific collecting permit (#SCCL-065321) and the US Geological Survey bird banding laboratory permit (#23253).

Results

The final sample of birds used in this study included 18 chickadees (nine flocks) and 22 titmice (eleven flocks). I coded more than 11,100 vocalizations between the two species after recording each flock for eight days (three days of acclimation for separate analyses and five days of trials). After removing calls from unknown birds and vocalizations made during acclimation, the remaining dataset of known birds during trial periods consisted of 6,122 calls (4,524 from titmice and 1,598 from chickadees). The average number of vocalizations per bird was approximately 89 calls for chickadees (ranging from 9 to 274) and approximately 206 calls for titmice (ranging from 0 to 1,607).

Call rate. The median call rate ranged from approximately 6 calls per minute to 0 calls per minute for titmice (**Figure 2.3**) and 2 calls to 0 calls per minute during sampling for chickadees (**Figure 2.4**). The overall individual daily repeatability for titmice was high (*ICC* = 0.9525, 95% CI = 0.014–0.997) and high for chickadees (*ICC* = 0.682, 95% CI = 0.235–0.891). See **Figure A-4** and **Figure A-5** for chickadee and titmouse call rate separated by birds housed together. The wide confidence intervals may be reflective of a handful of individuals with large variances in behavior and many individuals with small within-individual variances.

Note use. Maximum likelihood estimation for individual tufted titmice differed significantly from the full population likelihood (N =14 callers), X^2 (78, N = 14) = 19624.94, $p < 0.0001$ (**Figure 2.5**). Individual titmice were repeatable in their use of *I* notes ($R = 0.494 \pm 0.149$, 95% CI = 0.133–0.715, $p < 0.0001$), *A* notes ($R = 0.494 \pm 0.154$, 95% CI = 0.119–0.722, $p < 0.0001$), D_h notes ($R = 0.657 \pm 0.165$, 95% CI = 0.188–0.840, $p < 0.0001$), and *D* notes ($R = 0.614 \pm 0.135$, 95% CI = 0.293–0.802, $p < 0.0001$). *B* notes were also repeatable, but include the null hypothesis ($R = 0$) within the

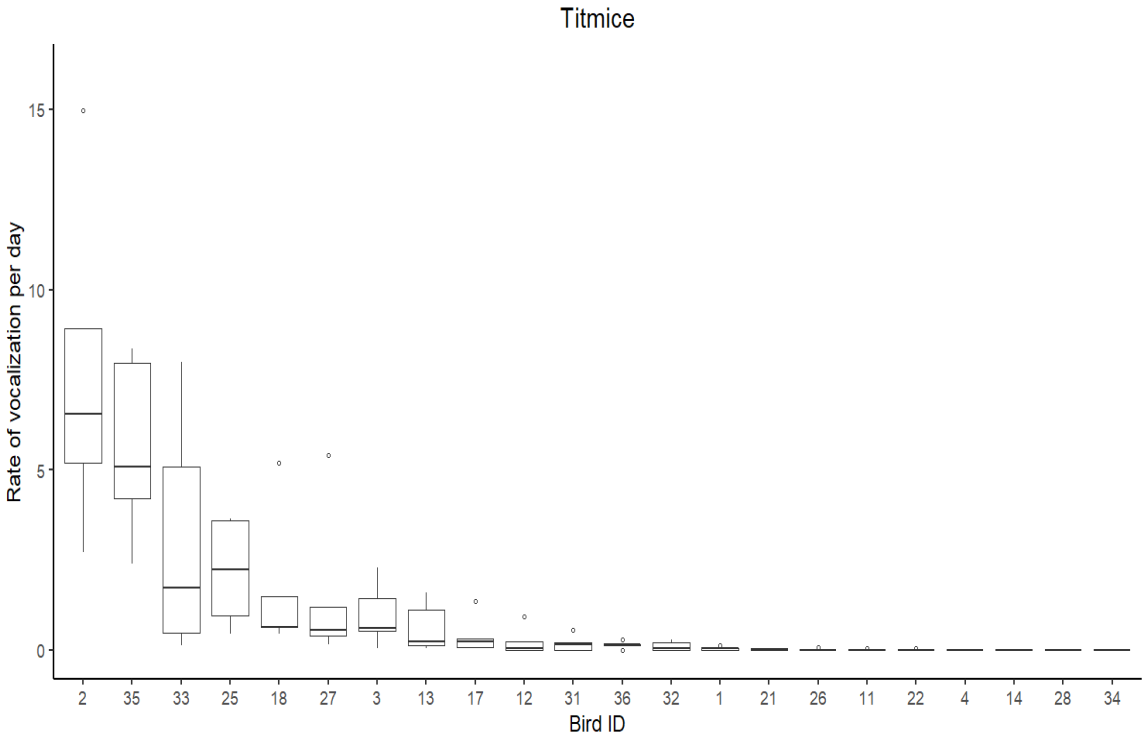

Figure 2.3. Call rates of tufted titmice per day (25 minutes of sampling). Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents five days of the bird's average call rate per minute, per day, including all calls made during the ten-minute focal sampling period and fifteen-minute all-occurrence sampling.

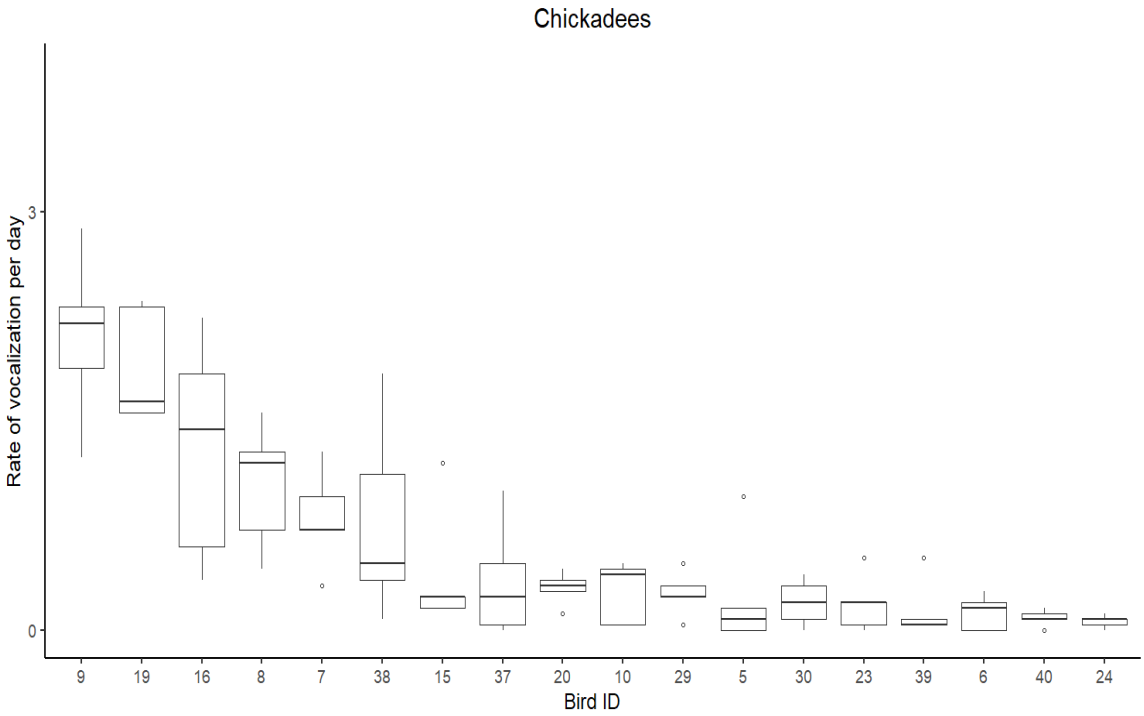

Figure 2.4. Call rates of Carolina chickadees per day (25 minutes per day). Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents five days of the bird's average call rate per minute, per day, including all calls made during the ten-minute focal sampling period and fifteen-minute all-occurrence sampling.

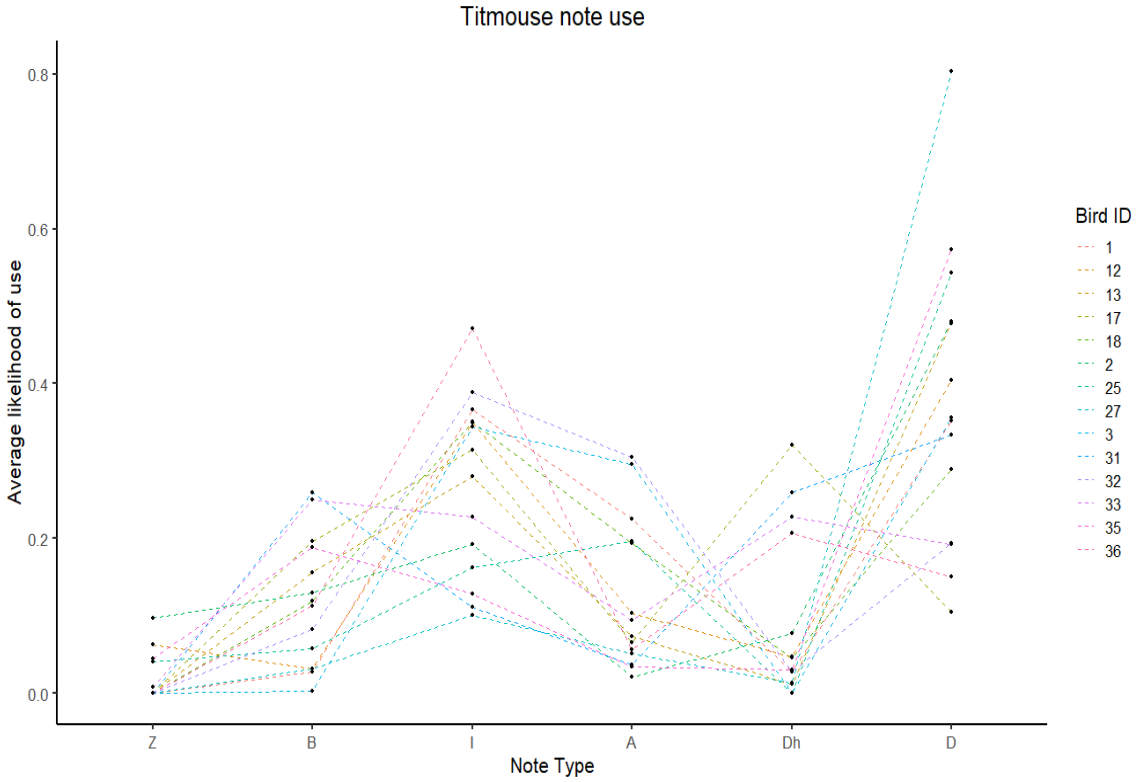

Figure 2.5. Maximum likelihood estimates of different notes for each titmouse. Black circles indicate maximum likelihood estimates. The different colors represent individual titmice and the lines link together likelihood estimates from a single bird.

confidence interval, (R = 0.415 ± 0.178, 95% CI = 0.0–0.682, p = 0.0008). *Z* notes were weakly repeatable and also include the null (ICC = 0.319, 95% CI = -0.357–0.775).

Individual Carolina chickadees likelihoods also differed significantly from the full population likelihood, X^2 (68, N = 18) = 8046.489, $p < 0.0001$ (**Figure 2.6**). Individual chickadees were repeatable in their use of *Intro* notes (R = 0.599 ± 0.115, 95% CI = 0.306–0.759, $p < 0.0001$), *C* notes (R = 0.461 ± 0.153, 95% CI = 0.097–0.69, $p <$ 0.0001), and *D* notes (R = 0.365 ± 0.124, 95% CI = 0.082–0.566, p = 0.0001). D_h notes were also weakly repeatable (ICC = 0.329, 95% CI = 0.121–0.509).

Call type. The five most common call types for titmice were [*I*][*A*][*D*] (581 calls; 19.7%), [*D*] (444 calls; 15.0%), [*B*][D_h] (431 calls; 14.6%), [*B*][*I*][*D*] (281 calls; 9.5%), and [*I*][*D*] (277 calls; 9.4%). The titmouse call types were repeatable: [*B*][D_h] calls (R = 0.708 ± 0.196, 95% CI = 0.087–0.897, $p < 0.0001$), [*I*][*A*][*D*] calls (R = 0.538 ± 0.164, 95% CI = 0.111–0.752, $p < 0.0001$) and [*D*] calls (ICC = 0.469, 95% CI = 0.257–0.639). [*I*][*D*] calls (R = 0.249 ± 0.155, 95% CI = 0.0–0.528, p = 0.0475) were not repeatable, and [*B*][*I*][*D*] calls (R = 0.387 ± 0.218, 95% CI = 0.0–0.658, p = 0.008) were weakly repeatable but include the null hypothesis (R = 0) in the confidence intervals.

Likewise, the five most common call types for the chickadee sample were [*I*][*D*] (725 calls; 48.5% of all calls), [*I*] (383 calls; 25.6%), [*I*][*C*][*D*] (305 calls; 20.4%), [*I*][*C*] (36 calls; 2.4%), and [*D*] (17 calls; 1.1%). The chickadee call types were generally repeatable, including [*I*] calls (R = 0.645 ± 0.136, 95% CI = 0.302–0.812, $p < 0.0001$), [*I*][*D*] calls (R = 0.435 ± 0.136, 95% CI = 0.126–0.644, $p < 0.0001$), and [*I*][*C*][*D*] calls (R = 0.550 ± 0.160, 95% CI = 0.122–0.751, $p < 0.0001$). [*I*][*C*] calls (R = 0.709 ± 0.251, 95% CI = 0.0–0.932, $p < 0.0001$) were repeatable and [*D*] calls were weakly repeatable (ICC = 0.328, 95% CI = -0.022–0.606), but both include the null hypothesis (R = 0) in the confidence interval.

Call uncertainty. The titmice that called had an average of 1.89 for U_0 (n = 14; range = 1.21–2.30) and the chickadees had an average U_0 of 1.15 (n = 18; range = 0.93–1.43). Chickadees had an average U_1 of 0.69 (n = 18; range = 0.28–1.09).

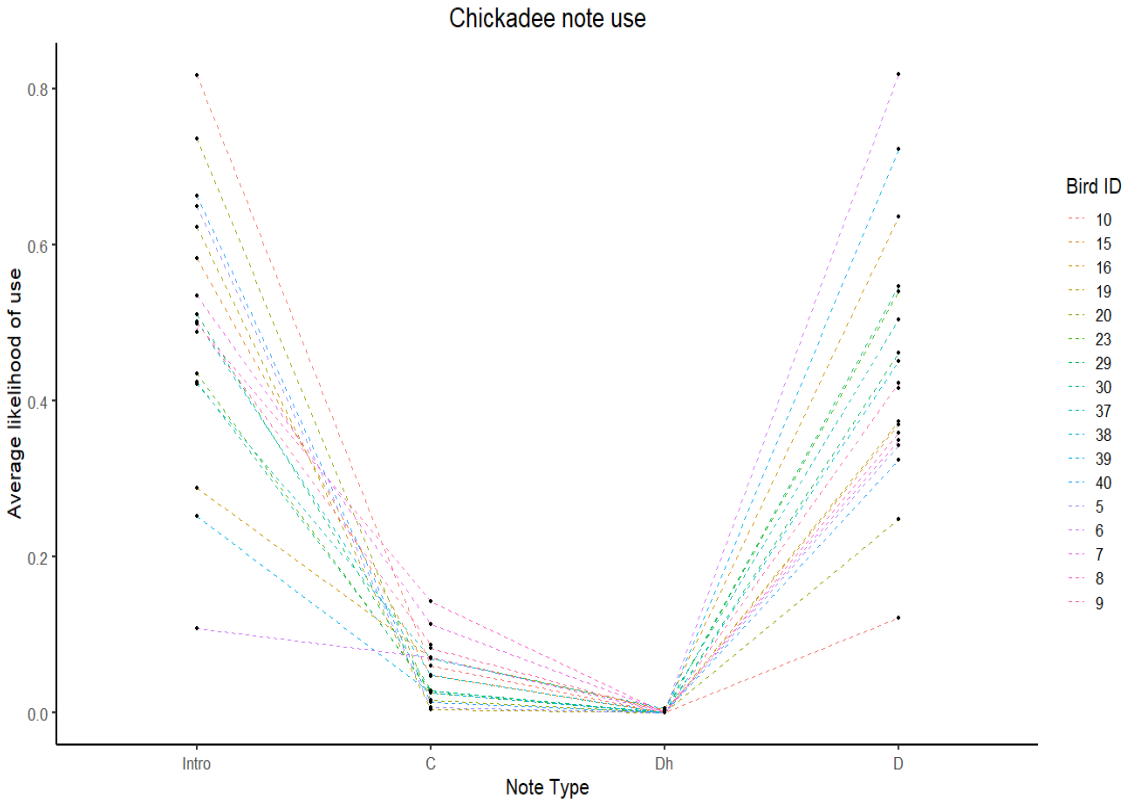

Figure 2.6. Maximum likelihood estimates of different notes for each chickadee. Black circles indicate maximum likelihood estimates. The different colors represent individual titmice and the lines link together likelihood estimates from a single bird.

Diversity index. The average diversity index for the titmice that called was 2.16 (n = 14; range = 1.30–2.71) and 1.60 for chickadees (n = 18; range = 1.22–2.02). The daily diversity index was not repeatable for chickadees (R = 0.126 ± 0.096, 95% CI = 0.0–0.35, p = 0.0916) and weakly repeatable for titmice (R = 0.309 ± 0.142, 95% CI = 0.013–0.567, p = 0.0105).

Transition probabilities. Based on the visual analysis of the transition matrices (chickadees – **Figure A-6**; titmice – **Figure A-7**), the ten most common titmouse note transitions were *Begin* → *I*, *I* → *A*, *I* → *D*, *Begin* → *B*, *B* → *I, B* → D_h,, *A* → *D, D* → *D, D* → *End,* and D_h → *End*. The ten most common note transitions for chickadees were *Begin* → *I*, *I* → *I*, *I* → *D*, *I* → *End*, *C* → *C*, *C* → *D, C* → *End, D* → *D*, *D* → *End*, and D_h → *D*. For both species, *D* → *D* and *D* → *End* were redundant with one another, so only the *D* → D transition was retained for the remaining analyses. See **Table 2.2** for the repeatability estimates for each pair of notes.

PCA. The PCA for titmice resulted in five components that contributed more than five percent of the total variance (85% of the variance cumulatively explained by these components). **Table 2.3** labels that five principal components and the top contributing variables for titmice. Titmouse PC1 indicates that birds that start their calls with *B* notes use less *A* notes overall. Similarly, PC4 shows that birds that use [*B*][*I*][*D*] calls and transition between *B* → *I* more, tend to use less *A* → *D* transitions. Birds that score high on PC2 are using more *D* notes and transition between *D* notes more frequently but use fewer D_h notes. In PC3, birds that use more *A* → *D* transitions also have greater diversity in their calls, but fewer [*D*] calls. Lastly, PC5 indicates that birds that used more [*I*][*D*] calls used more I notes overall, and were less likely to transition from *I* → *A*. For the titmouse GLMs, most of the models were not statistically significant at α =0.05. After controlling for the false discovery rate with the Benjamini & Hochberg Correction (1995), only PC2 scores were predicted by the main effects of wing chord length (X^2 = 8.63, p = 0.003) (**Figure 2.7**).

Chickadees also had five principal components that contributed more than five percent of the total variance (84% of the variance cumulatively explained by these components), and the most important variables for each component are listed in

Table 2.2. Repeatability estimates for the most common transition probabilities for each species. Repeatability estimates (R) were calculated in the *rptR* package. The 95% confidence interval (CI) was found via parametric bootstrapping. SE is the standard error. *Begin* indicates the start of the call and *End* indicates the end of the call. Chickadee *Intro* notes are abbreviated here as *I* notes. P-values smaller than 0.05 with confidence intervals that do not overlap with 0 are bolded.

Species	Pair	R	± SE	95% CI	P
Titmouse	*Begin* → *I*	0.391	0.137	0.087–0.611	**0.0007**
	I → *A*	0.430	0.138	0.121–0.657	**0.0005**
	I → *D*	0.087	0.100	0.00–0.341	0.24
	Begin → *B*	0.229	0.130	0.00–0.490	0.027
	B → *I*	0.136	0.112	0.00–0.393	0.12
	B → D_h	0.489	0.142	0.150–0.703	**< 0.0001**
	A → *D*	0.278	0.133	0.00–0.517	0.011
	D → *D*	0.549	0.135	0.231–0.746	**< 0.0001**
	D_h →*End*	0.533	0.135	0.213–0.745	**< 0.0001**
Chickadee	*Begin* → *I*	0.051	0.071	0.00–0.236	0.36
	I → *I*	0.336	0.117	0.097–0.541	**0.0009**
	I → *D*	0.426	0.121	0.151–0.623	**< 0.0001**
	I → *End*	0.225	0.111	0.00–0.430	0.008
	C → *C*	0.205	0.109	0.00–0.404	0.017
	C → *D*	0.112	0.091	0.00–0.316	0.13
	C → *End*	0.043	0.068	0.00–0.218	0.38
	D → *D*	0.154	0.101	0.00–0.361	0.074
	D_h → *D*	0.096	0.206	0.00–0.756	0.16

Table 2.3. Titmouse principal component scores and the top contributors.

Component	Variable	Contribution	Loading
PC1 (29.6 %)	Likelihood to use *A* note	10.69%	-0.327
	Probability of *Beginning* → *B* note	10.37%	0.263
PC2 (23.9%)	Likelihood to use *D* note	13.99%	0.374
	Probability of *D* → *D*	12.22%	0.350
	Likelihood to use D_h note	10.18%	-0.319
PC3 (16.2%)	Diversity index	14.69%	0.383
	Zero-order uncertainty	13.42%	0.366
	Proportion [*D*] calls used	12.11%	-0.348
	Probability of *A* → *D*	10.49%	0.324
PC4 (8.2%)	Probability of *B* → *I*	22.34%	-0.473
	Proportion [*B*][*I*][*D*] calls used	18.44%	-0.429
	Probability of *A* → *D*	10.17%	0.319
PC5 (7.0%)	Proportion [*I*][*D*] calls used	21.07%	0.459
	Probability of *I* → *A*	19.32%	-0.439
	Likelihood to use *I* note	13.28%	0.364

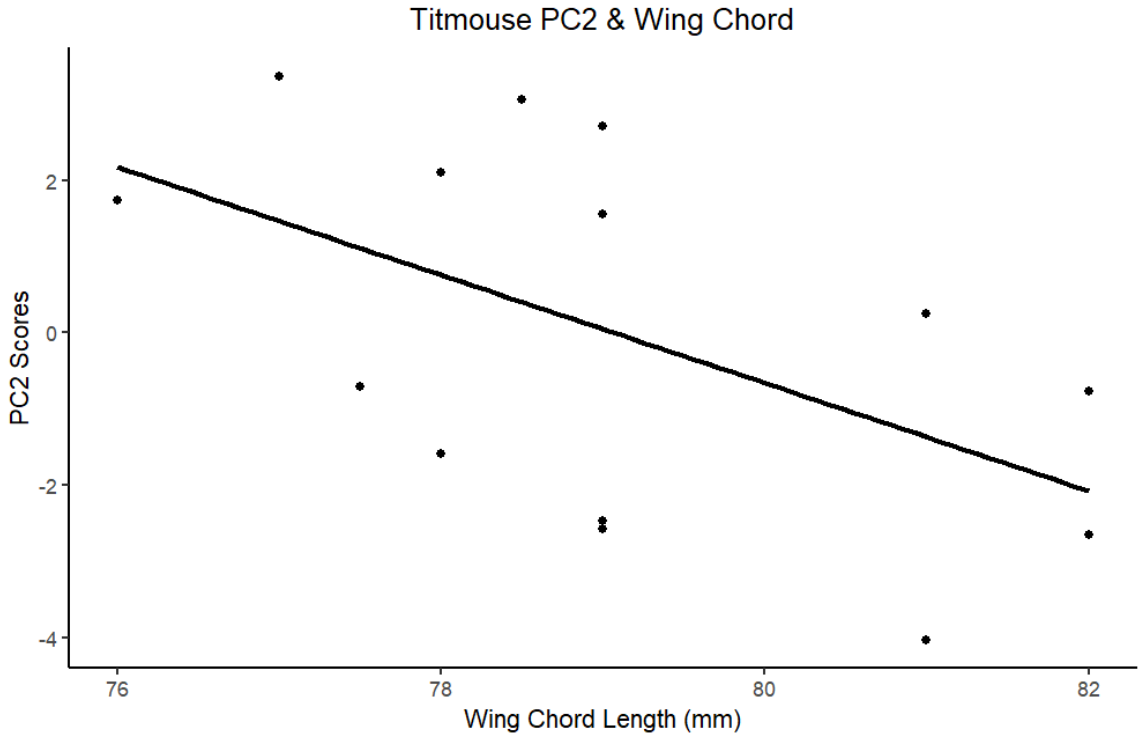

Figure 2.7. Titmouse PC2 scores and wing chord length. PC2 describes the birds' likelihood of using *D* notes and $D \rightarrow D$ transitions, as well as a lack of D_h notes. Smaller birds were more likely to use *D* notes and less likely to use D_h notes.

