SOCIAL NICHE CONSTRUCTION IN BORWN-HEADED COWBIRDS (*MOLOTHRUS ATER*)

Gregory Mark Kohn

Submitted to the faculty of the University Graduate School

in partial fulfillment of the requirements for the degree

Doctor of Philosophy

in the Department of Psychological and Brain Sciences

Indiana University

March 2015

Accepted by the Graduate Faculty, Indiana University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Doctoral Committee

Meredith J. West, Ph.D
Chairperson

Andrew P. King, Ph.D

Jeffrey R. Alberts, Ph.D

Colin Allen, Ph.D

David J. White, Ph.D

January 15th 2015

Gregory Mark Kohn

Social Niche Construction in Brown-headed Cowbirds (*Molothrus ater*)

Variation in reproductive behavior is essential to selection. Despite this, researchers know very little about the social factors shaping the development of such variation. Social niche construction reflects the ability of an individual to shape its social environment. A social niche reflects an individuals place within the larger social network of the group. Some niches reflect high levels of connectedness with others, whereas other niches reflect more selective connections. The early niche will shape the quality and frequency of social interactions, and may have a cascading influence onto later reproductive performance. In this dissertation I explored the sex differences in social niche construction within Brown-headed Cowbirds (*Molothrus ater*). Male and female cowbirds face divergent challenges when navigating the social environment. In this dissertation I investigated the different niches occupied by males and females over development, and how different niches predict later reproductive behavior.

Female cowbirds construct predictable niches, whereas males construct more plastic niches. During the fusion of two novel flocks females maintain stronger connections with familiar females in contrast to males. The ability to form reliable networks with familiar conspecifics may influence the predictability of individual behavior across contexts. Across changes in group size and composition both adult and juvenile females maintain correlated patterns of both social approach and affiliative head-down displays, whereas males did not. Such variation is able to predict a female's reproductive behavior across long timescales.

More frequent and closer interactions during the fall predict courtship behavior and pair bonds in juvenile females, and egg production in adult females. Such results suggest that the early niches and individual constructs may have evolutionary consequences by shaping the development of functionally relevant courtship and reproductive abilities.

Doctoral Committee

Meredith J. West, Ph.D
Chairperson

Andrew P. King, Ph.D

Jeffrey R. Alberts, Ph.D

Colin Allen, Ph.D

David J. White, Ph.D

Table of Contents

First chapter: General Introduction

“To understand the individual I must study him in his group setting; to understand the group I must study the individual whose interrelated actions constitute it”- Solomon Ash

1.1: Introduction

Recently there has been an increased interest in the development and functional consequences of individual variation in behavior. While the existence of variation between individuals is an essential component of the original formulation of natural selection, the origins of such variation have been contentious among theorists and researchers (Gottlieb 1992). The developmental psychologist James M. Baldwin (1896), ethologist C. Lloyd Morgan (1896) and paleontologist H. F. Osborne (1896) all independently formulated an idea that later became known as the Baldwin effect. Here behavior acquired consistently over development could change the strength or direction of selective pressures. Selection may favor individuals who can readily acquire beneficial behavioral traits over development, leading to the eventual canalization of those behaviors. While historically the relevance of the Baldwin effect has been debated, theoretical and empirical advances have led to a wider acceptance of the importance of developmental processes for evolution (West-Eberhard 2003). Despite this, few studies have investigated the development of behavioral differences in the ability to successfully survive and reproduce within naturalistic settings. In this dissertation I outline a series of studies that highlight how understanding behavioral development within semi-naturalistic groups provides new insights into the persistence and evolution of social behavior.

Social behavior is ubiquitous. Nearly all vertebrates spend significant periods of their life foraging, courting, playing, migrating, and fighting within close proximity of others. Therefore most, if not all, vertebrates possess a social life, and understanding the origins and diversity of different social lives is a central theme in the study of animal behavior. Within a species one can observe both regularities and differences in social interaction across individuals, groups, and populations. Some populations are noted for their solitary tendencies, while others possess more gregarious tendencies (Lott 1991). Some individuals may form enduring relationships with conspecifics, particularly mates, while others may only associate with conspecifics for short periods, with no evidence of individual preferences. Groups may vary in their size and composition. Many vertebrates inhabit fission-fusion groups, where smaller groups join together to form larger aggregations before splitting again into smaller groups (Aureli et al. 2008). The stability of such groups over time can range from just a few minutes to decades. The ability to navigate and adapt to the complexity of one's group constitutes the large majority of an individuals interactions with others, and is often the main focus of an individual's social life.

Social development is the ontogenetic process where individuals acquire the behaviors necessary to engage others within the group. Groups, containing species-typical patterns of interaction, are therefore the necessary precursors for social development. Stimulation from others is essential for expression of a wide spectrum of capabilities, from gene expression to the organization of physiological and endocrine systems to the emergence of perceptual and cognitive systems necessary to recognize other social agents and effectively interact with them (Gottlieb 1971; Johnston & Gottlieb 1985; Lickliter & Gottlieb 1988; Meaney & Szyf 2005). The structure of the group often regulates the timing and intensity of the social stimulation an individual receives, especially during early life. However, most studies of social development have focused on the contribution of social stimulation, in contrast to non-social stimulation, emergence of behavior. Often subjects are placed into an isolated context, and then compared with individuals who are raised within a typical social context (Braaten & Reynolds 1999; Searcy & Marler 1987). Isolation studies, while highlighting the plasticity inherent within developmental systems, rarely inform the exact mechanisms that are necessary and sufficient for the emergence of social behaviors.

While it is widely accepted that early experiences have a long-lasting influence on later behavior, the importance of social development for the evolution of behavior may be underestimated. Within most vertebrates successful reproduction requires sustained periods of social interaction with mates and rivals. Individuals who are able to effectively compete with rivals, and cooperate with mates, may exhibit higher reproductive success than others. Despite this, most studies of social evolution do not explicitly address the mechanisms whereby variation in the ability to successfully interact across a broad range of social contexts, or social competence, develops. While research on the development of social competence within humans has a long history, only recently have researchers begun to recognize its potential for informing our understanding of evolution. As evolution requires variation, understanding the ontogenetic origins and reproductive consequences of individual social behavior may help to explain the variation observed across individuals, groups, populations and species.

1.2 Behavioral Development and Evolution: A quick overview:

Until recently, development was seen as having little to no influence over evolutionary processes. Adaptive behavior, or behavioral traits that have been selected for survival and reproduction, were thought to be a product of innate genetic programs. Individuals with the correct suite of alleles for specific traits were able to better survive and reproduce, leading to increased expression of those alleles in subsequent generations. Over time, populations would converge towards an optimal mean, with behaviors representing an adaptive response to selective pressures. Behaviors acquired over development were thought to have no evolutionary potential, as there was no direct mechanism whereby variation in such behavior could be transmitted to other generations. New behavioral variants could therefore only be introduced through changes in DNA, either through random mutation or genetic drift. Furthermore, the environment was considered to be too unreliable to provide the consistent influences needed for the development of adaptive traits, while genetic transmission assured robust transmission. According to this account – typically called the modern synthesis- natural selection was seen as acting solely at the genetic level, with phenotypes being simple “vehicles” for genetic information (Dawkins 1976).

Increasingly, new research is questioning the gene’s privileged role in behavioral development. There are now many different recognized pathways where information can be transmitted between generations (Jablonka & Lamb 2005). From directed mutations, to epigenetic influences such as RNAi interference and DNA methylation, to the transfer of learned behaviors via social learning and the emergence of culture, information has many avenues to pass from parents to offspring. For instance, recent studies have shown that early maternal behavior can shape gene expression in the brains of their offspring (Meaney & Szyf 2005). In particular, decreased maternal responsiveness leads to increasing methylation of serotonin reuptake receptor genes, leading to differences in stress responses in their offspring that extend into adulthood. These developmentally-induced stress responses were then transmitted to the next generation. Thus, while DNA is an essential component in developing organisms, its expression requires, and is shaped by, a wide array of developmental resources.

The demise of the gene as the sole factor in inheritance has proved challenging for the theoretical assumption about evolutionary progress. No longer can the phenotype be considered an evolutionary dead end, but its actions have a significant influence on the emergence of adaptive traits within an individual's lifespan. Developmental systems theory provides a new platform for conceptualizing evolutionary processes. A core view of DST contends that traits are not merely inherited, but are reconstructed in a heterogeneous and causally bidirectional matrix of organism-environment relationships that defines the life history of an individual from conception to death. Waddington (1962; Waddington 1940) provided a popular depiction of a developmental system in his epigenetic landscape (Fig 1). Here development is conceptualized as ball rolling across an inclined landscape of peaks and valleys that represented the diverse array of influences an individual might encounter. These peaks and valleys determine the ball's trajectory as it rolls across the landscape, eventually placing the ball at different endpoints that represent alternative phenotypes. These phenotypes, the outcome of complicated developmental systems, are ultimately what survive and reproduce. Thus, natural selection is not just restricted to the level of the gene, individual, or group, but acts on the entire developmental trajectories that result in higher fitness.

Taking a developmental systems approach to evolutionary questions requires a reassessment of the role of behavior in evolution. Historically, studies of behavior have assumed that behavioral traits represented responses to selective pressures from the external environment. An organism's behavior therefore reflected a passive response to environmental challenge, and did not substantially alter the environments they experienced. Nonetheless, it is apparent from many studies that behavior plays a substantial role in modifying, creating, and selecting the environment surrounding themselves and others. Such processes, collectively called niche construction, were first introduced by Lewontin (Lewontin 1982; Lewontin 1983), but have been further developed by Odling-Smee, Laland and Feldman (2003). During niche construction, a behavior shapes the environment an individual experiences, and consequently guides the developmental trajectories of themselves and others towards specific phenotypes (Flynn et al. 2013). If some of these phenotypes are more successful, a feedback system can result where individuals continually construct the environments that assure the development of specific phenotypes across generations. Referring back to Waddington's epigenetic landscape, niche construction may allow individuals to "choose" between different landscapes they face, and also influence the landscapes of other conspecifics.

Traditionally niche construction has focused on the relationships between organisms and their physical environment. Some examples of this are the construction of nests, burrows, and lodges to provide a safe environment for raising offspring. Beavers construct dams that restructure the ecology of whole landscapes, and earthworms modify soil chemistry through their actions to make it more hospitable to themselves and other plants. Other types of niche construction involve moving between and selecting the environments they experience. This is also called *niche-picking* as individuals may not actively modify the environment in a substantial way (Stamps & Groothuis 2010). Habitat choice, dispersal tendencies, and migrations are all examples of niche picking. Often individuals with different dispersal tendencies exhibit substantially different behavioral repertoires, as exposure to different environments assures different ontogenetic influences (Cote et al. 2010). Thus, organisms are not simply passive recipients of environmental influences, but rather are active participants in their own development by actively constructing their relationships with the environment.

While recognition of niche construction as an important evolutionary process is becoming established, only recently have researchers seen its applications within the social environment (Flack et al. 2006; Flack et al. 2012; Saltz & Foley 2010; Saltz & Nuzhdin 2014). Social niche construction occurs when an individual modifies, constructs, or selects the social environment it or others experience. For instance, in some species members can choose to live within the group, or to live a more solitary existence outside the group. Within groups individuals can exert some control over who they interact with, and how they interact with them. Here, social niche construction focuses on how individuals shape their social network within the group, and their influence on the networks of other individuals. By social network I am referring to the cumulative dyadic connections an individual has with others in the group (Wasserman & Faust 1994). Differences in an individual's *connectedness* with conspecifics constitute a major aspect of their social niche, as discussed in detail below. Flack (2006) conducted an experiment where highly dominant policing male macaques were removed from the troop. This resulted in more aggressive interactions, and less cohesive social networks at both group and individual levels. By perturbing the size and composition of groups researchers can measure the resulting changes in an individual's social behavior, and the qualities of their social network. Some individuals may be able sustain equivalent networks across changes, others may "rewire" their connections with others when conditions change. Thus research on social niche construction aims to uncover the causes and consequences of an individual's social niche, and its implications for the expression and development of social behavior.

The social environment will change widely across development as individuals move from naïve juveniles to more experienced adults. As juveniles become more independent they will likely encounter a more diverse range of social situations. How individuals utilize their social behavior in response to these new situations may determine the characteristics of their social niche. Terms such as aggressive, cooperative, affiliative, introverted and extroverted are often used to describe differences in how individuals behave around others. Numerous studies have shown that repeatable differences in these traits, often called animal personality or temperament, may both shape, and be shaped by an individual's social niche (Elliot & Thrash 2010). By investigating these behavioral attributes along with the networks an individual constructs over development, one may be able to understand how social niches shape the ontogeny of individuals towards specific phenotypes relevant to later reproductive performance.

The ability to sustain or rewire one's social networks may have reproductive implications. For instance, Saltz (2010) discovered that male fruit flies who engaged in more aggressive interactions tended to form groups with fewer males. Within these groups more aggressive males were more reproductively successful, resulting in directional selection for niche constructing traits. Sih and Watters (2005) discovered that consistently more aggressive male water striders disrupted networks with their behavior so much that overall reproductive performance for all individuals decreased. Changes in dominance relationships often result in large changes in aggressive or affiliative tendencies, with corresponding differences in reproductive performance. Therefore an individual's opportunities for successful reproduction may reflect the different social niches they occupy within the group.

While some researchers have contested that the concept of social niche construction is so broad as to encompass all social behavior (Laland & Sterelny 2006), the purpose is not to define the boundaries between what does, or does not constitute social niche construction, but rather to highlight how this perspective can inform our understanding of the development and evolution of social behavior. To do so, however, one must first come up with a platform from which social niches can be measured, and understand the trajectories they take across development, and their influence on fitness.

1.3 The social niche:

General differences in social interaction patterns and preferences may influence an individual's performance across a wide range of modalities. Social life comes with many benefits and costs, and individuals have to manage these tradeoffs across development. Living in close proximity provides clear advantages in terms of reducing predation, finding food, reducing vigilance and creating opportunities for social learning (Krause et al. 2009). However, it can also generate increased risk of competitive interactions over food and mates (Etkin 1964; Székely et al. 2010). The ability to facilitate or inhibit their connectedness with conspecifics may change the costs and risks of life inside the group. For instance, individuals with connections to many individuals will have a higher risk of encountering aggressive interactions, but will be better able to access beneficial social information. By looking at the social niches constructed as individuals engage conspecifics over ontogeny, one may be able to understand the differences in how individuals cope with the challenges of social life.

The niche is a concept used primarily within ecology, and aims to capture all the relationships between an organism and its environment that constitute its "way of life" (Hutchinson 1957). As such the niche often reflects the *place*, or differences in the organism-environment relationships in contrast to others, and the *occupation,* or what an organism does in order to maintain or change those relationships over time (Alberts & Cramer 1988). While the concept is expansive, in practice, ecologists will estimate the qualities of a niche by looking at variation within a selected range of measurable organism-environment relationships, such as interactions with prey or predators, use of abiotic resources, or the types of environments a species frequents (Schoener & Cherrett 1989).

While the niche concept has largely been restricted to the physical environment, researchers are starting to apply the concept to include the relationships formed within the larger social environment. This social niche has been described as the "individual's vector of behavioral connections in the set of overlapping social networks in which it participates" (Flack et al. 2006). Despite increased interest, little is currently known about individual variation in social niches, and how such variation shapes the ontogeny of functionally relevant social skills used to navigate interaction with others and successfully reproduce.

Within this dissertation I use the concept of a social niche to describe the "place" that an individual inhabits within the larger group. This place ultimately reflects differences in who and how often individuals approach conspecifics. In particular I use two aspects of connectedness with others in order to estimate their niche, their *sociability* and their *social preferences* (Fig 2). Sociability reflects the frequency of an individual's overall approaches with others, whereas social preferences reflect the distribution of those approaches towards others.

A central aspect of sociability is the management of proximity with others. Close proximity affords significant benefits for assessing individual quality and accessing social information (Coussi-Korbel & Fragaszy 1995; Fernández-Juricic & Kacelnik 2004; White et al. 2007). Most animals possess rigid personal fields, or areas around individuals where they generally resist approaches from others, and the size and diversity of these fields determines how individuals interact (McBride 1971, 1976). Personal fields are defined by how individuals approach and withdraw from others. The propensity to approach others is an important component of both human and animal temperaments (Davidson 2006; Windle

1995) and its neural underpinnings have been well studied (Goodson et al. 2009; Goodson & Kingsbury 2011; Hood et al. 1995). During an approach, an individual moves in close proximity to a recipient who then has the choice of either staying, and thus allowing the approach, or withdrawing and averting the approach. A successful approach reflects the ability to maintain close proximity without eliciting withdrawal. Thus, looking at the between-individual differences in the initiation and reception of approaches is a useful metric in estimating sociability.

T. C. Schneirla laid out a framework whereby an individual's behavioral development could be categorized as a modification of basic approach-withdrawal systems that govern how individuals interact with their surrounding environment (Schneirla 1965). During early life, an individual's approach-withdrawal responses are largely controlled by the intensity of stimulation from the environment. Strong and sudden onset of stimulation will likely trigger a withdrawal response from the location of the stimulus, whereas light to moderate levels of stimulation will likely trigger an approach response. Such responses are usually a by-product of the early development of an organism's sensory and neural systems, but over time the responsiveness to a specific stimuli will become more specialized. Such underlying differences in approach-withdrawal systems may be a basic aspect of individual differences in behavior, and scaffold behavioral development. While much work has investigated the approach-withdrawal systems in both animals and humans (Blair et al. 2004; Hood et al. 1995), few studies have looked at how access to repeated interactions with known individuals shapes these systems. In particular, reliable and repeated interactions within the early social environment may shape the development of later social approach-withdrawal systems, leading to the emergence of consistent sociabilities.

Individual differences in sociability have been observed across a wide array of vertebrates (e.g., macaques (Capitanio 2002) chimpanzees (Koski 2011), sheep (Sibbald et al. 2005), cows (Gibbons et al. 2010), Japanese quail (Mills & Faure 2000), common lizards (Cote et al. 2008), greylag geese (Kralj-Fišer et al. 2007), mice (Brodkin 2007), and cowbirds (Kohn et al. 2011). By structuring the spatial proximity between conspecifics, differences in sociability can influence access to social resources. In Zenaida doves (*Zenaida aurita*), individuals from gregarious populations tend to perform better on social learning tasks than individuals from territorial populations (Dolman et al. 1996). More frequent interactions with a more diverse range of conspecifics may facilitate access to resources, while increasing the chances of competitive and aggressive interactions. Engaging in fewer interactions with fewer individuals may reduce the risk of dangerous interactions, but also decrease access to needed resources and information from others. Thus, stable differences in an individual's sociability may have a wide influence on an individual's performance across an array of different social challenges.

Social preferences, or differences in who individuals approach, represents the other axis of a social niche. While two individuals may engage in the same number of approaches, one individual may approach few individuals, whereas another may distribute those approaches across all group members. Here, social preferences represent a significant bias to approach a specific class of conspecifics within the group. On average, strong preferences will likely construct sparser overall social networks with pockets of cohesive sub-groups. Weaker social preferences will generally tend to construct overall cohesive networks, while minimizing the emergence of cohesive sub-groups (Fig 3, B2, B3). If the strength of social preferences remains consistent across changes in context, than the qualities of these networks will persist, creating different social environments.

In contrast to sociability much less is known about individual variation in the strength of social preferences. While sociability only reflects the willingness to approach social stimulation, social preferences require an organism to freely choose between interactions with a range of individuals, and consequently more naturalistic settings are needed for preferences to be observed. Despite this, the effects of social preferences can be observed in the non-random interaction networks between individuals that provide the group with an organization. Within many social mammals sex-and age-based assortment seems to be the norm, meaning that on average individuals must be able to maintain preferential associations with individuals of a similar age-sex class (Ruckstuhl 2007). In some species separate male and female groups exist and interaction between adults of different sexes occurs only during reproductive periods (Bon & Campan 1996). The average social preference expressed by individuals may have cascading influence into the organization of the group, and therefore provide different contexts where social development can occur.

1.4 Social niche specialization:

As individuals develop and gain new experiences, the characteristics of their social niches will change. How their niches change in relation to others is an important aspect of their behavioral development, and may have cascading influences into their later reproductive success. There are two broad ways in which niches change over time. In response to changes in social context individuals may seek to either maintain or change their niches in relation to others (Bergmüller & Taborsky 2010; Bolnick et al. 2003; Montiglio et al. 2013). The hallmark of a *specialized social niche* is its contextual generality. Here, across very different social contexts and over time individuals will exhibit repeatable differences in their sociability and social preferences (Fig 3, A1, A2). In contrast, *plastic social niches* are highlighted by their contextual specificity. This means that between-individual differences in sociability or social preferences reflect the current context, and will change in relation to others once the context shifts (Fig 3, A3).

Groups are never entirely static, but are in a continual process of turnover and renewal as individuals emigrate and die, or are integrated and born into the group. This is especially true for groups that exhibit fission-fusion processes, where smaller groups may join together to form larger aggregate groups. In order for individuals to maintain consistency within these fluctuating groups they may need to continually adjust their behavior in relation to others. While specialized niches will remain correlated over contexts, the average qualities of an individual's niche may undergo substantial changes (Dingemanse et al. 2010). For example, while on average individuals may increase their rate of social interactions during migratory periods, researchers might observe high correlations from migratory to non-migratory periods. Within this dissertation, a specialized niche does not connote a static one, but rather a consistent one. To understand how these specialized social niches emerge, I first need to see if the early social environment facilitates the expression of consistent differences in sociability and social preferences across individuals.