Table 2.4. Chickadee PC1 indicates birds that used *C* notes more often used fewer *D* notes overall. Likewise, PC4 suggests that birds that transition between $C \rightarrow D$ notes are less likely to transition from $C \rightarrow C$. PC2 loaded mostly on zero-order uncertainty. Birds that load higher on PC3 use fewer [*I*][*D*] calls and transition less between $I \rightarrow D$ notes. Lastly, birds that have higher PC5 scores have lower call rates and end their calls less with *C* notes. When testing the GLMs, again adjusted with the Benjamini & Hochberg Correction, PC2 was predicted by the weight × wing chord interaction term ($X^2 = 9.33$, $p = 0.002$)(**Figure 2.8**). See **Table 2.5** for details on all models and predictors for chickadees and titmice.

Discussion

The results support the hypothesis of calling being a personality-like trait by demonstrating that many calling characteristics appear to be repeatable within an individual in both study species. However, the way these call characteristics are used, and any potential patterns in the calling behavior, can be difficult to interpret at first glance. Some characteristics were repeatable but did not appear to contribute to the variation in overall calling behavior described by the PCA, such as titmouse call rates or the likelihood of an individual chickadee using an introductory whistle note. Some calling characteristics contributed to the PCA but were not repeatable like the use of [*I*][*D*] calls in titmice. Other behaviors were not repeatable at all or were variable enough that the null hypothesis could not be rejected, like the likelihood of using *B* notes in titmice or the use of [*D*] calls in chickadees. A lack of repeatability could be due to either individuals having a great deal of variation or all individuals doing the same thing.

Tufted titmice. Titmouse PC1, which contributes approximately 30 percent of the overall variation in calling behavior, suggests that birds that start calls with *B* notes are less likely to use *A* notes overall. Titmouse PC4 (about 8 percent of variation) also describes a tradeoff between using *B* notes and *A* notes. Birds that use more $A \rightarrow D$ note transitions use fewer [*B*][*I*][*D*] calls and fewer $B \rightarrow I$ note transitions. Interestingly, several of these have low repeatability (beginning calls with *B* notes, $A \rightarrow D$ note transitions, and [*B*][*I*][*D*] calls). Most birds appear to always transition from $A \rightarrow D$ if an *A* note is used, which may explain the lack of repeatability for these characteristics

Table 2.4. Chickadee principal component scores and the top contributors. *I* notes here are the consolidated *Intro* note category.

Component	Variable	Contribution	Loading
PC1 (28.3 %)	Likelihood to use *C* note	14.23%	0.377
	Likelihood to use *D* note	12.86%	-0.359
PC2 (24.4%)	Zero-order uncertainty	12.73%	0.357
PC3 (16.7%)	Proportion [*I*][*D*] calls used	17.56%	-0.419
	Probability of $I \rightarrow D$	10.51%	-0.324
PC4 (8.2%)	Probability of $C \rightarrow D$	29.51%	0.543
	Probability of $C \rightarrow C$	25.28%	-0.502
PC5 (6.8%)	Average call rate	23.20%	-0.482
	Median call rate	22.26%	-0.472
	Probability of $C \rightarrow End$	12.25%	-0.350

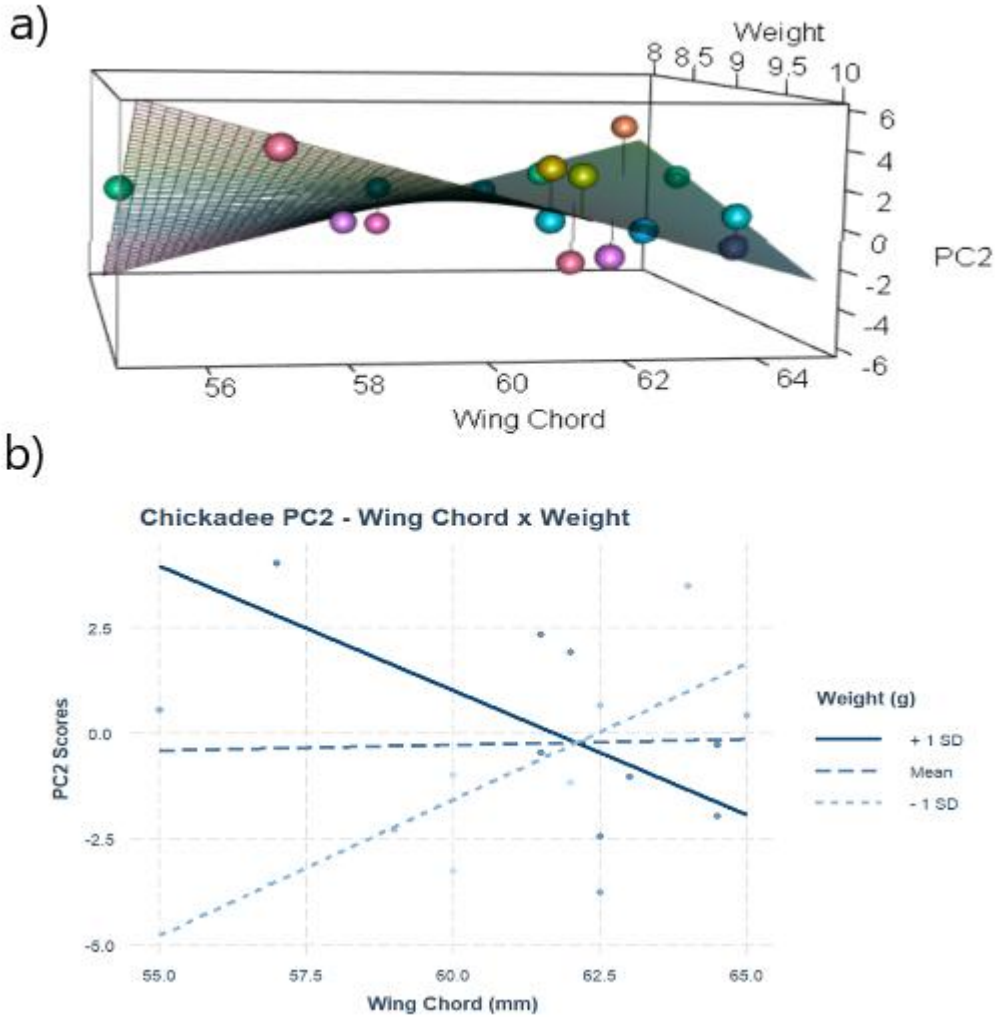

Figure 2.8. Chickadee PC2 scores and bird size. The interaction between weight (g) and wing chord length (mm) in relation to PC2 scores (zero-order uncertainty). a) is a 3D representation of the interaction. The plane is the best fit for the model. Spheres represent individual birds. b) is a flattened 2D representation of the interaction. Dot color is the bird's relative weight compared to the population average (range 8-10 g). Darker colors are heavier birds.

Table 2.5. Significance of size-related predictors in the GLM models for chickadees and titmice, based on PC scores for each bird. WC = Wing chord. Bolded p-values are retained after adjusting for multiple comparisons with the Benjamini & Hochberg Correction.

TITMOUSE				CHICKADEE			
PC	**Predictor**	X^2	***p***	**PC**	**Predictor**	X^2	***p***
PC1	Weight	0.158	0.28	PC1	Weight	1.12	0.29
	WC	0.005	0.94		WC	0.485	0.49
	Weight × WC	0.031	0.86		Weight × WC	0.096	0.76
PC2	Weight	4.13	0.042	PC2	Weight	2.45	0.12
	WC	**8.63**	**0.003**		WC	0.452	0.50
	Weight × WC	1.93	0.16		**Weight × WC**	**9.33**	**0.002**
PC3	Weight	0.013	0.91	PC3	Weight	5.82	0.016
	WC	3.26	0.071		WC	2.83	0.093
	Weight × WC	0.567	0.45		Weight × WC	1.34	0.25
PC4	Weight	0.497	0.48	PC4	Weight	0.092	0.76
	WC	0.737	0.39		WC	3.59	0.058
	Weight × WC	0.707	0.40		Weight × WC	0.018	0.89
PC5	Weight	0.472	0.49	PC5	Weight	0.059	0.81
	WC	0.067	0.80		WC	3.22	0.072
	Weight × WC	0.00003	1.00		Weight × WC	0.067	0.80

(**Figure A-7**). The lack of repeatability for beginning a call with *B* notes and the overall use of [*B*][*I*][*D*] calls is likely due to the prevalence of other common call types such as [*I*][*A*][*D*] calls and [*B*][D_h] calls that were used much more frequently. These latter calls are also much more repeatable than the [*B*][*I*][*D*] calls. Lastly, titmouse PC5 (7 percent of variation) suggests that titmice that use more [*I*][*D*] calls also use more *I* notes in general and fewer $I \rightarrow A$ transitions. [*I*][*D*] calls do not include *A* notes which explains this negative relationship. Titmouse calls typically do not include many notes (often one to three notes; Owens & Freeberg, 2007), so titmice may be constrained by the typical number of introductory notes and must swap additional *I* notes in a call for *A* notes. As before, [*I*][*A*][*D*] calls are much more common than [*I*][*D*] calls. Altogether, PC1, PC4, and PC5 indicate that individual titmice may preferentially use one of several call types. Call types that are used less frequently are also less repeatable, perhaps because the birds return to more common call types like [*I*][*A*][*D*] calls, [*B*][D_h] calls, and [*D*] calls. While the note coding scheme for this study is relatively novel, it is based on coding schemes that have been used for almost 20 years. There is no known research about the use of different call types, especially regarding individual differences in call type use.

Titmouse *D* notes and [*D*] calls that consist of strings of *D* notes are all highly repeatable. Titmouse PC2 (about 24 percent of variation) is characterized by individuals using more *D* notes and $D \rightarrow D$ transitions, and fewer D_h notes. All three call characteristics in this principal component were also highly repeatable within individual titmice. Previous work on titmouse calls has greatly focused on *D* note variation, particularly in terms of contextual variables such as predator presence or distress during handling (Nolen & Lucas, 2009; Freeberg & Branch, 2013; Landsborough et al., 2019), often finding that using more *D* notes in a call attracts more attention from flockmates (Courter & Ritchison, 2010; Landsborough et al., 2019). Wing chord length was related to PC2, where smaller birds use more *D* notes and more strings of *D* notes, and fewer D_h calls. Smaller birds are more often female, so this may indicate a sex effect with *D* and D_h note use. While few studies have examined sex differences in note use, these results of this study are surprising, as previous research on calling in distress contexts shows that male tufted titmice use more *D* notes and there were no sex effects on the use of D_h notes

(Freeberg & Branch, 2013). The current study obtained vocalizations during non-manipulated conditions rather than under stressful conditions such as capture, which could explain the discrepancy in results. Females and males may have different criteria that need to be met before using attention-grabbing calls. Future studies should continue to examine potential sex differences during baseline conditions in natural or naturalistic conditions to explore these findings further.

Titmouse PC3 (approximately 16 percent of variation) is defined by the most variables out of all the titmouse principal components. Individuals that have high PC3 scores have more complexity in their calls, indicated by greater diversity index in their calls and greater zero-order uncertainty in their calls. I was not able to calculate a repeatability for the uncertainty measure, but diversity index and [*D*] calls were repeatable. The birds that have more complexity in their calls also use fewer [*D*] calls overall and more $A \rightarrow D$ note transitions. Birds that use more single note type calls will have less complexity in their calls when complexity is measured as the proportional use of different note types. It is unclear why birds that use more $A \rightarrow D$ note transitions would be correlated with greater call complexity. [*A*][*D*] calls were not used very often, so *A* notes may more often follow other note types, ensuring a more proportional use of notes (minimum three out of six note types used) compared with similar note pairings like $I \rightarrow D$ when [*I*][*D*] calls are used frequently (two out of six notes types). In current research, any focus on call complexity differences in titmice are often at the species level and not on individual differences (Krams et al., 2012; Brooks & Freeberg, In press). Wing chord size (an estimate of sex) and weight were not related to call complexity, but there may be other underlying characteristics that affect what types of calls titmice use. More research should be done on these calls to understand which individuals prefer simpler calls, and which individuals use more complex calls.

Carolina chickadees. Similar to the findings for titmice, three of the chickadee principal components more clearly relate to different call types and note ordering rules. Chickadee PC1 (about 28 percent of variation in calling behavior) and PC4 (about 8 percent of variation) are very similar. Birds that score high on PC1 use more *C* notes and fewer *D* notes. These were both repeatable within individual chickadees. PC4 is

characterized by more $C \rightarrow D$ transitions and fewer $C \rightarrow C$ transitions, which were not repeatable call characteristics. Almost all chickadee calls were [*I*][*D*], [*I*], or [*I*][*C*][*D*] call types, and almost half of all calls were [*I*][*D*] calls. The transitions in PC4 may have a lack of repeatability due to the lack of calls using $C \rightarrow C$ transitions and almost all calls using $C \rightarrow D$ transitions. Both of these principal components suggest that chickadees may make tradeoffs between using *C* notes and *D* notes in a call. *D* notes in chickadees are also thought to be used for attention and arousal (Mahurin & Freeberg, 2008; Soard & Ritchison, 2009). Previous contextual analyses of chickadee calls suggest that *C* notes are used more when in flight (Freeberg, 2008). If the meaning of these note types are indeed different, then that would explain why they are not used at the same time. More work should be done to understand which individuals are more likely to attract flockmates via *D* notes and whether more active individuals are the ones using more *C* notes, and if these individuals differ from one another.

The third chickadee principal component based on note ordering and call types is PC3 (about 17 percent of variation in calling behavior). Birds that have high PC3 scores use fewer [*I*][*D*] calls and fewer $I \rightarrow D$ transitions. These individuals are likely using other call types like [*I*] calls and [*I*][*C*][*D*] calls that are also common. Because almost 50 percent of all chickadee calls were [*I*][*D*] calls, some individuals may be using these calls exclusively and not using the other call types. As before, more research is needed to understand which individuals are limiting their calls to [*I*][*D*] calls and which individuals are using other call types.

Chickadee PC5 (about 7 percent of variation) is characterized by call rates and the probability that *C* notes end the call. Only call rate was repeatable. Birds that score high on PC5 call less frequently and end their calls with *C* notes less often. Since *C* notes are less common, calls that end with *C* notes are less frequent (e.g., [*I*][*C*] calls or [*C*] calls). This lack of use would explain why it is not very repeatable. While not examined in this study, individuals that call more may also use a greater variety of call types. Further work would be needed to understand whether this is due to characteristics about individuals who call more, or if a greater variety of calls is likely to be observed merely due to sample size.

Lastly, chickadee PC2 (about 24 percent of variation) is explained by zero-order uncertainty. Chickadees that score high on PC2 have greater complexity in their calls as measured by the proportion of notes used in their calls out of all possible note types. PC2 was related to the interaction between wing chord size and weight. Small birds, likely female, that weigh more have greater complexity in their calls than small birds that weigh less. This trend flips when birds get larger, or when the birds are more likely to be male. Larger, heavier birds have less complex calls than larger, lighter birds. There may be a dominance effect happening that is causing this relationship with call complexity. In songbirds, heavier individuals may often be subordinate individuals maintaining greater fat stores to cope with diminished resource access (Clark & Ekman, 1995). Dominant individuals can exclude subordinates from food resources and do not need to maintain unwieldy fat stores to survive. When very subordinate, birds may be excluded so often that they are not able to increase their fat stores and must find alternative strategies such as leaving the flock (Barbosa et al., 2000; Krams et al., 2020). Males are typically dominant to females in both species (Hogstad, 1989). When taken in consideration with the findings from this study, dominant males and perhaps more dominant females (that are still subordinate to males) have greater complexity in their calls and subordinate males and perhaps subordinate females have lower call complexity. Previous work on the calls of Carolina chickadees and tufted titmice found minimal effects of sex alone in the *chick-a-dee* calls (Freeberg et al., 2003; Owens & Freeberg, 2007; Coppinger et al., 2020), so the findings reported here should be compared with known dominance hierarchies to better elucidate these patterns.

Communicative personality. For both Carolina chickadees and tufted titmice, it appears that individuals can combine the available notes into a wide variety of calls, but they may prefer to use one or two call types. Individuals from the same species can differ in their preferred call types. While this does not disprove the potential for the chick-a-dee call system to be open-ended (there were some individuals in this study that occasionally used reversals in the note ordering rules), it does suggest that there are perhaps additional constraints in the use of these signals that are not currently being considered within the field of communication. These signaling systems may be less plastic than originally

thought. These constraints on the number and type of calls used would also be reflected in the other communicative measures, like note use and uncertainty measures that were important for both species. Currently, there has been little focus on individual differences in signal use and potential preferences. The most analogous research to this work with the *chick-a-dee* calls in the parid system are syllable use in birdsong and language preferences that are correlated with human personality types.

In certain species of songbirds, such as the saffron finch (*Sicalis flaveola pelzelni*) and the northern mockingbird (*Mimus polyglottos*), individuals have large repertoires and can use the songs in flexible combinations. In both of these species, males predictably change their vocal behavior throughout the breeding season, but also demonstrate individual differences in the syllables used, the transitions between songs, bout length, and versatility (Derrickson, 1988; Saldívar & Massoni, 2017). Some individuals prefer to reuse preferred syllables, whereas others do not use many repetitions and instead run through their entire repertoire before significant repetitions occur (Saldívar & Massoni, 2017). Likewise, in humans, burgeoning research into language and personality has suggested that certain words or phrases are more likely to be used by certain behavioral types. For example, positive emotion words, social references, and feelings of certainty may be more likely to be used by extraverted individuals than introverted ones (Pennebaker & King, 1999; Argamon et al., 2005). While individual differences in language are attributed to personality quickly in the human literature, nonhuman researchers are often reticent to explain variation between individuals as related to personality. The current work on chickadees and titmice takes a step towards understanding these phenomena in nonhuman animals.

A communicative behavioral syndrome could explain the consistent individual differences in vocal output found here, including the presence of non-callers. If calling behaviors are repeatable and individuals fall along a gradient of behavioral output, there may be times where the animals are behaving in suboptimal ways (Sih et al., 2004b). Individuals are constrained by their behavioral traits and cannot exhibit optimal behavior in all different contexts (i.e., behaviors are less plastic than originally believed) (Sih et al., 2004a). Constraints in communicative behaviors could mean that animals are being

too vocal when they should be quiet, such as when there is a predator nearby, or too quiet when they should be vocal, like when trying to maintain flock cohesion or find mates. In addition, if there are constraints in the rate and composition of calls the birds produce, the birds may use inappropriate calls for a given context. However, more research is needed to understand if these communicative behaviors are consistent across different contexts, indicating potential constraints due to the presence of a behavioral syndrome.

The current findings only demonstrate that communicative behaviors can be repeatable and that there are differences between individuals. It does not yet demonstrate the presence of a behavioral type such as a behavioral syndrome or personality. To discover whether one or more of the repeatable variables in this study could be a behavioral syndrome or personality trait, more research needs to be done comparing these characteristics over different contexts and across different individuals or species. The other studies in this dissertation attempt to answer some of these questions. There are some limitations in this current study design that should be addressed in future comparisons. The birds in this study were held in naturalistic environments and were not in familiar territory. The flocks also only consisted of conspecific pairs when natural parid flocks often consist of several individuals from both species, as well as other occasionally present satellite species. The birds will likely behave differently in larger, mixed-species flocks in the wild. Lastly, some of the variation that was found in chickadee calls may be due to limitations in the coding scheme after condensing the variety of introductory note categories used in other studies into one summary category. There are several different coding schemes that have been used by other researchers, and breaking the introductory notes into two or more categories may change the observed patterns.

Conclusion

The call systems of both species are complex and allow the birds to use the calls in flexible ways. The results from this non-manipulated study suggest that call type, note use (particularly *D* notes), zero-order uncertainty, and call rate are important variables for distinguishing between individuals. Finding that individuals use these in repeatable ways across several days and times indicates that there may be underlying factors driving the

use of these calls, such as dominance status or the potential for a personality-like component. In my subsequent studies, I examine whether repeatability in these variables is consistent across social conditions, how it relates to other known behavioral syndromes and assays, and the influence of dominance status on communication.

CHAPTER THREE
COMMUNICATIVE REPEATABILITY ACROSS SOCIAL CONTEXT

Abstract

Chickadees and titmice are repeatable in their calling behavior within a single context, however behavioral syndrome research requires that the behaviors be consistent across two or more contexts. This study examines calling behavior (call type, note use, call rate, and call complexity) in Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) across two social conditions, conspecific pairs and mixed-species groups. To do this, I measured the repeatability (within-individual variance versus population-level variance) and the consistency (change in calling behavior overall) between the two social conditions. I also compared the call characteristics to other known behavioral syndromes, including activity level, exploratory behaviors, and coping strategy under stress. Wild chickadees and titmice were captured from natural mixed-species flocks and held in naturalistic outdoor aviaries. All birds were recorded for five days in a conspecific pair and five days in a mixed-species group, for a total of ten days of audio recording per bird. No other manipulations were made during audio recording. Activity scores were calculated by measuring the number of flights and hops during ten-minute focal sampling periods, the latency to explore a novel environment was used for an exploration score, and a stress score was obtained by measuring the bird's response during handling, including the use of distress calls and biting behavior. Repeatability estimates *R* or the intraclass correlation coefficient *ICC* were used to calculate repeatability of calling, and one and two-way ANOVAs were used for comparison across social conditions or with the other behavioral syndromes. Most call characteristics for both species were repeatable and consistent across context, though rarer call and note types were less repeatable. None of the call characteristics were related to other behavioral syndrome scores. These findings continue to support the possibility that communication could be a novel behavioral syndrome.

Introduction

When considering whether or not a behavioral characteristic could be a personality trait or a behavioral syndrome in vertebrates, it is usually not enough to show that the behavior is consistent across a short period of a couple of days. Ideally, the behavior would also be repeatable across two or more contexts or in response to various

stimuli over many days, weeks, months, or years (Sih et al., 2004a). As an example, the activity levels of streamside salamander larvae (*Ambystoma barbouri*) are correlated across different contexts, including time spent in a refuge and in the presence of predators (Sih et al., 2003). These findings are notable because more active larvae are at greater risk of predation, and yet the behavior still exists in the population. While studying these salamanders, Sih et al. (2003) also found that there was a heritable component to this activity syndrome, indicating that there may be distinct behavioral types in this population. The presence of distinct behavioral types potentially has wide-ranging implications for the formation and structure of groups. Individuals with similar behavioral types may prefer to cluster together (Johnson et al., 2017), affecting which conspecifics they interact with the most. While many studies focus on a single behavioral syndrome, individual variation in behavior may be more complex than the simple dichotomous set of traits that are often described.

Since behavioral syndromes have gained popularity in behavioral research, it has become apparent that several syndromes are often correlated with one another. For example, bolder individuals are also more likely to be fast explorers (Kudo et al., 2021), and due to this strong relationship, some researchers include exploratory behaviors as a subcomponent of the bold-shy syndrome (Kerman et al., 2016; Portugal et al., 2017). Several studies warn against lumping syndromes together to prevent confounding two or more phenomena (Carter et al., 2012; Padovani et al., 2020). Other correlated behavioral types that are frequently compared to the bold-shy syndrome are aggression (often positive correlation with boldness, Tamin et al., 2023), stress/reactivity (negative correlation, Atwell, 2012), and activity (Archard & Braithewaite, 2011). One relatively new angle in the personality/behavioral syndrome literature is the idea that communication is repeatable and possible related to behavioral syndromes.

A large focus of animal communication research over the years has been to understand how communication differs or stays the same between contexts at the species level, such as the foundational experiments on the use and semantics of signals (Seyfarth et al., 1980), but interest in individual differences and repeatability primarily increased due to the popularity of behavioral syndromes in the 2000s. Research into communicative

repeatability in collared flycatchers (*Ficedula albicollis*) found that many components of an individual's song are sensitive to environmental and contextual conditions (Zsebők et al., 2017). Other recent studies have concluded that calling behavior may be related to known behavioral syndromes, such as bold-shy and exploration syndromes, in species like European house crickets (*Acheta domesticus*; Wilson et al., 2010), domesticated pigs (*Sus scrofa domestica*; Friel et al., 2016), long-tongued bats (*Glossophaga soricina handleyi*; Schabacker et al., 2024), and superb fairy-wrens (*Malurus cyaneus*, Colombelli-Négrel et al., 2025). These studies suggest that bolder, more exploratory animals tend to call more and use more elements in their signals.