Individuals are born into, and utterly dependent on, the social environment for survival. Access to social interaction is assured by the behavior of parents and siblings (West & King 1987), and the organization of interaction during this period, and even pre-natally, is essential for the ontogeny of species-typical behavior. Studies by Gottlieb (Gottlieb 1971, 1980, 1993), Lehrman (Lehrman 1959; Lott & Lehrman 1967), Alberts (Alberts 1978; Alberts & Gubernick 1983; Alberts 2007) and others (Bertin & Richard-Yris 2005; Cheng 1992; Meaney & Stewart 1979), have highlighted how repeated interactions between parents and siblings assures the ontogenetic reconstruction of behavioral patterns necessary to survive until independence. For instance, wood duck embryos depend on repeated auditory stimulation from their parents and siblings to develop a preference for their mother's call (Gottlieb 1963). Wood ducks nest in trees within flooded forests, and during hatching the mother will descend from the nest to the water and begin calling. Juveniles must utilize their pre-natal exposure to their mother's call in order to leave the nest and locate the mother below. Failure to do so would result in near-certain predation. Thus, from an early age, individuals are exposed to, and dependent upon, a consistent social environment. Nonetheless, little is known about how interaction within these early social environments shapes the expression of consistent individual differences in sociability and social preferences observed during adulthood.

Early environments are often more predictable than those encountered later in development. Parental influences and motor limitations constrain the types of interaction an individual can encounter early on. Individuals who experience a more unpredictable early environment will have to change their behavior in response to interactions with novel conspecifics. As such, it may be difficult for individuals to maintain consistent patterns of social interaction, resulting in more plastic social niches. Within more predictable social environments individuals will experience repeated interactions with known individuals. Here it may be easier to learn about the behavioral characteristics of conspecifics, differentiate one's behavior from them, and sustain those differences over time, resulting in more specialized social niches. For example, colonial spiders housed in more stable social environments, with only familiar conspecifics, exhibited a higher degree of behavioral consistency in contrast to spiders housed in unpredictable social settings, with frequent introductions of novel individuals (Laskowski & Pruitt 2014). Thus, predictable social environments may be the contexts where predictable differences in sociability and social preferences can emerge.

One way that niches become differentiated is through competition. As niches reflect differences in how individuals interact with their environment, overlapping niches may create competition over access to either resources or information. In order to avoid the costs of competition individuals may shift their behavior and occupy an alternative niche. This process, often called the competitive exclusion principle, or Gause's law (Gause 1934; Hardin 1960), has long been used to conceptualize ecological niche differentiation, but its application to social niches is comparatively recent (Bergmüller & Taborsky 2010; Montiglio et al. 2013). Nonetheless, competition over access to social resources such as maternal care, mates, or social learning opportunities may cause individuals to differentiate their social behavior in relation to others. Within mammals the early huddle is a good example of a predictable early social environment. Inside the huddle individuals may compete over access to thermally advantageous positions, as well as access to the mother's nipples (Alberts 1978, 2007; Bautista et al. 2008). In response to the competitive pressures individuals may modify their approach-withdrawal responses, with some individuals consistently holding different positions at the periphery or center of the huddle (Nicolás et al. 2011). These differences in early position in turn predict the consistency of an individual's later behavior across a wide range of modalities well into adulthood (Reyes-Meza et al. 2011). Within stable groups individuals often utilize different strategies when foraging. Some individuals will adopt a producer strategy, where they compete with others to utilize a new food resource, while others adopt a scrounger strategy where they scrounge for food once a producer has used it, thus avoiding competition while limiting access to new food resources (David et al. 2011; Giraldeau & Caraco 2000). Within predictable social environments competition may therefore be a mechanism where different social niches are expressed.

While parents and siblings often provide environmental predictability early on, such predictability can also be achieved through later social preferences. As discussed earlier, consistent preferences may construct reliable sub-groups, leading to a more predictable social experience. In particular, preferences for previous associates may assure that individuals have access to repeated interactions with known conspecifics. Upon leaving the protection of their immediate family, individuals may encounter unfamiliar conspecifics, and be forced to adapt to novel social contexts. Individuals who seek out social novelty may be more likely to encounter a diverse range of individuals, and therefore experience a more unpredictable environment. In contrast individuals, who seek out familiar conspecifcs with similar characteristics, may experience a more predictable social environment. If significant familiar preferences are maintained across group changes, then selective sub-group networks between familiar individuals will emerge. If significant familiar preferences are not sustained across group changes, then individuals will engage a wider diversity of both familiar and novel conspecifics causing networks within the group to become more homogenized. Thus, the expression of consistent familiarity preferences may create the sub-groups where specialized social niches can be expressed through repeated interactions with others.

Disentangling the influence of repeated associations on the specialization of social niches requires observing behavior across an array of different contexts. Throughout this dissertation I investigate the consistency or plasticity of sociability and familiarity preferences across varying timescales; from changes in group size and composition within a season, to changes exhibited across seasons and years. Such consistency was observed both within juveniles and adults of either sex in order to explore the developmental trajectories of social niches as males and females age. I also investigate whether groups maintain significant social preferences for both same sex and familiar conspecific across group perturbations. If repeated associations facilitate the emergence of specialized niches I should expect that: 1) significant familiarity preferences within the group reflect consistent between-individual differences in social niches from an early age and, 2) the strength of the between-individual differences will become stronger (Fig 2, A1), or at least remain consistent (Fig 2, A2), over development within a stable social group. If individuals maintain consistent social niches without exhibiting significant familiarity preferences then niches may reflect prior individual differences in experience, or pre-natal influence, that are sustained despite changing associations.

1.5 Social skills:

Throughout their lives individuals will face considerable challenges while navigating the social environment in pursuit of resources and mates. Groups often change in size and composition, and the behavioral state of conspecifics can shift over a period of seconds, such as going from foraging to predator avoidance, to more gradual changes, such as seasonal changes in reproductive and migratory state. Such fluctuations make the social environment considerably more complex and unpredictable than other factors. Some individuals may "optimize" their behavior based on the current social context, or possess social skills, and gain access to social resources such as mates, pair bonds and foraging opportunities. Social skills reflect differences in the ability to assess and respond appropriately to stimuli based on the available social information (King & West 1987; Taborsky & Oliveira 2012). Competent individuals will possess skill-sets that allow them to interact successfully across a diverse array of contexts, from foraging, to fighting, to flocking and mating. As differences in sociability and social preferences may expose individuals to different social challenges, I expect that individuals who occupy different niches may develop different skill-sets appropriate to those niches.

As reproduction is the currency of evolutionary progress, the skills needed for successful reproduction are among the most important to acquire. While the importance of social skills in shaping reproductive success is often assumed (King & West 2002; Taborsky & Oliveira 2012), few studies have looked at the developmental factors shaping variation in reproductive behavior. Successful reproduction often requires reciprocal courtship interactions, and the maintenance of close relationships for extended periods. Here individuals must coordinate and respond appropriately to another's behaviors, whether initiating a courtship display with a preferred mate, competing with others for access to mating opportunities, or engaging in joint parental care of offspring. While reproduction is inherently social, few studies have linked variation in non-reproductive social behavior to variation in courtship skills during reproductive periods

Competence reflects differences in behavioral performance across various contexts. One way to assess an individual's competence is by observing their behavior in response to non-reproductive challenges, such as integrating into a new group, along with their behavior during reproductive challenges, such as forming a successful pair bond. Individual with social niches characterized by more approaches with a wider range of conspecifics during non-reproductive periods may have more experience with a wider diversity of contexts than others. In turn these individuals may possess better skills when in comes to navigating the array of challenges faced when courting and competing with others during reproductive periods. Individuals with niches characterized with fewer interactions with specific individuals may be less able to compete with others during reproductive periods (However, by potentially avoiding direct competition these individuals may live longer and enjoy reliable rates of reproductive output over longer timescales). In this dissertation I will explore the possibility that reproductive behavior may be a more specialized expression of a general social niche, one that reflects the ability to engage and respond appropriately in close social interactions across a wide range of modalities.

The relationship between an individual's social niche and their social skills may exhibit a positive feedback relationship. Social niches characterized by a high frequency of interactions with a wide diversity of conspecifics may foster the development of skills used to manage such diversity. For instance, highly social, low preference niches may foster the development of affiliative behaviors that in turn are used to increase both the frequency and diversity of interactions with others. If such processes occur, then early social niches should be predictive of the development of affiliative skills. The development of those skills may cause the between-individual differences in sociability and social preferences to be more expressed, leading to an increased diversification of social niches over time (Fig 1, A1). In contrast, if individuals occupy a niche characterized by interactions with few individuals, they may develop the skills to avoid others, and increase the time spent with a few selected individuals. For instance, studies in quail have uncovered that individuals who are highly gregarious are less likely to be able to sustain a pair-bond during breeding periods than individuals who restrict their interaction to a more limited set of individuals (Schweitzer et al. 2010).

1.5 The Cowbird:

The Brown-headed Cowbird (*Molothrus ater*) is a common North American blackbird that ranges from the boreal forest of Canada to the tropical regions of Mexico. It is one of the eight recognized cowbird species that inhabit the Americas. Cowbirds are of considerable interest to both biologists and psychologists because of their obligate brood parasitic nature. Female cowbirds must lay their eggs within host nests, and depend on host species to raise their offspring. In no cases have cowbirds been observed to exhibit any parental care, even after the administration of hormones which commonly elicit parental care within other brood parasitic species (Dufty & Wingfield 1986; Scott & Ankney 1983).

Due to the cowbird's brood parasitic nature it has become an interesting species to investigate the factors shaping behavioral development.

While some cowbird species, such as the Giant Cowbird (*Molothrus oryzivorus*), specialize in a few host species, the Brown-headed Cowbird is far les selective, and has been observed to parasitize hundreds of different species (Ortega 1998). Such plasticity in host selection means young cowbirds will experience a very diverse early social environment, as eggs from a single female could be raised by a range of different host species, each with differences in their parental behavior. The instability of a cowbird's early experience has lead some theorists to postulate that cowbird behavior must be the result of innate genetic programs that allow cowbirds to both identify conspecifics, and know how to interact with them. For example Ernst Mayr (1974), one of the leading architects of the modern synthesis, once stated that, "the gestalt of his own species is firmly embedded in the genetic program with which the cowbird is endowed from the very beginning…As far as mate selection is concerned…There is no input from experience". As such, the cowbird was traditionally lauded as a prime example of a species where behavior should be experience-independent, as their social and reproductive skills were predetermined upon conception in response to the selective pressures of an unpredictable early environment.

This view is, however, simply false. Research by Meredith West, Andrew King and Todd Freeberg have demonstrated that reliable patterns of interaction with conspecifics are essential for the development of even basic species-typical skills, such as species identification, mate choice, and vocal competence (Freeberg et al. 1995; Freeberg 1996;

Freeberg et al. 2001; King et al. 1996). For instance, if juvenile male cowbirds are raised with heterospecific females, in this case domesticated Canaries (*Serinus canaria*), they fail to develop the ability to effectively court conspecific females (Freeberg et al. 1995). Males raised with canaries were significantly more likely to direct songs and copulatory attempts to canaries in contrast to conspecific females, whereas males housed with conspecific females were more likely to direct songs towards other males. Thus, where theorists expected to find the best example of experience-independent behavior, social experience remains central to the development of the most basic behaviors needed to successfully navigate the social environment and reproduce.

Cowbird courtship revolves around a female's response to male song displays. While males may sing throughout the year, the majority of songs are performed during the breeding season from May to mid July. Male song contains a series of note clusters followed by a high-pitched whistle (King et al. 1981). The acoustics of the cowbird's song assure that only individuals in close proximity are able to hear the full range of sound, and therefore song is often performed within a few inches of others. Overall, males use two different types of song, an undirected song, that is sung while alone, and a directed song display, that is used when engaging another individual with song. During a directed song display a male orients his beak within 45 degrees of another individual, and delivers a song while bowing, fluffing out his feathers, and spreading his wings (Friedmann 1929). Songs directed towards males often end with the tail being raised, whereas songs to females often do not exhibit significant tail raises in order to reduce withdrawal (O'Loghlen & Rothstein 2010). Males also exchange directed song displays in a tit-for-tat manner within counter-singing matches. The ability to counter-sing effectively may be one of the more important courtship skills that males need to develop. Female cowbirds use a male's counter-singing ability when making mate choice decisions, and the level of counter-singing within the flock is a strong predictor of egg production. Studies have shown that within aviaries characterized by a higher proportion of counter-singing that females produce more eggs than in flocks with lower levels of counter-singing (White et al. 2010b).

Female responses to male song are essential ingredients in a cowbird's species typical development. While female cowbirds do not sing, they do provide both visual and acoustic feedback to males that reinforce preferred song variants, attract male attention, sustain pair bonds, and coordinate behavior. During the fall males will often cycle through their song repertoires and improvise new song variants when engaging females. Favorable song variants may elicit a "wing-stroke" from females that is characterized by a slight elevation of the wing over a few milliseconds in response to song (West et al. 1998). Males often exhibit large behavioral responses to wing-strokes from females, and males who receive more wing-strokes will develop higher quality song variants within their repertoire (West & King 1988). There is some evidence that females may also attend to the wing-strokes of other females (Gros-Louis et al. 2003), potentially allowing for the transmission of mate preferences between females (West et al. 2006).

Most of the previous work on cowbird vocal development has focused on the social contributions to the development of male singing behavior. Nonetheless, an increasing amount of studies are looking at the ontogenetic correlates of variation in female vocal skills (Kohn et al. 2013b, Submitted; Maguire et al. 2013). While males must learn to engage a wide diversity of conspecifics using song, and modulate the use of their song based on the sex and identity of the recipient, females must selectively utilize their vocal responses to song in order to reinforce a preferred males attention and foster stronger pair bonds. During the breeding season females use a “chatter” vocalization both while alone, and in response to male songs. Chatters have been known to attract male attention in the field, and are individually distinct allowing for individual recognition (Burnell & Rothstein 1994). While it has been suggested that they play a role in the formation of pair bonds, studies have shown that females may use the chatters of others in order to guide their own mate preferences (Freed-Brown & White 2009). Playbacks of songs followed by a chatter elicit higher rates of copulatory postures than playbacks of the same songs without chatter vocalizations. While the chatter may be an important contributing factor to their reproductive performance within the flock, less is known about its development in comparison to male song, and how exposure to chatter vocalizations may shape the ontogeny of both male and female reproductive behavior.

In order to understand how cowbirds become reproductively competent adults, I first need to understand how they become integrated into cowbird flocks, and how differences in social experience shape the ontogeny of later courtship behaviors. For most birds little is known about the within-group association patterns outside of breeding periods. Nonetheless, social interaction during these periods may play an important role in shaping social development and later reproductive performance (Kohn et al. 2013a, b). After breeding, cowbirds join mixed sex and/or age flocks. These flocks often contain a mix of both resident and migratory birds from other populations. As they move southward from September to late November, these flocks will join with others to form larger migratory aggregations (Friedmann 1929; Ortega 1998). Such fission-fusion dynamics may foster the adoption of plastic and unselective interaction preferences to adapt to changing conditions, or strong familiarity preferences in order to sustain preferential contact with prior associates despite changing conditions. Thus one of the first steps in looking at cowbird social development is by focusing on how differences in the quality of an individual's social niche during the fall is able to shape the development of social behavior used during reproductive periods.

The first challenge for all cowbirds may be locating and integrating into established cowbird flocks. After fledging juveniles have been observed both alone, within smaller flocks composed completely of juveniles, as well as within larger mixed age and sex flocks (Friedmann 1929). While the processes whereby fledgling cowbirds initially find other cowbirds are unknown, I do have some suggestions on how integration might initially occurs. Cowbird parasitism often occurs on forest edges, which is also where cowbird flocks often frequent. Similar food demands may mean that cowbirds will be statistically more likely to encounter other cowbirds than other species when fledging. Cowbirds also possess a species-specific affiliative display known as the head-down (Fig 3), which will be discussed in detail later in this dissertation. Young individuals may use the head-down to explore their early social environments, and juveniles will direct head-downs towards both heterospecifics and conspecifics. Only conspecifics will actively reciprocate the display, making it a species-specific social signal that may facilitate species identification and foster integration into cowbird flocks.

For juveniles, access to reliable patterns of interaction with experienced adults is important for the development of later courtship and reproductive performance. For adults interactions with inexperienced juveniles may both aid (White et al. 2002b) and inhibit (West et al. 2002) their reproductive performance. Once integrated into cowbird flocks juvenile cowbirds must navigate a wide diversity of different interactions with other individuals. How and whom individuals interact with during this period may have important developmental consequences, as for many cowbirds this will be their first time experiencing interaction with adults of both sexes. For instance, juvenile males housed with more sociable adult females engaged in higher rates of counter singing, and were more competitive in mating competitions than males housed with less sociable females (King et al. 2003). Most studies looking at early interactions involve "social-knock outs" where a class of individuals is removed from the groups, and the resulting deficits on social development among other group members is measured (West et al. 2011). In particular the removal of experienced adult males significantly alters the social development of juvenile males. Juvenile males housed without access to experienced adult males developed different social interaction patterns then those typically observed. These naïve juveniles were less likely to have near neighbor interactions with other male, use fewer songs in interactions, and were much less aggressive then the experienced juvenile males (White et al. 2002c). Such results suggest that access to the full range of social experiences, including interactions with experienced adults may have a significant influence on aspects of a male's sociability.

In cowbirds social interactions will have a cascading influence into their later social and reproductive behavior (White, et al. 2007). As access to social stimulation from others is an essential factor governing cowbird behavioral development, different social niches may foster different developmental trajectories by guiding an individual's exposure to others. In the studies presented here I investigate how differences in an individual's ability to approach and interact with conspecifics during the fall shapes their reproductive performance months later during the breeding season. The challenges cowbirds face across the fall and breeding season are very different. During the fall, cowbirds need to engage others within changing fission-fusion flocks. Here individuals may need to use behavioral skills that facilitate close interaction with others, while minimizing the risks of aggressive encounters. During the breeding season individuals need to compete with other and successfully court preferred mates. Competent cowbirds may be better able to respond to both of these challenges.

In contrast to males little is known about behavioral development of females. While it is becoming increasingly recognized that the importance of female behavior is often underestimated, studies on social development within female birds have been few. While flock living is known to change a female's mate preferences, and that access to social cues from other females play a role in the ontogeny of their mate preferences in cowbirds, less is known about the within group interaction networks that females participate in across development across most bird species. Throughout this dissertation I will focus on how the between-individual differences in the social niches across the sexes contribute to the development of their reproductive behavior. While this dissertation contains some insights into how individual differences in social behavior among males shape their reproductive performance, most of the findings focus on how the existence of specialized female social niches are predictive of later courtship skills and reproductive output.

1.7: General Layout of the dissertation

In this dissertation I aim to investigate the formation of specialized social niches within Brown-headed Cowbirds, and how these niches influence an individual's reproductive performance through the development of social skills relevant to them. My first aim is to look at the consistency of a cowbird's fall sociability and social preferences across development. My second aim is to see if variation in fall specialized social niches are able to predict the emergence of later courtship skills and reproductive output during the breeding season.

The second chapter is focused on investigating the characteristics of a cowbird's social niche across development. This chapter cover two studies: The first study looks at the consistency in sociability, measured in the number of social approaches an individual initiates and receives, and the strength of same sex social preferences across flocks of juveniles and adults. Here I uncover that females, but not males, sustain repeatable between-individual differences in sociability across fission-fusion groups changes. Furthermore, these studies also show that females are able to sustain strong sex and familiarity based social preferences across fission-fusion changes, and therefore construct predictable sub-groups over time.

The third chapter will focus on the reproductive consequences of such variation in adult social niches. Two studies will be presented that demonstrate how consistent social variation in fall interaction networks is able to predict reproductive and courtship behaviors months into the future for both females and males. The first study demonstrates that individual variation in female sociability in consistent across years, and is able to predict the number of eggs produced both at the flock and individual levels. The second study shows how between individual differences in an affiliative display, the head-down also predicts the number of eggs produced, but also the emergence of competent counter singing skills within adult males.

The fourth chapter takes a more developmental turn, and looks at how interaction patterns within juveniles predict the emergence of courtship skills during the first year of life. Here the focus is on understanding how individual social variation may influence the genesis of competent courtship behaviors before sexual maturity. I show that variation in the use of head-downs within juvenile females remains consistent, and is able to predict the ontogeny of the chatter vocalization within the first breeding season.

The fifth chapter ties together the findings from the third and fourth chapters, by looking at how consistent variation in the use of chatters shapes egg production in adult females. The studies covered here will show how consistent variation in female courtship behavior shapes the formation and maintenance of strong pair bonds, leading to higher egg production. The discussion ties the studies together by highlighting how an understanding of individual developmental trajectories, may assist in our understanding of the evolutionary process shaping both social behavior and social organization.

The sixth chapter will discuss the implications of these findings for our conceptualization of individual behavioral development, and its potential to shape evolutionary processes. In particular I highlight how understanding the social contribution arising both intrinsically and extrinsically are essential the development of fitness differences between individuals. Therefore, selection may act on the repeated and reliable ontogenetic reconstruction of favorable social niches across generations.

1.8 Figures:

Figure 1.

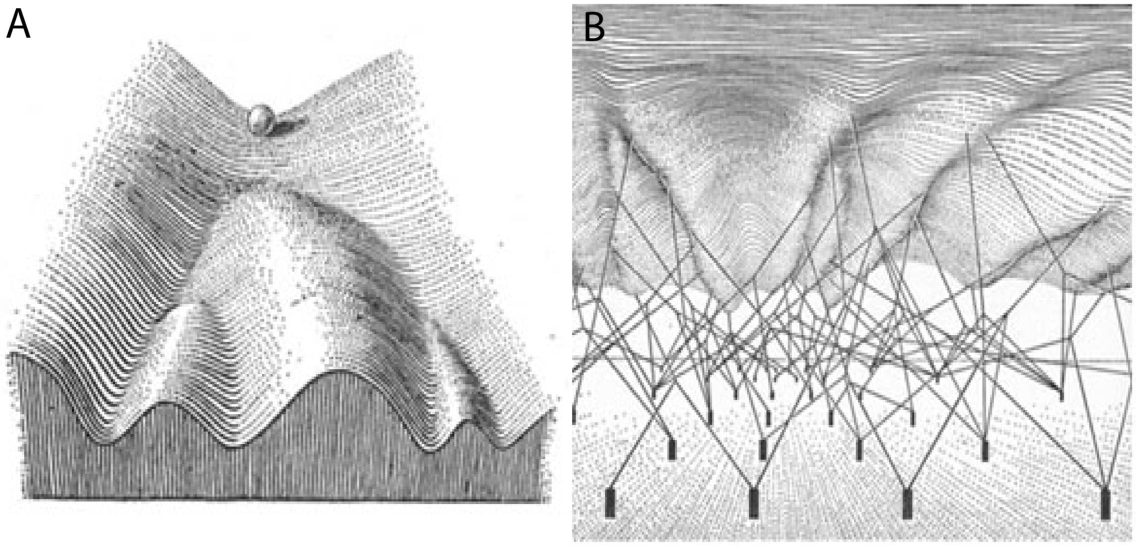


Figure 1. Waddington's Epigenetic landscape taken from his book *Organisers and genes* (Waddington 1940). The ball in picture A represents the current position in an individual's developmental trajectory, or its current phenotype. As the ball rolls down the landscape it reaches many bifurcations that may shift the development of its phenotype. The contours of the landscape are shaped by the relationship of the individual's genes with its environment. This is highlighted by the pegs, or the individual's genes, and ropes, representing the gene by environment relationship, in picture B.

Figure 2. Measuring social niches

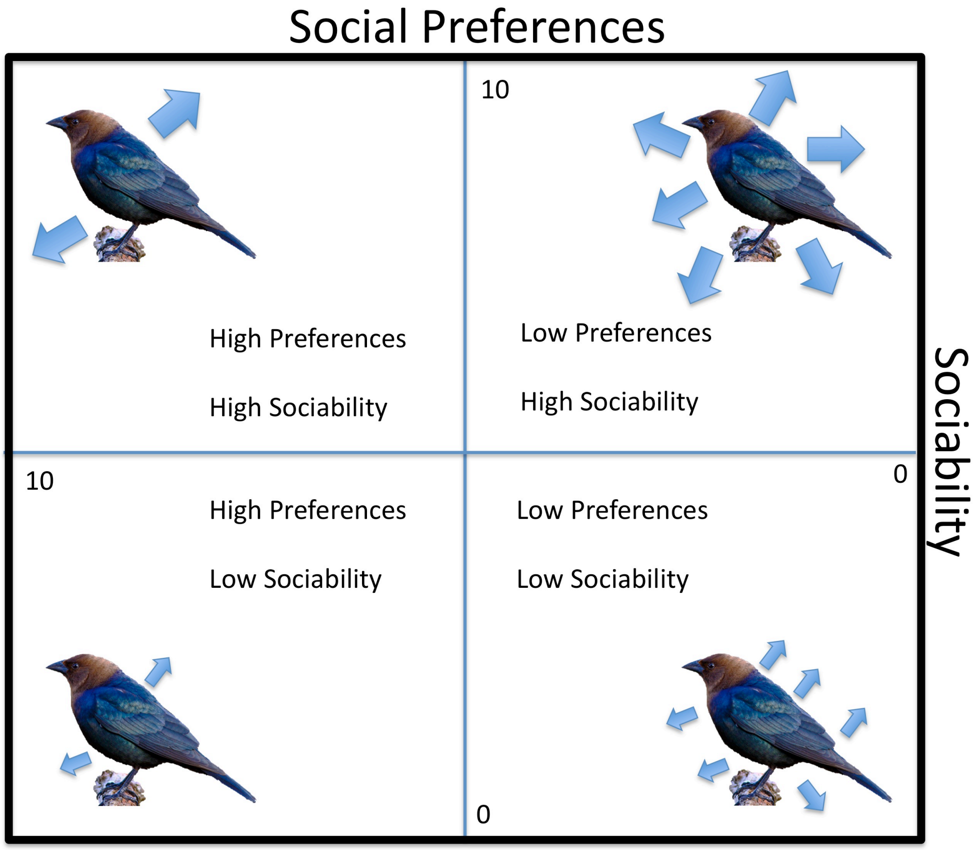


Fig 2. This diagram represents one estimate of an individual's social niche within the larger group. The size of the arrows represents the frequency of social interaction, while the number of arrows represents the connections with others in the group. High preference scores (those approaching 10) reflect individuals who have strong biases in who they interact with, while high sociability scores represent higher rates of social interaction.

Figure 3.

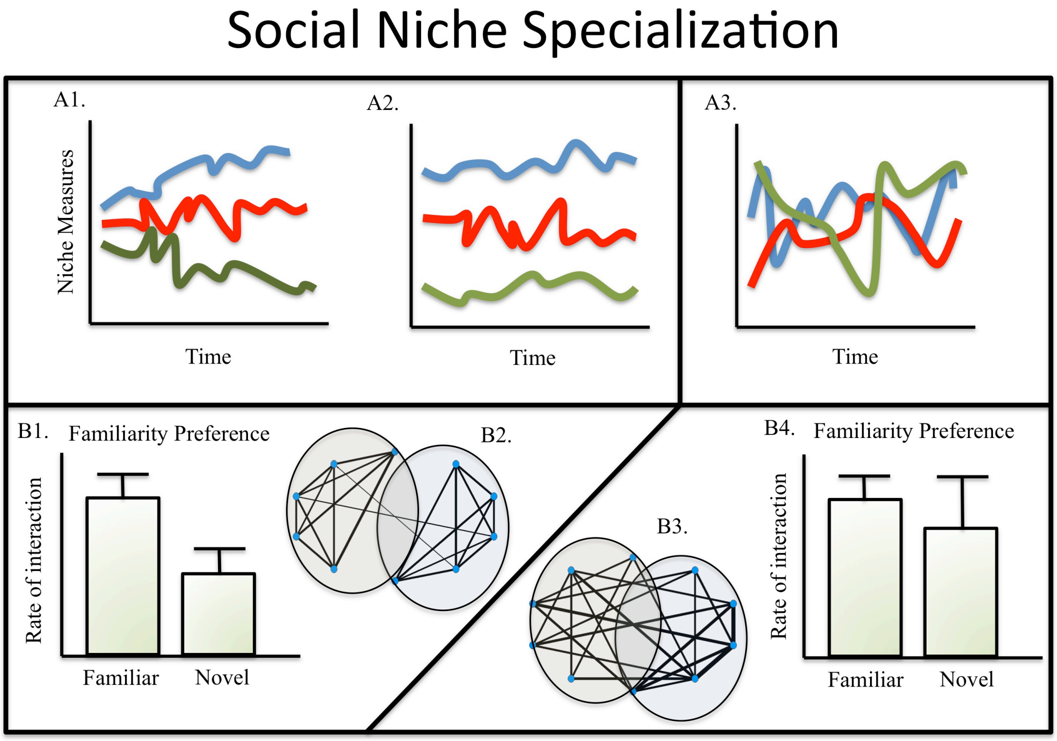


Fig 3. According to the social niche specialization hypothesis, when two groups join together, stronger familiar preferences should create greater between-individual variation over time. The social networks represented by diagrams B2 and B3 represent the social integration of two prior groups represented by the circles. In B2 individuals maintain preferential assortment patterns with familiar conspecifics (B1), whereas in B3 individuals show no preference for prior associates (B4). Groups with strong preferences for familiar conspecifics during integration should exhibit consistent between-individual behavioral differences over time (A1 and A2), whereas groups with no familiar preferences during social integration should change their niche over time (A3).

Second Chapter: Social niches in fall cowbird flocks

2.1: Introduction

The introduction of this dissertation stressed the importance of social niches for developmental and evolutionary processes. This chapter will cover a series of studies that investigate the strength and consistency of an individual's social niche in relation to other group members. Many vertebrates inhabit loosely structured groups that exhibit fission-fusion processes in which the number and composition of members change over short timescales. Often during fission and fusion, smaller sub-groups coalesce into larger groups before fragmenting again into smaller sub-groups. Significant changes in social density and composition may rapidly induce changes in individual social interaction patterns, potentially causing groups to become less cohesive and even dissolve (Calhoun 1962; Flack et al. 2006; Fushing et al. 2014; Sih & Watters 2005). Thus, in order to understand how social organization persists, I must look at the responses of individual social niches to group changes. During fission-fusion processes, individuals can respond to changes by attempting to maintain equivalent interaction patterns in relation to others, or by changing their interaction patterns in order to adapt to the demands of a new social composition. The studies covered in this chapter investigate the consistency of social interaction patterns and preferences across fission-fusion changes within different age / sex categories that come to define an individuals social niche.

Within the confines of traditional laboratory research, it is often difficult to generalize results onto more naturalistic contexts where individuals have more agency over whom, how, and when they interact with others. Nonetheless, the limitations of field studies often make it difficult to observe and follow individuals over longer time periods, making longitudinal studies of individual social behavior difficult. Charles Otis Whitman, one of the pioneers of animal behavior, was the first to suggest that semi-naturalistic social conditions could be recreated within "biological farms" where one could "observe and experiment under conditions that ensure *free behavior*" (Whitman 1899). The compromise between field and laboratory settings offered by the semi-naturalistic approach may allow us to gain more generalizable insights into the factors shaping social behavior. Within this dissertation the approach has been to recreate, to the best of our ability, the naturalistic groups observed under some contexts in the wild. These groups can then be manipulated in an equivalent fashion to changes observed in wild groups, to see how the birds reorganize their behavior in response to changes in group size and composition.

The studies covered in this chapter investigate the consistency and plasticity of adult and juvenile social niches when the social environment is perturbed. By perturbing an existing group by removing or adding individuals I can assess if a social niche maintains rank-ordered consistency across changes in social context. Throughout this dissertation a stable social niche is defined by correlated patterns of sociability and social preferences across different contexts, whereas a plastic niche reflects non-correlated patterns of sociability and preferences across contexts. Such methods have been used extensively within primates to understand the role individuals play within the social group. In macaques, social perturbations have been used to assess the role of policing behavior (an individual who intervenes during aggressive encounters) in maintaining group cohesion. Removing policing males destabilizes individual social networks, leading to a less cohesive group, and more aggressive interactions (Flack et al. 2006). Studies in cowbirds used perturbation techniques to understand the role of specific individuals in shaping the behavioral development of conspecifics (Gros-Louis et al. 2006; King et al. 2003; White et al. 2007). Here juveniles were raised in a group where specific age-sex classes were removed, and compared to other juveniles who were raised in a control group. Often the removal of experienced adults hampers the development of social skills in juveniles, as it deprives individuals of the social contexts needed to acquire the feedback from others.

An individual's sex is also an important determinant of the social niches they construct within the group. Even during non-reproductive periods males and females face different challenges when interacting with others. Across some social species females play an important role in constructing core groups, whereas males may disperse from their natal group to avoid inbreeding, and form new associations (Pusey 1987). Such patterns suggest that females may benefit from forming stable relationships with other females (Silk et al. 2009), whereas males may benefit from being able to interact with a diverse range of individuals (White et al. 2009). Within cowbird flocks males maintain stronger dominance relationships with others, whereas females do not exhibit dominance relationships. Males will benefit from engaging and interacting with others during periods of change in order to increase one's social status within the flocks, while the arrival of new and potentially aggressive males may pose significant risks for females. Furthermore close female-female interaction during the fall is known to shape later mate preferences (West et al. 2006), and females may maintain close associations with females in order to access information about potential mates. Therefore, in response to changing social compositions, I hypothesize that females will maintain stronger and more consistent social approach patterns and preferences than males. As males must reassess their relationship with others when the social composition changes, I hypothesized that perturbing the social environment will cause males to change the frequency and preferences of social approaches in relation to others when conditions change.

This chapter covers two studies, the first study focuses on the consistency of social approach tendencies, and the second study investigates the consistency of social preferences for familiar conspecifics. In the first study, two flocks, one with familiar adults and one with naive juveniles, were separated into two smaller flocks and then recombined. Here the main goal was to investigate the differences in the social niches that adults and juveniles, and males and females construct across similar fission-fusion changes. I expected that adult females would be able to maintain robust levels of sociability in comparison to adult males. As juveniles may not yet have developed the full social repertoire needed to sustain interaction with a wide diversity of conspecifics, I also predicted that juvenile social niches would exhibit greater flexibility and less internal coherence than adults. In particular I expected juveniles to change their approach rate in relation to others across group changes. A second aim of this study was to uncover whether individuals exhibited any significant preferences to assort with same-sex individuals when the conditions changed. Previous studies have shown significant age-sex based assortment patterns in cowbird flocks, but little was know about its occurrence at early ages. This study will show if sex assortment preferences are exhibited within solely juvenile flocks, and if changes in group size and composition change the strength of those preferences.

In my first study social network measures were used in order to operationalize individual differences in sociability across contexts. Centrality measures are designed to capture how an individual relates to others in a group (Freeman 1979). Here sociability had two components, one is individual gregariousness and the other is an individual's attractiveness. When approaches are directed towards specific individuals, degree centrality uses the frequency of approaches directed toward others to calculate gregariousness, and the frequency of approaches that are received from others to calculate attractiveness. Degree centrality is therefore a useful construct for measuring an individual's social niche by capturing both directions in how individuals relate to others (Faust & Skvoretz 2002; Flack et al. 2006). I expected to find stable variation in the characteristics of social niches, with some individuals being more gregarious or attractive than others. Degree centrality also allows us to quantify these niche characteristics and see if they are related (or internally coherent). For instance, gregarious individuals may also be highly attractive. Thus, using degree centrality, I can uncover the characteristics and stability of an individual's niche.

The second study investigates the strength and persistence of social preferences across social contexts. The instability of fission-fusion groups presents challenges in with who to engage and and how often. Homophily, or associating with conspecifics who share at least one characteristic as yourself, is a common factor in both human (McPherson & Smith-Lovin 1987) and animal groups (Kohn et al. 2011; Ruckstuhl 2007). Such shared characteristics may range from similar size or sex, to similar behavioral characteristics, or previous associations. In fission-fusion groups, individuals are often faced with a shifting landscape of both familiar and novel conspecifics. Consistent preferences for familiar individuals may create sub-groups that are sustained over time, while potentially decreasing the overall cohesiveness and persistence of larger aggregations.

Living in close proximity can create competition over resources, and lead to increased risks of aggressive encounters with conspecifics (Aureli et al. 2008; van Schaik & van Noordwijk 1988). The formation of familiar sub-groups within larger aggregations can function to make social interactions more predictable, lessen the chances of aggressive encounters, and lower stress levels (Marler 1976; Strodl & Schausberger 2013; Takeda et al. 2003). Such conditions may also allow for more effective transfer of social information, increased behavioral coordination, and efficient foraging (Lachlan et al. 1998; Laland & Williams 1997). Nevertheless, strong familiar sub-groups may also hinder the integration of new individuals, making larger aggregations less cohesive, and more prone to fragmentation (Lusseau 2003; Wasserman & Faust 1994). As large aggregations offer increased protection from predators, and decreased individual vigilance, modulation of familiarity preferences may sustain the benefits of remaining within a larger group. Thus, the persistence and strength of familiarity preferences across fission-fusion changes reflects the challenges and risks individuals face when engaging novel conspecifics. In the current study I investigated the strength and stability of social preferences within brown-headed cowbirds. In particular, I tested whether individuals maintain consistent and preferential associations with familiar conspecifics when flock conditions change.

My second study contained two experiments. First, I investigated if individuals exhibited an overall preference for approaching novel or familiar conspecifics. During 2012, I conducted introduction experiments in two cowbird flocks, a familiar and unfamiliar flock. Each flock was created through the fusion of two smaller sub-flocks. In the familiar flock, the sub-flocks had previously been housed together for an extensive period before the study, and were thus deemed familiar, while in the unfamiliar flock, both sub-flocks had never previously interacted. Next I investigated the persistence of familiarity preferences across multiple introductions. During 2013, four flocks were created through a series of introductions where they could either interact with familiar or unfamiliar conspecifics. I measured whether preferences to interact with familiar conspecifics persisted across the introductions.

2.2: The consistency of individual sociability

Methods:

Subjects: All birds were originally captured either in Philadelphia County, Pennsylvania or Monroe County, Indiana and housed in aviaries in Monroe County, Indiana. All subjects were *Molothrus ater ater*. Previous social and song development studies with both populations have found no song, structure or social differences (unpublished data, King). I used 33 female and 29 male cowbirds. The adult flocks contained 21 adult females and 17 adult males, and the juvenile flocks contained 12 juvenile females and 12 juvenile males. At the beginning of the study, adults ranged in age from 3 to 11 years with an average age of 6 and juveniles ranged in age from 55 to 75 days old with an average age of 73 days. Adult birds were housed together for a year and juveniles were housed together for one month prior to the present study. After being caught, juveniles were housed separately from adults and had no direct interactions with adults after capture. Each bird was marked with uniquely colored leg bands to allow for individual recognition. All birds were provided daily with a diet of vitamin treated water (Aquavite Nutritional Research), red and white millet, canary seed and a modified Bronx Zoo diet for blackbirds.

Aviaries: I used three aviaries that were visually isolated and substantially acoustically attenuated or isolated from each other, each with identical dimensions (9.1 x 21.4 x 3.4 meters). Environmental conditions were similar throughout all aviaries with shrubs, trees, grass, covered feeding stations and access to indoor enclosures. All aviaries allowed birds to be exposed to ambient climatic conditions, wild cowbirds, and the sight and occasional interaction with predators.

Data collection: An approach was scored when one individual approached another individual with any part of its body within a radius of 30cm. The identity of the individual who initiated the approach and the individual who was approached was recorded. Throughout the study, I utilized a scan-sampling procedure: behaviors were recorded as they were observed using voice recognition technology described in detail by White et al (2002). When used in combination with voice recognition technology scan-sampling can accurately acquire a more comprehensive dataset than focal sampling. All observations were conducted between 07:00-10:30 when cowbirds are most active. All observations were counterbalanced so that each observer took the same number of scan-sampling blocks in each aviary at the same time of day. All work was conducted under ABS guidelines and approved by the Institutional Care and Use Committee of Indiana University (05-010).

Experiment 1: Adults

Stage one: Baseline period. On September 2nd, 2009, all individuals were moved into Aviary 1. From September 3rd to September 18th, 2009, two observers conducted daily counterbalanced observations, each recording approaches collecting a total of 126 seven-minute observation blocks.

Stage two: Fission Period. On September 18th, I separated the birds into Aviaries 1 and 2 based on their frequency of approaches during the Baseline period so that both flocks contained a similar range of approaches. Aviary 1 contained 11 females and 9 males, and Aviary 2 contained 10 females and 8 males. From September 19th to November 21st, two observers conducted daily counterbalanced observations, each recording approaches, and collected a total of 573 seven-minute observation blocks (286 blocks in Aviary 1, 287 blocks in Aviary 2).

Stage three: Fusion Period. On November 21st, the partition separating the two aviaries was opened and both flocks were allowed to interact. From November 21st to December 4th, two observers recorded approaches in both Aviaries 1 and 2. A total number of 108 seven-minute observation blocks were collected during the Fusion stage.

Experiment 2: Juveniles

Stage one: Baseline period. From September 7th to October 11th, 2010, three observers conducted daily observations in Aviary 1 each recording approaches, collecting a total of 165 seven-minute observation blocks.

Stage two: Fission Period. On October 13th, I separated birds into Aviary 1 and Aviary 2 based on their frequency of approaches during the Baseline period, so that both flocks contained individuals with a similar range of approaches. Both aviaries contained 12 males and 12 females. From October 13th to October 24th, three observers conducted daily counterbalanced observations recording approaches, and collected a total of 195 seven-minute observation blocks (98 blocks in Aviary 1, 97 blocks in Aviary 2).

Stage three: Fusion Period. On October 27th, all birds were moved into Aviary 1. From October 27th to November 6th, three observers conducted daily observations recording approaches, and collected a total of 166 seven-minute observation blocks.