Similar results have been found in the communication systems of species in the family Paridae. Faster explorers in great tits (*Parus major*) increased their signaling output more than slow explorers during the breeding season (Naguib et al., 2016). Bolder Carolina chickadees (*Poecile carolinensis*) also had a tendency to call more during predator presentations and during baseline conditions (Williams, 2009). Lastly, *chick-a-dee* calls and alarm calls from black-capped chickadees (*Poecile atricapillus)* during predator playbacks were positively correlated with exploratory behavior (Guillette & Sturdy, 2011). Many of the studies examining the relationship between other behavioral syndromes and communication have focused on exploration or boldness, however several of these studies hint at potential implications for activity levels, aggression, and stress responses in the concluding statements. None of these studies, however, compare communication across different social contexts and few measure other behavioral syndromes as a part of the methodology.

In this study, I examined whether the calling behaviors from study one were consistent across social contexts. To do this, I captured wild Carolina chickadees and tufted titmice (*Baeolophus bicolor*) from naturally occurring flocks and placed them into one of two social conditions, conspecific pairs or mixed-species groups. After several days of recording the birds' vocalizations in their flock configuration, I reconfigured the flocks to record the same individuals in a different social environment. While coding the data I focused on the variables that were repeatable and that contributed to the overall variation from study one (note type, call rate, zero-order uncertainty, diversity index, and

call rate). I compared these data to the same individual's behavioral scores for several commonly studied behavioral syndromes. The goal of this study was to assess whether calling behaviors in chickadees and titmice were consistent over time and context (i.e., a novel behavioral syndrome), and if these behaviors wwere correlated with other behavioral syndromes.

H_{1A}: Calling behavior is correlated across social context.

If calling behavior is correlated across social contexts, then I expect to see that birds that call more in the conspecific context are also calling more in the heterospecific context. Likewise, birds may consistently prefer to use one type of call regardless of the social environment. These scores merely need to be correlated across context, meaning that it is possible for behaviors to change between contexts as long as they are changing in the same direction for most individuals. There are no known studies examining whether calling behavior in parids is consistent across social groups. However, in disc-winged bats (*Thyroptera tricolor*), an individual's contact calling rates are repeatable and are not affected by the identity of a receiver (Chaverri & Gillam, 2015; Chaverri et al., 2024). If supported, this hypothesis suggests that these calling characteristics may have a personality-like component.

H_{1B}: Calling behavior is correlated with another behavioral type.

There may be correlations between communication and other known behavioral types. Like the other species detailed earlier, several studies have discovered that the calls and songs of species in the family Paridae are correlated with their exploratory behavior (*Poecile atricapillus*, Guillette & Sturdy, 2011; *Parus major,* Naguib et al., 2010, Amy et al., 2010). Freeberg & Branch (2013) also found that distress calls of titmice (a type of stress response) were repeatable within individuals. These studies suggested the possibility of a personality-like component for communication but they primarily explored the relationship between vocalizations and exploration in laboratory birds. Other syndromes have not been considered yet.

If this hypothesis were supported, then one or more of the calling characteristics would be correlated with the other behavioral syndromes, activity, exploration, or coping strategy. For example, chickadee *C* notes are expected to be correlated with activity

levels because *C* notes are often used in flight contexts (Freeberg, 2008). By extension, the results of study one suggest that *C* notes and *D* notes are negatively correlated, so *D* notes may likewise be negatively correlated with activity levels.

H_0: There are no correlations in signaling behavior across any context.

It is possible that the birds have such flexible calling systems that their calls not correlated across context, and their calls do not correlate with known behavioral syndromes. If this were the case, the birds may use completely different calls between the two social conditions (conspecific flocks and mixed-species flocks). All individuals could have different call rates between the two conditions, with no clear directionality. For example, titmouse A would increase its call rate from conspecific to mixed-species conditions, titmouse B would decrease, and titmouse C would stay the same. Lastly, there would be no correlations between calling behaviors and activity level, exploration behavior, or coping strategy under stress. Previous research into dawn chorusing behavior in the closely related great tits suggest that while chorusing was repeatable within an individual, it was not related to exploration (Naguib et al., 2019).

Methods and Materials

Subjects and housing

Conspecific pairs of chickadees and titmice were captured from permanent feeder sites between October 2024 and March 2025 at the University of Tennessee Forest Resources, AgResearch, and Education Center (UTFRREC) in Oak Ridge, Tennessee. Captive birds were held in aviaries for approximately two weeks before release. Chickadees and titmice are resident species in East Tennessee and have small home ranges, so the platforms are spaced more than 375 m apart to ensure flock independence between sites (Bartmess-LeVasseur et al., 2010). Two size-matched birds from each species were taken from each site (four birds total). Chickadees must have been within a 2 mm wing chord difference to be considered size-matched, and the larger titmice needed to be within 3 mm wing chord difference to be size-matched. This means that unlike study one, conspecific pairs could be female-unknown or male-unknown sex pairs. The final sample of birds used in this study was 48 birds (24 chickadees and 24 titmice).

As in study one, every captured chickadee or titmouse had its wing chord measured to estimate sex and received a unique plastic color band combination on one leg. Titmice were considered male when their wing chord was greater than or equal to 81 mm and female when the wing chord was less than or equal to 76 mm; chickadees were considered male when their wing chord was greater than 61.5 mm and female when their wing chord was less than 59.5 mm (Coppinger et al., 2020). Birds were labeled as unknown sex when they fell into the middle range where wing chord overlaps between the sexes. When two size-matched conspecific birds were caught within 30 minutes of each other, they were transported to one of six nearby semi-naturalistic, outdoor aviaries that each measure approximately 6 m × 9 m × 3.5 m. Once captured, birds were randomly placed into aviaries as either conspecific pairs or a four-bird mixed-species flock. Five flocks began as single species pairs and seven flocks began as mixed-species flocks.

All aviaries had a covered indoor section that the birds could use as shelter, as well as several natural and naturalistic perches with vegetative cover. The aviaries were kept stocked with ad libitum black oil and safflower seed, fresh water, and the birds were provided with mealworms approximately every day as a part of a separate study. All birds housed in the aviaries were kept for a minimum of fifteen days, though some flocks were kept longer if weather conditions delayed data collection. Each flock was given a minimum of four days for acclimation to the aviary. The first day after capture the birds were left alone, and then for three subsequent days I replicated the procedure to acclimate the birds to all components of the observational study (i.e., equipment was set up and I spoke aloud for approximately 35 minutes). After all ten days of observations were completed, the birds were recaptured using baited treadle traps in the aviaries, weighed, and released at their original site of capture.

Procedure

The main procedure for study two was very similar to the procedure from study one. See **Table 3.1** for the study timeline. On observation days, I entered the aviary between 0800 and 1300 hours (Eastern Standard Time) with the equipment presented during acclimation. I set up the equipment and then sat in the designated corner to

Table 3.1. Study two timeline. This is the timeline for a flock that was not held longer due to inclement weather or other events that extended the sampling period.

Day of capture	Activity
1	Capture, banding, and handling audio
2	Acclimation
3	Acclimation
4	Acclimation
5	Audio sampling and activity scores
6	Audio sampling and activity scores
7	Audio sampling and activity scores
8	Audio sampling and activity scores
9	Audio sampling and activity scores, handling audio, exploration assay, and flock reconfiguration
10	Acclimation
11	Audio sampling and activity scores
12	Audio sampling and activity scores
13	Audio sampling and activity scores
14	Audio sampling and activity scores
15	Audio sampling and activity scores, weighing, handling audio, and release

observe the birds. A Sennheiser ME-64 electret microphone was placed in a microphone stand located in the middle of each aviary for all recordings. The microphone was connected to a Marantz PMD661 Professional Solid-State Recorder. The sample rate was 22,050 with 16-bit resolution.

Every observation day consisted of ten minutes of focal sampling for each bird in the aviary followed by 15 minutes of all-occurrence sampling. The order of the observations for focal sampling alternated randomly so that each bird was sampled first during a roughly equal number of days. During the focal samples, I visually followed the focal bird with binoculars and stated aloud when the focal individual was calling or singing. During all-occurrence sampling, I noted calls and songs from all birds in the aviary. Unknown vocalizations and vocalizations from birds outside the aviary were also noted. After five days of audio sampling (capture days five through nine), the birds would be recaptured, and the social configuration of the flocks would be altered. All birds were moved to a new aviary at this time to ensure that all individuals were starting in a novel environment. Birds that started in the mixed-species flock condition would be split into two conspecific flocks (i.e., one chickadee pair and one titmouse pair). Likewise, birds that started in conspecific pairs would be reunited with the pair of the other species. All birds were housed with familiar birds from their home territory for all conditions.

Once in the new housing configurations, the flock(s) were given one day without observer presence to acclimate to the new aviary and social environment (capture day ten). On capture day 11, I started collecting audio data again with the same procedure as capture days five through nine. Each observation day consisted of ten minutes of focal sampling for each bird in the aviary followed by 15 minutes of all-occurrence sampling. The order of the observations for focal sampling alternated randomly so that each bird was sampled first during a roughly equal number of days. During the focal samples, I visually followed the focal bird with binoculars and state aloud when the focal individual was calling or singing. During all-occurrence sampling, I noted calls and songs from all birds in the aviary. Unknown vocalizations and vocalizations from birds outside the aviary were also noted. After five days of audio sampling (capture days 11 through 15),

the birds were recaptured and released at their home site. As in study one, I was not able to calculate inter-observer reliability for the live data coding part of the study.

In addition to the audio sampling procedure described previously, I also collected data for comparison with other behavioral syndromes. During initial capture (capture day one), the reconfiguration day (capture day nine), and final release (capture day fifteen), the birds were recorded while being held for a minimum of one minute (three minutes per bird). During the handling audio file, I noted whether the bird was biting or not. In addition, on the reconfiguration day (capture day nine), the birds were placed into a novel environment and video recorded for a minimum of five minutes. The novel environment was a medium sized bird cage (approximately 0.8 m × 0.5 m × 0.45 m) that had never been used with these birds. The birdcage had two wooden perches that spanned the entire length of the cage, and both perches were marked with permanent marker into thirds (**Figure A-8**). The exploration testing occurred in one of the aviaries with at least one other flock member in the aviary to prevent confounding effects from isolation (Benson, 2024). Once the bird was finished with the novel environment testing it was released into its new aviary and flock condition.

Lastly, each bird's activity level was recorded during focal audio sampling (capture days five through nine and eleven through fifteen). While following the focal birds visually each day, I also used a handheld tally counter to record each hop or flight. All movements needed to be farther than one body length away to be included. An activity score was calculated for each bird every day of audio sampling, resulting in ten total activity scores per bird (five from the conspecific condition and five from the mixed-species condition).

Call analysis and note classification

Calls were manually classified within the spectral view window (Blackman-Harris windowing function at a resolution of 256 bands) in CoolEdit Pro, version 2 (Syntrillium Software, Scottsdale, AZ, USA). As in study one, titmouse calls were analyzed using the modified coding scheme from Owens & Freeberg (2007). The four introductory note categories are *A*, *I*, *B*, and *Z*, in order of increasing duration. I defined *A* notes as notes that are less than 75 msec in duration. *I* notes are notes with durations

between 75 msec and 144 msec. *B* notes are notes with durations that are between 145 msec and 214 msec. *Z* notes are notes with durations of 215 msec or greater. Also included were *D* notes, broad-frequency notes with a harmonic-like structure, and D_h notes, hybrid notes that transition from introductory note to *D* note, in our categorization of the titmouse *chick-a-dee* call. Inter-observer reliability was high for titmouse calls (Cohen's Kappas: *Z* notes = 0.93; *B* notes = 0.93; *I* notes = 0.89; *A* notes = 0.93; D_h notes = 1.0; *D* notes = 1.0). Chickadee calls were analyzed using a condensed coding scheme. I condensed all introductory note categories into a single whistle note category, *I*. I also included structurally complex *C* notes, broad-frequency *D* notes, and D_h hybrid notes that transition from an introductory whistle note to *D* note. Inter-observer reliability for chickadee note types was good. Cohen's Kappas ranged from 0.88 for *C* notes to 1.0 for D_h notes (*Intro* notes = 0.90; *D* notes = 0.97). In the audio files collected during handling to measure stress response, I also included a category called *high notes* to indicate a high-risk distress call by the birds. These notes are often rapid and higher pitched than other introductory notes. See Chapter 2, **Figure 2.1** for spectrograms of titmouse calls and **Figure 2.2** for spectrograms of chickadee calls.

Video analyses

The videos were coded in Boris (v 8.25.4; Friard & Gamba, 2016). Behavioral assays began when the bird was released from the hand or bag into the novel environment. The total number of flights and hops were recorded as well as the locations of the hops (top, bottom, left wall, right wall, front, back, and perch locations one through six). Walking across an area was not recorded. I calculated the exploration score by finding the latency to visit all locations within the cage. Birds that did not visit all sites were assigned the maximum potential latency score (301 seconds). See **Table 3.2** for the ethogram used for video analyses.

Statistical analyses

Once all the calls were coded, I focused on the call characteristics that were important to overall call variation in the PCA from study one and that were generally repeatable. These characteristics were call type, note use, zero-order uncertainty, diversity index, and call rate. I calculated repeatability using the intraclass correlation

Table 3.2. Exploration ethogram. The ethogram that was used to code the novel environment test videos. See Figure A-8 for an image of the testing arena. There are two perches spanning the center of the arena at different heights, with the perch closest to the camera as the lower perch. Both perches are divided into thirds with a black marker. The new locations on the perches are given a numeric ID for video coding. The outer surfaces of the area are given letter IDs and are designated based on directionality from the camera viewpoint. The small seed and water containers were empty and are considered part of the front of the arena for coding purposes. All movements were coded, including short hops that stayed in the same location code.

Boris code	Behavior/location
1	The bird is on the left side of the upper perch
2	The bird is in the middle area of the upper perch
3	The bird is on the right side of the upper perch
4	The bird is on the left side of the lower perch
5	The bird is in the middle area of the lower perch
6	The bird is on the right side of the lower perch
t	The bird is on the top/ceiling of the arena
g	The bird is on the floor/ground of the arena
r	The bird is on the right wall of the arena
l	The bird is on the left wall of the arena
f	The bird is on the front wall of the arena (closest to camera)
b	The bird is on the back wall of the arena (farthest from camera)

coefficient (*ICC*) or the repeatability estimate (*R*) for all call characteristics. I ran two repeatability tests for all calling variables. One test was on the conspecific condition data to ensure that repeatability was comparable to study one findings, and one was on the full data set for each species. The repeatability of the full data was calculated without including condition to examine whether repeatability goes down when social context changes.

To further explore these patterns, I created generalized linear models (GLMs) to compare the variables across social contexts using the *base* package in R. I included species, condition, and their interaction as independent variables for call rate, diversity index, and call uncertainty. For call characteristics that were not comparable across species (note use and call type), the models did not include species and were kept as simple one-way ANOVAs. When there were several comparisons being made, I used the Benjamini-Hochberg False Discovery Rate correction (1995).

I also included whether the birds were biting during handling, their calling behavior during handling, activity levels, and latency to explore a novel environment in the analyses. I calculated repeatability estimates for all but the novel environment test with *R* and *ICC* to ensure that I was capturing these known behavioral syndromes. The novel environment was only assayed once so that it remained novel and thus does not have repeated measures. Once all behavioral tests were initially analyzed, I created models with all call characteristics that were consistent across social condition (if any) as the dependent variable and the bird's behavioral scores as predictors to understand any relationship between the different syndromes. I corrected for multiple comparisons with the Benjamini-Hochberg correction (1995).

Call rate. As in study one, calls and songs were filtered by individual ID for each day of sampling. Calls included in these analyses were limited to those made during each ten-minute period and fifteen-minute all-occurrence sampling period per day. Calls made during other bird's focal sampling period or after the sampling period were not included. Each bird had one call rate per day, over ten days total (five intervals per condition).

For the repeatability analyses, I used the R stats package *ICCCounts* (version 1.1.2; Carrasco, 2024) to measure the repeatability in the total number of vocalizations

per day. I used the same zero-inflated negative binomial model with additive extradispersion from study one.

Note use. For the repeatability analyses, I found the number of each note used per day, per bird. I used the *rptR* package in R (version 0.9.22; Stoffel et al., 2017) to find the repeatability estimate for each note type. All models were run with the Poisson family, log link, and parametric bootstrapping to calculate the confidence intervals (n = 1000 repetitions). *Z* notes for titmice were unable to be modeled in *rptR* due to zero-inflation, so an ICC score was calculated for these notes with the package *ICCCounts* using a zero-inflated Poisson model.

Call type. I recorded the quantity and order of the notes within each call. I used a cutoff of 150 msec between notes to differentiate between different calls (rounded from the 147 msec cutoff used Courter & Ritchison, 2010). Call type here refers to the unique ordering of notes without regard to the number of notes in the call. For example, a titmouse call with the notes *BIIADDD* and *BBIAD* would both have the call sequence type [*B*][*I*][*A*][*D*]. All *chick-a-dee* calls with a known caller were included in these analyses, including any calls with a positive identification that were made during another bird's focal sampling session.

As in the first study, I focused on the five most common call types for each species. I calculated the total number of times each of the call types was used per trial day. I used the *rptR* package to calculate the repeatability for conspecific flocks and repeatability across conditions. All models were run with the Poisson family, log link, and parametric bootstrapping to calculate the confidence intervals (n = 1000 repetitions).

Call uncertainty. The complexity of the calls, measured by the potential bits of information available in the system, was estimated by calculating the uncertainty in the calls. For this study, only zero-order uncertainty (U_0) was included. Uncertainty was found using the UNCERT program written by E.D. Hailman and J.D. Hailman (Hailman *et al*. 1985). Zero-order uncertainty examines how much information is in these calls due to the proportional use of different note types. The highest U_0 would occur if all note types were equally likely to occur. In Carolina chickadees, for example, this would mean that *I* notes, *C* notes, D_h notes and *D* notes are all equally likely to be used across all the

calls for a given individual. For zero-order uncertainty, greater uncertainty indicates greater communicative complexity. Zero-order uncertainty was calculated for each condition per individual, and one average U_0 was calculated by finding the weighted mean between the two conditions.

Diversity index. The Inverse Simpson's diversity index (DI; Simpson, 1949) of the calls was calculated per individual using SPSS version 27.0 for Windows. The diversity index is determined by the number of note types used out of all possible note types and whether the notes are used in equal amounts. Each bird had one DI score per day and two overall DI scores, one per condition, averaging across all days the bird called. These overall scores were weighted towards days with more calls. Birds that did not call did not have a DI score for that day. I used the daily diversity index scores for repeatability analyses with the *rptR* package in R. For these analyses, I ran *rptR* models with the Gaussian family and parametric bootstrapping to calculate the confidence intervals (n = 1000 repetitions).

Activity level. Ten activity level scores were calculated per bird (one per day for each of the trial days). I ran a *rptR* model with the Gaussian family and parametric bootstrapping (n = 1000 repetitions). All activity scores were included in the analyses. I calculated an average activity score for each bird to use in the GLMs. Birds with more flights and hops (higher scores) were considered to be more active birds than individuals that moved less.

Exploration. I calculated the latency for each bird to explore 12 locations in a novel environment within a five-minute timeframe. The birds with a shorter latency were considered to be fast-explorers and those with longer latencies, including birds that did not reach all areas of the novel environment, were considered slow-explorers. Latency was used directly in the GLMs as a measure of exploratory behavior.

Behavior during handling. Birds were handled a maximum of three times during the study procedure. Handling sessions were often different lengths of time depending on how long it took to measure and color band the bird. I started coding the audio file at 0:10 seconds to account for any variation in getting the bird out of the bag and into the hand. I recorded all notes used for one minute, ending files at 1:10. Thirteen of the 137 handling

audio files ended early (1 to 4 seconds) due to technical issues, and the start time for these data were moved earlier to include all 60 seconds.

I focused on *D* notes and whistle-like *seet* alarm notes for both species. *D* notes are often used in lower risk, aggressive mobbing contexts and *seet* notes are often paired with freezing behavior and are used more in high-risk contexts (Templeton et al., 2005). I found the proportion that these note types were used per bird during handling. I also calculated the rate of note use for these birds across the 60-second sampling period. Lastly, biting was measured as a binary variable where the birds were biting at least once during the handling period, or not at all. In terms of their coping strategy, individuals that called more or those that were biting were considered more active and those that bit and called less were more passive. Within the calling birds, *D* note use was considered slightly more active than the *seet* notes because of the association between *D* notes and aggression in contexts of risk. Birds were assigned a unique score for coping strategy by adding together their note rate (notes/sec), biting score (1 or 0), and their maximum likelihood of using a *D* note (0 to 1). Birds with more active coping strategies would have higher scores. These compound coping scores are used in the GLMS to understand how coping strategy relates to calling behavior during non-manipulated contexts.

I calculated the repeatability estimates for the likelihood of each bird using *D* notes and biting with *rptR* models. *D* notes and *seet* notes are redundant with one another for these maximum likelihood estimates. I used the binary family with logit link for biting repeatability and a Gaussian family for maximum likelihood of *D* notes. Note rate repeatability was calculated with *ICCcounts* and was a zero-inflated negative binomial model with additive dispersion.

Animal use statement

I have adhered to all applicable institutional, national, and international guidelines for the use of animals. This study was conducted under protocols approved by the University of Tennessee Institutional Animal Care and Use Committee (#1248 and #1326). Birds were collected and banded under US Fish and Wildlife Service scientific collecting permit (#SCCL-065321) and the US Geological Survey bird banding laboratory permit (#23253).

Results

The final sample of birds used in this study included 24 chickadees and 24 titmice (twelve mixed-species flocks). One chickadee died after reconfiguration and the subsequent mixed-species flock consisted of only three individuals. Additionally, four birds used in study two were recaptures from the first study (two titmice and two chickadees), however all recaptures were housed with different flockmates and the manipulations in study two were novel for all individuals. I coded more than 20,600 vocalizations between the two species after recording each flock for ten days (i.e., five days in conspecific pairs and five days in mixed-species flocks). After removing calls from unknown birds and other vocalizations from known birds, the remaining dataset of *chick-a-dee* calls during trial periods consisted of 13,135 calls (7,944 from titmice, 5,191 from chickadees). The average number of calls per bird was approximately 216 calls for chickadees (ranging from 0 calls to 742 calls per bird) and approximately 331 calls for titmice (range 0 to 1687 calls per bird). The sample size for call rate analyses was the full 24 birds per species, but two titmice did not call at all and were removed from the other analyses (N = 22). The repeatability of the calls made during the conspecific conditions was calculated as a replication of the study one results. These replication data are available in **Table A-1** (titmice) and **Table A-2** (chickadees).

Call rate. The average call rate for individual titmice ranged from approximately six calls per minute to zero calls (**Figure 3.1**). The range for chickadees averaged from around three calls per minute to zero calls (**Figure 3.2**). See **Figure A-9** for call rates split out by flock. When comparing across the two conditions, repeatability was high (titmice, $ICC = 0.630$, 95% CI = 0.095–0.883; chickadees, $ICC = 0.529$, 95% CI = 0.130–0.780).

After removing the chickadee that died halfway through the data collection, the glm predicted by condition, species, and the interaction between the two only had a significant main effect of species, $X^2 = 6.06$, $p = 0.014$. Titmice called more in both conditions (mixed-species condition, M = 0.938 calls per minute; conspecific condition, M = 0.981 calls per minute) than chickadees (mixed-species condition, M = 0.451 calls per minute; conspecific condition 0.854 calls per minute) (**Figure 3.3**).

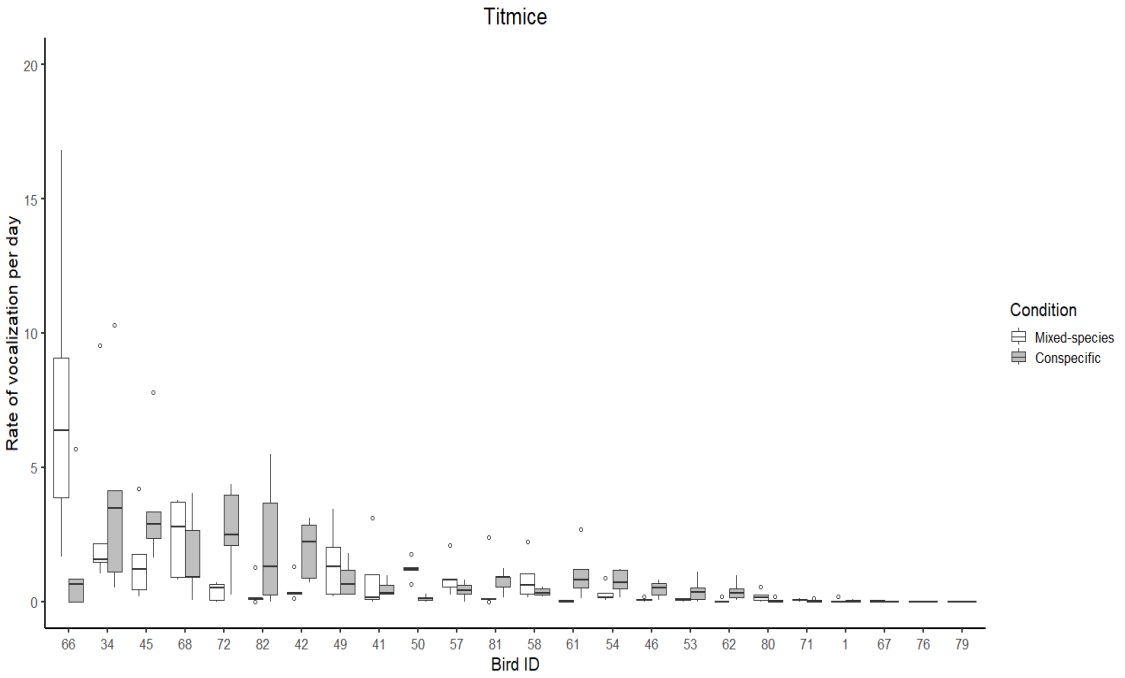

Figure 3.1. Call rates of tufted titmice per day (25 minutes per day). Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents five days of the bird's average call rate per minute, per day, including all calls made during the ten-minute focal sampling period and fifteen-minute all-occurrence sampling. White boxes are calls made during the five days of mixed-species condition and the gray boxes are calls from the conspecific conditions.