*Analysis :*I checked all data for normality using a Kolmogorov-Smirnov test. To uncover the influence of age, sex and period on the degree of sex assortment I conducted General Linear Mixed Model. The proportion of approaches towards females was the dependent variable, with period (baseline, fission, fusion), age (adult, juvenile) and sex (male, female) and the fixed factors and individual included as a random factor. I conducted a further Bonferroni–adjusted post-hoc pairwise comparison based on the estimated marginal means to uncover the degree and direction of difference between the variables. Significant values for both fixed factors and post-hoc comparisons were determined using two tailed p-values with $\alpha = 0.05$ with confidence intervals reported for the estimated marginal means. Comparison of the approach proportions between aviaries during the Fission period revealed no significant differences in adult or juvenile flocks (Adults: Mann-Whitney U-Test: $U = 158$, $N1 = 20$ $N2 = 18$, $P = 0.52$, Juveniles: $U = 75$, $N1 = 12$ $N2 = 12$, $P = 0.87$). Therefore data from the Fission period was combined for our model.

Using the approach data, I calculated degree centrality for each individual during each period. Because interactions in this study were directed, degree centrality was parsed into indegree and outdegree centrality. If a focal individual approached more individuals more frequently, they would have a higher *outdegree* centrality, and if a focal individual attracted more approaches from more individuals, they had a higher *indegree* centrality (Faust & Skvoretz 2002). Outdegree centrality corresponds with an individual's gregariousness, and indegree centrality corresponds with their attractiveness (Wasserman & Faust 1994). For the Fission period, both indegree and outdegree centrality were calculated for each of the two separated flocks, and for the Baseline and Fusion periods, it was calculated for the entire flock. Spearman correlations were used to investigate whether there was a relationship between an individual's outdegree and indegree in each period, and whether an individual's indegree/outdegree centrality demonstrated repeatability across periods.

To test if individuals approached the same individuals at similar frequencies across periods, I used a *Kr* row-wise matrix correlation with 4 000 permutations. The *Kr* correlation was developed to compare directed interaction matrices and can be used to demonstrate if stable interaction preferences among pairs of individuals are sustained across contexts. Significant *Kr* correlations approaching 1.0 indicate that most individuals interacted with the same individuals between the different periods. I compared male-male, female-female, male-female and female-male interaction matrices from the baseline and fusion periods for both the adult and juvenile flocks. This will show if individuals approached the same males or females when the flocks were recombined.

Observer bias was tested using Kruskal-Wallis tests (Juvenile Flocks, Baseline: H 2 = 0.339, $P = 0.56$, Fission: H 2 = 1.280, $P = 0.26$, Fusion: H 2 = 0.083, $P = 0.77$) revealing no significant differences between observers in the number of approaches observed in each period (Ottoni et al. 2005). Interclass correlation components (ICC) were used to test observer reliability showing all observers ranked birds based on the number of approaches similarly in each period (ICC: adults = 0.85, $P < 0.0001$, juveniles = 0.73, $P = 0.002$).

All statistical analysis was conducted using the R statistical computing platform version 2.11.0 (the R project website, http://www.r-project.org/) and SPSS (2005) and degree centrality measures were calculated using UCInet (Borgatti et al. 2002).

Results:

Frequency of approaches:

Adult Flock: During Baseline, I recorded a total of 2,732 approaches; during Fission, I recorded 19 039 approaches; and during Fusion, I recorded 3,405 approaches. Across all conditions, I recorded a total of 5,587 female to male (FM) approaches, 6,866 female to female (FF) approaches, 5,618 male to male (MM) approaches and 7,105 male to female (MF) approaches. I recorded an average rate of 22 approaches per block during Baseline; 33 approaches per block during the Fission period; and 32 approaches per block during the Fusion period.

Juvenile Flock: During Baseline, I recorded a total of 2,005 approaches; during Fission, I recorded 2 791 approaches; and during Fusion, I recorded 3,255 approaches. Across all periods I recorded a total of 1,150 FM approaches, 2,892 FF approaches, 2,448 MM approaches and 1,561 MF approaches. I recorded an average rate of 12 approaches per block during Baseline; 14 approaches per block during the Fission period, and 20 approaches per block during the Fusion period.

Comparison of proportion of approaches in Adult and Juvenile Flocks:

Our model demonstrated that the fixed effects of period (F (2, 116) = 6.038, P = 0.003) and sex (F (1, 58) = 91.285, P < 0.0001) significantly influenced the proportion of approaches towards females, whereas age had a marginally significant effect (F (1, 58) = 3.917, P = 0.053). Post hoc analysis demonstrated that females (M = 0.66, SE = 0.015, 95% CI [0.63, 0.69]') sustained a significantly higher (*Mean Difference* = 0.21, SE = 0.022, P < 0.0001) proportion of approaches towards females in contrast to males (M = 0.45, SE = 0.016, 95% CI [0.42, 0.48]). Juveniles (M = 0.57, SE = 0.017, 95% CI [0.54, 0.61]) exhibited a tendency (*Mean Difference* = 0.044, SE = 0.022, P = 0.053) to have a higher proportion of approaches towards females than adults (M = 0.53, SE = 0.014, 95% CI [0.50, 0.56]). The fusion period exhibited a significantly lower (Baseline-Fusion: *Mean*

Difference = 0.042, *SE* = 0.015, *P* = 0.02, Fission-Fusion: *Mean Difference* = 0.048, *SE* = 0.015, *P* = 0.005) proportion of approaches towards females in comparison to all other periods (Baseline: *M* = 0.56, *SE* = 0.014, 95% CI [0.54, 0.59], Fission: *M* = 0.57, *SE* = 0.014, 95% CI [0.54, 0.60], Fusion: *M* = 0.52, *SE* = 0.014, 95% CI [0.49, 0.55]). Thus, our model demonstrates that although the overall proportion of approaches towards females changed with the social perturbations, females preferentially approached other females.

Our model also discovered a significant interaction between sex and age (*F* (1, 58) = 33.946, *P* < 0.0001, Fig 2.1) on the proportion of approaches towards females. Juvenile females maintained the highest proportion of approaches to females (*M* = 0.74, *SE* = 0.024, 95% CI [0.69, 0.79]), whereas juvenile males maintained the lowest (*M* = 0.40, *SE* = 0.024, 95% CI [0.36, 0.45]). Post-hoc analysis revealed that juvenile females maintained significantly higher proportion (*Mean Difference* = 0.172, *SE* = 0.030, *P* < 0.0001) of approaches towards females in comparison to adult females (*M* = 0.57, *SE* = 0.018, 95% CI [0.53, 0.61]), whereas adult males (*M* = 0.49, *SE* = 0.02, 95% CI [0.45, 0.53]) sustained a significantly higher proportion (*Mean Difference* = 0.085, *SE* = 0.032, *P* = 0.01) of approaches towards females than juvenile males. In both the adult and juvenile flocks females maintained a significantly higher (juveniles: *Mean Difference* = 0.338, *SE* = 0.034, *P* < 0.0001, adults: *Mean Difference* = 0.082, *SE* = 0.027, *P* = 0.004) proportion of approaches towards other females in contrast to males. These findings demonstrate that an individual's age and sex influenced how they allocated their approaches, and that juvenile females biased their approaches towards other juvenile females over juvenile males (Fig 2.1).

Degree centrality:

Adults: Adult females maintained equivalent patterns of interaction throughout the study: Across all three periods, I observed significant correlations in adult female indegree and outdegree centrality ($N = 21$, Table 2.1), and within all periods, adult female outdegree centrality was significantly correlated with indegree centrality (Spearman rho: Baseline, r s = 0.61, $N = 21$, $P = 0.004$; Fission, r s = 0.75, $N = 21$, $P < 0.0001$; Fusion, r s = 0.76, $N = 21$, $P < 0.0001$). Consequently, adult females constructed stable social niches as gregariousness was correlated with attractiveness in all periods.

Adult males were less able to construct equivalent patterns of interaction when the social context changed. While adult male outdegree centrality was significantly correlated over the three periods, there was no significant relationship in a male's indegree centrality across periods (Table 2.1). Male outdegree centrality was only significantly correlated with indegree centrality during the Fission period (Fission, r s = 0.73, $N = 17$, $P = 0.001$). Thus, adult males did not maintain stable niches and their gregariousness was not correlated with their attractiveness in all periods.

Juveniles: Juvenile females maintained equivalent social niches throughout the study. Across all periods, I observed significant correlations in juvenile females' indegree and outdegree centrality ($N = 12$, Table 2.2). However, the characteristics of juvenile female niches differed from adult females. Juvenile female outdegree centrality was significantly correlated with indegree centrality only during the Baseline period (Baseline: r s = 0.6, $N = 12$, $P = 0.04$, Fig 2.2). Therefore, while juvenile females maintained stable social niches, although their gregariousness was not correlated with their attractiveness throughout the study.

Juvenile males did not maintain equivalent social niches. Outdegree centrality was correlated over the Baseline-Fission and Fission-Fusion periods, and their indegree centrality was correlated only over the Baseline-Fusion periods (Table 2.2). The characteristics of juvenile male social niches changed over time. Juvenile males' outdegree centrality was significantly correlated with their indegree centrality during the Baseline and Fusion periods (Baseline: r s = 0.65, $N = 12$, $P = 0.01$, Fusion: r s = 0.59, $N = 12$, $P = 0.045$, Figure 2.2). Thus, like adult males, a juvenile male's gregariousness was not correlated with their attractiveness throughout the study.

Individual Association Patterns: Adult females exhibited a low but significant ($\tau_{kr} = 0.172$, $P < 0.001$) tendency to approach the same adult females between Baseline and Fusion periods, but exhibited no tendency to approach the same adult males ($\tau_{kr} = 0.06$, $P = 0.1237$). Adult males also exhibited a low but significant tendency to approach the same adult females ($\tau_{kr} = 0.207$, $P < 0.001$) but exhibited no tendency to approach the same adult males ($\tau_{kr} = 0.001$, $P < 0.494$). There was no tendency for juvenile females to approach the same juvenile males ($\tau_{kr} = 0.02$, $P = 0.389$) or females ($\tau_{kr} = -0.037$, $P = 0.685$), and there was no tendency for juvenile males to approach the same males ($\tau_{kr} = -0.011$, $P = 0.55$) or females ($\tau_{kr} = 0.033$, $P = 0.35$) across the baseline and fusion periods. Thus, most individuals did not approach the same individuals when the flocks were recombined.

2.3 The consistency of social preferences

Methods:

Subjects: All birds were originally captured in Philadelphia County, Pennsylvania or in Monroe County, Indiana. Each bird was provided with uniquely colored leg bands for individual recognition. All birds were of the subspecies, *Molothrus ater ater*, with an average age of 6 years (range: 1-12 years). Pennsylvania and Indiana populations have no known differences in song behavior (Freeberg & White 2006).

Aviaries: Each aviary (9.1 x 18.3 x 3.4 m) contained perches, vegetation (e.g. trees, shrubs, & grass), an observation platform, a roofed feeding station, and access to an indoor shelter. By removing a partition within the indoor shelters Aviaries 1 and 2, and Aviaries 3 and 4, can be connected forming two larger aviaries. Aviary 5 was visually and spatially (by 85 m) isolated from the rest of the aviaries (Fig 2.3 A). Birds were provided with *ad libitum* access to vitamin-treated water (Aquavite Nutritional Research, South Whitely, Indiana) and a modified Bronx zoo diet for omnivorous birds with canary seed and red and white millet. Birds were exposed to ambient climatic conditions and native insects and invertebrates.

Data Collection: Behavioral interactions were recorded using scan-sampling using voice recognition technology. When used in combination with voice recognition technology scan-sampling can provide a more comprehensive data set than focal sampling (White & Smith 2007). A single observation block lasted seven minutes, and observers recorded social approaches between dyads. An approach was scored when one individual approached a conspecific within a radius of 30 cm around its body, and that individual remained in close proximity for at least one second. Thus, a successful approach demonstrates an individual's ability to maintain close proximity with another conspecific without eliciting an immediate withdrawal response. All observation blocks were conducted between 0700 and 1030 hours.

Reliability: During 2012 observer reliability between the two observers (GMK and GRM) was high at 94% (ICC=0.941, F=33.2, p=0.00843), and during 2013 observer reliability (GMK and FRM) remained high at 83% (ICC=0.83, F=10.9, $p < 0.0001$).

2012 experiment:

Baseline period: On 3 November 2012, new flocks were created into the four aviary subsections of the large aviary complex. All birds separated between Aviary 1 (9 females, 8 males) and 2 (9 females, 9 males) were familiar with each other, as they had been housed together for one year and 4 months prior to separation. These flocks would be used for the Control introduction (Fig 2.3 B). Birds in Aviary 3 (9 females, 6 males) and 4 (9 females, 5 males) were unfamiliar with each other, and had never previously interacted. Previously, birds in Aviary 3 had been housed together for one year and four months, while birds in Aviary 4 had been housed together for six months in Aviary 5. These flocks would be used for the Novel introduction (Fig 2.3 B). All birds were allowed three days to adjust to their new conditions before data collection began. During the baseline period, from November 6th to November 13th 2012, two observers conducted daily counterbalanced 7-minute block observations where approaches were recorded. Two observers recorded a total of 91 blocks (Aviary 1-21 blocks, Aviary 2-20 blocks, Aviary 3-25 blocks, Aviary 4-25 blocks).

Novel introduction: On 14 November, a partition separating Aviaries 3 and 4 was opened and both flocks were allowed to interact. From November 14th to November 18th 2012, two observers conducted counterbalanced 7-minute observations, during which all approaches were recorded. A total of 70 blocks was recorded between the two observers.

Control introduction: On November 20th, the partition separating Aviaries 1 and 2 was opened and both flocks were allowed to interact. From November 20th to November 27th 2012, two observers conducted counterbalanced 7-minute observations, during which all approaches were recorded. A total of 73 blocks were recorded between the two observers.

2013 experiment:

Baseline period: On October 2nd 2013, birds were separated into the four aviaries within the large aviary complex. All birds separated into Aviaries 1 (10 females, 7 males) and 2 (5 females, 8 males), and in Aviaries 3 (11 females, 7 males) and 4 (6 females, 7 males) had never previously interacted. Prior to separation birds from Aviaries 1 and 3 were housed together for four months within the large aviary complex, whereas birds from Aviaries 2 and 4 had been housed together for two months in Aviary 5 (Fig 2.3 C). Individuals were randomly assigned to each new flock to assure the resulting flocks maintained equivalent levels of approach tendencies. All birds were allowed to acclimate to the new surroundings from October 2nd to October 19th.

First introduction: On October 20th, the partitions separating Aviaries 1 and 2 as well as Aviaries 3 and 4 were opened allowing the pairs of flocks to interact and to form Aviaries 1-2 and 3-4, respectively (Fig 2.3 C). From October 20th to October 28th 2013, two observers conducted observations. A total of 328 blocks were recorded between the two observers (164 in Aviary 1-2 and 164 in Aviary 3-4).

Second introduction: On 4 November, birds originally from Aviary 2 were moved into Aviary 3-4 and birds originally from Aviary 4 were moved into Aviary 1-2 (Fig 2.3 C). From November 4th to November 17th 2013, two observers conducted observations, and a total of 306 blocks were recorded between the two observers (138 in Aviary1-2 and 138 in Aviary 3-4).

Analysis:

2012 experiment: For both the Novel and Control introductions individuals housed within the same baseline flock were designated as *familiar*, whereas interactions with individuals from another baseline flock were designated as *unfamiliar*. As the number of familiar and unfamiliar individuals was not equal, I used the rate of approaches towards familiar and unfamiliar conspecifics. The rate was calculated by first dividing the number of approaches towards either familiar and unfamiliar conspecifics by the number of familiar or novel individuals present in the aviary, which was then divided by the number of sampling blocks.

I used generalized linear mixed models using a Poisson distribution to assess the factors shaping approach tendencies. The dependent variable was the rate of approaches per individual, and the explanatory factors included an individual's sex, the identity of the individual being approached (familiar or unfamiliar), the experimental condition (Novel or Control introductions), and all two-way interactions between these variables. Models were simplified through the selection of terms based on minimizing the Akaike's information criteria (AIC). If removal of a factor increased the AIC value, then that explanatory factor remained in the model. A minimal model was defined when the removal of any remaining non-significant explanatory factors increased the AIC value. Variable selection was done using both drop1 and stepAIC functions in R (R Development Core Team 2012) with identical results. Post hoc analysis was conducted using Spearman's correlations on continuous explanatory factors, and Wilcoxon signed-rank and Mann-Whitney U tests for categorical explanatory factors. Confidence intervals for Spearman's coefficients were calculated using resampling techniques. For the Wilcoxon signed-rank test zeros were handled using the Pratt method (Pratt 1959). Effect sizes (*r*) were obtained for the Wilcoxon signed-rank test through calculating the Z-score using permutation methods (wilcoxonsign_test in the coin package) and dividing the Z-score by the square-root of the sample size (Cohen 1988).

2013 experiment: For the second experiment I conducted two GLMMs with a Poisson distribution to assess the factors shaping approach tendencies. The dependent variable in the first model was the approach rate per dyad towards females, and the second model was the approach rate per dyad towards males. The explanatory factors in both models were the individual's sex, the introduction (first or second introduction), the social identity of the individual being approached (familiar or unfamiliar) and all two-way interactions between the variables. In each model, the identity of the individual and the aviary was included as a random variable. Model simplification and post-hoc tests were the same as the 2012 model.

To assess the repeatability in the strength of individual familiarity preferences across contexts I used intraclass correlation coefficients and Spearman's correlations across the two introductions. Our measure of familiarity preference was the proportion of approaches an individual initiated towards familiar conspecifics by the number of total approaches. I conducted the analysis separately for both males and females. Significant differences in the consistency of preferences across males and females were assessed using 95% confidence intervals around the correlation coefficients. Non-overlapping confidence intervals indicate a significant difference in the consistency of familiarity preferences across males and females.

Results:

Sex differences in approach behavior:

2012 introductions: I observed a total of 6,003 approaches during this study, including 1.661 approaches during the baseline period and 4,342 approaches during Novel and Control introductions. There was no significant difference in the numbers of approaches between the Novel and Control introductions (Mann-Whitney U test: $N_1 = 29$, $N_2 = 35$, $U = 45$, $P = 0.65$), and no significant differences in the rate of approaches initiated by either males or females ($N_1 = 28$, $N_2 = 36$, $U = 55$, $P = 0.45$). In both the Novel and Control introductions females exhibited a significant preference to approach other females (Wilcoxon signed-rank test: Control: Z = 2.0474, $N = 18$, P = 0.0396, Novel: Z = 3.5933, $N = 18$, P < 0.0001), whereas males displayed no significant preference to interact with either sex in the Control introduction ($Z = -1.1838$, $N = 17$, $P = 0.2532$), but displayed a significant preference to interact with females in the Novel introduction ($Z = 2.228$, $N = 11$, $P = 0.02441$)

2013 introductions: I observed a total of 17,198 approaches during this study, including 7,939 approaches during the first introduction, and 9,259 approaches during the second introduction. I uncovered no significant differences in the rate of approaches initiated by either males or females (First intro: $N_1 = 29$, $N_2 = 32$, $U = 475$, $P = 0.87$, Second intro: $N_1 = 29$, $N_2 = 32$, $U = 403$, $P = 0.38$). Across all introductions females maintained strong preferences to interact with other females (First intro: $Z = 3.983$, $N = 32$, $P < 0.001$, $r = 0.70$, Second intro: $Z = 4.2823$, $N = 32$, $P < 0.001$, $r = 0.76$), whereas males did not exhibit any sex preferences (First intro: $Z = -0.8761$, $N = 29$, $P = 0.39$, $r = 0.16$, Second intro: $Z = -1.674$, $N = 29$, $P = 0.095$, $r = 0.31$).

Familiarity preferences:

2012 introductions: Our minimal model contained only two factors, one was experimental condition (GLMM: *Coef* = -0.16, *Z* = -0.891, *P* = 0.37) and a significant interaction effect between experimental conditions and familiarity preference (*Coef* = 0.19, *Z* = 1.983, *P* < 0.047). In the Novel introduction females exhibited an overall significant preference for interacting with familiar versus unfamiliar conspecifics (*Z* = -2.919, *N* = 18, *P* = 0.002, *r* = 0.71, Fig 2.4). When I looked at the interactions by the sex of the recipient I discovered that females exhibited a significant preference to interact with familiar females (*Z* = 3.027, *N* = 18, *P* = 0.001, *r* = 0.71) but not familiar males (*Z* = 1.20, *P* = 0.25, *N* = 18, *r* = 0.28). Neither males nor females exhibited any significant preference to interact with familiar or unfamiliar individuals in the Control introduction (Females: *Z* = -0.41, *P* = 0.70, *r* = 0.1, Males: *Z* = -0.167, *P* = 0.89, *r* = 0.04)

2013 Introductions: Both male and female models showed a significant main effect of familiarity on an individual's approach behavior (Table 2.3). Across all introductions females were more likely to approach both familiar males and females over unfamiliar males and females (Table 2.4). Our male model also uncovered a significant interaction effect between familiarity and introduction. Males exhibited a strong and significant bias to approach both familiar males and females during the first introduction (Table 2.4), but during the second introduction no significant preferences for familiar or unfamiliar conspecifics were observed (Table 2.4). From the first to second introduction males increased their rate of approaches towards both unfamiliar males (*Z* = 4.076, *N* = 29, *P* < 0.0001, *r* = 0.76) and unfamiliar females (*Z* = 2.687, *N* = 29, *P* = 0.006, *r* = 0.50).