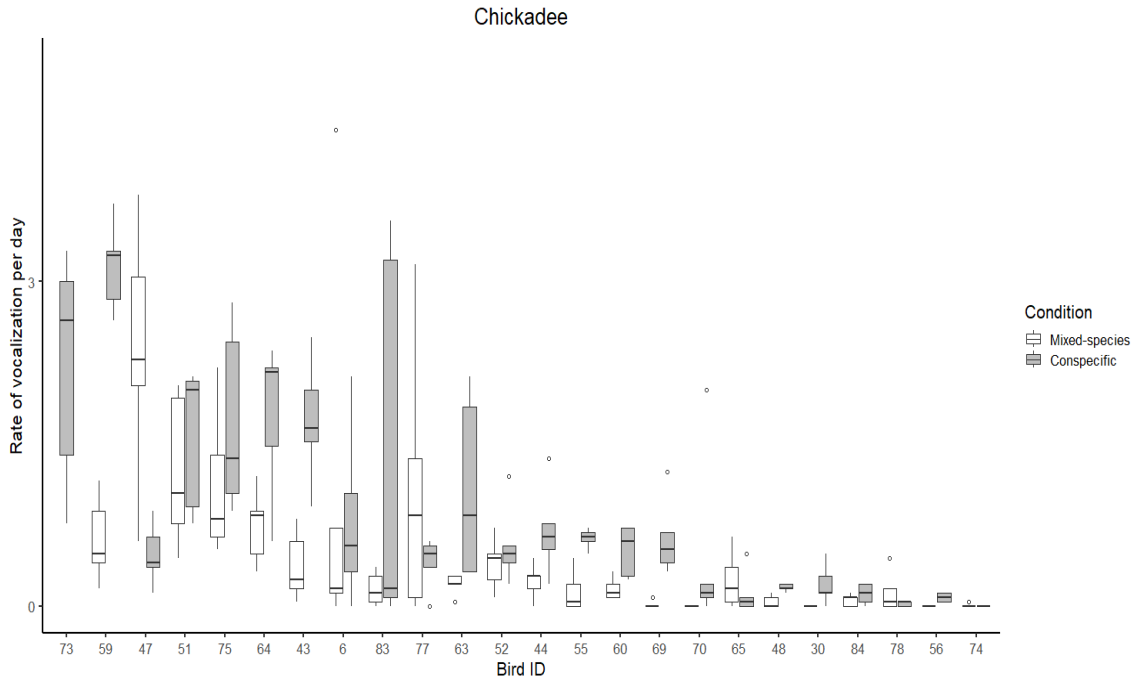

Figure 3.2. Call rates of Carolina chickadees per day (25 minutes per day). Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents five days of the bird's average call rate per minute, per day, including all calls made during the ten-minute focal sampling period and fifteen-minute all-occurrence sampling. White boxes are calls made during the five days of mixed-species condition and the gray boxes are calls from the conspecific conditions. Bird 73 died after the conspecific condition.

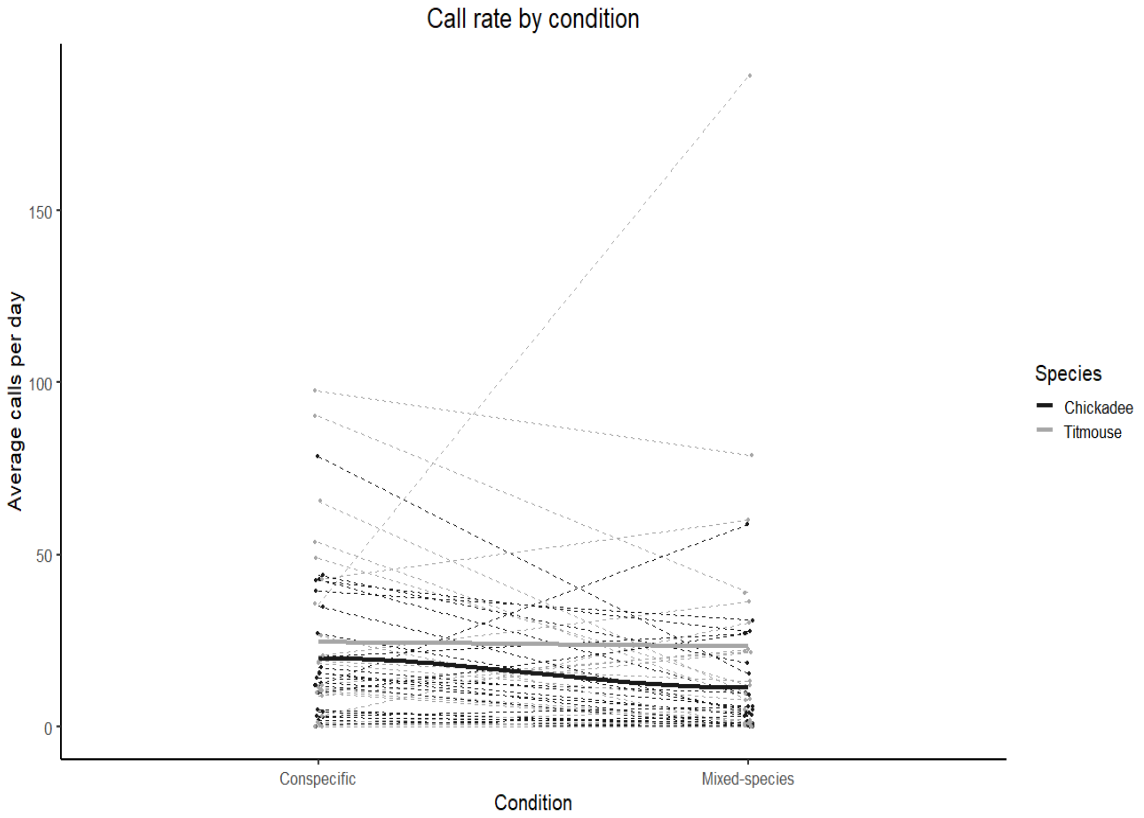

Figure 3.3. Average number of calls per day across social conditions. Gray dashed lines are individual titmice and black dashed lines are individual chickadees. The solid gray and black lines indicate the population average for titmice and chickadees, respectively.

Note type. When comparing the use of notes by individual titmice, *B* notes ($R = 0.564 \pm 0.177$, 95% CI = 0.279–0.725, $p < 0.0001$), *D* notes ($R = 0.535 \pm 0.091$, 95% CI = 0.320–0.677, $p < 0.0001$), and D_h notes ($R = 0.576 \pm 0.113$, 95% CI = 0.315–0.740, $p < 0.0001$) were highly repeatable across the two flock conditions. Likewise, *A* notes ($R = 0.415 \pm 0.100$, 95% CI = 0.198–0.585, $p < 0.0001$) and *Z* notes ($ICC = 0.428$, 95% CI = 0.274–0.561) were moderately repeatable, and *I* notes ($R = 0.373 \pm 0.094$, 95% CI = 0.167–0.521, $p < 0.0001$) were weakly repeatable. The one-way ANOVAs suggest that none of the note types differed between the two conditions (*Z* notes, $X^2 = 0.186$, $p = 0.67$; *B* notes, $X^2 = 0.011$, $p = 0.91$; *I* notes, $X^2 = 1.43$, $p = 0.23$; *A* notes, $X^2 = 0.619$, $p = 0.43$; D_h notes, $X^2 = 3.08$, $p = 0.079$; *D* notes, $X^2 = 0.077$, $p = 0.78$).

Most chickadee notes were also repeatable within an individual, including *Intro* notes ($R = 0.547 \pm 0.088$, 95% CI = 0.334–0.673, $p < 0.0001$), *C* notes ($R = 0.631 \pm 0.095$, 95% CI = 0.401–0.767, $p < 0.0001$), and *D* notes ($R = 0.438 \pm 0.091$, 95% CI = 0.230–0.577, $p < 0.0001$). D_h notes appeared repeatable but included the null hypothesis ($R = 0$) within the confidence interval ($R = 0.640 \pm 0.208$ 95% CI = 0.0–0.811, $p < 0.0001$). After running the GLM models, D_h notes and *C* notes did not differ significantly by condition (D_h notes, $X^2 = 1.96$, $p = 0.16$; *C* notes, $X^2 = 0.609$, $p = 0.43$). *Intro* notes were marginally significant but was rejected after correcting for multiple comparison ($X^2 = 4.44$, $p = 0.035$). Lastly, the use of *D* notes was significantly different between conditions ($X^2 = 10.848$, $p = 0.0009$) and was retained after the Benjamini-Hochberg correction. Chickadees used roughly twice as many *D* notes during the conspecific condition (M = 100.47 notes per bird) as the mixed-species condition (M = 46.08 notes per bird) (**Figure 3.4**).

Call type. The five most common call types used overall by titmice were [*I*][*A*][*D*] (2,230 calls; 28.1%), [*D*] (2,073 calls; 26.1%), [*I*][*D*] (658 calls; 8.3%), [*I*][D_h] (635 calls; 8.0%), and [*B*][D_h] (548 calls; 6.9%). When comparing the call types between the two conditions, the top five calls were the same (but in a different order) except [*I*][*D*] calls (215 calls; 5.9%) were slightly less common than [*B*][*I*][*D*] calls (225 calls; 6.2%) in the conspecific condition. See **Table 3.3** for the top ten calls per condition for both species. [*I*][*A*][*D*] calls were repeatable across both conditions ($R = 0.441 \pm 0.099$, 95%

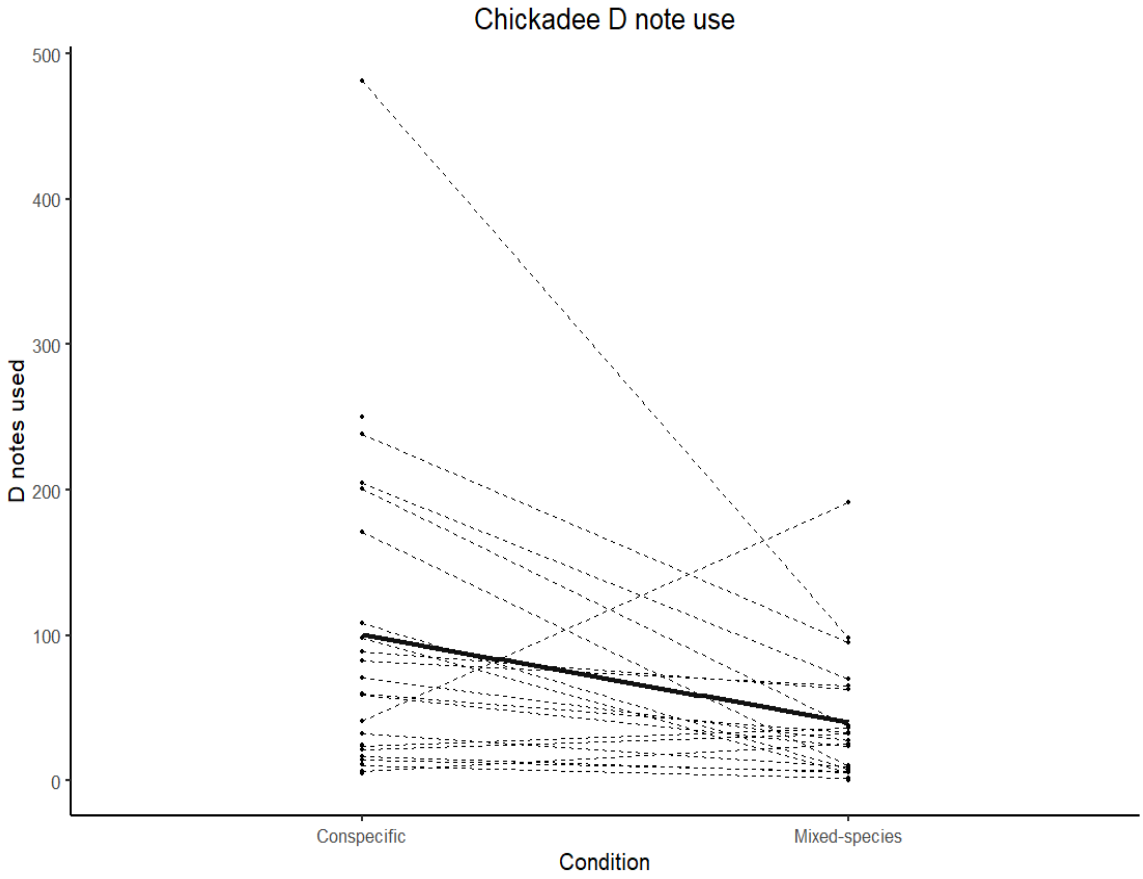

Figure 3.4. Average number of D notes used across social conditions. Black dashed lines are individual chickadees. The solid black line indicates the population average.

Table 3.3. Call type use between conditions. The top ten call types used by each species per condition, and the frequency that the species used that call type, in percentage.

	Condition				
	Conspecific			Mixed-species	
Species	**Percent**	**Rank**	**Call type**	**Rank**	**Percent**
Titmice	32.0	1	[*I*][*A*][*D*]	2	24.7
	25.9	2	[D]	1	26.3
	6.2	3	[*B*][*I*][*D*]	6	5.8
	6.1	4	[*B*][D_h]	5	7.6
	6.0	5	[*I*][D_h]	4	9.7
	5.9	6	[*I*][*D*]	3	10.3
	4.6	7	[*A*][*D*]	8	3.4
	3.7	8	[*Z*][*B*][*D*]	16	0.2
	2.7	9	[*Z*][*B*]	18	0.1
	1.6	10	[*Z*][*I*][*D*]	7	4.4
	0.7	14	[*B*][D_h][*D*]	9	1.9
	1.0	12	[*I*][D_h][*D*]	10	1.3
Chickadees	46.0	1	[*I*][*D*]	1	38.7
	28.2	2	[*I*][*C*][*D*]	2	29.1
	11.9	3	[*I*]	3	18.2
	4.2	4	[*D*]	5	2.3
	3.2	5	[*I*][D_h][*D*]	6	1.9
	2.5	6	[*I*][*C*]	4	6.0
	1.5	7	[D_h][*D*]	9	0.5
	1.1	8	[*C*][*D*]	8	1.2
	0.4	9	[*C*]	7	1.5
	0.3	10	[*I*][*D*][*I*][*D*]	12	0.1
	0.1	12	[*I*][*D*][*I*]	10	0.2

CI = 0.210–0.588, $p < 0.0001$), as were [*I*][*D*] calls ($R = 0.472 \pm 0.124$, 95% CI = 0.183–0.648, $p < 0.0001$), [*I*][D_h] calls ($R = 0.517 \pm 0.135$, 95% CI = 0.172–0.684, $p < 0.0001$), [*B*][D_h] calls ($R = 0.580 \pm 0.146$, 95% CI = 0.152–0.732, $p < 0.0001$), and [*D*] calls ($R = 0.684 \pm 0.108$, 95% CI = 0.391–0.812, $p < 0.0001$).

The one-way ANOVAs indicated that the social condition did not significantly influence the proportion that titmice use [*I*][*A*][*D*] calls ($X^2 = 2.13$, $p = 0.14$), [*I*][D_h calls ($X^2 = 0.685$, $p = 0.41$), [*B*][D_h] calls ($X^2 = 0.504$, $p = 0.48$), and [*D*] calls ($X^2 = 0.183$, $p = 0.67$). The proportion of [*I*][*D*] calls used appeared to be influenced to flock composition, ($X^2 = 3.93$, $p = 0.047$), but was rejected after correcting for multiple comparisons with the Benjamini-Hochberg Correction (1995).

The top five chickadee call types were [*I*][*D*] calls (2,264 calls, 43.6%), [*I*][*C*][*D*] calls (1,480 calls; 28.5%), [*I*] calls (725 calls, 14.0%), [*I*][*C*] calls (191 calls; 3.7%), and [*D*] calls (187 calls; 3.6%). These call types were the same between conditions, except birds used more [*I*][D_h][*D*] calls (113 calls; 3.2%) than [*I*][*C*] calls (89 calls, 2.5%) in the conspecific condition. See **Table 3.3** for the top ten calls per condition. [*I*][*C*][*D*] calls ($R = 0.757 \pm 0.085$, 95% CI = 0.544–0.863, $p < 0.0001$) and [*I*] calls ($R = 0.604 \pm 0.107$, 95% CI = 0.351–0.758, $p < 0.0001$) were highly repeatable, and [*I*][*D*] calls ($R = 0.404 \pm 0.091$, 95% CI = 0.193–0.551, $p < 0.0001$) were moderately repeatable. As in study one, [*I*][*C*] calls and [*D*] calls were also repeatable but include the null hypothesis ($R = 0$) within the confidence interval: [*I*][*C*] calls ($R = 0.439 \pm 0.176$, 95% CI = 0.0–0.635, $p < 0.0001$), [*D*] calls ($R = 0.384 \pm 0.169$, 95% CI = 0.0–0.573, $p < 0.0001$).

For chickadees, the proportion of [*D*] calls ($X^2 = 0.844$, $p = 0.36$) and [*I*][*C*][*D*] calls ($X^2 = 1.28$, $p = 0.26$) were not related to flock composition. The proportion of [*I*] calls was not significant at 0.05, but trended towards significance ($X^2 = 3.80$, $p = 0.051$). Lastly, the proportion of [*I*][*D*] calls ($X^2 = 10.79$, $p = 0.001$) and [*I*][*C*] calls ($X^2 = 5.66$, $p = 0.017$) significantly differed across social condition. After correcting for multiple comparisons, only the use of [*I*][*D*] calls were significantly different across social context. Individual chickadees were more likely to use the [*I*][*D*] calls when in conspecific pairs (M = 15.02 calls per day) rather than in the mixed-species groups (M = 7.47 calls per day).

Uncertainty and diversity index. Zero-order uncertainty was repeatable for both species (titmice, 0.657 ± 0.134, 95% CI = 0.324–0.843, $p = 0.00099$; chickadees, 0.670 ± 0.136, 95% CI = 0.336–0.866, $p = 0.0018$). In the comparison across conditions, there was a main effect of species ($X^2 = 25.26$, $p < 0.0001$). Social condition was nonsignificant ($X^2 = 0.073$, $p = 0.79$) and there was no significant interaction ($X^2 = 0.167$, $p = 0.68$). Titmice had greater uncertainty in their calls than chickadees (titmice, M = 1.57; chickadees, M = 1.23).

The daily diversity index across both social conditions was repeatable for both titmice ($R = 0.490 \pm 0.092$, 95% CI = 0.279–0.645, $p < 0.0001$) and chickadees ($R = 0.413 \pm 0.089$, 95% CI = 0.225–0.576, $p < 0.0001$). After comparing the relationship between species, condition, and diversity index with a GLM, there was only a main effect of species ($X^2 = 45.32$, $p < 0.0001$). Social condition had no effect ($X^2 = 0.837$, $p = 0.36$) and there was no significant interaction term ($X^2 = 0.158$, $p = 0.69$). Titmice had greater diversity in their calls than chickadees (titmice, M = 2.19; chickadees, M = 1.68).

Other behavioral syndromes. Activity level was weakly repeatable across individual across the ten days of observation ($R = 0.385 \pm 0.058$, 95% CI = 0.258–0.484, $p < 0.0001$). Individuals ranged from an average of 26 movements per day to 175 movements per day (titmouse, M = 80 movements per focal sampling period; chickadee, M = 101 movements). For coping strategies under stress, biting was repeatable within an individual ($R = 0.498 \pm 0.138$, 95% CI = 0.162–0.682, $p < 0.0001$) and the proportion of D notes used in the distress call was highly repeatable ($ICC = 0.999$, 95% CI = 0.618–1.00). Nineteen birds bit every time they were recording during handling (11 titmice, 8 chickadees), and 11 birds never bit at all (6 chickadees, 5 titmice). Separately, most chickadees never called at all during handling (N = 22 birds), whereas all but one titmouse called, and the average number of notes used ranged from 4 per minute to 83 per minute. Within those calls, no chickadees used *D* notes, and titmice ranged from zero *D* notes in their calls to almost entirely *D* notes (97 percent of the call). Lastly, during the exploration assay, 19 birds explored all 12 regions of the novel environment within a five-minute interval (300 seconds). The fastest of these individuals visited each area after 80 seconds in the arena. Twenty-nine birds did not explore all designated areas before the

end of the trial. Of these, twelve birds visited all but one of the locations (11/12 locations). Sixteen birds had two or more locations left to explore by the end of the trial, with the slowest explorers only visiting half of the enclosure before time ran out (6/12 locations).

These behavioral scores were averaged across all days and used in GLMs to understand the relationship with the birds' communicative behavior. None of the variables were related to the measured behavioral syndromes. See **Table A-3** for the results of the titmouse models and **Table A-4** for the results of the chickadee models.

Discussion

The results of this not only replicated the results of study one but also indicate that much of a bird's communicative behavior is relatively consistent across different social contexts. Hypothesis 1_A predicted that calling behavior would be correlated across social conditions and this was supported by these results. All titmouse call characteristics were repeatable and consistent across the two social conditions. Chickadees were mostly repeatable and consistent, but some call characteristics like the D_h notes were not. The way that repeatability was calculated here requires individuals to have a smaller variance in behavior than the population level variance. A lack of repeatability could be due to either individuals having a great deal of variation or all individuals doing the same thing. Hypothesis 1_B, predicting calling behavior would be correlated with other behavior syndromes was not supported.

A few results applied to both species. First, titmice call more than chickadees regardless of condition, and the average number of calls for chickadees in the mixed-species group was lower than the conspecific condition. These findings lend support to the audience effect hypothesis proposed for these mixed-species flocks (Coppinger et al., 2020). Second, chickadees also had a lower diversity index score and lower zero-order uncertainty than titmice. Perhaps chickadees are including less information in their call and note use. A more likely alternative is that this result is due to the coding schemes used for the two species. Titmice had six possible note types and chickadees had four note types. Future research should examine the diversity of these calls when there are equal categories to remove the potential confounding factor.

Tufted titmice. Titmouse call rate, note use, call type, and call complexity were all repeatable within individual birds. These call characteristics also did not significantly differ between conspecific pairs and mixed-species groups. This differed slightly from study one where some call characteristics were not repeatable, such as the use of *B* and *Z* notes. [*B*][*I*][*D*] and [*I*][*D*] calls in the first study were also not repeatable. [*B*][*I*][*D*] calls were used less frequently by the birds in this study and did not make the top five call types overall. In contrast, [*I*][*D*] calls were in the top five and were repeatable and consistent in across conditions, though the consistency across context was near statistical significance. This is likely because [*I*][*D*] calls were the third most common call type in the mixed-species condition but only the sixth most common in the conspecific condition. [*B*][*I*][*D*] calls were used in opposite ways, as the sixth most common call type in the mixed-species condition and the third most common in the conspecific condition. The use of these longer intro note types, *Z* and *B*, are less common than the use of the shorter note types, *I* and *A*. Repeatability will be poorer for notes that are rarer because the overall population variability is small. These notes may have been more repeatable during the second study due to the larger sample size. Alternatively, the few birds that do use *Z* and *B* notes may be using these calls more under certain contexts, such as when flock sizes are smaller or when only with conspecifics. Previous work on the function of titmouse notes suggests that longer note types may be correlated with fear or the sex of the bird (Branch & Freeberg, 2012; Freeberg & Branch, 2013). Future research should continue to examine the relationship between social grouping, group size, and the use of long introductory notes. Researchers should particularly look at the use of [*B*][*I*][*D*] calls and [*I*][*D*] calls in these contexts.

Carolina chickadees. While many of the chickadee call characteristics were repeatable and consistent across condition like the titmouse calls, several of the note types and call types were not repeatable or were inconsistent. Across both study one and study two [*I*][*C*] calls and [*D*] calls were not repeatable within an individual. Chickadees used these two call types much less frequently than the more common call types like [*I*][*C*][*D*], potentially leading to a lack of repeatability if most individuals are behaving the same way (by not using these calls). Likewise, D_h notes were not repeatable for

chickadees, but very few birds use these notes, as seen in study one. The other call types and note types that are more common are more repeatable.

The use of [*I*][*D*] calls, while relatively repeatable within an individual, were not used consistently across the different social conditions. Chickadees used more [*I*][*D*] calls in the conspecific pairs than in the mixed-species groups. Similarly, *D* notes were repeatable, but more *D* notes were used during the conspecific condition than the mixed-species condition. These findings imply that some birds tend to use more *D* notes or [*I*][*D*] calls than others. Birds that use more of these calls in the conspecific condition also used more of these calls in the mixed-species condition, relative to birds who rarely used these calls. However, even though the birds' behavior is consistent relative to other individuals, the actual number of calls per individual differs between conditions. *D* notes in chickadees are thought to be used to get attention from flockmates (Courter & Ritchison, 2010; Landsborough et al., 2019). It is possible that birds are using more of these *D* notes in the conspecific pairs to attract more flockmates, including potentially heterospecific flockmates specifically because there are no other species in their flocks. Over wintering periods, including when this study was conducted, chickadees act as nuclear species driving mixed-species flocking (Morse, 1970; Contreras & Sieving, 2011). In East Tennessee, the mixed-species flocks have an average of about five birds, ranging between two and seventeen birds depending on the number of satellite species (Brooks & Freeberg, 2024; Freeberg et al., 2024). If *D* notes were used in this context to form the flocks and attract other individuals, it is not surprising that the larger, more diverse flocks in the mixed-species condition would use fewer of these notes. [*I*][*D*] calls could be associated with an increase in *D* notes in general or perhaps these calls are important for communicating between conspecifics in general. More work should be done to understand the relationship between [*I*][*D*] calls and flock size or composition, as well as *D* note use in these contexts.

Other behavioral syndromes. The lack of a relationship between calling behavior and the measured behavioral syndromes was unexpected. The research on parid communication and behavioral syndromes has been primarily done on chickadees and tits (Williams, 2009; Naguib et al., 2016) and less is known about titmouse calls in this

context. However, given the close relationship between these species and the similarity in call system, it would perhaps be expected that titmice would show similar behavioral trends, such as more exploratory birds having higher calling rates (Guillette & Sturdy, 2011). On the other hand, there are known species differences in behavior that may be reflected here. For example, titmice are often more passive than chickadees in risky situations (Nolan & Lucas, 2009). However, the relative lack of prior research into titmouse behavioral syndromes and how they differ from other parid species does not explain why chickadee calling behavior in this study does not align with previous findings from other studies.

Other reasons why the calls might not be correlated with the behavioral syndromes as expected could be that the behavioral measurements were taken in more naturalistic settings or because of differences in the methodology. Many of these prior studies on behavioral syndromes took place in a laboratory setting with greater control over the environment and used fewer observations to calculate behavioral scores. As research into behavioral syndromes like exploration and bold-shy becomes more prevalent, it is likely that researchers will use a single assay to approximate the behavioral types (Niemelä & Dingemanse, 2018). These single measures can be risky, however, if they assume that a single day is a true representation of the individual's average behavior (Dingemanse & Wright, 2020). I calculated the behavioral scores for coping strategy and activity by averaging several days together and used one assay for exploration. It is possible that the single assays or behavioral scores in this study or other studies are not representative of the true behavior and that is why some studies find a significant relationship and others find no relationship. More research should be done on calling behavior and the potential correlation, or lack thereof, with other behavioral syndromes to understand these relationships further. Another direction that would be beneficial would be to examine calling behavior with other behavioral syndromes not studied here, including the popular bold-shy syndrome.

Broader implications. The results of this study continue to support the possibility of a behavioral syndrome in communicative behavior in these species. Previous work on the repeatability of communication has focused primarily on how call rate is correlated

with other known behavioral syndromes in a variety of species (e.g., crickets, Wilson et al., 2010; bats, Schabacker et al., 2024), but few studies have considered communication as a standalone syndrome. Likewise, in human personality research, patterns in communication are often categorized as part of extraversion (Goldberg, 1990). However, this may be shortsighted if communication is not always explained by other behavioral syndromes, as was found in the current study. What may originally have been thought of as a subcomponent of one behavioral syndrome could also be a separate correlated behavioral syndrome. As seen with exploration and boldness, combining behavioral syndromes may confound results and make it more difficult to examine interspecific differences in behavior (Carter et al., 2012; Padovani et al., 2020).

It is important to continue to explore the repeatability of these behaviors and how they may or may not relate to other behavioral types not only in chickadees and titmice, but also in a variety of other taxa and communication modalities. Much of communication literature focuses on acoustic communication, however other modalities are also widely used, including visual, chemical, and vibrational communication (Bradbury & Vehrencamp, 1998). Many species also produce signals in two or more modalities, including the parid species studied here. For example, tufted titmice are primarily known for communicating through their acoustic *chick-a-dee* signals, but they also appear to use their eponymous tufts, or crests, to communicate visually (Smith, 2007; Borger, 2020). An exciting question to explore would be whether the acoustic behavioral trends correlate with communicative behaviors in other modalities within the same individual or species. Lastly, it is also critical to continue to explore the relationship between communication behavior and other individual-level characteristics that are not behavioral syndromes, such as dominance status or physiological condition. Pursuing these research directions would provide valuable insight into communicative and social behavior.

Conclusion

Chickadees and titmice have versatile calling systems that allow these species to vary their calls based on the social and environmental context. Despite this flexibility, the results of this study suggest that individuals in these species tend to use call

characteristics (such as call rate, note use, call type, and call complexity) differently from one another and that these differences are relatively consistent in various social groupings. The other notable finding is that these call characteristics did not correlate with other behavioral syndromes like activity level, exploratory behavior, or coping behavior under stress. These results—repeatability across contexts and a lack of correlation with other syndromes—suggest that communication should be viewed as a novel behavioral syndrome separate from other currently studied syndromes. Next steps are to examine whether these repeatable call characteristics are correlated with other individual statuses or traits such as dominance. Chapter four attempts to answer this question by comparing note use, call type, call rate, and call complexity with each bird's dominance status.

CHAPTER FOUR
COMMUNICATION AND DOMINANCE STATUS

Abstract

Many animals live in dominance hierarchies that determine the outcome of their social interactions. Dominance status can also affect how an animal communicates with other members in its group. In this study, I examined how the call characteristics of Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) are related to dominance status. To do this, I combined the acoustic sampling data from study one and study two. I also calculated each bird's dominance status with a randomized Elo-score based on the number of dominance interactions that the bird was involved in. Dominance interactions were recorded verbally during audio recording and visually by video recording at the feeding platforms in each aviary where a high-quality resource was available in limited quantity. These dominance interactions included behaviors like chasing and supplanting (or being chased and supplanted). I used these scores as predictors in generalized linear models (GLMs). The dependent variables were the call characteristics that were found to be repeatable in the first two studies (call rate, zero-order uncertainty, diversity index, call type, and note use). I also used the subset of birds from study two to examine the potential interaction between dominance rank and social condition on communicative behavior. Titmice had more call characteristics associated with dominance rank than chickadees. Compared to subordinates, dominant titmice called more and used more *D* notes, *I* notes, and *B* notes. Dominant titmice also used more [*D*] calls than subordinate titmice. Lower ranked titmice use more [*I*][*A*][*D*] calls, [*I*][D_h] calls, and had greater complexity (diversity index and zero-order uncertainty) in their calls than dominant titmice. Chickadee calls were not related to dominance status other than call rate: dominant chickadees called more than subordinates. While dominance appears to be an important factor for calling behavior, especially in titmice, it did not fully explain the behavioral patterns seen in this study and in the previous studies. There may be other underlying traits, such as a behavioral type or syndrome, that help explain these patterns.

Introduction

Animals often change their communicative behavior based on the identity of the individuals they interact with, including familiarity with that individual (Ferkin, 1988; Coppinger et al., 2019), the sex (Nakamichi, 1989; Slater et al., 2009), or the species (Vander Meiden et al., 2023). Another major influence on social interactions is an individual's relative dominance status. Dominance has historically been considered both part of personality (Gosling & John, 1999) and a separate temporary status that is determined by behavioral traits such as aggression or boldness (Snijders et al., 2017). This conflict in the definition of dominance has led to a lack of clarity in the animal personality literature. For this study, dominance will not be considered a personality trait, however there is a growing literature that looks for correlations between behavioral traits (like exploration or boldness) and relative dominance status (Dingemanse & da Goede, 2004; Jolles et al., 2013). Behavioral traits may be correlated (Arakawa, 2006; Favati et al., 2014; Snijders et al., 2017) or not correlated with status (Devost et al., 2016; Portugal et al., 2017). The current study adds to the literature comparing dominance within groups to behavioral syndromes.

Dominance within a group is often depicted as a linear hierarchy that is mostly stable once formed, and the animals at the top of the hierarchy (i.e., dominant) have greater access to resources and territory than those at the bottom of the hierarchy (Schjelderup-Ebbe, 1975; Wagner & Gauthreaux, 1990; Krams et al., 2020). Dominance interacts with sex, species, and familiarity to determine the social interactions between individuals in complex groups, including mixed-species groups (Wittemyer & Getz, 2007; Surbeck & Hohmann, 2013; Rabinowicz et al., 2020; Coppinger et al., 2023). Hierarchies can range from strongly linear with rigid rankings to hierarchies where individuals frequently experience challenges and rank changes (Boehm, 1993; Kavanagh et al., 2021; Blersch et al., 2024). Within these two extremes exists a spectrum of intermediate hierarchies, and behavior is sensitive to the various gradations in structure (Strauss et al., 2022).

Communicative behaviors are no exception, and there is a growing understanding of how communication is affected by dominance status. In many species there are often

calls that are used primarily in a dominance context, such as appeasement calls or aggressive displays (Bradbury & Vehrencamp, 1998). Calling characteristics, including the types of calls, are often correlated with the rank of the signaler. Across species, dominant individuals may call more or use more of certain note types (Bolt, 2013; Massey-Abernathy & Haseltine, 2019). In addition, the use of these calls can be also determined by the rank of the dyadic partner. For example, common ravens (*Corvus corax*) use more defensive calls when in an antagonistic encounter with a higher-ranking individual, and the most calls are used when the difference in relative rank between the dyad members is very large (Szipl et al., 2017). Lastly, the information produced by dominant individuals may be viewed as more valuable than the calls from subordinate individuals. The calls of subordinate dwarf mongooses (*Helogale parvula*) acting as sentinels are treated as less trustworthy than dominant sentinels, leading to increased vigilance when subordinate sentinels are calling (Kern et al., 2016). However, while these findings are common patterns of behavior, the interactions between dominance and communication can be species specific. It is important to understand the unique behavioral repertoire of the study species before examining dominance hierarchies.

In the family Paridae, larger birds are often dominant to smaller birds within and between species (Morse, 1978; Hogstad, 1989). These larger, more dominant individuals may suppress the calls of subordinates, a type of audience effect (Coppinger et al., 2020). Other audience effects in parids include birds using different calls and strategies depending on the status of potential competitors (Møller, 1987; Freeberg, 2006; Suzuki & Kutsukake, 2017) or birds altering the number of vocalizations used depending on the perceived audience (Bai et al., 2021). Some vocalizations in the parid repertoire are used almost exclusively for agonistic dominance interactions, such as the chickadee *gargle* call (Ratcliffe et al., 2007). Still, less is known about the effects of dominance on the *chick-a-dee* call itself, and how dominance interacts with communication in mixed-species groups (Coppinger et al., 2020).

In this study, I compared the calling behavior of captive Carolina chickadees (*Poecile carolinensis)* and tufted titmice (*Baeolophus bicolor*) in the context of their relative dominance status. The purpose of this study was to explore potential links

between the communication syndrome found in the first two studies with dominance status, especially after some findings from study one suggested a potential relationship between dominance and calling behavior. The birds in this study were aggregated from study one (conspecific pairs) and study two (conspecific pairs and mixed-species groups). In the dyadic conspecific flocks, calling behavior was compared between high- and low-status individuals. In the mixed-species flocks, I examined whether communicative behavior was graded from most dominant to most subordinate. The individuals from study two were measured in both conspecific and mixed-species social contexts. This subset of birds was used to examine whether a change in relative dominance rank altered communication. I measured the dominance hierarchies of each flock by calculating an Elo-rating for each bird.

H_1: Calling behavior is correlated with dominance status.

If calling behavior is correlated with dominance status, then birds with high social status will call in different ways from birds with low social status. If these birds follow trends in other species, the birds that are high status will call more than low-ranking birds (Krams, 2000; Kondo & Hiraiwa-Hasegawa, 2015). There may also be a difference in the types of calls that these birds use, for example, high status individuals could use more *D* notes, or low status birds could have lower complexity in their calls. In study one, the results of the chickadee PCA suggested that there could be an interaction between dominance status and sex for zero-order uncertainty (see **Figure 2.8** in Chapter Two).

H_2: A change in relative dominance status erodes patterns in communication.

If a change in dominance status erodes behavioral syndromes, as found in Rudin et al. (2017), then calling behavior will change if the relative status of the individual changes. The birds from study two experienced a change in social condition between mixed-species groups and conspecific pairs. Titmice are typically dominant to chickadees (Hogstad, 1989), so it is expected that the hierarchy in the mixed-species group will have one titmouse that is the most dominant and one chickadee as the most subordinate. There will be one subdominant titmouse, likely ranked second, and one subdominant chickadee, likely ranked third. There is also a potential for a very dominant chickadee to occasionally outrank a very subordinate titmouse, regardless of body size. In the

conspecific pairs, there will be one individual with a higher status than its partner. Parids tend to have stable hierarchies (Ratcliffe et al., 2007), so it is predicted that the relative order of the hierarchy will not change between conditions because these birds are all familiar with one another and are coming from the same natural flock.

When switching conditions, I expect the lower ranked chickadee will remain the lowest ranked individual in the flock and the highest ranked titmouse will remain the highest ranked individual. The two intermediate individuals will likely experience more of a status change between social conditions because the lower ranked titmouse would, presumably, no longer be the lowest ranked individual in the group, and the highest ranked chickadee would not be the highest ranked. If the findings from Rudin et al. (2017) hold true for a communication behavioral syndrome, then animals that experience no change in relative status (such as the highest and lowest ranked birds) would have more stable communication behavior than the intermediately ranked birds that experience a change in status.

H_0: Calling behavior is not related to dominance status.

If there is no relationship between dominance status and calling, then dominant and subordinate birds will not differ in their calling behavior. For example, the dominant titmouse would have roughly the same call rate as the subordinate titmouse. This lack of relationship could occur if dominance is not reflected in the *chick-a-dee* calls, but rather in other call types such as the *gargle* call that is often tied to aggression (Ficken et al., 1987). Dominance could also be communicated via other modalities like body language (visual communication). Titmice are able to raise and lower the crest on the top of their heads and the crests and their relative angles have been found to be correlated with dominance status (Queller & Murphy, 2017).

Methods

Subjects and housing

All individuals from studies one and two were included in this study. Conspecific pairs of chickadees and titmice were captured from permanent feeder sites across two overwintering periods—October 2023 to March 2024 and October 2024 to March 2025—at the University of Tennessee Forest Resources, AgResearch, and Education Center

(UTFRREC) in Oak Ridge, Tennessee. All birds were caught in size-matched conspecific pairs. For the second study chickadees must have been within a 2 mm wing chord difference to be considered size-matched, and the larger titmice needed to be within 3 mm wing chord difference to be size-matched. The birds in the first study were sex matched, which was similarly based on wing chord measurements but more restrictive on potential pairings. All titmouse pairs and all but two of the chickadee pairs in the first study also met the requirements for inclusion in the second study. The two exceptions were a pair of female chickadees (59 mm and 55 mm wing chords), and a pair of male chickadees (62 mm and 65 mm wing chords).

When two usable conspecific birds were caught within 30 minutes of each other, they were transported to one of six nearby semi-naturalistic, outdoor aviaries that measure approximately 6 m × 9 m × 3.5 m. Conspecific pairs were also used during the mixed-species condition in study two, but instead of one pair per aviary, one pair of chickadees and one pair of titmice were placed in the same aviary. All aviaries had a covered indoor section that the birds could use as shelter, as well as several natural and naturalistic perches with vegetative cover for the birds. The aviaries were kept stocked with ad libitum black oil and safflower seed, fresh water, and the birds were provided with mealworms approximately every day.

Once captured, birds were placed into aviaries as either conspecific pairs (study one and study two) or a four-bird mixed-species flock (study two). In study two, five flocks started as conspecific pairs and seven flocks started as mixed-species flocks. All birds housed in the aviaries were kept for a minimum of nine days. Study two birds were housed for a minimum of 15 days, and some flocks were kept longer if weather conditions delayed data collection. Each flock was given a minimum of four days for acclimation to the aviary. The first day after capture the birds were left alone, and then for three subsequent days I replicated the procedure to acclimate the birds to all components of the observational study (i.e., equipment was set up and I occasionally spoke aloud for approximately 35 minutes). Audio data was collected on each bird for the remaining five or ten days depending on the study, including ten minutes of focal sampling and fifteen minutes of all-occurrence sampling of the whole flock each day.

Video sampling occurred daily after the audio samples had been collected. After all observations for each flock were completed, the birds were recaptured using baited treadle traps in the aviaries, weighed, and released at their original site of capture.

Procedure

Aviaries were fitted with mock cameras to acclimate the birds to the presence of a camera near the feeding platform. These mock cameras were made out of Styrofoam and painted to look like an active GoPro camera (**Figure A-10**). These models were permanently installed throughout the overwintering period using a GoPro Flexible Grip Mount approximately 0.5 m away from the ad libitum food source. When starting the video sampling, the model cameras were swapped with a GoPro Hero11 Black camera (See **Figure A-11** for an example of the recording setup).

Video recordings occurred on the same day as the audio recordings from study one and two (See **Table 4.1** for a schedule of the daily data sampling). Once audio sampling started, any dominance interactions that occurred during the sampling period, including the individuals involved and the direction of antagonism, were verbally described. These descriptions were captured on the audio recordings and were coded at the time of the data analyses from study one and two. After the audio sampling finished, I removed the audio recording equipment from the aviary and installed the GoPro on the mount. At this time, the flocks were also provided with a limited number of live giant mealworms (approximately five for flocks of two and approximately ten for flocks of four). Mealworms were presented to the birds in a small, transparent glass bowl with no covering. Once the mealworms were prepared, the GoPro was turned on and I left the aviary to reduce observer effects. The birds were recorded for a minimum of 30 minutes and any uneaten mealworms were removed from the aviary.

Because video recordings were taken immediately after audio sampling procedures, birds in study one were recorded for five days, with a minimum of 150 minutes of video data per conspecific pair. In study two, birds were recorded for ten days (five in conspecific flocks and five in mixed-species flocks), with a minimum of 450 minutes of video data per set of four birds. Verbal descriptions of dominance interactions were aggregated with video observations to create a dominance dataset.

Table 4.1. Daily data collection procedure. This is the procedure that each day of data sampling followed across all studies.

Time	Operational definition
Before audio collection	Set up audio equipment
10 minutes	Focal audio sample bird one
10 minutes	Focal audio sample bird two
10 minutes	Focal audio sample bird three (if applicable)
10 minutes	Focal audio sample bird four (if applicable)
15 minutes	All occurrence audio sampling of all birds
After audio collection	Remove audio equipment; place mealworms and camera
30 minutes	Video recording behavior; human absent
After video collection	Remove camera and mealworms; place model camera

Video analyses

Video analyses were conducted in Boris (v 8.25.4; Friard & Gamba, 2016). I recorded all dyadic dominance interactions visible on camera, including supplants, chases, evades, and flees. The recorded interactions primarily took place on or near the feeding platform because it was difficult to ascertain bird identity at greater distances. I also recorded when any of the birds took one of the provided food types: mealworms or seeds. See **Table 4.2** for the ethogram used during video coding.

Call analysis and note classification

Audio data were initially coded and analyzed in study one and two. Calls were manually classified within the spectral view window (Blackman-Harris windowing function at a resolution of 256 bands) in CoolEdit Pro, version 2 (Syntrillium Software, Scottsdale, AZ, USA. There were four introductory note categories for titmice, including *A*, *I*, *B*, and *Z*, in order of increasing duration. *A* notes were defined as notes that are less than 75 msec in duration. *I* notes had durations between 75 msec and 144 msec. *B* notes were between 145 msec and 214 msec in duration. *Z* notes had durations of 215 msec or greater. Also included were *D* notes, broad-frequency notes with a harmonic-like structure, and D_h notes, hybrid notes that transition from introductory note to *D* note. For chickadees, I condensed all introductory note categories into a single whistle note category, *I*. I also included structurally complex *C* notes, broad-frequency *D* notes, and D_h hybrid notes that transition from an introductory whistle note to *D* note. See Chapter 2, **Figure 2.1** for spectrograms of titmouse calls and **Figure 2.2** for spectrograms of chickadee calls.

Statistical analyses

To calculate the dominance scores for the birds, I used the randomized Elo-rating method in the *aniDom* R package (version 0.1.5; Farine & Sánchez-Tójar, 2022). I used this method because Elo-ratings are less sensitive to small sample sizes. All birds were initially assigned a predefined point rating, and then the bird's rating increased or decreased based on the outcome of the observed interactions and whether the outcome was expected (Neumann et al., 2011). For instance, higher ranked individuals are expected to win an interaction against lower ranked individuals, and reversals result in a

Table 4.2. Dominance ethogram. This ethogram describes the dominant and subordinate behaviors that were coded in the video data in study three. Behaviors with * indicate behavioral states.

Code	Behavior	Operational definition
1	Present*	The subject is standing, walking, hopping on the platform or flying within approximately six inches over the feeding platform.
2	Absent*	The subject is not on or above the feeding platform and is either flying or perched on another surface
3	Seed	The subject takes a seed
4	Mealworm	The subject takes a mealworm
5	Chasing*	The subject is chasing another bird in flight
6	Chased*	The subject is being chased by another bird in flight
7	Supplant	The subject has supplanted another bird, replacing the bird in its exact location and the supplanted bird leaves within two seconds of the subject landing
8	Evade	The subject has been supplanted or another bird lands nearby and the subject immediately hops or flies to another location on the feeding platform
9	Flee	The subject has been supplanted or another bird lands nearby and the subject immediately flies off, away from the feeding platform

loss of points for the higher ranked individual and an increase of points for the lower-ranked individual. In the rare case of a tied hierarchy, Elo-rating also allows for tied outcomes (Neumann et al., 2011). The randomized component of this Elo-rating method accounts for any temporal biases in the data and can account for uncertainty in the hierarchy. The latter is done by dividing the data into two halves and calculating the Spearman rank correlation coefficient between the halves (Sánchez-Tójar et al., 2018). This randomization is important because the dominance data used in this study was collected over two overwintering periods (late fall into early spring) leading to likely temporal and seasonal impacts on behavior.

After calculating the dominance ranks, I used GLMs in the *base* package to examine how the dominance relationships in the flock correlate with the calling behavior (rate and note type usage) of all individuals in the flocks. In the models, the rankings of each bird and the species were used as predictors. I used the Akaike information criterion (AIC) to reduce the full model, if necessary. For the primary analyses, only the hierarchies from the conspecific pairs were used to ensure that the samples from study one and study two are comparable. I used the mixed-species hierarchy information to examine the impact of a changing dominance status due to differing social conditions for the birds from study two. To do this, I created GLM models that used the rank of the birds and the social condition as predictors for calling behavior. I corrected for multiple comparisons with the Benjamini-Hochberg Correction (1995). Tukey's Honestly Significant Difference (HSD) tests were used for significant main effects and I used marginal means in the *emmeans* package (version 1.11.0; Lenth, 2025) to examine any significant interaction terms.

Animal use statement

I have adhered to all applicable institutional, national, and international guidelines for the use of animals. This study was conducted under protocols approved by the University of Tennessee Institutional Animal Care and Use Committee (#1248 and #1326). Birds were collected and banded under US Fish and Wildlife Service scientific collecting permit (#SCCL-065321) and the US Geological Survey bird banding laboratory permit (#23253).

Results

The final sample of birds used in this study was 84 birds (40 chickadees and 44 titmice; two chickadees and two titmice were used in both studies). Six chickadee flocks (12 birds) and four titmouse flocks (eight birds) from study one did not have any visible dominance interactions during audio sampling or video recordings. Additionally, one bird from study two died during the flock reconfiguration (on approximately day ten). This bird and its conspecific partner also did not have a known dominance relationship, leaving 62 birds with a known dominance hierarchy.