Repeatability of familiarity preferences:

2013 Introductions: Across the first two introductions females exhibited significant repeatability in their preference to approach familiar conspecifics (*ICC* = 0.637, $P < 0.0001$, 95 % CI = 0.365- 0.81), whereas males did not (*ICC* = -0.05, $P = 0.606$, 95 % CI = -0.41- 0.32, Fig 2.5). As the confidence intervals are non-overlapping this also indicates that males were significantly less consistent when compared to females. Furthermore, females also exhibited rank ordered consistency in their tendency to approach familiar conspecifics (Spearman rank correlation: *rho* = 0.60, $N = 32$, $P = 0.0005$, 95% CI = 0.36 – 0.76), whereas males did not (*rho* = -0.20, $N = 29$, $P = 0.304$, 95% CI = -0.51 – 0.15).

To further investigate the change in male preferences, I conducted an additional analysis to see if the strength of a male's familiarity preference during the first introduction reflected a significant increase in their tendency to approach unfamiliar individuals in the second introduction. The approach rate towards unfamiliar individuals during the second introduction minus the rate-per-dyad to unfamiliar individuals in the first introduction was used as the rate of change across introductions. I found a significant positive correlation between the strength of a male's familiarity preference during the first introduction and an increase in approaches to unfamiliar males (*rho* = 0.43, $N = 29$, $P = 0.025$) and females (*rho* = 0.46, $N = 29$, $P = 0.015$).

2.4 General Discussion:

Complex social organization requires the persistence of stable interaction patterns to canalize developmental pathways and transfer information (Hinde 1976; West-Eberhard

2003). Both studies demonstrated that females are able to maintain consistent social interaction patterns and preferences across changes in group size and composition. In contrast male interaction patterns and preferences were not consistent across group changes. Differences in sociability and social preferences will determine the opportunities to learn from others by affording qualitatively different social experiences (Alberts & Cramer 1988). The consistency of female sociability suggests that females play an important role in shaping social structure and information transfer within cowbird flocks through the repeated construction of stable individual social niches. The flexibility of male sociability and preferences suggests that males may benefit from adjusting their social niches in response to changes in context. Thus, in order to face the demands of a fluctuating social environment males and females may need to acquire different skills in order to sustain or change their behavior in relation to others.

Sociability in cowbirds:

The first study demonstrated that both adult and juvenile females maintained robust patterns of sociability over fission-fusion perturbations. Female proximity may be one of the more salient features involved in shaping the development of song, behavior and social organization within cowbird flocks (Smith et al. 2000). Male-female social interactions are performed within inches of other individuals. For example, females respond to preferred male song variants with very rapid wing flicks called “wing-strokes” (West & King 1988). Males who attend to female wing-strokes receive feedback about the quality of their song, and produce higher quality song variants. Thus, female proximity affords access to communicative signals that shape the development of female song preference. In large flock settings, females a) adopt the mate preferences of other females (Freed-Brown et al. 2006; West et al. 2006); b) prefer male song when it is coupled with another female's vocalizations; and c) respond to other females' wing-strokes (Gros-Louis et al. 2003). The predictability of female social interactions may provide the economy of perception, and consistent access to social information needed to guide the development of female song and mate preferences (Gibson 1966).

While female sociability remained robust, the organization of behavior within females changed as they aged. Here I discovered that gregariousness in adult females was correlated with their attractiveness as indegree centrality was correlated with outdegree centrality in all periods. In contrast, juvenile female gregariousness did not reflect their attractiveness. An important milestone in female cowbird social development is learning to manage proximity with others (King et al. 2003). As females lack dominance relationships, females who initiate more approaches may seem more approachable by conspecifics. As females may exhibit preferences for interacting with familiar females (see section below), the ability to initiate more approaches towards more individuals may foster increased attention, by making oneself more familiar with a wider diversity of conspecifics. As substantial social interaction is necessary for the development of familiarity preferences in many species, juveniles may not yet have the ability to recognize and preferentially attend to previous associates in contrast to novel individuals. Thus, the qualities of a female's social niche may reflect their level of social competence, with juveniles' niches changing as they learn to differentiate familiar females and become more discriminative in whom they approach.

Male sociability exhibited a higher degree of contextual specificity than females. While adult male gregariousness remained consistent, perturbing the group changed a male's relative attractiveness in relation to others. Juvenile males did not exhibit any consistent patterns of indegree or outdegree across the three contexts. There was also no consistent relationship in a male's gregariousness and their attractiveness. Thus, males who initiated the most approaches to others were unlikely to receive equivalent amounts of approaches in return. Such flexibility in male interaction patterns suggests that males and females face qualitatively different challenges when the social composition changes. As males maintain dominance relationships with conspecifics, the status of others may reflect who individuals choose to approach, with individuals initiating more approaches to males of a similar social status, while avoiding approaching more dominant males. If changes in social composition cause disruption in the ordering of male dominance relationships, individuals may change the males they approach based on their new status. Male sociability, particularly their attractiveness, may therefore reflect the fluctuating dominance relationships that occur when the social composition changes.

Social preferences in cowbirds:

While sociability captures the frequency of an individual's interactions, their social preferences capture non-random interaction patterns of individuals within the group. The strength and persistence of social preferences will shape the organization and social networks within the flock. Across many species female social preferences may have an enduring influence on the social organization of groups. Within many fission-fusion societies females play a significant role in creating and maintaining group boundaries. In primates, ungulates, and elephants (*Loxodonta africana*) strong and reliable bonds between females form a core group that remains stable, even during the fusion of two groups (Archie et al. 2011; Couzin 2006; Griffiths & Magurran 1998; Henzi & Barrett 2007). Males often exhibit a tendency to disperse from their natal groups, and must be able to assess and successfully initiate interaction with a wide diversity of conspecifics (Pusey 1987). Thus, the different challenges faced across the sexes may influence whom individuals preferentially choose to approach or avoid within the flock.

Our first study investigated if cowbirds maintained preferences for interacting with the same suite of individuals when the composition changed. The results suggest that both adult and juvenile cowbirds of both sexes did not generally tend to approach the same individuals when the flocks were recombined. Thus, during the fall, females were able to maintain their sociability within a de-individualized context. Nonetheless, in the first study all individuals had been housed together for an extended period of time, and were familiar with all group members. As discussed below, when provided with the option, females do prefer to engage familiar over unfamiliar cowbirds. It is possible that cowbirds maintained a small number of preferential relationships with more familiar conspecifics during the fall, and that these relationships take time to be re-established after a period of separation. Thus, further studies are needed to address the presence and significance of strong dyadic relationships between two individuals in relation to others during fall.

Autumn cowbird flocks are characterized by sex and age biased assortment patterns (Gros-Louis et al. 2003; Smith et al. 2002). Many species, including humans, exhibit sex-biased social structures (Bon & Campan 1996; La Freniere et al. 1984; Ruckstuhl 2007).

By preferentially assorting with their own sex, the proximal social ecologies surrounding males and females differ. Both the first and second studies demonstrated significant preferences for same sex conspecifics. These findings replicate the Smith et al. (2002) finding by documenting pronounced sex assortment within a semi-naturalistic flock. The first study confirmed that sex assortment was especially pronounced within juveniles and adult females in larger flocks, while the second study showed that sex preferences in females are maintained when individuals were exposed to novel individuals.

The persistence of sex assortment in adult females at large group sizes suggests females may preferentially assort with their own sex when interacting with novel and potentially aggressive males. There are many competing hypotheses that attempt to describe patterns of sex assortment observed in many species (Ruckstuhl 2007). When assortment originates from females' social preferences it is often assumed that females avoid the intrusive behavior of males, and therefore preferentially associate with other females by default. When in the presence of males, female Japanese quail (*Coturnix japonica*) preferentially formed associations with other females, whereas when males were not present, females tended to avoid each other (Persuad & Galef 2003). In small-spotted catsharks (*Scyliorhinus canicula*), well-connected female networks remained stable despite introductions of new males into the group (Jacoby et al. 2010). Nonetheless, female cowbirds may also preferentially assort with other females in order to share information and mate preferences with other females. The construction of all female sub-groups may provide the right context for the exchange of communicative signals between females. Thus, by avoiding the intrusive behavior of males, females create a self-organized forum where they may exchange information on male quality from experienced to naïve juveniles (Gros-Louis et al. 2003; West et al. 2006)

Juvenile flocks exhibited higher levels of sex assortment over more periods than adults, and therefore sex-biased interaction preferences emerge without adult influence. The high levels of sex assortment within juvenile females may still reflect avoidance of the intrusive behavior of juvenile males. Within mixed aged flocks juvenile females often quickly integrate into adult female subgroups (Freed-Brown et al. 2006), suggesting that the motivations behind juvenile and adult female assortment are similar. The strength of sex assortment in juveniles suggests that females may continually communicate their song/mate preferences with other females before initiating interactions with males. Unlike adults, juvenile males maintained higher levels of sex assortment. Across many species juvenile males may rely on interaction within male subgroups to develop later social skills. Juvenile cowbirds may preferentially approach individuals of their own sex because they engage in similar kinds of behaviors. Jacklin & Maccoby (1978) documented that sex-segregation in pre-school play groups resulted from differences in behavioral compatibility and Hassett et al (2010) showed that variation in behavioral compatibility constructs male-only peer groups in Rhesus Macaques (*Macaca mulatta*). In many social mammals males often leave the natal group upon weaning or sexual maturity, and join exclusively young male cohorts. The male’s interactions within these male cohorts plays a significant role in shaping their later development. Thus, the presence of early sex-biased interaction preferences may structure the developmental trajectories and social niches of the sexes.

The second study demonstrated that females also exhibit strong and consistent preferences to interact with familiar individuals, fostering the creation of stable social networks between familiar females. This suggests that female cowbirds can construct reliable familiar sub-groups within the shifting composition of fission-fusion flocks. Unlike females, males did not exhibit consistent familiarity preferences. The individual variation in the strength of a male's familiarity preference was not significantly repeatable, and males increased their approaches towards unfamiliar individuals during the second introduction. Males therefore changed how they interacted with novel individuals in response to either prior experience with unfamiliar conspecifics, or changes in the social dynamics of the group.

Differences in strength and consistency of familiarity preferences across the sexes are important components in the social organization of fall flocks. Outside of breeding periods female cowbirds do not exhibit dominance relationships with other females, and female-to-female aggression is very rare. This suggests that familiarity preferences among females may reflect more than just avoiding aggressive interactions. Strong familiar networks can provide the consistent interactions, and more limited attentional demands necessary to learn and improve species-typical skills and coordinate activities with others. During autumn female cowbirds advertise, modify, and share mate preferences through close interaction with other females. Females communicate mate preferences through visual cues known as "wing-strokes" that can only be accessed in close proximity (West & King 1988). The constantly changing compositions of fall flocks may present females with information overload, and frequent associations with familiar females may limit their attention to local individuals who possess relevant local specific knowledge. Individuals who interact more frequently, but possess strong preferences, may access the benefits of constructing strong relationships with familiar conspecifics. However, individuals with weaker preferences may be the first to access new social information and cope with the new challenges of a changing social composition. Variation in the strength of an individual's familiarity preference may interact with their sociability to shape their later social and reproductive performance. While additional studies need to be conducted that address the consequences of variation in social preferences for later development and reproduction, our results demonstrate that females exhibit repeatable differences in the strength of those preferences.

Unlike females, males did not exhibit consistent familiarity preferences. In 2013, significant familiarity preferences were observed during the first introduction, but disappeared in the second introduction as males increased their approaches towards novel individuals. Males with the strongest familiarity preferences during the first introduction also exhibited the strongest increase in their approach rates towards unfamiliar males and females across introductions. In many species of mammals and birds individuals construct dominance relationships with group-members. Here changing social conditions may present opportunities to increase one's social status within the group fostering increased "social flexibility" in response to changing conditions (Schradin 2013).

Unstable hierarchies may also create more risk of aggressive encounters, as individuals compete with each other for higher social status. As male cowbirds form dominance relationships with others in the flock, and therefore it may be advantageous for males to engage unfamiliar individuals to quickly integrate them into new dominance relationships. Previous social experience can also shape a male’s interaction preferences well into adulthood. White et al (2010a) found that males housed in a flock with a changing social composition constructed more diversified social networks and had higher mating success in the breeding season than males housed in a stable unchanging flock. Males may benefit from fostering connections with a wide diversity of different conspecifics, as such connections may aid in the development of later social skills. Thus, males may be an important factor in social integration, by being more willing to engage novel individuals and incorporate them into new patterns of organization when the social composition changes.

Individual differences in social behavior are the necessary conditions for the evolution of social behavior. The studies presented here suggest that individuals construct qualitatively different social niches in response to group level changes. Whereas female social niches emphasize contextual generality by maintaining robust patterns of sociability and social preferences, male niches emphasize contextual specificity by flexibly responding to changes in context. Such differences suggest that reliable female interaction networks are the common denominator in sustaining cowbird social organization; whereas male interaction networks may be an important factor in social integration and group responses to changing conditions. As cowbirds are heavily dependent on culturally transmitted behavior to become reproductively competent, it appears that evolution has selected for a non-hierarchical but specialized social interaction networks to guide the development of species typical behavior. The next section will look at how variation in individual social niches during the fall is able to predict the emergence of reproductive performance months into the future.

2.5 Figures and Tables

Figure 2.1

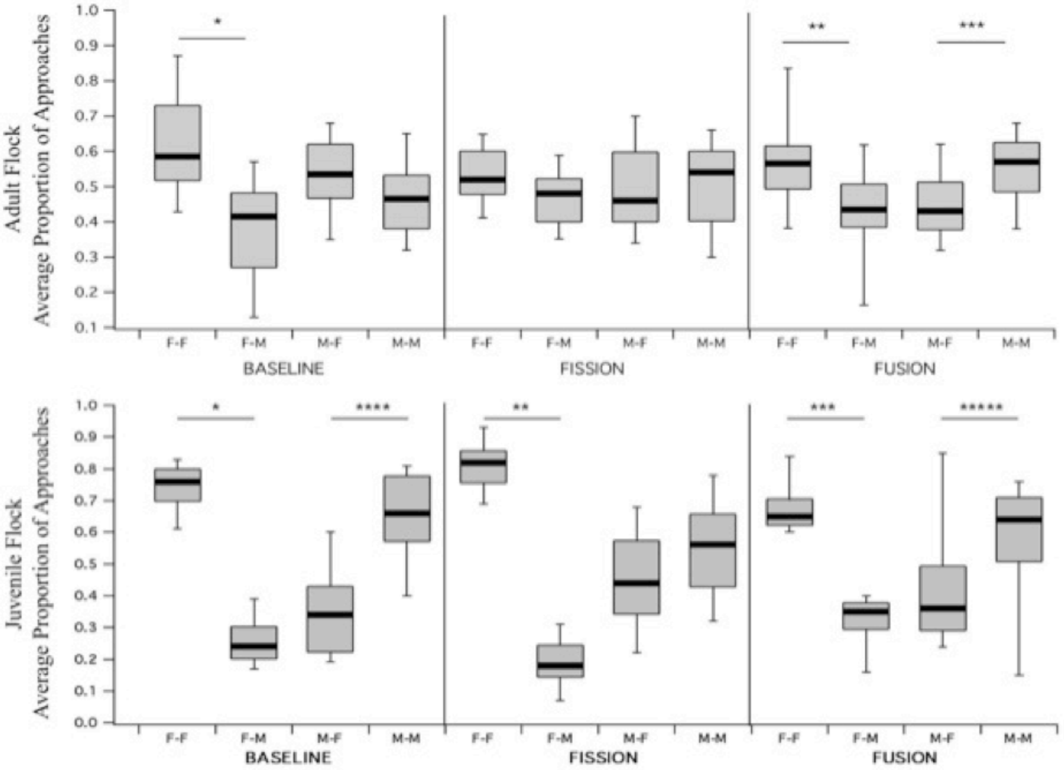


Figure 2.1: Box plots of proportion of male and female directed approaches for all three periods in the adult and juvenile flocks. The whiskers are 5th and 95th percentile. The box shows the median proportion of male/female approaches. In the adult flock significant differences in approach behaviour were observed during Baseline (* = Z =-3.354, N=21, p = 0.001), and Fusion (** = Z= -2.381, N=21, p = 0.017, *** = Z =-2.249, N=17, p = 0.025) periods. Juvenile females exhibited significant differences in all rounds (* = Z=-3.059, N=12, p=0.002, ** = Z=-3.059, N=12, p=0.002, *** = Z=-3.061, N=12, p=0.002), and males during the Baseline and Fusion period (**** = Z= -2.078, N=12, p = 0.006, *****= Z=-2.118, N=12, p=0.034).

Figure 2.2:

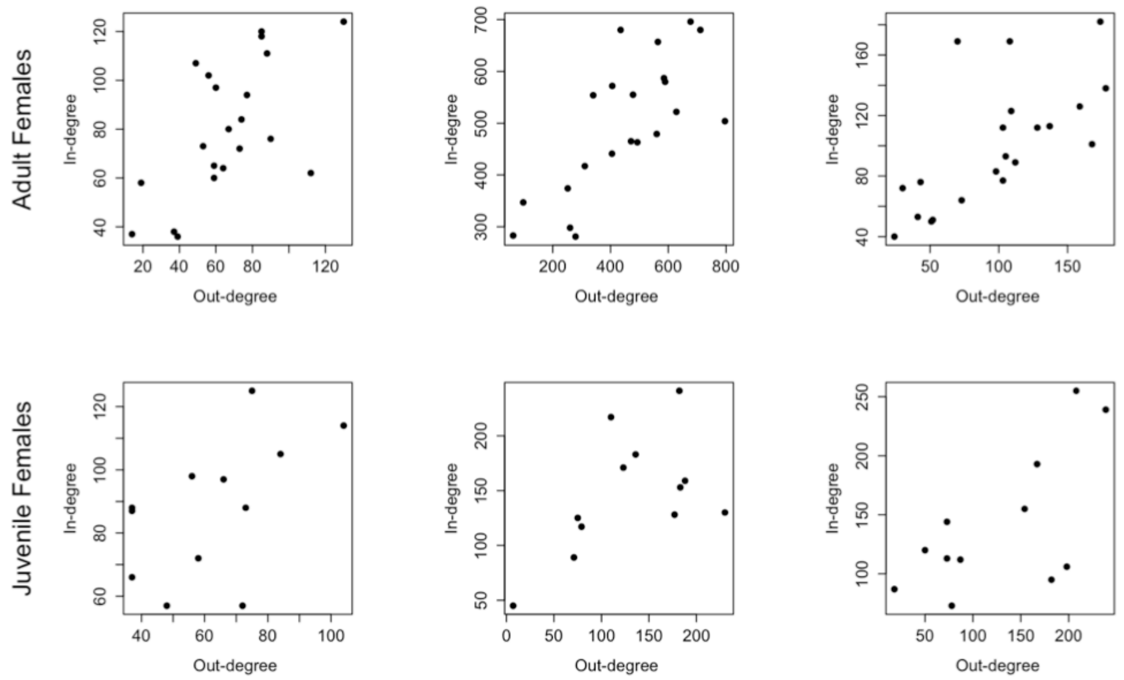


Figure 2.2: Scatter plots of individual indegree and outdegree centrality for adult and juvenile females over all three periods. Significant correlations between indegree and outdegree were observed for adult females during all periods (Spearman: Baseline, rho = 0.61, p=0.004, Fission, rho= 0.75, p<0.0001, Fusion, rho=0.76, p<0.0001), and for juvenile females during Baseline period only (Spearman: Baseline, rho = 0.6, p=0.04, Fission, rho= 0.55, p=0.06, Fusion, rho=0.47, p=0.12).

Table 2.1: Adult degree centrality correlations between periods

		Baseline-Fission	Fission-Fusion	Fusion-Baseline
Adult Males	Indegree	0.32	0.35	0.02
	Outdegree	0.64*	0.67**	0.75***
Adult Females	Indegree	0.63**	0.80***	0.68**
	Outdegree	0.71***	0.81***	0.73***

Table 2.1: Spearman rho correlations in indegree and outdegree centrality for adult males and females over the three conditions. Significant correlations are noted with an (*): * = ($P < 0.05$), ** = ($P < 0.005$), *** = ($P < 0.0005$)

Table 2.2: Juvenile degree centrality correlations between periods

		Baseline-Fission	Fission-Fusion	Fusion-Baseline
Juvenile Males	Indegree	0.62*	-0.06	-0.38
	Outdegree	0.82**	0.72*	0.55
Juvenile Females	Indegree	0.80*	0.77**	0.65*
	Outdegree	0.85**	0.79**	0.75*

Table 2.2: Spearman rho correlations in indegree and outdegree centrality for juvenile males and females over the three conditions. Significant correlations are noted with an (*): * = ($P < 0.05$), ** = ($P < 0.005$), *** = ($P < 0.0005$)

Figure 2.3:

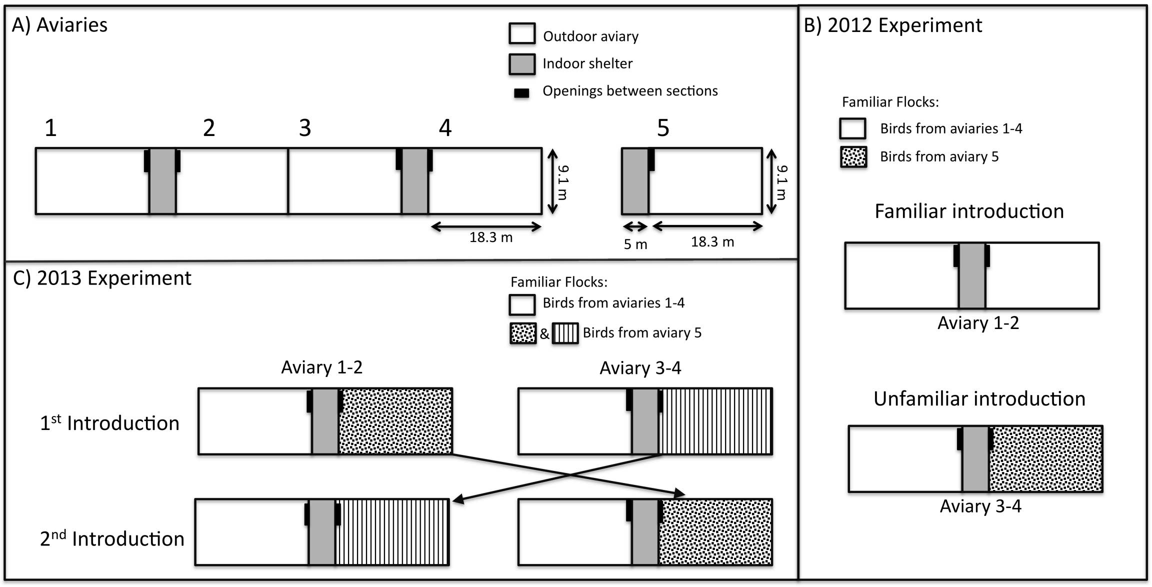


Figure 2.3: A) This is the diagram of the aviaries used during the aviary including the large aviary complex consisting of aviaries 1-4, and aviary 5. B) This diagram shows the experimental setup for the aviaries used during the 2013 experiment and C) diagram of the experimental setup for first and second introductions within the large aviary complex in the 2013 experiment.