Conspecific dyads. There was a significant interaction between species and rank for call rate ($X^2 = 11.89$, $p = 0.0005$). Titmice (M = 26.1 calls per day) per called more than chickadees (M = 17.9 calls per day). I separated the species into separate models to examine the relationship between rank and calling behavior. The Tukey HSD post hoc tests indicate that in titmice, dominant birds (Rank 1, M = 42.3 calls per day) called more than subordinate birds (Rank 2, M = 7.51 calls per day, $p < 0.0001$). In chickadees, dominant birds (Rank 1, M = 23.8 calls per day) called more than subordinate birds (Rank 2, M = 15.1 calls per day, $p = 0.023$). See **Figure 4.1** for the relationship between calling, rank, and species.

I adjusted the analyses of the note use per day to avoid confounding birds that use a particular note type more often with birds that call more in general. To do this, I divided the total number of notes for each note type by the total number of calls per day, per bird, to find the average number of notes used per call each day. Titmouse *B* notes ($X^2 = 9.25$, $p = 0.002$) and *I* notes ($X^2 = 37.90$, $p < 0.0001$), *A* notes ($X^2 = 14.44$, $p = 0.0001$), and *D* notes ($X^2 = 20.68$, $p < 0.0001$) were significantly predicted by dominance rank after adjusting for multiple comparisons with the Benjamini-Hochberg Correction. *Z* notes ($p = 0.051$) and D_h notes ($p = 0.051$) trended towards significance. Dominant birds used more *D* notes (M = 2.14 notes per call per day, $p < 0.0001$) and *B* notes (M = 0.18 notes per call per day, $p = 0.0028$) than subordinate birds (*D* notes, M = 1.13 notes per call per day; *B* notes, M = 0.096 notes per call per day). Subordinate birds used more *I* notes (M = 0.84 notes per call per day, $p < 0.0001$) and *A* notes (M = 0.65 notes per call per day, $p =$

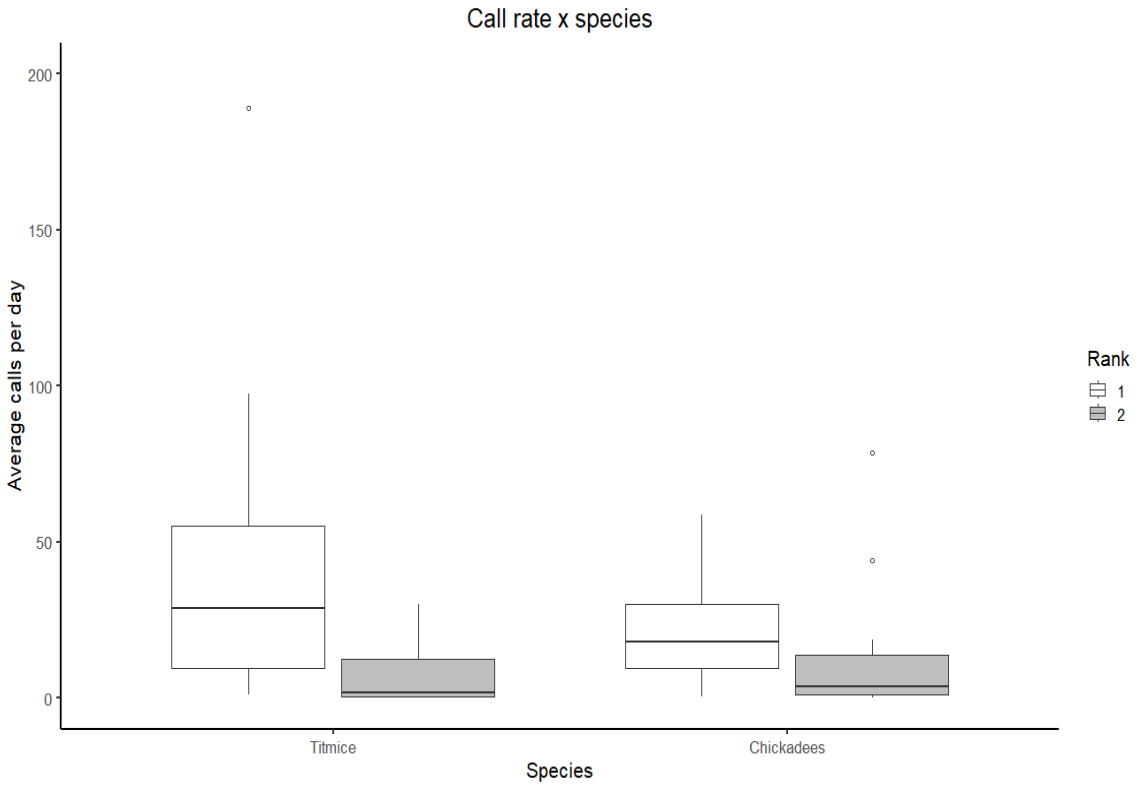

Figure 4.1. Average number of calls per day, per dominance rank, in conspecific pairs. Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents the average number of calls made by the birds with that social rank, including all calls made during the ten-minute focal sampling period and fifteen-minute all-occurrence sampling. White boxes are dominant birds (rank 1), and the gray boxes are subordinate birds (rank 2) based on the conspecific dominance hierarchies. Chickadees were assigned ranks 3 and 4 for the mixed-species condition, keeping the same order. Titmice call significantly more than chickadees and dominants for each species call more than subordinates.

0.0002) than dominant titmice (*I* notes, M = 0.61 notes per call per day; *A* notes, M = 0.44 notes per call per day).

After correcting for multiple comparisons, chickadee *D* note ($X^2 = 6.62$, $p = 0.01$) and *C* note ($X^2 = 5.07$, $p = 0.024$) use were correlated with rank. Dominant chickadees used more *C* notes (M = 0.43 notes per call per day, $p = 0.026$) and *D* notes (M = 2.92 notes per call per day, $p = 0.011$) than subordinates (C notes, M = 0.22 notes per call per day; *D* notes, M = 2.17 notes per call per day).

In the combined audio data from the conspecific pairs in the earlier studies, the top five call types for titmice were [*I*][*A*][*D*] (1,745 calls, 35.0%), [*D*] (1,385 calls, 27.8%), [*B*][D_h] (652 calls, 13.1%), [*B*][*I*][*D*] (506 calls, 10.1%), and [*I*][*D*] (492 calls, 9.9%). In the one-way ANOVAS, [*D*] calls ($X^2 = 27.71$, $p < 0.0001$) and [*I*][*A*][*D*] calls ($X^2 = 26.54$, $p < 0.0001$) were significantly correlated with dominance status. Dominant birds were more likely to use more [*D*] calls (M = 29.7% of calls per day, $p < 0.0001$) and fewer [*I*][*A*][*D*] calls (M = 37.7% of calls per day, $p < 0.0001$) than subordinate birds ([*D*], M = 2.8% of calls per day; [*I*][*A*][*D*], M = 69.3% of calls per day). For the chickadee call type analyses, the top five call types were [*I*][*D*] (1,733 calls, 47.2%), [*I*][*C*][*D*] (907 calls, 24.7%), [*I*] (531 calls, 14.5%), [*D*] (153 calls, 4.2%), and [*I*][D_h][*D*] (114 calls, 3.1%). Dominance status was not related to any of the chickadee call types.

In the models for both zero-order uncertainty and diversity index, there were significant main effects of species (U_0, $X^2 = 6.41$, $p = 0.011$; DI, $X^2 = 4.11$, $p = 0.043$) but no effect of dominance rank and no significant interaction. Titmice had greater zero-order uncertainty (M = 1.5, $p = 0.012$) and diversity index (M = 1.95, $p = 0.046$) scores than chickadees (U_0, M = 1.17; DI, M = 1.66), likely due to difference in the number of notes measured.

Mixed-species groups. For the comparison between flocking condition, I assigned dominance ranks based on the birds' species and conspecific Elo-rating. Out of 56 observed interactions between chickadees and titmice across the experimental flocks, titmice were dominant to chickadees in all of the interactions. Thus, titmice were assigned ranks one and two, and chickadees were assigned ranks three and four based on their relative Elo-score in the conspecific flocks. The number of calls used per day was

significantly related to the dominance status of the bird ($X^2 = 22.87$, $p < 0.0001$) but was not correlated with the social condition ($X^2 = 0.788$, $p = 0.37$) or the interaction between rank and condition ($X^2 = 0.599$, $p = 0.90$). Post hoc tests indicate that the dominant titmouse (rank 1; M = 40.1 calls per day) differed from the subordinate titmouse (rank 2, M = 7.88 calls per day, $p = 0.0002$) and the subordinate chickadee (rank 4, 10.9 calls per day, $p = 0.001$), but was not quite statistically different from the dominant chickadee (rank 3, 21.4 calls per day, $p = 0.07$). Ranks 2, 3, and 4 did not differ from one another (rank 2–rank 3, $p = 0.29$; rank 2–rank 4, $p = 0.98$; rank 3–rank 4, $p = 0.53$). (**Figure 4.2**). The note use analyses were also calculated per call per day, as in the conspecific flock analyses above. After adjusting for multiple comparisons, all titmouse note types were significantly related to relative rank (*Z* notes, $X^2 = 6.29$, $p = 0.012$; *B* notes, $X^2 = 5.72$, $p = 0.017$; *I* notes, $X^2 = 20.21$, $p < 0.0001$; *A* notes, $X^2 = 11.42$, $p = 0.0007$; D_h notes, $X^2 = 10.25$, $p = 0.0013$; *D* notes, $X^2 = 31.18$, $p < 0.0001$), and there was a also significant interaction between rank and condition for *I* notes ($X^2 = 9.04$, $p = 0.0026$). There were no other significant interaction terms and no significant main effects of condition. Dominant titmice used more *Z* notes (M = 0.044 notes per call per day, $p = 0.013$), *B* notes (M = 0.18 notes per call per day, $p = 0.018$) and *D* notes (M = 2.14 notes per call per day, $p < 0.0001$) than subordinate titmice (*Z* notes, M = 0.00 notes per call per day; *B* notes, M = 0.096 notes per call per day; *D* notes, M = 1.13 notes per call per day). Subordinate titmice used more *A* notes (M = 0.65 notes per call per day, $p = 0.0009$) and D_h notes (M = 0.24 notes per call per day, $p = 0.0016$) than dominant birds (*A* notes, M = 0.442 notes per call per day; D_h notes, M = 0.118 notes per call per day). For *I* notes, subordinates used more *I* notes during the conspecific condition (M = 0.94 notes per call per day) than the mixed-species condition (0.73 notes per call per day, $p = 0.032$). Dominant titmice did not differ in the use of *I* notes across condition (conspecific, M = 0.56 notes per call per day; mixed-species, M = 0.66 notes per call per day). In the conspecific condition, subordinates used more *I* notes than dominant titmice ($p < 0.0001$), but the two ranks did not differ from one another in the mixed-species condition ($p = 1.00$). See **Figure 4.3** for the main effect of rank for the titmouse notes. Chickadee note use was not related to the relative rank of the bird.

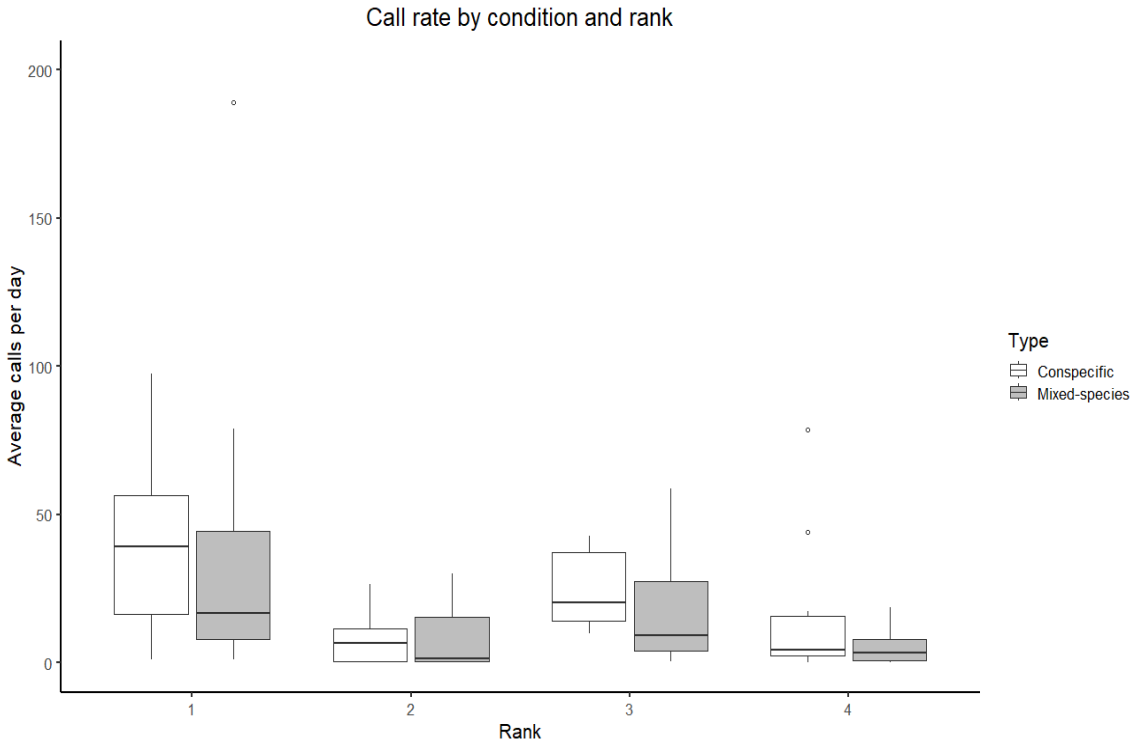

Figure 4.2. Average number of calls per day, per dominance rank, across social conditions. Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents the average number of calls per day. Birds that rank first and second are always titmice. Ranks three and four are chickadees.

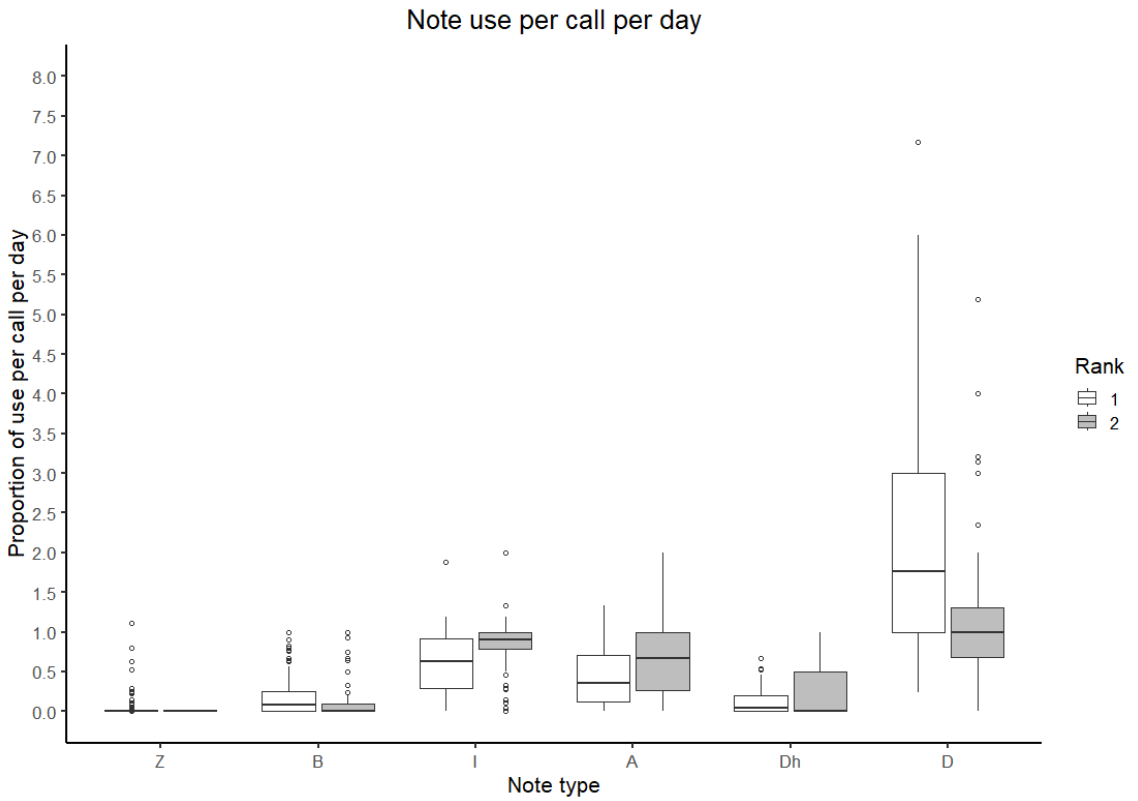

Figure 4.3. The average number of titmouse notes per call, per day by dominance rank. Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents the average number of notes used per call per day. White boxes are the dominant titmouse (rank 1), and the gray boxes are the subordinate titmouse (rank 2). All note types differed significantly between the two ranks.

For call type, I ran all models for the top five call types for both species with the social condition and the bird's rank as predictors. The call types used in these analyses are those found in study two: [*I*][*A*][*D*], [*D*], [*I*][*D*], [*I*][D_h], and [B][D_h]. After correcting for multiple comparisons with the Benjamini-Hochberg Correction, dominance status was correlated with the use of [*I*][*A*][*D*] calls ($X^2 = 7.06$, $p = 0.0078$) and [*I*][D_h] calls ($X^2 = 15.28$, $p < 0.0001$). [*D*] calls were significantly related to a main effect of dominance status ($X^2 = 32.91$, $p < 0.0001$) and the interaction between social condition and dominance ($X^2 = 6.48$, $p = 0.011$). All other predictors in the models were not significantly related to the call types. Lower ranked birds were more likely to use both [*I*][*A*][*D*] calls (M = 56.6% of calls per day, $p = 0.009$) and [*I*][D_h] calls (M = 5.7% of calls per day, $p = 0.0002$) than dominant individuals ([*I*][*A*][*D*], M = 42.2% of calls per day; [*I*][D_h], 16.9% of calls per day). Dominant individuals used more [*D*] calls per day than subordinate individuals in both the conspecific condition (Rank 1, M = 37.9% of calls per day; Rank 2, 1.3% of calls per day, $p < 0.0001$) but not the mixed-species condition (Rank 1, M = 31.4% of calls per day; Rank 2, 17.3% of calls per day, $p = 0.10$). The ranks did not significantly differ between conditions after running the marginal means (which uses a Bonferroni correction for multiple comparisons)(rank 1, $p = 1.0$; rank 2, $p = 0.075$). For chickadees, the top five call types from study two were, in order, [*I*][*D*], [*I*][*C*][*D*], [*I*], [*I*][*C*], and [*D*] calls. No call characteristics were related to social condition or dominance rank after adjusting for multiple comparisons, though [*I*][*D*] calls trended towards significance ($X^2 = 8.40$, $p = 0.0038$, $p_{adj} = 0.056$).

In the models for both zero-order uncertainty and diversity index, there were significant main effects of dominance rank (U_0, $X^2 = 32.90$, $p < 0.0001$; DI, $X^2 = 54.39$, $p < 0.0001$) but no effect of social condition and or interaction. Dominance rank here also reflects species differences. After examining the results via post hoc tests, the subordinate titmice (rank 2; M = 1.69) had greater zero-order uncertainty in their calls than the dominant titmice (rank 1; M = 1.48), and the two chickadees (rank 3, M = 1.28; rank 4, M = 1.16). The dominant titmouse had greater zero-order uncertainty than the two chickadees, but the chickadees did not differ from one another (**Figure 4.4**). The same pattern occurs for diversity index, where the subordinate titmice (rank 2; M = 2.36) has

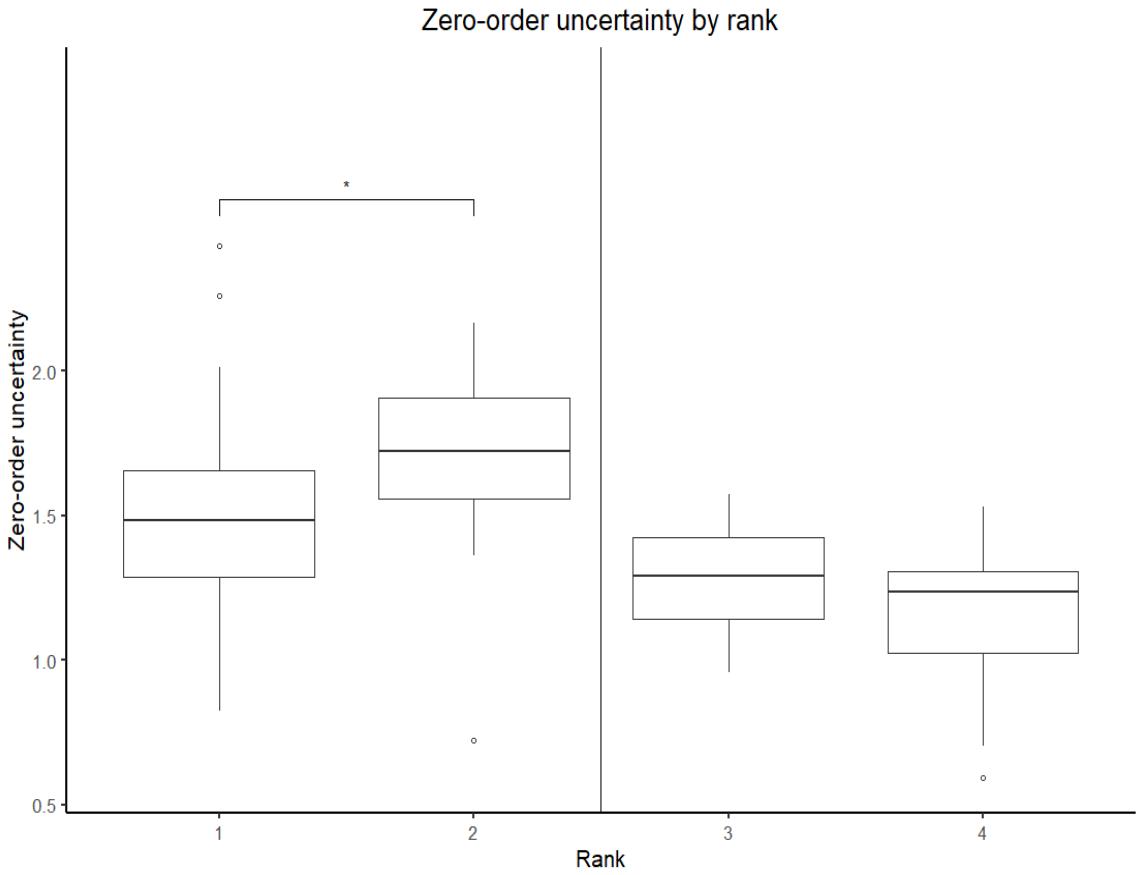

Figure 4.4. Zero-order uncertainty, per dominance rank. Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents the overall zero-order uncertainty for each dominance rank, averaged across condition. Ranks 1 and 2 are titmice and ranks 3 and 4 are chickadees. The brackets at the top indicate significant differences at $p = 0.05$. Significance in cross-species comparisons are not included due to different coding methodologies.

greater diversity in their calls than the dominant titmice (rank 1; M = 2.06, $p = 0.03$), and the two chickadees (rank 3, M = 1.68, $p < 0.0001$; rank 4, M = 1.68, $p < 0.0001$). The dominant titmouse also had greater call diversity than the two chickadees (rank 3, $p = 0.0023$; rank 4, $p = 0.003$), and the chickadees did not differ from one another ($p = 1.0$).

Discussion

For many of the call characteristics examined in this study, relative dominance status was not correlated with the communicative output from the birds, aligning with the null hypothesis. However, for certain call characteristics, dominance appeared to play a role in the birds' communication, supporting Hypothesis 1. Also, titmouse *D* notes in this study may reflect a change in communicative behavior following a change in dominance status, tentatively supporting Hypothesis 2. In general, titmice had more dominance related call characteristics than chickadees.

Tufted titmice. Several titmouse call characteristics were predicted by dominance status, including call rate, diversity index, zero-order uncertainty, note use, [*I*][*A*][*D*] call use, [*D*] call use, and [*I*][D_h] call use. Dominant titmice are more likely to call more and to use more [*D*] calls, *D* notes, *Z* notes, and *B* notes than subordinate titmice. Surprisingly, subordinate titmice had greater diversity index, zero-order uncertainty, *I* notes, *A* notes, D_h notes, and used more [*I*][*A*][*D*] calls and [*I*][D_h] calls than dominant individuals. These patterns in call complexity are likely explained by the increased proclivity of subordinate birds to use rarer notes (like D_h notes) and calls with more note types. These results with the *D* notes, D_h notes, and [*D*] calls support the principal components results from study one, where the use of *D* notes and [*D*] calls are negatively correlated with D_h notes. However, the use of the calls in this study appears to reverse the relationship previously found between bird size and PC2 (i.e., smaller birds use more *D* notes and calls, and fewer D_h notes). These findings should be replicated with larger sample sizes to tease apart these potential interactions. Dominant birds use more of the longer note types (notes longer than 145 msec) than subordinate birds. Future studies should also more explicitly examine whether note length is correlated with dominance.

Variation in tufted titmouse *D* notes suggests that birds may change aspects of their communicative output after a change in their relative dominance status. In the

conspecific pairs, the subordinate titmouse is at the bottom of the hierarchy. These individuals are then ranked second in the mixed-species flock condition. Subordinate titmice used more *D* notes in the mixed-species condition than the conspecific condition, unlike the dominant birds that did not change their behavior across social context. Titmice may be increasing their *D* notes as their dominance status increases. In research on other behavioral syndromes, changes to dominance status reduced the repeatability of behavioral syndromes (Rudin et al., 2017). It is possible that these changes in status undermine communicative repeatability as well. Future researchers should consider manipulating the dominance status of titmice to examine this phenomenon further. One method that could be used would be to assess the dominance status of all titmice in natural flocks and then measure calling behavior (particularly *D* notes) in manipulated dyads, with a focus on intermediately ranking birds that may being either subordinate or dominant depending on the partner. *D* notes in titmice are important to understand because researchers have often focused on these notes in studies of predator avoidance and foraging (Hetrick & Sieving, 2012; Freeberg et al., 2014).

Lastly, call rate was significantly related to dominance status. Titmice called more than chickadees and within species, dominant individuals called more than subordinate individuals. Titmice are larger and dominant to chickadees (Mostrom et al., 2020; Ritchison et al., 2020), likely driving the difference in calling between the two species. While there is no known prior research explicitly examining whether dominant titmice call more than subordinate titmice, previous work by Freeberg & Branch (2013) found that males call more than females in situations of high risk, and the authors suggest that this may be due to a dominance effect. In addition, there is evidence that other species in the family Paridae demonstrate similar trends (Krams, 2000), lending support to the results of this study.

Carolina chickadees. Most of the chickadee call characteristics were not predicted by an individual's relative dominance status, regardless of whether the birds were measured in a conspecific pair or in a mixed-species group. Call rate was significantly related to dominance status, with dominant individuals calling more frequently than subordinate individuals, as seen in other parid species (Krams, 2000).

Dominant chickadees were also more likely to use *C* notes and *D* notes than subordinate birds. Like titmice, chickadee *D* notes have been the focus for much research on identity and (Freeberg et al., 2003; Bloomfield et al., 2005), and it is important to understand what information may be encoded in these notes. *C* notes are slightly less studied, but previous research has suggested that these notes could also be important for encoding information about identity in *chick-a-dee* calls (Freeberg et al., 2003). The relatively poor relationship between dominance status and most of the chickadee calling behaviors may occur due to several factors. First, chickadees may use other call types other than the *chick-a-dee* call to signal status, such as the *gargle* call. *Gargle* calls are complex calls that often occur as a string of several different syllable types like broadband syllables and buzzing syllables (Baker & Gammon, 2007). These calls have long been associated with agonism and dominance interactions (Odum, 1941), and it is possible that chickadees only use *gargle* calls to signal status. While it was not part of the analyses for these studies, I recorded approximately 1,000 *gargle* calls between study one and study two. Researchers should continue to study the *gargle* call and its place in the chickadee repertoire to understand whether use of *gargle* calls reduces the need to encode status information in *chick-a-dee* calls.

Chickadees could also encode dominance information in other characteristics of the *chick-a-dee* call that were not measured. Previous research has shown that Paridae species use fine acoustic properties of their calls to communicate a wide variety of contexts (Guillette et al., 2010; Suzuki, 2014; Kalb et al., 2019; Jung, 2020). It is unknown whether dominance is encoded in the fine acoustic structure of the notes in *chick-a-dee* calls, but other chickadee species do share this information in the structure of their *feebee* songs (Christie et al., 2004). Future research should continue to explore the fine acoustic structure of chickadee calls, with a focus on whether the identity information that is encoded also includes relative dominance status.

The last factor that could be affecting the lack of dominance information in chickadee calls is the relative dominance status of the whole species. Carolina chickadees are subordinate to most of the species that are often part of the overwintering mixed-species flocks (Miller et al., 2017). It is possible that chickadees have less dominance-

related information in their calls because they are dominant over relatively fewer birds. It would be a valuable avenue of future research to examine whether more dominant species have greater dominance information encoded into their calls than subordinate species. This research should be done in a comparative fashion across species and taxa to ensure that the findings are broadly applicable. It is not known whether this phenomenon occurs in most species, however, there is some evidence that more despotic species with rigid hierarchies tend to use more dominance-related calls (Kavanagh et al., 2021).

Broader implications. This study adds to the growing literature comparing dominance status to behavioral syndromes (Favati et al., 2014; Portugal et al., 2017; Snijders et al., 2017) and communicative behaviors (Krams, 2000; Kitchen et al., 2003; Bolt, 2013; Kavanagh et al., 2021). Dominance status appears to be correlated with calling behavior in species specific ways (Dingemanse & da Goede, 2004; Devost et al., 2016). This reflects the inconsistency in relationship between dominance and other behavioral syndromes. In some species there are correlations between dominance and other syndromes (Kortet & Hedrick, 2007; Dahlbom et al., 2011), and in other species there are no correlations (Jolles et al., 2013; Portugal et al., 2017). Future research should work to understand why some species have correlations between communicative signals and dominance and others do not.

There may be other factors that have are associated with calling behaviors in other species include cortisol response in marine mammals (Eskelinen et al., 2022), testosterone levels in rodents and birds (Hunt et al., 1997; Pasch et al., 2011), and genetics in rodents (Blumstein et al., 2013). More work should be done with the parid system and with other taxa to explore calling behavior as a behavioral syndrome and how it relates to other physiological characteristics.

Conclusion

Dominance status often influences how animals interact with one another, and this can include how animals communicate within a social group. Studies one and two suggested there may be a communication behavioral syndrome due to the repeatability of the characteristics across social conditions. In this study, dominance status was correlated with several of the call characteristics for titmice (call rate, diversity index, zero-order

uncertainty, the note types used per call, [*I*][*A*][*D*] call use, [*D*] call use, and [*I*][D_h] call use), but only three call characteristics for chickadees (*C* notes, *D* notes, and call rate). It is also important to note that changes in dominance status did not appear to widely affect the calling behavior of the birds, however titmice used more of the functionally important *D* notes as they became more dominant within the flocks. Future work should continue to explore the possibility of a communicative behavioral syndrome and potential associations with other behavioral traits and statuses.

CHAPTER FIVE
CONCLUSIONS

Animals often behave in predictable ways that fall into behavioral categories, called personality traits or behavioral syndromes (Sih et al., 2004a; Gosling, 2008). As the field of animal personality has grown, a handful of behavioral syndromes have become the focus of the field. These include the bold-shy syndrome, exploratory syndrome, activity syndrome, and proactive-reactive syndrome (Blight et al., 2016; Huang et al., 2016; Kerman et al., 2016; Kelleher et al., 2018). Researchers also often compare the syndrome they are studying to dominance, an often closely related behavioral category (Dahlbom et al., 2011; Jolles et al., 2013; Snijders et al., 2017). More recently, researchers have been examining the relationship between known behavioral syndromes and communication behavior (Wilson et al., 2010; Naguib et al., 2016; Schabacker et al., 2024). Some of these findings suggest that communication could be a standalone behavioral syndrome (Guillette & Sturdy, 2011), but most researchers continued to explore communication as an extension of other syndromes. In my dissertation, I investigated the possibility of a novel communication behavioral syndrome in Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*), two closely related species with complex communication systems and important ecosystem roles tied to their communication systems (Freeberg, 2008; Hetrick & Sieving, 2012; Krams et al., 2012). I also compared the different call characteristics of each species to other behavioral syndromes and to the birds' dominance status.

In chapter two, I captured conspecific wild chickadees and titmice and placed them into naturalistic aviaries to measure whether individuals in these species differed from one another in their calling behavior, and whether these differences were repeatable across several days of testing during unmanipulated conditions. Other species in the family Paridae have been shown to have communicative repeatability in their calling or singing behaviors (Guillette & Sturdy, 2011; Naguib et al., 2016), but many of the call characteristics utilized in this study have never been used for repeatability studies. The goal of this first study was to discover which Carolina chickadee and tufted titmouse call characteristics were repeatable. These characteristics were then narrowed down with principal components analysis to those that were most important for the overall variation in each species' call systems. Lastly, I used generalized linear models to explore which of

the principal components were related to the size of the bird. The results of this study suggested that many call characteristics in these species were repeatable, particularly call rate, note use, call type use, and call complexity measures. Birds may make tradeoffs between certain note types or call types more often, and much of the birds' calling behavior did not appear to be related to the size of the bird.

In chapter three, I extended the methodology from study one to investigate how communication changes between different social conditions. To be considered a behavioral syndrome the behavior must be correlated across two or more contexts (Sih et al., 2004a). Wild chickadees and titmice were placed into aviaries, and the calling behavior of each bird was recorded in two flocking conditions: conspecific pairs and mixed-species groups flocks. I calculated the repeatability of the call characteristics from study one across both social conditions and separately, whether the calls differed between conditions. The results suggested that most of the call characteristics were still repeatable within an individual, different for each bird in the flock, and for the most part, birds did not change their calling behavior with a changing social context. Some of the chickadee call characteristics were used more under the conspecific condition rather than the mixed-species condition, likely due to audience effects (Coppinger et al., 2020). These results suggest that there may be a communicative behavioral syndrome. Additionally in study two, I compared chickadee and titmouse call characteristics to other commonly studied behavioral syndromes: exploration, activity, and coping strategy. Calling behavior was not related to any of the other behavioral syndromes.

In chapter four, I explored whether the repeatable call characteristics from the earlier studies were related to the birds' relative dominance statuses. I recorded all known dominance interactions and calculated an Elo-rating and dominance rank for each bird based on the outcomes of those interactions. I used these ranks as a predictor for the calling characteristics in generalized linear models. Dominance appeared to be correlated with several of the titmouse call characteristics, but not all. Dominant individuals tended to use more calls and more of certain note or call types than subordinates, a pattern that has been found in several other species (Preuschoft & van Schaik, 2000; Fichtel et al., 2024). Unexpectedly, subordinate titmice had greater communicative complexity than

dominant individuals. Chickadee calling behavior did not appear to be related to dominance status except for call rate, *D* note use, and *C* note use. I also examined whether there was an interaction between dominance rank and social condition on a bird's calling behavior, with particular interest in changing rank. One call characteristic, titmouse *D* note use, appeared to be influenced by the relative increase in subordinate titmouse rank between social conditions.

Overall, the results of these studies found that communication in these species is repeatable and consistent across different social contexts. Additionally, some of these calling behaviors are related to the size or dominance status of the bird, but many are not. These calling behaviors made during unmanipulated contexts also did not appear to be correlated with exploration, activity level, or coping strategy. Taken together, these findings provide support for a novel behavioral syndrome that is separate from other currently studied behavioral syndromes or behavioral characteristics. The presence of a standalone communication behavioral syndrome also helps explain past research that examines the repeatability or consistency of communication. Previous research comparing communication to behavioral syndromes has been inconsistent. Some studies find that bolder, more exploratory animals are more likely to use alarm calls and other studies show that shyer animals are more likely to use alarm calls (Hyman et al., 2013; Kerman et al., 2016). These discrepancies suggest that communication is not part of these other syndromes, and we should perhaps consider communicative repeatability as a separate and equal trait.

Broader implications. Communication is crucial for many aspects of an animal's life, including group formation, mate attraction, foraging, predator deterrence, and other behaviors (Bradbury & Vehrencamp, 1998). As a repeatable behavioral syndrome or personality trait, we can ask questions about which animals are producing which signals, and how these differences in communication affect social behaviors. Framing communicative behaviors as a personality trait would change how we study conspecific and heterospecific interactions and how we interpret other behavioral syndromes. For example, animals have been found to form groups based on their personality traits (boldness, Pike et al., 2008; exploration, Aplin et al., 2013). Similar work could be done

to understand whether this non-random assortment also applies to a communication syndrome, causing the formation of groups consisting of vocal animals and groups of quieter individuals. Animals or groups of animals that call more or use more of particular call types may be important to study for elucidating social cohesion and interactions. These individuals could act as information "keystones," providing a disproportionate amount of information to the flock or community. On the other hand, it is also important to understand the animals that call less, especially when this reduced signaling does not appear to be explained purely by other attributes. One particularly interesting outcome of these studies is the presence of individuals who never called at all, even when other members of the flock were similarly silent. This suggests that this phenomenon is not due to suppression in the presence of a vocal partner (a type of audience effect).

In the field of animal communication it is typically assumed that all animals produce signals of some kind, whether for finding mates, individual recognition, or maintaining territory (Bradbury & Vehrencamp, 1998; Tibbetts & Dale, 2007). However, this dissertation and other work (Weary et al., 1998; Miller-Sims & Bottjer, 2012; Coppinger et al., 2018) suggest that there are individuals that consistently do not signal at all. In many of these other studies, non-signalers are excluded from the data analyses. This has profound implications for our understanding of communication. By removing these individuals from data sets, we are losing an added layer of complexity within these systems and ignoring the underlying reasons why those individuals may not be calling. There are several crucial questions that should be answered moving forward in the field of animal communication and individual repeatability. Why do some individuals rarely or never call? Are these individuals using other modalities for communication? If not, are they relying more heavily on non-communicative alternative strategies for social cohesion, mating, foraging, or other activities? What percentage of a population are non-signalers? And if we ignore non-signalers when conducting research, what other valuable information about these individuals are we missing? Future research should address these questions and examine the potential pitfalls of neglecting the full variation in communicative behaviors.

In other fields, researchers have discovered fascinating behaviors when they reduce biases against behaviors that "should not exist" and examine the full range of behavioral variation in the study system. For example, in round gobies (*Neogobius melanostomus*), males are often large and aggressively territorial of their mates, however there is an alternative male strategy that would be easily missed—a small percentage of males are cryptic, meaning they remain small and maintain the same coloration as females (Cerwenka et al., 2021). These cryptic phenotypes are not expected, especially when the norm is a large and aggressive male, and would be easily neglected if researchers limited studies to the phenotypic majority. Likewise, interspecies play between nonhuman animals was also dismissed for decades, and any evidence of this play was considered unusual or purely anecdotal (Brooks & Burghardt, 2023). However, interspecies play is more common than originally believed and is demonstrated by a wide range of taxa including mammal, bird, and reptile species (Brooks & Burghardt, 2023). This phenomenon of neglecting behaviors perceived as rare or unusual has also occurred in the animal communication literature. Female birdsong was dismissed as abnormal for many years until researchers decided to take a closer look at the behavior, finding that female birdsong is not only widespread, but perhaps even the ancestral state for songbirds (Barros et al., 2024). In each of these cases, studying phenomena that are rare or uncommon has led to exciting new avenues of research. Likewise, researching the animals that do not call, rather than rejecting them from our study populations, would undoubtably lead to many more discoveries on how animals behave and communicate.

Limitations and future directions. In this dissertation, there were a few limitations that may have affected the outcome of these studies. First, the numbers of notes recorded in the chickadee and titmouse call systems were uneven (four for chickadees, six for titmice), likely confounding comparisons of call complexity in these species. I also used uneven flock sizes due to constraints on the number of size-matched birds that could be taken from a single flock. Future studies could reduce the emphasis on bird size due to the lack of relationship between most call characteristics and bird size. This would allow for larger conspecific flock sizes to reduce potential conflation between flock diversity and flock size. I also only observed birds over spans of approximately two

weeks. It would be beneficial to conduct a longitudinal study examining these call characteristics and their repeatability over longer periods of time. Lastly, these studies took place within naturalistic aviaries. These studies should be repeated with field studies to investigate whether these trends are consistent in natural settings.

Additional studies into communication and individual repeatability should be done to continue to understand the communicative behavioral syndrome. While I examined dominance, size, and various behavioral syndromes as potential correlates of communicative differences, future researchers should also consider alternative characteristics that have been associated with communication in other species. These could be characteristics like age and sex (Erwin & Mitchell, 1973), hormonal differences (Pasch et al., 2011; Eskelinen et al., 2022), or hereditary patterns of behavior (Blumstein et al., 2013). I only examined acoustic communication; however, many species use different modes of communication or combine two or more modalities together (Bradbury & Vehrencamp, 1998). It is critical for future work on communicative behavioral syndromes to examine other modalities of communication and to replicate these studies with other species. As an example, white-breasted nuthatches (*Sitta carolinensis*) are one of the species most commonly found in the parid mixed-species flocks ((Gentry) Richardson et al., 2022). Nuthatches are less known for their vocalizations (*quank* calls) than chickadees and titmice but still encode some information in their calls (Ritchison, 1983; Bartmess-LeVasseur et al., 2010). If the studies here were replicated with nuthatches, I predict that there would be similar results to the current findings. Namely, call rate should differ between individuals and be repeatable in these differences. I also expect that birds would use *quank* notes in different ways (e.g., some birds might use consistently more *quank quank* calls and others might use rapid *quank* calls). If these predictions are accurate, it would parallel the current findings in chickadees and titmice. If these suggested future studies continue to suggest that these relationships are not fully explanatory, like the results in this dissertation, then this would continue to support the possibility that communication is a novel behavioral syndrome.

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APPENDIX

Appendix I: Additional Figures for Chapter One

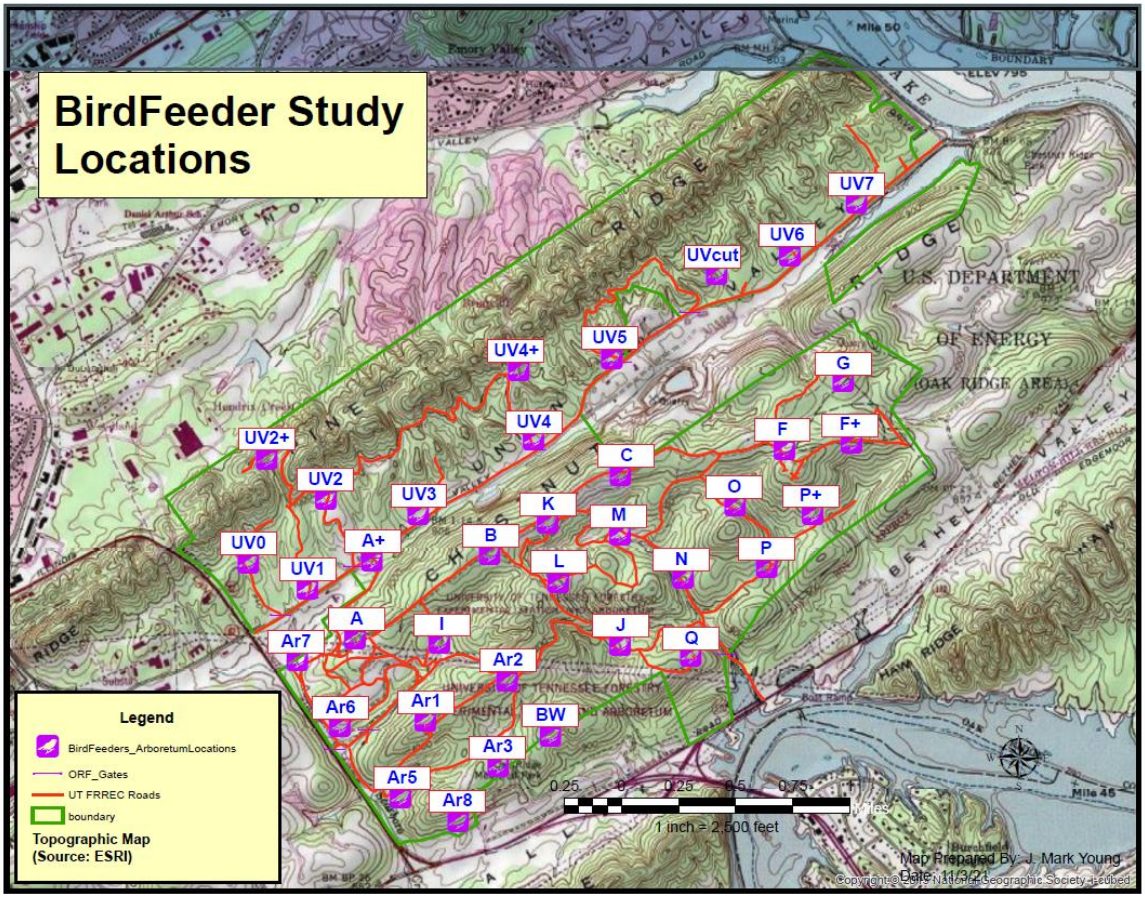

Figure A-1. Map of the feeding and banding sites at the University of Tennessee Forest Resources, AgResearch and Education Center. The field site consists of 2,204 acres and all aviaries are located in the area between sites "A" and "I".



Figure A-2. Image showing one of the naturalistic aviaries. There are six aviaries of similar dimension, approximately 6m × 9m × 3.5m. All aviaries were kept stocked with fresh water and *ad libitum* birdseed. Aviaries also contained a combination of natural and artificial vegetation.

Appendix II: Additional Figures for Chapter Two

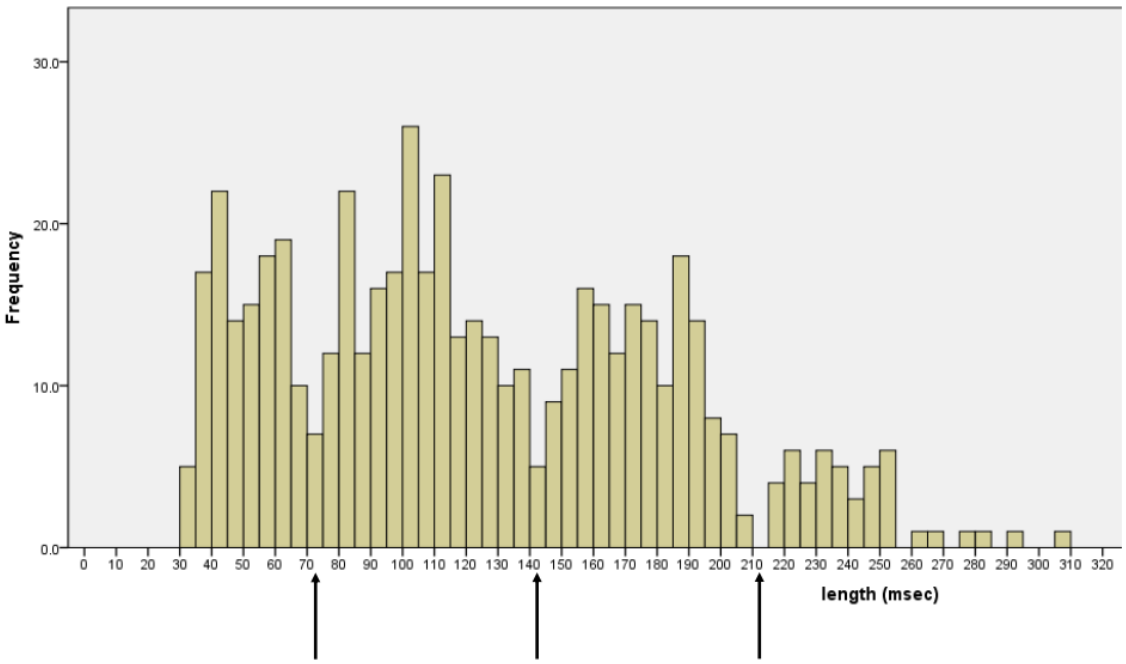

Figure A-3. Histogram of tufted titmouse intro note lengths. Notes measured in msec and arrows pointing to the natural breaks where categories were split. The categories are as follows: *A* notes ≤ 74 msec, 75 msec ≤ *I* notes ≤ 144 msec, 145 msec ≤ *B* notes ≤ 214 msec, 215 msec ≤ *Z* notes.