Figure 2.4:

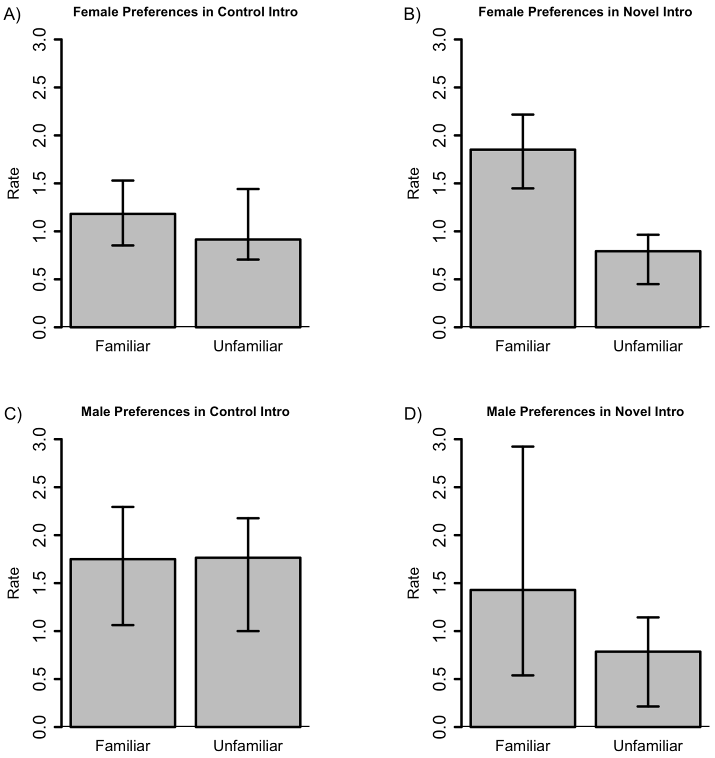


Figure 2.4: Differences in the female (A & B) and male (C & D) preferences across the Control (A & C) and Novel (B & D) introductions. Bars represent the median rate of approaches per individual to towards familiar or unfamiliar individuals within the Control and Novel introductions. Bars represent the 95% confidence interval around the median.

Figure 2.5:

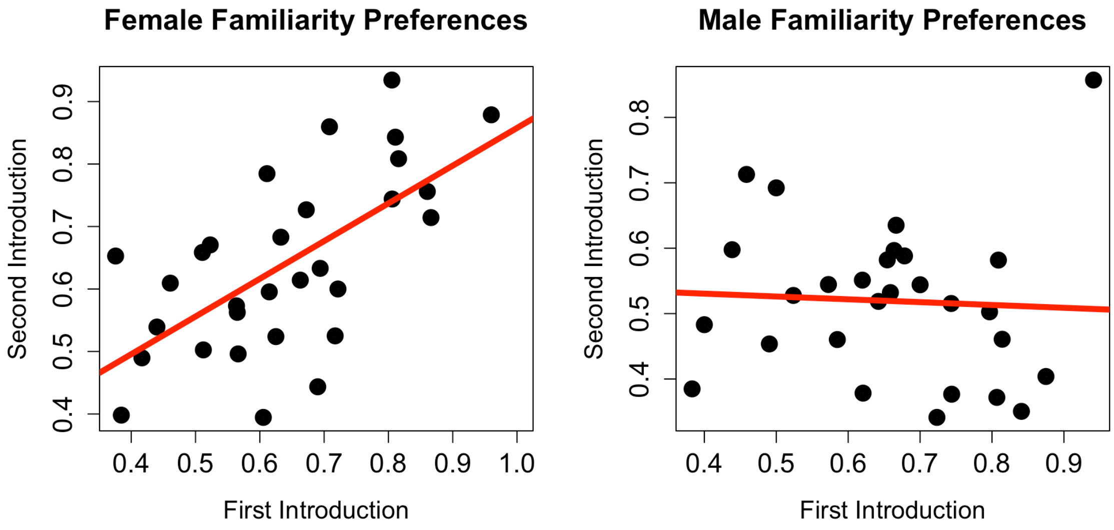


Figure 2.5: Consistency of familiar approach preferences across the first and second introductions for both males and females. Line represents a linear regression fitted to the data in order to illustrate the direction of the effects across introductions.

Table 2.3:

Model	Factor	Coef	Std. Error	Z-value	P-value
Females	**Sex**	**-0.339**	**0.179**	**1.88**	**0.059**
	Familiarity	**-0.517**	**0.084**	**6.138**	**< 0.0001**
	Famil : Intro	**0.308**	**0.088**	**3.493**	**0.0004**
Males	**Sex**	**0.48**	**0.24**	**1.958**	**0.05**
	Introduction	**0.31**	**0.075**	**4.068**	**< 0.0001**
	Familiarity	**0.85**	**0.10**	**8.169**	**< 0.0001**
	Famil : Intro	**0.67**	**0.12**	**5.424**	**< 0.0001**

Table 2.3: Model results from the second experiment.

Table 2.4:

	First Introduction			**Second Introduction**		
F-F	**$Z = 2.4403$**	**$P = 0.01$**	**$r = 0.43$**	**$Z = 3.0278$**	**$P = 0.007$**	**$r = 0.54$**
F-M	**$Z = 3.9838$**	**$P < 0.0001$**	**$r = 0.70$**	**$Z = 2.19$**	**$P = 0.03$**	**$r = 0.39$**
M-M	**$Z = 4.1314$**	**$P < 0.0001$**	**$r = 0.76$**	**$Z = 0.2391$**	**$P = 0.818$**	**$r = 0.05$**
M-F	**$Z = 4.3033$**	**$P < 0.0001$**	**$r = 0.70$**	**$Z = 0.353$**	**$P = 0.736$**	**$r = 0.07$**

Table 2.4: Wilcoxon singed-rank tests looking at the rate-per-dyad approaches to familiar or novel individuals for female to female (F-F), female to male (F-M), male to male (M-M) and male to female (M-F) approaches.

Third Chapter: Fall social niches predict reproductive performance in adults

3.1 Introduction:

How individuals engage, interact, and form relationships with conspecifics is a major determinant of their reproductive success. From courtship to pair bond formation to successful copulation, reproduction requires that individuals initiate and sustain close social contact with conspecifics. Despite this, little is known how variation in social interaction during non-reproductive periods may predict later variation in an individual's reproductive output. In the last chapter I investigated the characteristics and consistency of individual social niches across changes in autumn flocks. In this chapter I will explore how individual variation in fall social niches and affiliative skills are able to predict the reproductive output and courtship behavior months later during the breeding season.

Courtship is a prelude to successful reproduction. In cowbirds and many other species, courtship often requires direct interaction with potential mates, as well as the skills to respond appropriately to changes in the behavior of mates. The strength of individual's relationship with others can have a large impact on the number of offspring they can produce. Consistent individual differences in social behavior may have implications across different modalities. As successful reproduction requires the ability to engage others, I expect that consistent differences in fall social behavior predict reproductive performance over long timescales. This chapter covers two studies. In both studies I explore the interaction between autumnal social behavior and reproductive performance in cowbirds by manipulating the flock composition during the breeding season based on male and female behavior during the fall. The first study investigates the stability of fall sociability across long timescales, and how variation in fall sociability may shape the rate of egg production of both individual females and groups during the breeding season. The second study looks at how consistent variation in a fall affiliative displays, the head-down, predicts reproductive performance during the breeding season, and social niches during the fall. Because males form dominance relationships with others, approaches may be perceived as agonistic in nature. By looking at variation in head-down usage in contrast to the social niches I may uncover if a male's place within the fall group reflects later performance, or whether differences in their ability to sustain affiliative contact with others play a complimentary role.

Previous research has documented that affiliative displays, or behaviors used to initiate and sustain close contact with conspecifics while minimizing aggression, are widespread across a range of social species. In birds and primates, affiliative displays are used to establish and maintain pair bonds with others, increase group cohesion, manage stress, and reduce agonistic interactions (Carter et al. 1999; Stöwe et al. 2008). For example, allo-grooming in many mammals has been shown to assist in the formation of coalitions, solidify social ranks, and facilitate the survival of offspring (Silk et al. 2003a; Silk 2007), while allo-preening in birds has also been shown to facilitate offspring survival (Emery et al. 2007; Lewis et al. 2007). Individual differences in affiliative behaviors are often used to assess an individual's sociability (Koski 2011; Silk et al. 2003b; Silk et al. 2010). Nevertheless, few studies have explicitly looked at the consistency and repeatability of affiliative behaviors over time, and how differences in the consistency of an individual’s affiliative behaviors may shape their later reproductive output.

Brown-headed cowbirds engage in an affiliative display known as the head-down. During a head-down, an individual freezes in a low crouched position with its head pointed downwards so that the back of the head and neck are positioned in close proximity, if not touching, a neighboring individual for at least one second. Reports of head-down displays in both wild and captive populations of brown-headed (Hunter 1994; Webber 1983), bronzed (*Molothrus aeneus*) (Garrett & Molina 2005), shiny (*Molothrus bonariensis*) (Post & Wiley 1992), giant (*Molothrus oryzivorus*) (Payne 1969) and bay-winged (*Molothrus badius*) (Selander 1964) cowbirds suggest it has a widespread social role. Repeated use of the behavior has been shown to facilitate close proximity between individuals (Stevenson 1969), integrate others into the flock (Rothstein 1977, 1980b), and have appeasing influence on others (Robertson & Norman 1976; Scott & Grumstrup-Scott 1983). Head-down displays are very seasonal with nearly all displays occurring during the fall and winter when cowbirds assemble into large flocks (Ortega 1998). Some have suggested that the display functions to sustain close proximity while reducing aggressive behavior during periods when social cohesion is necessary (Ortega 1998). Head-down displays can also be reciprocated, when individuals respond to another’s head-down with a matching display (Figure 3.1). Most displays last for a few seconds, but I have observed head-downs that have lasted for upwards of 10 minutes. Head-down displays emerge early in development (Lowther & Rothstein 1980a), with reciprocated displays observed in 43 day old hand-reared birds housed without adult contact (Miller, unpublished data). The head-down shares many postural and functional similarities with affiliative behaviors seen in other bird species (Selander & LaRue 1961; Selander 1964).

The use of the head-down may be important for sustaining close social contact with others, and may reflect an individual's social niche. Individuals who are more likely to approach and be approached by others may exhibit higher rates of head-downs to manage the increased risk of engaging in aggressive encounters. As such, I may observe that more sociable niches with higher rates of head-downs may be better at managing the costs and risks of social interaction, and exhibit better courtship skills during the breeding season. The first step is to see if fall social niches, particularly sociability, predict higher rates of reproductive performance. This is the focus of the first study in this chapter. The next step is to see of the use of head-downs reflects the characteristics of the social niche, and if this is able to predict later reproductive output and courtship skills. This is the focus of the second study of this chapter.

Our first study was conducted over a two-year period. During both years I documented autumnal patterns of individual sociability in flocks of cowbirds that were allowed to associate freely. In the spring of 2011, I created three flocks based on sociability scores during the previous fall. Females were separated into high, intermediate and low sociable flocks, while male sociability was spread evenly across the three flocks. Because of the importance of female proximity in shaping courtship behaviors, I hypothesized that more sociable females would construct more opportunities to interact, court, and produce more eggs than less sociable females. I predicted that high levels of female sociability would lead to more male counter-singing even though male sociability was equivalent across the three flocks. I also examined if sociability reflected how selective individuals were when approaching others during the spring. In particular, I expected that more sociable cowbirds would also be less selective in their approaches and therefore be able to assess more potential mates. I expected that courtship and egg production would differ across the three flocks with increased egg production in flocks with females who were more sociable.

The second study looks at how consistent variation in a fall pro-social, or affiliative, display may shape the emergence of reproductive competence much later during the fall. While male social niches are characterized by greater flexibility than females, males that use head-downs more consistently may be able to obtain the close social experiences needed to develop better courtship skills. In our second study, our first objective was to document the consistency and repeatability of the head-down rates across multiple social contexts. During the fall, I subjected a large flock to a fission-fusion perturbation to investigate if rates of head-downs remain correlated across changes in social context. Our second objective was to investigate the relationship between these tendencies and reproductive performance. In the spring, I separated individuals into high, intermediate or low flocks based on their frequencies of head-downs during the fall. Within each flock I recorded male courtship behavior and female egg production to document if variation in fall head-down displays predicts variation in spring reproductive behavior.

3.2: Sociability and reproductive performance in female cowbirds

Methods:

Subjects: All birds were cowbirds, *Molothrus ater ater*, originally captured in Philadelphia County, Pennsylvania or Monroe County, Indiana, USA and housed in aviaries in Monroe County, Indiana. Previous studies have shown no differences in the song or social behavior within the *Molothrus ater ater* subspecies (King & West, 1990). I used 34 male and 38 female cowbirds during the course of this study. At the beginning of April 2011, all individuals ranged in age from 2 to 13 years, with an average age of 5 years. After capture, all birds were fitted with a unique series of colored leg bands to allow for individual identification. Some birds died during the study; between fall 2009 and fall 2010 six birds died, and between fall 2010 and spring 2011 ten birds died. All flock sizes and compositions were well within the normal range for this species (Friedmann, 1929). I provided all birds with a daily diet of vitamin treated water (Aquavite Nutritional Research Association, South Whitley, IN, USA), red and white millet, canary seed and a modified Bronx Zoo diet for blackbirds.

Aviaries: I used four aviaries in this study. Each aviary had identical dimensions (9.1 x 21.4 x 3.4 m), and similar environmental conditions with shrubs, trees, a covered feeding station, and access to indoor enclosures. The size of the aviaries and availability of cover provided individuals with significant degrees of freedom to either interact or avoid interacting with others. All aviaries allowed birds to be exposed to ambient climatic conditions and the presence of wild cowbirds and predators. During the spring, each aviary was supplied with 6 artificial nests. All nests were supplied with yogurt-covered raisins as decoy eggs. Nests were video monitored to determine the identity of females laying eggs using Geovision software (Geovision Inc. 2008, 9235 Research Drive, Irvine, CA, USA) on Dell Vostro 230 computers running a 32-bit Windows 7 operating system.

Data Collection: During observations, I recorded either approaches or songs. All observations were conducted using a scan sampling procedure with voice recognition technology. An approach was scored when one individual approached a conspecific within a radius of 30 cm around their body. I recorded three types of song: directed song, undirected song and counter-singing matches. A directed song occurred when a male sang while oriented on an axis of 0° to 45° towards a conspecific. An undirected song occurred when a male sang without orienting towards a conspecific. A counter-singing match was tabulated if a male reciprocated a directed song within 15 seconds. Copulations were also recorded during both approach and song observations. Approach behaviors were recorded during a 7-minute scan sampling block while song interactions were recorded during a 15-minute scan sampling block. All observations were conducted between 0700 and 1030 hours. During the spring, each nest was checked daily from 0700 to 0730 hours for the presence of newly laid eggs. Cowbird eggs were collected daily and decoy eggs were resupplied so that each nest maintained one to three decoy eggs. All nests were moved to a different position after 8 days.

Procedure:

Fall observations 2009: From September 18th to November 21st I observed two aviaries. Aviary 1 contained 11 males and 9 females, and aviary 2 contained 8 males and

10 females. Two observers conducted observations where approaches were recorded (observation blocks: 286 in aviary 1, 287 in aviary 2).

Fall observations 2010: From September 7th to November 13th I observed two aviaries. Aviary 1 contained 32 birds, including 15 females and 17 males, and aviary 2 contained 34 birds, including 19 females and 15 males. All birds from aviary 1 had been observed the previous fall, while all birds from aviary 2 had not been observed previously. During observations three observers recorded approaches (observation blocks: 103 in aviary 1, 254 in aviary 2).

Sociability calculations: Using the approach data, I calculated both the approach rate initiated and the approach rate received per observation block for each individual during fall 2009, fall 2010 and spring 2011. For each season, I took the total number of approaches an individual either initiated or received and divided it by the total number of observation blocks. I calculated an individual's sociability by summing their approach rate initiated and the approach rate received.

Female manipulation 2011: On March 25th, all individuals were separated into three flocks based on their sociability in fall 2010. The 12 most sociable females from the top third of the distribution were assigned to the high sociable aviary (hereafter high/intermediate/low aviaries), 9 females of intermediate sociability from the middle third of the distribution were assigned to the intermediate aviary, while the 11 least sociable females in the lower third of the distribution were assigned to the low aviary.

Male manipulation 2011: I distributed males across the three aviaries so that they contained a similar distribution of sociability (X^2 (2, N = 24) = 2.18, p = 0.34), the high aviary contained 9 males, the intermediate aviary contained 8 males, and the low aviary contained 9 males.

Spring observations 2011: During the pre-breeding season from April 1st to April 30th, three observers recorded approach interactions in all three aviaries (observation blocks: 30 in the high aviary, 15 in the intermediate aviary, 33 in the low aviary). During the breeding season from May 1st to June 9th, four observers recorded song interactions in all three aviaries (93 blocks in all aviaries).

Spring nest monitoring 2011: All nests were video monitored from May 24th to June 10th to capture the identity of laying females and the number of eggs laid. During video analysis, I used the individual band combination to identify the laying females.

Analysis: Due to small sample sizes and non-normality of data I primarily used non-parametric statistics. Spearman rank correlations were used to look at the consistency of approach rates initiated and approach rates received over fall 2009, fall 2010 and spring 2011. Mann-Whitney U-tests and Kruskal-Wallis tests were used to look at differences in eggs laid, approach rates, and sex-assortment across aviaries during the spring.

A Fisher's Exact Test with a Monte Carlo simulation was used to compare the egg distributions (the number of eggs laid for each female) across the three aviaries.

A generalized linear model (GLM) was used to uncover the factors influencing female egg laying. The dependent variable in our GLM was binary, and was whether a female laid or did not lay eggs during the video recording period. The explanatory variables were aviary (high, intermediate, or low), the number of songs that each female received from males, the number of males that sang to a female, and the number of copulations each female had. I simplified our GLM through stepwise elimination of non-significant variables. Our model used a binomial error distribution with a link-logit function, and during model simplification I used log-likelihood ratio tests with a chi-square distribution to assess the influence of specific explanatory variables. Spring sociability was calculated by summing the approach rates initiated and approach rates received from April 2011. Within aviaries, I used Spearman rank correlations to investigate if spring sociability correlated with individual egg production.

During spring 2011, I tabulated to total number of songs directed toward females and males, as well as the number of undirected and songs sung in counter-singing matches. Kruskal-Wallis tests were used to look at differences in the amount of female directed, male directed, undirected and counter-singing matches across the three aviaries.

In order to investigate social selectivity, I rank ordered the number of approaches to each conspecific from lowest to highest during spring 2011. For each individual, I also calculated a social selectivity quotient where I subtracted the proportion of approaches directed towards the top 50% of recipients from the proportion of approaches directed towards the bottom 50% of recipients. When flock size was uneven, I rounded the bottom 50% of recipients upwards. Individuals with higher social selectivity quotients had distributed more approaches towards fewer individuals. Kruskal-Wallis tests and Mann-Whitney U-tests were used to see if the females differed in their selectivity quotients during the spring 2011. All analysis was conducted using R version 2.11.1 (the R project website, http://www.r-project.org/) for Mac.