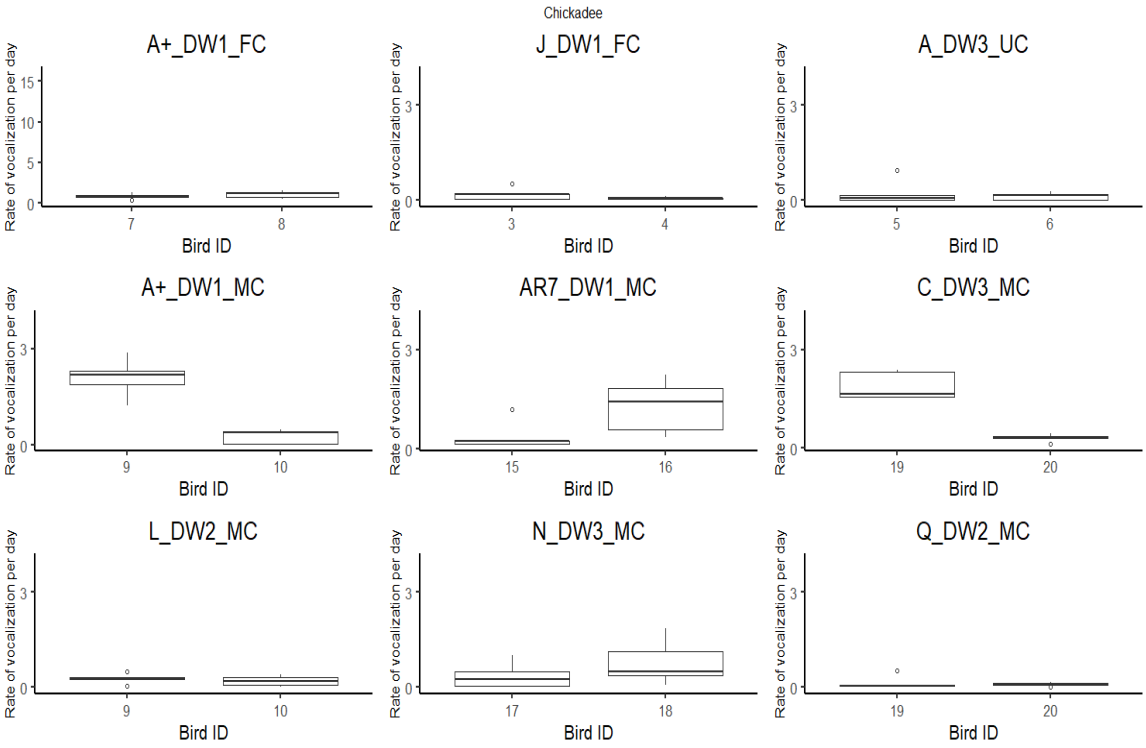

Figure A-4. Call rates of Carolina chickadees split by conspecific pairs. Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents one individual sampled across 25 five-minute intervals.

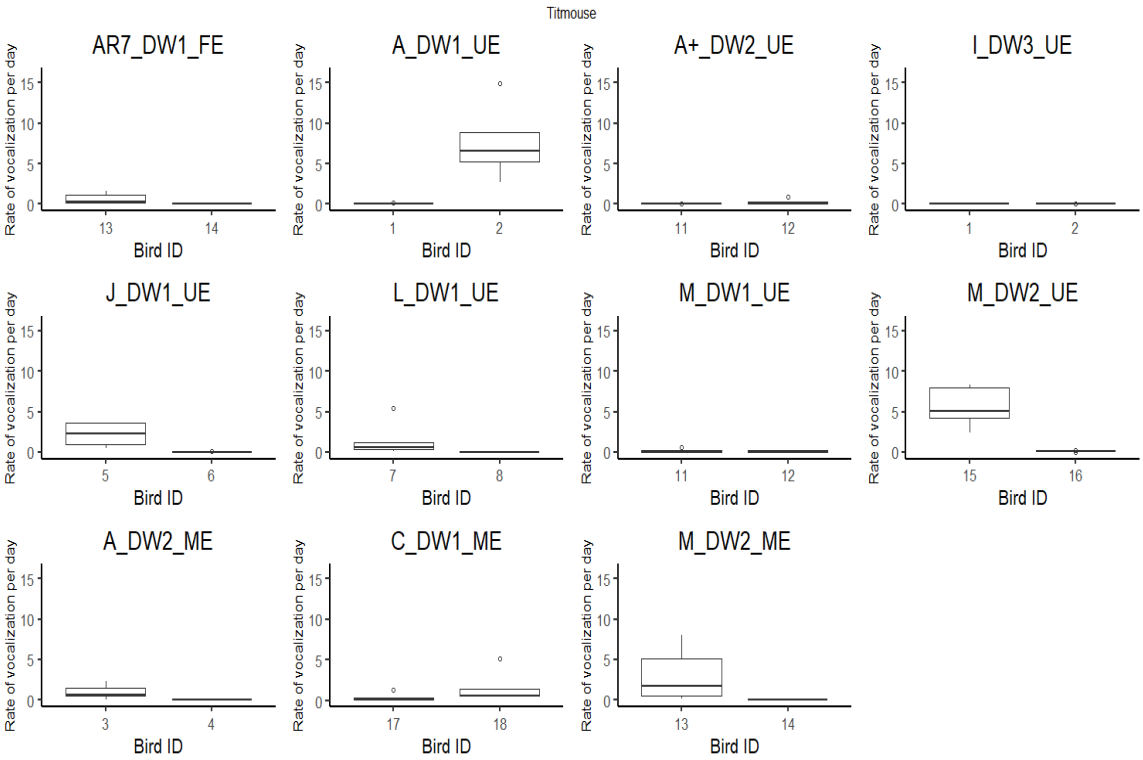

Figure A-5. Call rates of tufted titmice split by conspecific pairs. Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents one individual sampled across 25 five-minute intervals.

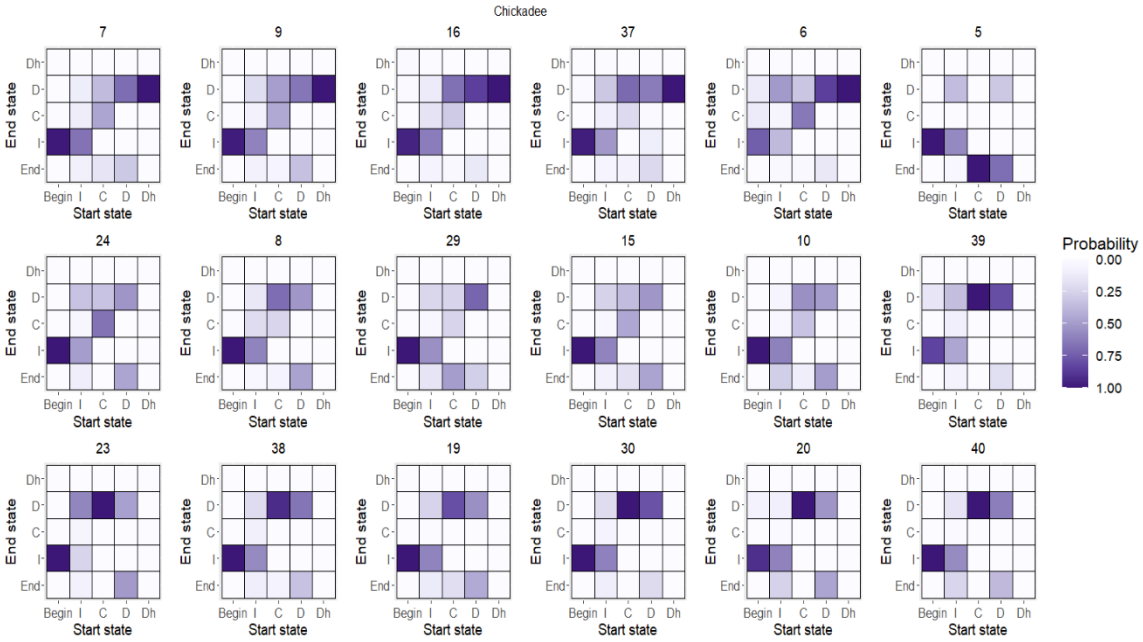

Figure A-6. Transition matrices for chickadees. The beginning note is on the X-axis and the ending note is on the Y-axis. White and other light colors are low transition probabilities between the two states, darker colors indicate higher probabilities.

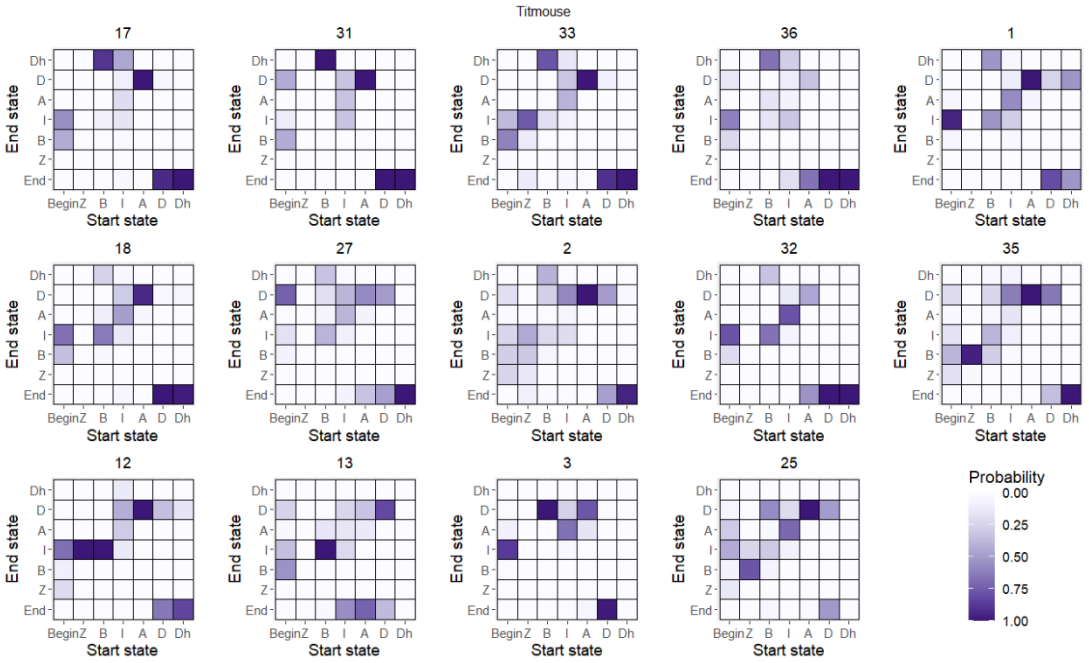

Figure A-7. Transition matrices for titmice. The beginning note is on the X-axis and the ending note is on the Y-axis. White and other light colors are low transition probabilities between the two states, darker colors indicate higher probabilities.

Appendix III: Additional Figures for Chapter Three



Figure A-8. Image of the novel test enclosure for the exploration behavioral assay. This approximately 0.8 m × 0.5 m × 0.45 m enclosure was novel for all birds in the study. Birds were placed in this enclosure and video recorded for five minutes before release in a new aviary.

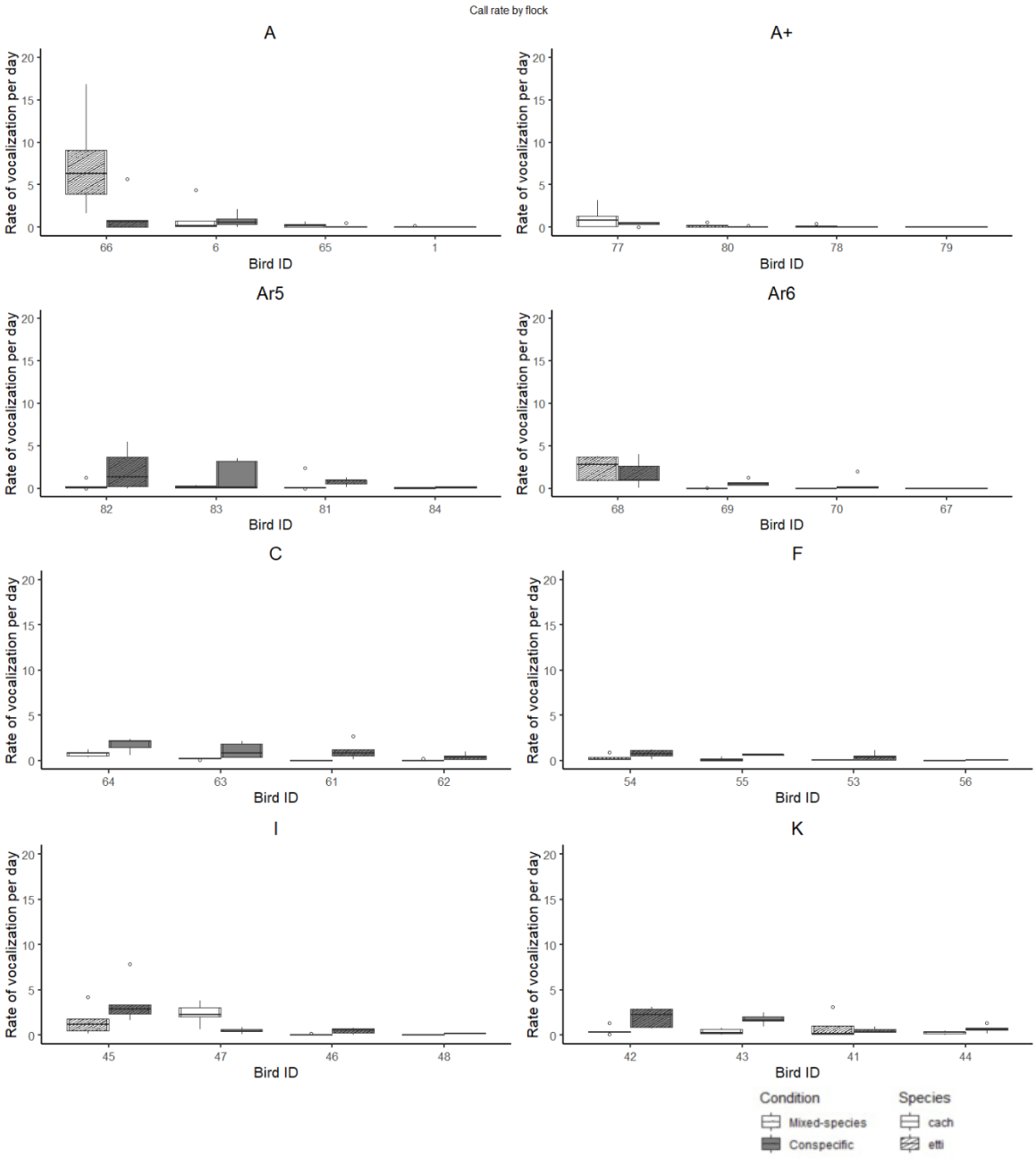

Figure A-9. Call rates split by flock. Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents one individual, sampled across the ten-minute focal period and the fifteen-minute all-occurrence period for five days. Gray boxes are calls made during the conspecific condition and white boxes are the mixed-species condition. Boxes with the shaded diagonal lines are titmice. Bird 73 died after the mixed-species condition.

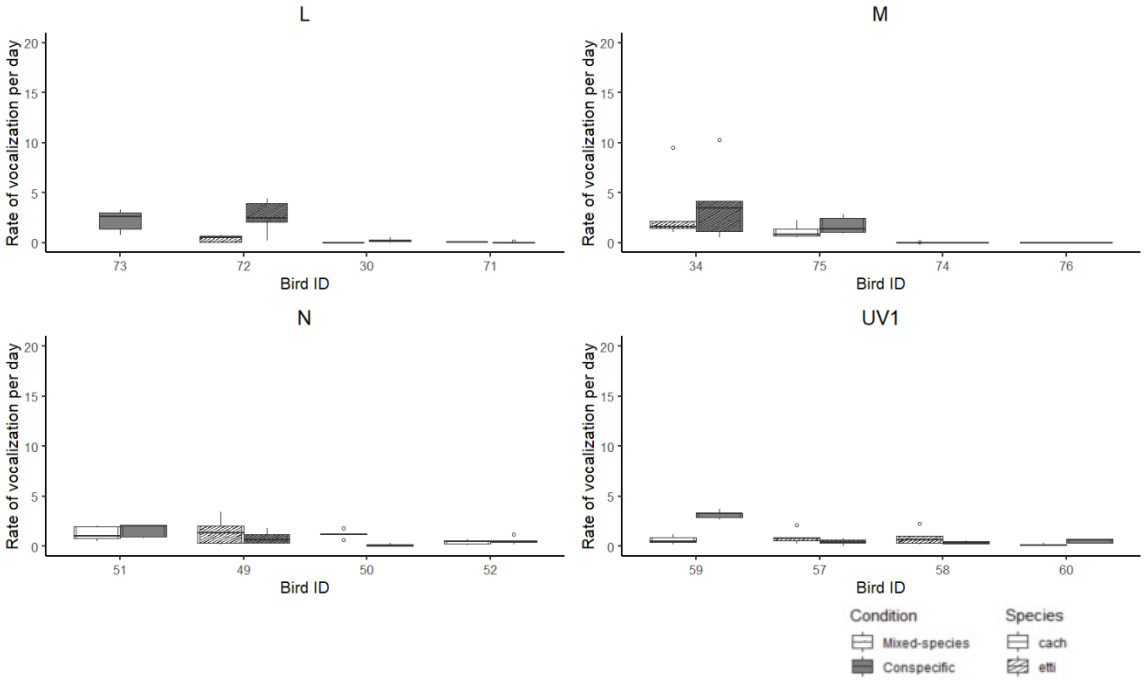

Figure A-10 (cont.). Call rates split by flock. Each box represents the 25% and 75% quartiles, thick horizontal lines are the median, whiskers are ranges not counting outliers, and circles are outliers. Each plot represents one individual, sampled across the ten-minute focal period and the fifteen-minute all-occurrence period for five days. Gray boxes are calls made during the conspecific condition and white boxes are the mixed-species condition. Boxes with the shaded diagonal lines are titmice. Bird 73 died after the mixed-species condition.

Table A-1 Replication of the repeatability in titmouse conspecific pairs from study two. Repeatability estimates (R) were calculated in the *rptR* package. The 95% confidence interval (CI) was found via parametric bootstrapping. SE is the standard error. Some variables were zero-inflated and repeatability was calculated with the Intraclass Correlation Coefficient with the *iccCounts* package. For these values only confidence intervals were calculated in the package. Confidence intervals that do not include zero with a P-value smaller than 0.05 (if applicable) are bolded.

Variable	R/ICC	± SE	95% CI	P
Call Rate	0.696		**0.080–0.927**	
[*I*][*A*][*D*] calls	0.525	0.120	**0.235–0.697**	**< 0.0001**
[*I*][*D*] calls	0.460	0.155	**0.087–0.679**	**0.0001**
[*D*] calls	0.841	0.109	**0.559–0.937**	**< 0.0001**
[*B*][D_h] calls	0.875	0.188	**0.180–0.980**	**< 0.0001**
[*I*][D_h] calls	0.622	0.164	**0.189–0.817**	**< 0.0001**
Z notes	0.428		**0.274–0.561**	
B notes	0.694	0.135	**0.352–0.850**	**< 0.0001**
I notes	0.268	0.115	**0.020–0.457**	**0.0032**
A notes	0.545	0.121	**0.242–0.772**	**< 0.0001**
D_h notes	0.710	0.133	**0.354–0.871**	**< 0.0001**
D notes	0.516	0.115	**0.264–0.686**	**< 0.0001**
Diversity Index	0.547	0.107	**0.293–0.715**	**< 0.0001**

Table A-2 Replication of the repeatability in chickadee conspecific pairs from study two. Repeatability estimates (R) were calculated in the *rptR* package. The 95% confidence interval (CI) was found via parametric bootstrapping. SE is the standard error. Some variables were zero-inflated and repeatability was calculated with the Intraclass Correlation Coefficient with the *iccCounts* package. For these values only confidence intervals were calculated in the package. Confidence intervals that do not include zero with a P-value smaller than 0.05 (if applicable) are bolded.

Variable	R/ICC	± SE	95% CI	P
Call Rate	0.736		**0.329–0.912**	
[*I*][*C*][*D*] calls	0.836	0.078	**0.617–0.924**	**< 0.0001**
[*I*][*D*] calls	0.557	0.109	**0.283–0.712**	**< 0.0001**
[*I*] calls	0.709	0.115	**0.408–0.853**	**< 0.0001**
[*I*][*C*] calls	0.511	0.246	0.0–0.760	0.006
[*D*] calls	0.593	0.187	**0.079–0.814**	**< 0.0001**
Intro notes	0.706	0.083	**0.494–0.816**	**< 0.0001**
C notes	0.781	0.084	**0.559–0.887**	**< 0.0001**
D_h notes	0.867	0.176	**0.282–0.969**	**< 0.0001**
D notes	0.582	0.071	**0.169–0.438**	**< 0.0001**
Diversity Index	0.486	0.105	**0.256–0.659**	**< 0.0001**

Table A-3. Behavioral syndrome predictors in the GLM models for titmouse call characteristics. U_0 = Zero-order uncertainty, DI = Diversity Index. No p-values were retained after adjusting for multiple comparisons with the Benjamini & Hochberg Correction. *Indicates models that included both species as a variable.

Variable	Predictor	X^2	p	Variable	Predictor	X^2	p
Call rate*	Exploration	0.07	0.79	Z	Exploration	0.597	0.44
	Activity	0.009	0.92		Activity	0.914	0.34
	Coping	1.96	0.16		Coping	0.006	0.94
[I][A][D]	Exploration	0.019	0.89	B	Exploration	0.054	0.82
	Activity	2.43	0.12		Activity	0.477	0.49
	Coping	2.87	0.09		Coping	0.019	0.89
[I][D]	Exploration	0.596	0.44	I	Exploration	0.967	0.32
	Activity	0.410	0.52		Activity	0.033	0.86
	Coping	0.250	0.62		Coping	0.985	0.32
[B][D_h]	Exploration	0.860	0.35	A	Exploration	0.007	0.93
	Activity	0.020	0.89		Activity	2.17	0.14
	Coping	0.197	0.66		Coping	4.43	0.03
[I][D_h]	Exploration	4.49	0.03	D_h	Exploration	3.50	0.06
	Activity	0.0013	0.97		Activity	0.054	0.82
	Coping	0.154	0.69		Coping	0.009	0.92
[D]	Exploration	0.777	0.38	D	Exploration	0.941	0.33
	Activity	0.931	0.33		Activity	0.659	0.41
	Coping	0.498	0.48		Coping	0.553	0.45
DI*	Exploration	0.655	0.42	U_0*	Exploration	1.21	0.27
	Activity	0.219	0.64		Activity	0.248	0.62
	Coping	4.021	0.04		Coping	1.62	0.20

Table A-4. Behavioral syndrome predictors in the GLM models for chickadee call characteristics. U_0 = Zero-order uncertainty, DI = Diversity Index. *I* notes here are the *Intro* note category. No p-values were retained after adjusting for multiple comparisons with the Benjamini & Hochberg Correction. *Indicates models that included both species as a variable.

Variable	Predictor	X^2	*p*	Variable	Predictor	X^2	*p*
Call rate*	Exploration	0.07	0.79	*Intro*	Exploration	0.771	0.38
	Activity	0.009	0.92		Activity	0.071	0.79
	Coping	1.96	0.16		Coping	2.27	0.13
[*I*][*C*][*D*]	Exploration	0.318	0.58	*C*	Exploration	0.0001	0.99
	Activity	0.016	0.90		Activity	0.030	0.86
	Coping	1.15	0.28		Coping	0.127	0.72
[*I*][*D*]	Exploration	0.552	0.46	D_h	Exploration	0.269	0.60
	Activity	0.044	0.83		Activity	0.361	0.55
	Coping	0.603	0.44		Coping	0.224	0.63
[*I*][*C*]	Exploration	0.015	0.90	*D*	Exploration	0.007	0.93
	Activity	0.188	0.66		Activity	0.093	0.76
	Coping	0.013	0.91		Coping	0.119	0.73
[*I*]	Exploration	2.22	0.14	DI*	Exploration	0.655	0.42
	Activity	0.06	0.79		Activity	0.219	0.64
	Coping	4.54	0.03		Coping	4.021	0.04
[*D*]	Exploration	0.158	0.69	U_0*	Exploration	1.21	0.27
	Activity	0.280	0.60		Activity	0.248	0.62
	Coping	0.320	0.57		Coping	1.62	0.20

Appendix IV: Additional Figures for Chapter Four



Figure A-11. Camera and mock camera for study three. On the left is a model camera that was placed in the aviaries for the duration of the study, except when replaced with the GoPro Hero11 Black camera (right) that was used for recording dominance interactions.



Figure A-12. Recording set up for study three. A GoPro was placed on a nearby bracket (approximately 1 to 2 ft away from food) and mealworms were placed in a clear glass bowl next to the ad libitum seed on the feeding platform.

VITA

Heather Brooks was born to Rebecca Bigelow and Dr. Ian Brooks outside of Philadelphia in 1995 and grew up in Champaign, Illinois. She attended Champaign Central High School and attended the University of Illinois Urbana-Champaign (UIUC). She graduated with a Bachelor of Science in Natural Resources and Environmental Science with a minor in Integrative Biology in 2017. She spent many years working in animal husbandry with all kinds of critters including farm animals, small pets, and laboratory animals. After graduating from UIUC, she worked at Brookfield Zoo Chicago and the Smithsonian National Zoological Park in animal behavior intern positions with carnivores and marine mammals. Right at the start of the COVID-19 pandemic when Heather was living in New York City, she found out she was accepted to the doctoral program at the University of Tennessee, Knoxville with Dr. Todd Freeberg. Heather is interested in mixed-species social behavior, particularly communication, and how these behaviors can be used to improve conservation and welfare efforts.