Results:

Social approach: I observed a total of 19,036 approaches during fall 2009, 3,252 approaches during fall 2010, and 3019 approaches during spring 2011. Analysis of approach rates for fall 2009 and fall 2010 is published in Kohn et al. (2011) and demonstrated that fall approach rates remained correlated across changes in social context. During spring 2011, there were significant differences in the approach rates that females initiated (X^2 (2, N = 32) = 13.31, $p = 0.001$) and received (X^2 (2, N = 32) = 15.87, $p < 0.001$) across the three aviaries. Females in the high aviary both received and initiated more approaches than the intermediate and low sociable aviaries (Initiated: High: *Mdn* = 2.59, *IQR* = 2; Intermediate: *Mdn* = 1.13, *IQR* = 0.733; Low: *Mdn* = 0.59, *IQR* = 1.03; Received: High: *Mdn* = 3.41, *IQR* = 1.20; Intermediate: *Mdn* = 1.67, *IQR* = 1.07; Low: *Mdn* = 1.56, *IQR* = 1.41; Approaches initiated: High vs. Intermediate: $U = 95$, $p < 0.004$; High vs. Low: $U = 118$, $p < 0.001$; Approaches received: High vs. Intermediate: $U = 93$, $p < 0.004$; High vs. Low: $U = 126$, $p < 0.001$). Across all aviaries, females exhibited high levels of sex assortment (High: $Z = -3.49$, $p < 0.00$; Intermediate: $Z = -2.75$, $p = 0.006$; Low: $Z = -2.61$, $p = 0.009$), with higher approach rates towards females (High: *Mdn* = 2.1, *IQR* = 1.72; Intermediate: *Mdn* = 0.87, *IQR* = 0.73; Low: *Mdn* = 0.5, *IQR* = 0.72) in contrast to males (High: *Mdn* = 0.47, *IQR* = 0.45; Intermediate: *Mdn* = 0.2, *IQR* = 0.2; Low: *Mdn* = 0.17, *IQR* = 0.38). There were also significant differences in the approach rates males received (X^2 (2, *N* = 24) = 7.77, *p* = 0.02), with males in higher aviaries receiving more approaches from females than males in the lower aviaries (High: *Mdn* = 2.241, *IQR* = 1.10; Intermediate: *Mdn* = 1.25, *IQR* = 0.58; Low: *Mdn* = 0.87, *IQR* = 0.92). I found no differences in the number of approaches males initiated across the three aviaries (X^2 (2, *N* = 24) = 1.93, *p* = 0.38).

Sociability across years: Patterns of female sociability remained consistent across all years, while male sociability was less consistent between years. I discovered significant correlations in both the approach rate initiated and the approach rate received for females from fall 2009 to April 2011 (Table 3.1). Male sociability did not exhibit consistently significant correlations; while male approach rate initiated and approach rate received exhibited significant correlations between fall 2009 and fall 2010, I observed only one significant correlation in male approach rate initiated from fall 2010 to April 2011 (Table 3.1).

Egg production: Flocks with more sociable females produced more eggs, and contained a higher number of laying females. I collected 65 eggs in the high aviary, 36 eggs in the intermediate aviary, and 32 eggs in the low aviary. From our video recordings, I discovered that the distribution of eggs between the aviaries was significantly different from expected frequencies (X^2 (2, *N* = 32) = 7.33, *p* = 0.03, Fisher's Exact Test: *p* = 0.03), with females in the high aviary laying significantly more eggs than females in the low aviary (High: *Mdn* = 1, *IQR* = 0.25; Low: *Mdn* = 0.0, *IQR* = 0.2; U = 96.5, n_1 = 12, n_2 = 11, *p* = 0.048). Our GLM model demonstrated a significant influence of aviary (*T* = -2.153, *p* =

0.03), and a marginally significant influence of the number of songs a female received (*T* = 1.910, $p = 0.056$), on the number of laying females. Model comparisons demonstrated a significant change in the residual deviance when both aviary (X^2 (2, $N = 32$) = -9.1364, $p = 0.01$) and songs received (X^2 (2, $N = 32$) = -7.4079, $p = 0.007$) were removed from the model. Post-hoc analysis demonstrated that laying females received significantly more songs in contrast to non-laying females (Laying females: *Mdn* = 272, *IQR* = 162; Non-laying females: *Mdn* = 88, *IQR* = 137.5; $U = 42$, $n_1 = 15$, $n_2 = 17$, $p = 0.0013$). The high aviary had a significantly higher number of laying females in contrast to both the intermediate and low aviaries (Fisher's Exact Test: $p = 0.016$, Figure 3.3).

Within aviaries, individual egg production reflected individual sociability measured in April 2011. I found that more sociable females laid more eggs within the high (rho = 0.77, $p = 0.003$) and intermediate (rho = 0.63, $p = 0.06$) aviaries, but not within the low aviary (rho = -0.27, $p = 0.41$).

Song comparisons across aviaries: There were no significant differences in male song across the three aviaries. I collected a total of 21280 songs throughout the breeding season; males in the high aviary sang the most songs ($N = 8489$) followed by the low ($N = 6812$) and intermediate ($N = 5979$) aviaries. There were no significant differences in the amount of counter-singing (X^2 (2, $N = 24$) = 5, $p = 0.08$), or directed songs towards males (X^2 (2, $N = 24$) = 1.17, $p = 0.556$) or females (X^2 (2, $N = 24$) = 0.2, $p = 0.9$) across the three aviaries. Furthermore, I observed no differences in the proportion of songs directed to males or females (X^2 (2, $N = 24$) = 1.90, $p = 0.386$) or within counter-singing matches (X^2

(2, $N = 24$) = 2.965, $p = 0.227$) between the three flocks. Thus, distributing male sociability evenly across aviaries resulted in similar patterns of singing behavior.

Social selectivity: Females in flocks with less sociable females were more selective in their interactions in comparison to flocks of highly sociable females. During spring 2011, females in each aviary differed in their social selectivity quotients (Female-Female selectivity: X^2 (2, $N = 32$) = 20.0, $p < 0.001$; Female-Male selectivity: X^2 (2, $N = 24$) = 15.3, $p < 0.001$) with females in the low flock being significantly more selective in comparison to the high flock (Female-Female selectivity: High: *Mdn* =35.6, *IQR* = 18; Low: *Mdn* = 83.77, *IQR* = 9; $U = 1$, $n_1 = 11$, $n_2 = 12$, $p < 0.001$; Female-Male selectivity: High: *Mdn* =54.31, *IQR* = 37.9; Low: *Mdn* = 100, *IQR* = 25.9; $U = 19.5$, $n_1 = 11$, $n_2 = 12$, $p = 0.007$). I found no significant differences in male social selectivity across the three aviaries during the spring.

3.3: Fall affiliative displays predict reproductive performance

Methods

Subjects: I used 21 adult female and 17 adult male cowbirds. Birds were originally captured in Philadelphia County, Pennsylvania or Monroe County, Indiana and housed in aviaries in Monroe County, Indiana. Birds ranged in age from 3 to 11 years with an average age of 6 years. Previous studies have shown no differences in the song or social behavior between the Pennsylvania and Indiana populations (Freeberg & White 2006). All individuals had been housed together for a year prior to the present study. Each bird was marked with uniquely colored leg bands to allow for individual recognition. All birds were provided daily with a diet of vitamin (Aquavite, Nutritional Research) treated water, red and white millet, canary seed and a modified Bronx Zoo diet for blackbirds.

Aviaries: I used the aviary complex described in detail in Smith et al. (2002). In the present study, I used three aviaries within the complex, each with identical dimensions (9.1 x 21.4 x 3.4 meters). Aviaries 1 and 2 were separated by an indoor enclosure, and aviaries 2 and 3 were separated by wire mesh that permitted visual contact. Ecological conditions were similar throughout all aviaries with shrubs, trees, grass, a covered feeding station and access to an indoor enclosure. All aviaries allowed birds to be exposed to ambient climatic conditions, wild cowbirds, and the sight and occasional interaction with predators.

Behavioral observations: To record behavior during the fall and the spring I utilized a scan sampling procedure: the entire flock was scanned and behaviors were recorded as they were observed. During scan sampling blocks in fall of 2009 I recorded approach interactions and head-down displays. An approach was scored when one individual approached a conspecific within a radius of 30 cm around its body. During both approaches and head-downs, the identity of the individual who initiated the behavior, and the individual who was the recipient were recorded. A reciprocated head-down was scored when a recipient of a head-down concurrently returned the display. Fall observation blocks were seven minutes long.

During scan sampling blocks in spring of 2010 I primarily recorded male vocal behavior. In particular I recorded the identities of the male singing and the individuals receiving the song. A directed song was recorded when one individual oriented on a 45 degree angle from a neighboring individuals and performed a song display that included fluffing up and bowing while singing a song. Males could direct songs towards males or females singly, or use directed songs within counter-singing matches with another male. A counter singing-match consists of two males exchanging directed songs in a tit-for-tat manner. A counter-singing match was recorded when a recipient of a directed song reciprocated with his own directed song within at least 15 seconds. An undirected song was recorded when an individuals sang a song while not oriented towards any neighboring individual. Outside of song I also recorded male copulations. All observations were conducted between 7:00-10:30 in the morning when cowbirds are most active. Spring observation blocks were fifteen minutes long.

All scan sampling blocks were conducted using voice recognition technology. When used in combination with voice recognition technology scan-sampling can accurately acquire a more comprehensive dataset than focal sampling (White & Smith 2007). I used the procedure and equipment described in detail by White et al. (2002a). All behaviors were recorded using IBM (White Plains, NY) ViaVoice Millennium Pro Edition voice recognition software operating on a Pentium III, 500-MHz IBM compatible computer. Behavioral observations were spoken into a Telex FMR 150 (Lincoln, NE) wireless microphone, transcribed into Microsoft Word 2004, edited for voice recognition errors and then imported into a database (4th Dimension 2004.8; ACI Inc). Observer reliability was tested using intraclass correlation coefficients between the two observers (GMK and APK) for the fall and spring and revealed a high level of agreement (Fall: ICC = 0.86, $p < 0.0001$, Spring: ICC = 0.87, $p < 0.0001$).

Procedure:

Fall baseline data collection: On September 2nd 2009, all individuals were moved into aviary 1. From September 3rd to September 18th, two observers conducted daily counterbalanced observations, each recording approach behaviors and head-downs. Observers collected a total of 126 seven-minute observation blocks.

Fall fission perturbation: On September 18th 2009, I separated the birds into two aviaries based on their frequency of approaches during the baseline period so that both flocks contained a similar distribution of approaches. Aviary 1 contained 11 females and 9 males, and aviary 2 contained 10 females and 8 males. From September 19th to November 20th 2009, two observers conducted daily counterbalanced observations and each collecting a total of 286 seven-minute observation blocks, recording approach behaviors and head-downs.

Fall fusion perturbation: On November 21st 2009, the partition separating the two aviaries was opened and both flocks were allowed to interact. From November 21st to December 4th, two observers recorded approach behaviors and head-downs in both aviaries. Observers collected a total of 108 seven-minute observation blocks during the fusion stage.

Spring breeding season head-down segregation: Individuals were ranked by the total amount of head-downs they initiated during the baseline, fission and fusion periods in the fall. On April 4th 2010 each individual was assigned to one of three new aviaries based on the frequency of head-downs they performed during the fall. The high aviary contained the birds that initiated the most head-downs (6 females and 5 males, head-down range: females = 68-193, males = 175-270), birds in the intermediate aviary initiated a moderate number of head-downs (7 females and 6 males, head-down range: females = 34-68, males = 106-158), and birds in the low aviary initiated the lowest number of head downs (7 females and 6 males, head-down range: females 0-28, males 27-95). From April 5th until June 13th two observers, working concomitantly, recorded a total of 411 fifteen-minute observation blocks. From April 29th to June 13th I collected all eggs laid.

Egg collection: From April 28th to June 13th 2010, each aviary was supplied with eight prefabricated nests. White yogurt covered raisins were used as decoy eggs, previous studies have shown that cowbirds readily remove yogurt covered raisins from nests and treat them as they would host eggs (Kohn et al. 2011; White et al. 2010b). One decoy egg was added to each nest daily for five days to simulate the normal laying pattern seen in many passerines. Nests were moved to different locations every 10 days. At 7:00 am each morning all cowbird eggs were collected and replaced with a decoy egg. All eggs were then placed in a Petersime Model 1 incubator (Petersime Incubator Company, Gettysburg Ohio). After eight days of incubation eggs were removed and candled in order to determine if they were fertile.

Data analysis: Given the low numbers of individuals and non-normality of data I primarily used non-parametric tests (using two tailed p-values). Friedmann and Wilcoxon signed-rank tests were used to investigate the differences in the rates of head-downs (number of head-downs per observation block for each individual) between males and females during the baseline, fission and fusion periods. Spearman's correlations were used to look at the relationship between the rates of head-downs across the three periods, and between individual approach behavior and rates of head-downs. Repeatability of rates of head-downs across periods was assessed using two-way random intraclass correlation coefficients.

Generalized linear models (GLM) were used to look at differences in the rate and proportion of counter-singing bouts between the spring aviaries. Our GLM for the rate of counter-singing utilized a quasi-Poisson distribution to control for over-dispersion with a log link function, with the rate of songs in counter-singing bouts per observation block as the dependent variable. Our GLM for the proportion for songs in counter-singing matches used a binomial distribution with a logit link function with the proportion of total songs within counter-singing matches as the dependent variable. For both models the explanatory factors were the spring aviary, the rate per block of male directed songs (outside counter-singing matches), female directed songs, and undirected songs as explanatory variables. Each model was simplified in a stepwise procedure by removing non-significant variables and comparing simplified models with a chi-square log likelihood test (Crawley 2005). I used variance inflation factors to assess potential multicolinearity in out explanatory factors for each model. A variance inflation factor of 10 or above indicates potential multicolinearity and makes model interpretation difficult (Chatterjee & Hadi 2013). In all of our models the variance inflation factor remained below 2 demonstrating no effects of multicolinearity. Further post hoc analysis was conducted using Kruskal-Wallis and Mann-Whitney U-tests. Chi-square goodness-of-fit tests were used to look at the differences in egg production across the aviaries.

Results:

Fall head-downs: I observed a total of 3,499 head-downs during the fall of 2009. There was a total of 598 female to female (FF: median = 21, IQR = 22), 773 female to male (FM: median = 30, IQR = 35), 886 male to male (MM: median = 29, IQR = 69), and 1242 male to female head-downs (MF: median = 77, IQR = 56). Males exhibited higher rates of head-downs than females (U = 83.5, n1 = 21, n2 = 17, p = 0.006). Neither males nor females displayed any significant sex bias in their head-down rates (Rate FF vs. Rate FM: t = 70.5, n = 21, p = 0.33, Rate MF vs. Rate MM: t = 106, n = 17, p = 0.17). Our fission-fusion perturbation significantly influenced the overall rates of head-downs (X^2 = 39.07, n = 21, p < 0.001, males: X^2= 32.12, n =17, p < 0.001) with the highest rates of head-downs observed during the fission period for both sexes (Fig 3.2). During the fission period I uncovered no significant differences in rates of head-downs across aviaries for both males (w = 40, p = 0.77) and females (w = 57, p = 0.92).

Most individuals engaged in reciprocated head-downs. A total of 33% (n = 1128, median = 27.5, IQR = 30) of all head-downs, including 38% (n = 525, median = 25, IQR = 19) of female, and 28% of male (n = 603, median = 31, IQR = 28) head-downs were reciprocated head-downs. There were a total of 143 reciprocated female to female (RFF: median = 5, IQR = 8), 382 reciprocated female to male (RFM: median = 17, IQR = 24), 325 reciprocated male to male (RMM: median = 12, IQR = 29), and 278 reciprocated male to female head-downs (RMF: median = 16, IQR = 17). Females had higher rates of reciprocated head-downs with males than with females (Rate RFF vs. Rate RFM: t = -2.516, n = 21, p = 0.012), but males exhibited no significant sex bias in their reciprocated head-downs (Rate RFF vs. Rate RFM: t = -0.284, n = 17, p = 0.776).

I found that rates of head-down displays were significantly repeatable across the baseline, fission and fusion periods for both females (ICC = 0.46, f = 3.56, p =0.003) and males (ICC = 0.40, f = 2.96, p =0.004). Furthermore I found significant correlations in the rates of head-downs across all periods for both males and females (Table 1). Thus, Head-down rates were both consistent and repeatable across the fall.

Social approach and head-downs: The frequency that females engaged in head-downs reflected their overall social approach tendencies. Females who performed a higher number of head-downs both initiated and received more approaches from others than females who performed fewer head-downs (approaches initiated vs. head-downs: r = 0.81, n = 21, p < 0.0001, approaches received vs. total head-downs: r = 0.66, n = 21, p < 0.001). Within each period, female approach numbers correlated positively with the rates of head-downs (Table 3.3), and therefore female head-down frequencies reflected their propensity to approach conspecifics. The number of head-downs a male initiated did not correlate with how frequently they approached others and how frequently others approached them (approaches initiated vs. head-downs: r = 0.29, n = 17, p = 0.26, approaches received vs. head-downs: r = 0.08 n = 17, p = 0.77). Therefore male head-down frequencies did not significantly reflect their propensity to approach conspecifics.

Spring singing behavior: I recorded a total of 29,551 songs during the spring, with a total of 15,100 songs directed towards males and 9186 songs directed towards females and

5265 undirected songs (Table 3.4). In each aviary, males directed more songs towards males than towards females (Low Aviary: $t = -2.201$, $n = 6$, $p = 0.03$, Intermediate Aviary: $t = -1.992$, $n = 6$, $p = 0.046$, High Aviary: $t = -2.023$, $n = 5$, $p = 0.043$). I uncovered no difference in the number or proportion of female (Number: $H_2 = 0.5739$, $p = 0.75$; Proportion: $H_2 = 1.1634$, $p = 0.559$) or male directed song (Number: $H_2 = 5.119$, $p = 0.08$; Proportion: $H_2 = 0.4875$, $p = 0.7837$) across the three aviaries.

Flocks exhibited a progressive increase in the amount of counter-singing from the low to high flocks. Our GLM indicated a significant influence of both aviary ($t = 5.810$, $df = 16$, $p < 0.0001$) and the rate of songs sung to males outside counter-singing bouts ($t = 5.368$, $df = 16$, $p = 0.0001$) on the rate of songs in counter-singing matches. I observed a total of 6965 directed songs within counter-singing matches, with 1741 songs (median = 286, IQR = 151) in the low aviary, 2093 (median = 389, IQR = 227) songs in the intermediate aviary, and 3131 songs in the high aviary (median = 633, IQR = 608, Table 3.2).

Males in the high flock placed more emphasis on counter-singing in contrast to the males in the intermediate and low flocks. Our GLM on the proportion of songs within counter-singing matches indicated a significant influence of aviary ($t = 7.566$, $df = 16$, $p < 0.0001$). There were significant differences between the three aviaries in the proportion of songs within counter-singing matches ($H_2 = 6.9477$, $p = 0.031$, Fig 3.6) with the high aviary displaying a higher proportion of songs in counter-singing matches than the low and intermediate aviaries (Low vs. High Aviary: $U = 2$, $n1 = 6$, $n2 = 5$, $p = 0.02$, Intermediate vs. High Aviary: $U = 3$, $n1 = 6$, $n2 = 5$, $p = 0.03$).

Males who initiated more head-downs during the fall had a higher proportion of songs in counter-singing matches than other males. Across all aviaries I discovered a significant correlation between the number of fall head-downs and the proportion of songs within counter-singing matches during the spring ($r = 0.48$, $p = 0.05$). I uncovered no relationship between the number of fall head-downs and the proportion of undirected ($r = -0.35$, $p = 0.17$), male directed ($r = 0.17$, $p = 0.51$), and female directed song ($r = -0.22$, $p = 0.38$).

Egg production and Copulations: Females in the spring aviaries produced significantly different numbers of eggs, with 76 eggs in the low aviary, 107 eggs in the intermediate aviary, and 138 in the high aviary (chi-square goodness-of-fit test: $X^2 = 17.96$, $p < 0.0001$, Fig 4). The low aviary produced 29 fertile eggs, the fewest of the three aviaries (38% fertility rate), followed by the intermediate aviary that produced 38 (36% fertility rate) fertile eggs, and the high aviary that produced 60 fertile eggs (43%, fertility rate). While the number of fertilized egg laid differed across the three aviaries (chi-square goodness-of-fit test: $X^2 = 17.96$, $df = 2$, $p < 0.0001$) the proportion of fertilized eggs laid did not differ across the three aviaries (chi-square goodness-of-fit test: $X^2 = 0.67$, $df = 2$, $p = 0.72$). I observed no differences in the number of copulations across aviaries ($H_2 = 0.14$, $p = 0.93$), although the observed instances of copulation was low, with an average of 3 for the high, 3.17 for the intermediate, and 1.7 for the low aviaries.

3.4 Discussion

By bringing individuals closer together, sociability will shape opportunities for learning social skills, or the appropriate behavioral responses to others. Here I demonstrated that sociability and affiliative displays during the fall predicted reproductive behavior months later. In cowbirds, social experiences with others before the breeding season can influence later reproductive skills (White et al. 2002c; White et al. 2010a). To my knowledge, this is the first experimental documentation that individual sociability shapes reproductive behavior in birds.

During the first study female cowbirds maintained comparable levels of social approach across years. Flocks of highly sociable females contained more laying females who laid more eggs than flocks with less sociable females. In addition, within the high flock, spring sociability correlated with individual egg production and showed a tendency to correlate with egg production in the intermediate flock. Evenly distributing male sociability across aviaries garnered no significant differences in male singing behaviors that predict reproductive success (White et al., 2010). Furthermore, females differed in how choosy they were when approaching others. Less sociable females were more selective by distributing their approaches across a smaller range of conspecifics than more sociable females.

During the second study I demonstrated that higher rates of head-down displays predict later courtship skills, in particular the ability to counter-sing. The rate at which males initiated head-down displays remained consistent across fission-fusion changes. During the spring, flocks composed of high frequency head-downers displayed higher rates and proportions of songs within counter-singing matches and exhibited higher egg production in comparison to other flocks. Across all flocks, males who initiated more head-downs in the fall had a higher proportion of their songs within counter-singing matches. Thus, fall head-down displays recorded in September, October, and November were predictive of competent social behavior six months later during May and June of the following year.

Discussion for the First Study:

In our first study cowbirds varied in how often and how widely they distribute their approaches. Within highly sociable flocks, females were less choosy in whom they approached, and approached others more often, in contrast to less sociable flocks. Frequent but selective approaches often signify strong individual relationships, whereas frequent but distributed approaches signify gregariousness (Hinde 1976). Thus, females increasingly distributed their approaches more gregariously from low to high flocks. More gregarious female cowbirds will have more opportunities to assess songs from a diversity of males, which may influence their subsequent reproductive decisions. Variation in female selectivity is an important component of mating systems, and while most cowbirds maintain selective monogamous relationships, promiscuous relationships have also been observed (Ortega 1998). Female cowbirds also exhibit significant variation in which song variants evoke copulatory responses with some females being consistently more selective than others (Hamilton et al. 1997). In the present study, it is impossible to know all the costs and benefits of being a highly sociable but less selective female, versus being a less sociable but more selective female, as selectivity is necessary for mate choice decisions and forming strong relationships (Insel & Young 2001). Nevertheless, our findings that more sociable cowbirds are also less selective when approaching others appears to have demonstrated divergent strategies that individuals employ to navigate the social environment and mate.

I found no significant differences in male singing behavior, selectivity, or the number of male initiated approaches across the three aviaries. Consequently, differences in female reproductive performance across flocks were unlikely to be a direct product of male singing or approach behavior. This contrasts with previous experiments showing that close female proximity increases male-directed song and counter-singing matches (King et al. 2003). However, unlike previous studies that used only juvenile males, all males in this experiment were familiar adults. Therefore, stable singing patterns may emerge later in development, and not be as responsive to female proximity as juvenile singing patterns. Overall, these findings suggest that stable variation in female approach tendencies, and not changes in male behavior, is the primary attribute influencing female egg production.

Separating cowbirds based on their sociability resulted in divergent patterns of egg production during the spring. In cowbirds, flocks of highly gregarious females will contain more opportunities to approach, assess, and mate with others in contrast to flocks of less gregarious females. This was reflected in both studies as the number of laying females progressively increased from the low to high flocks. Furthermore, in our first study, within both the high and intermediate flocks more sociable females laid more eggs than less sociable individuals. These results suggest that the social niches females occupy may have effects on both the group and individual level, such that groups containing more social females exhibit a higher correlation between individual sociability and egg production. The cohesive more distributed social networks within high flocks may have created increased competition over limited social resources, as many more individuals will be able to assess and interact with potential mates and competitive rivals. In such saturated networks individuals may be able to differentiate themselves from others, resulting in greater variation in reproductive performance among individuals. Such a process may be akin to the social niche specialization hypothesis, wherein stable social groups facilitate the emergence of distinct social roles, except here the emergence of a strongly connected more sociable group elicits greater individual differences in reproductive performance, while maintaining higher average reproductive performance in relation to other groups.

Discussion of the second study:

Our second study demonstrated that the head-down display is a robust component of the behavioral repertoire of cowbirds. Head-down rates remained correlated and repeatable across multiple social contexts and over time for both males and females. Females who initiated more head-down displays were more likely both to approach and to be approached by others. Most individuals participated in reciprocated displays, but females were more likely to reciprocate head-downs from males than from females. While the mean frequency of head-downs changed across the different contexts, both males and females maintained correlated and repeatable rates of head-down displays throughout the fall. Furthermore neither males nor females exhibited any sex bias in the head-downs they initiated, demonstrating that head-downs are used generally to initiate close contact with all conspecifics. Outside of fighting and copulations, the head-down is the only behavior that brings individuals into physical contact and sustains that contact for extended periods of time. During the fall cowbirds converge into large flocks and the head-down display is used to navigate an increasingly complex social environment. Some have suggested that the display may be particularly advantageous during roosting, obtaining food while group foraging (Scott & Grumstrup-Scott 1983), structuring social order (Rothstein 1980b), and assessing new individuals (Rothstein 1977). While the current study did not address the functional benefits of head-down displays, its individual consistency suggests that individuals may reliably seek out closer social interactions than others.

Male approach rates did not correlate with their head-down rates, and male cowbirds are more likely to use head-down displays in contrast to females. Previous studies have shown that repeated head-down use facilitates closer proximity between conspecifics (Selander & LaRue 1961; Stevenson 1969), and appeases aggressive tendencies in others (Scott & Grumstrup-Scott 1983). If the head-down provides a cue that subsequent interactions will not be aggressive (Ortega 1998) it will shape how males and females engage conspecifics and provide a “gateway” to a large diversity of different interactions involving close proximity. Unlike females, male cowbirds form strong dominance relationships with conspecifics, and this may lead to male approaches being perceived as more agonistic than female approaches. Studies have shown that male approaches are used to displace others (Rothstein et al. 1986), and thus higher male approach rates may not reflect an increased willingness to initiate close social contact. Therefore, more sociable males may use head-down displays more frequently than females as a means of minimizing withdrawal of conspecifics that may interpret their close proximity as agonistic. Furthermore, as males are more dominant, females may perceive close male proximity as more agonistic, and therefore be more likely reciprocate head-down initiated by males than females.

The head-down display disappears during the breeding season and thus cannot play a direct role in structuring breeding opportunities. Nonetheless, the use of head-down displays during the fall may facilitate the close interactions needed to learn social skills, and have cascading influence on reproductive performance. The ontogeny of social skills, requires individuals to seek out, engage, and learn from others. Different social experiences can shape the expression of later social skills. For instance, cichlid fish (*Neolamrologus pulcher*) raised with adults exhibited more appropriate behavioral responses when competing with others (Taborsky et al. 2012), and male cowbirds who experienced a more varied social environment outcompeted others for access to mates (White et al. 2010a). Head-down displays, by fostering close social interaction, will be an important influence on an individual's experience and access to social learning opportunities. While the current study did not investigate the developmental or proximate mechanisms linking head-down displays with reproductive behavior, it is the first demonstration in birds that affiliative displays can predict reproductive skills across contexts and over long periods of time.

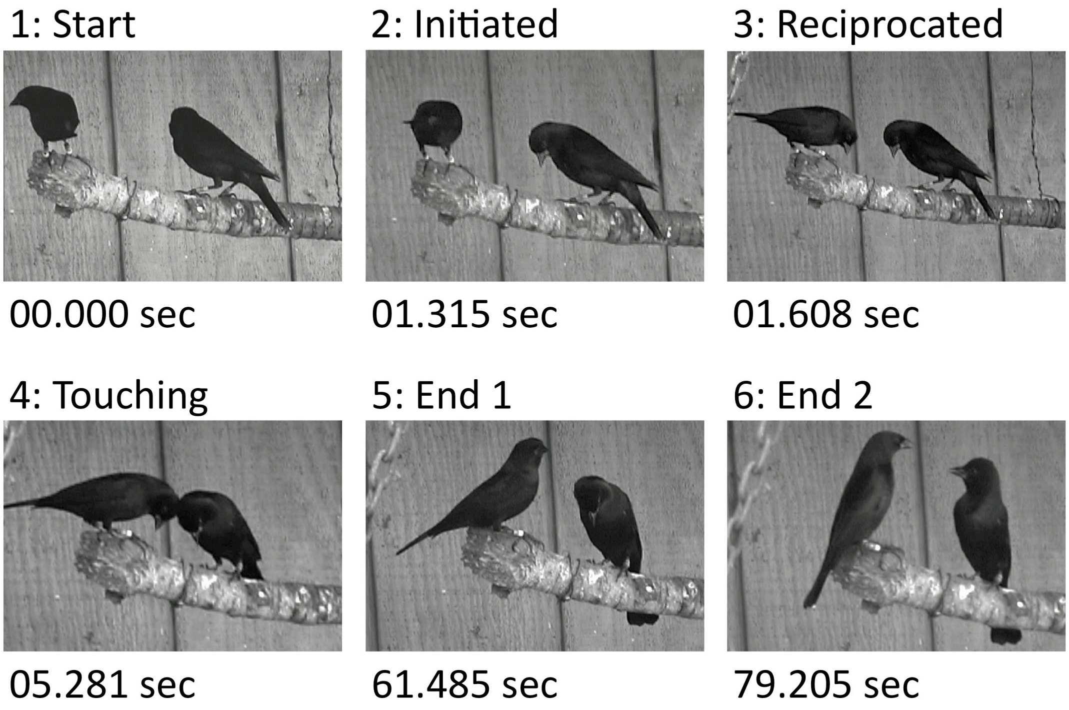
Counter-singing is an essential component of male courtship behavior. Flocks composed of the high head-downing birds exhibited significantly higher proportion of songs within counter-singing matches. Furthermore, male sociability during the fall correlated with the proportion of songs in counter-singing matches, but not the proportion of female, male, or undirected songs. Counter-singing is a predictor of male reproductive success, stimulates egg production in females, and is learned through close interaction with others (White et al. 2010b). White et al. (2002c) found that juvenile males who interacted with adults prior to the breeding season engaged in more frequent and longer counter-singing matches than juveniles who did not interact with adults. In order to counter-sing effectively, males must remain in close proximity with other males and respond appropriately without withdrawing or escalating to aggression. Thus a male's affiliative behavior may shape his ability to counter-sing, as more affiliative males may be more willing to remain in close proximity to another singing male. This study suggests that a male's affiliative displays during the fall are an important predictor of their later reproductive skills during the breeding season.

Females in flocks composed of higher head-downing birds produced more eggs than other flocks. While male counter-singing has been shown to reflect increased female egg production, previous studies have also demonstrated that exposure to highly interactive females can also increase levels of counter-singing (King et al. 2003). The design of this study does not address if male counter-singing stimulates females to lay more eggs or if more reproductively competent and sociable females stimulate males to engage in more counter-singing. Furthermore, the identities of the laying females were not known in the present study and therefore it is unknown if more sociable females within each flock also produced more eggs. Future studies that independently manipulate male and female affiliative behavior, while identifying laying females are needed to understand the direction of effects. Nonetheless, these results do suggest that sociability can create opportunities to acquire social engagement skills and that, taken as a whole, will lead to better courtship and reproductive success.

Here I demonstrated that variation in social niches and affiliative behaviors, in a context not associated with mating, is predictive of reproductive consequences many months and even years in the future. All functions of social life require individuals to manage, control and construct spatial relations between conspecifics. The ability to sustain close proximity with others is one of the most basic skills individuals must master, and creates a foundation where other behaviors arise. From protection from predators, to play (Burghardt 2005), to social bonding (Stöwe et al. 2008), the approach-withdrawal systems used to manage proximity between individuals are central in constructing a social niche. That approach alone was predictive of reproductive output in females indicates that these behaviorally economical approach-withdrawal systems, could provide a widespread mechanism for variation in reproductive behavior. The niches constructed by more sociable cowbirds will have more opportunities to reproduce, and therefore possess better social skills to take advantage of those opportunities. Furthermore, groups with more sociable composition may experience heightened competition over social resources resulting in exacerbated differences across individuals in their reproductive performance. The studies covered here suggest that selection may act on the social niches constructed by more sociable individuals to facilitate the acquisition of better courtship skills over the course of development.

3.5 Figures and Tables:

Figure 3.1



1: Start
00.000 sec

2: Initiated
01.315 sec

3: Reciprocated
01.608 sec

4: Touching
05.281 sec

5: End 1
61.485 sec

6: End 2
79.205 sec

Fig 3.1: Sequential progression of a head-down display. The display starts with two male cowbirds facing different directions (1: Start). The individual on the right initiates (2: Initiated) a reciprocated display (3: Reciprocated) and then moves (while maintaining the head-down posture) in close proximity to the individual on the left until the crest of their heads touch (4: Touching). After maintaining the display for around a minute, the individual on the left goes out of the display (5: End 1), pecks lightly at the individual on the left right (not shown) until he goes out of the display. The individual on the left then adopts a alert posture, while the individual on the right adopts a raised head posture with crest feathers raised (6: End 2).

Figure 3.2

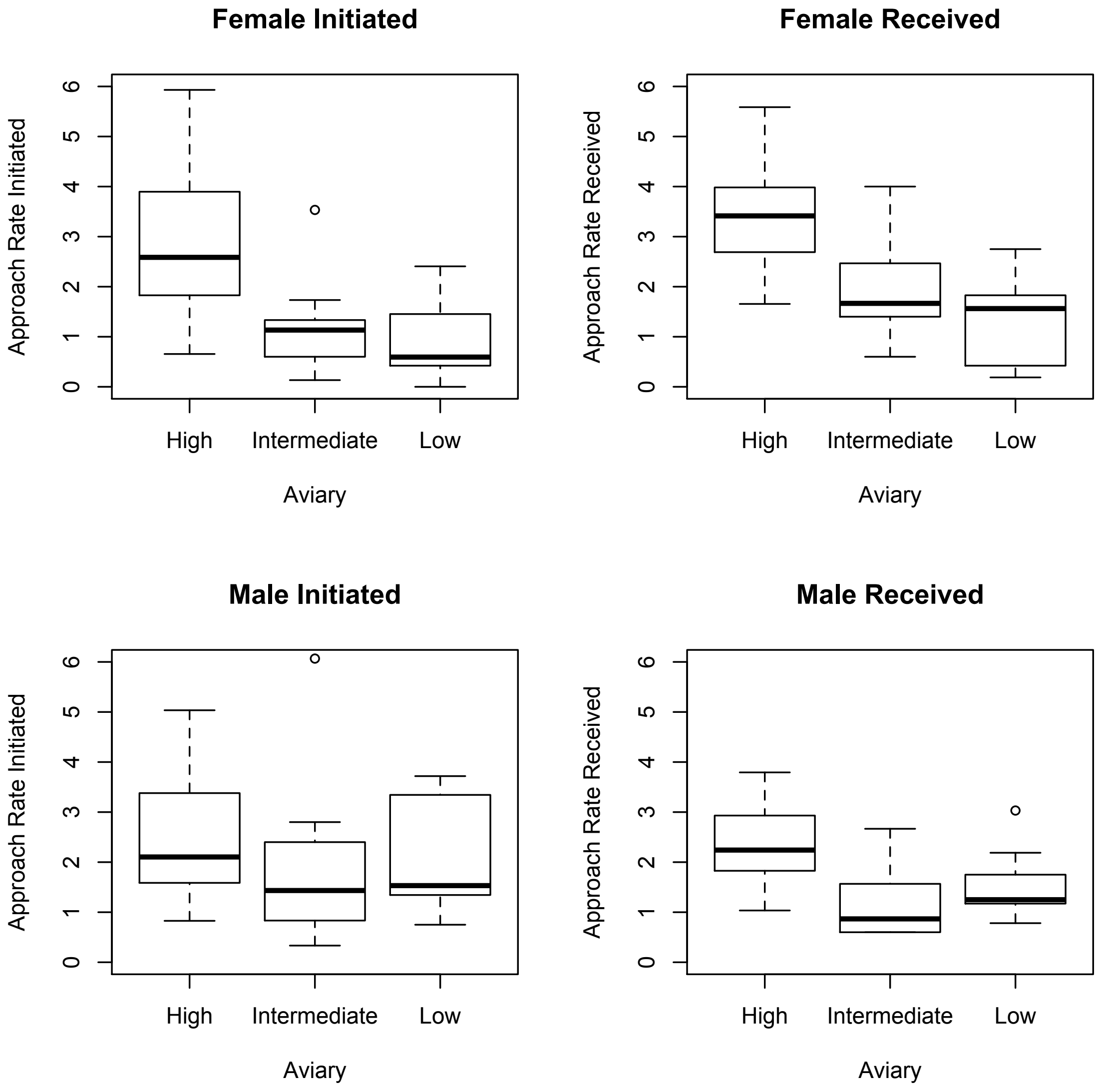


Figure 3.2: The approach rates for the female-initiated, male initiated, female received and male received for the high intermediate and low aviaries during spring 2011.

Figure 3.3:

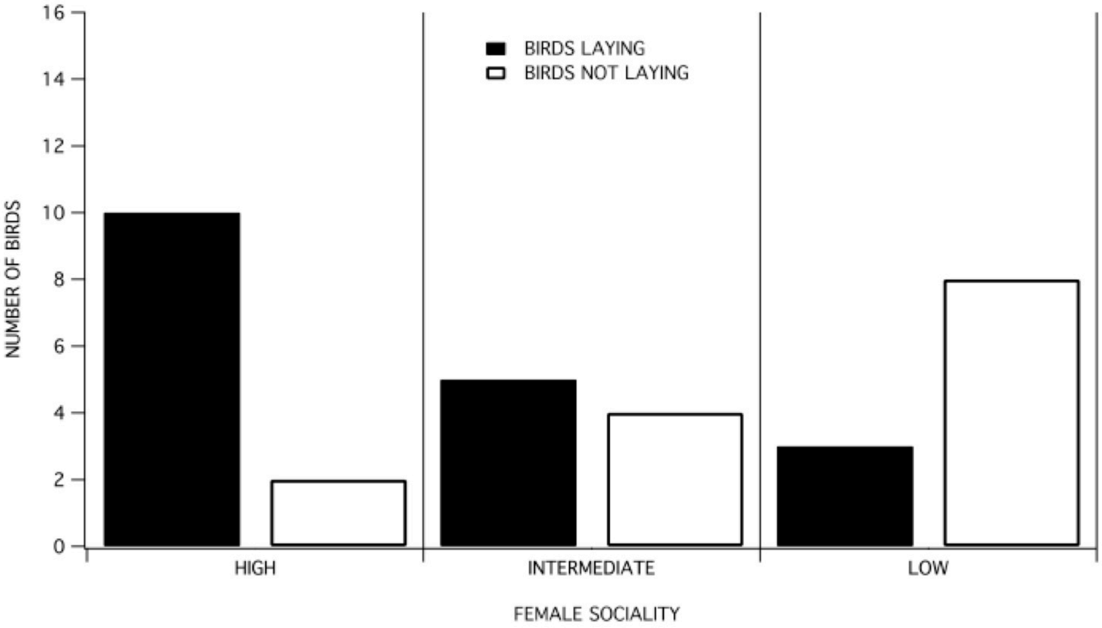


Figure 3.3: Number of females that either did or did not lay eggs within the high, intermediate and low aviaries.

Table 3.1:

Sex	Centrality	Fall 2009 –Fall 2010	Fall 2010 – April 2011	Fall 2009 – April 2011
Female	in-degree	0.93***	0.67**	0.71**
	out-degree	0.79***	0.64**	0.69**
Males	in-degree	0.55*	0.11	0.31
	out-degree	0.75**	0.57*	0.49

*P<0.05, **P<0.01, ***P<0.001

Table 1: Spearman's rank correlations for in-degree and out-degree centrality for females and males over the three years.

Figure 3.4:

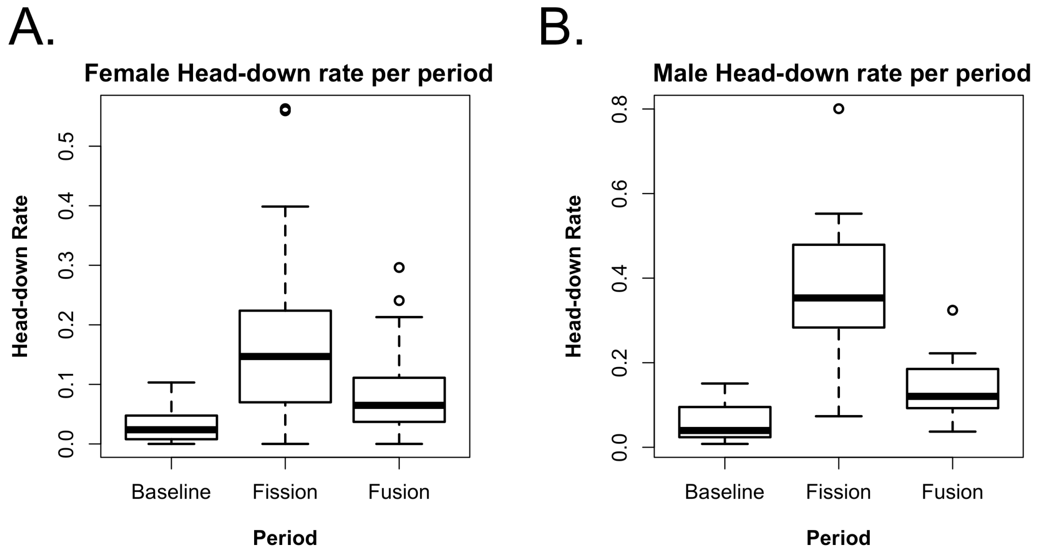


Figure 3.4. The rates of head-down displays per block across the baseline, fission, and fusion periods for both females (A: Baseline: *Md* = 0.024, IQR = 0.04, Fission: *Md* = 0.15, IQR = 0.15, Fusion: *Md* = 0.07, IQR = 0.074) and males (B: Baseline: *Md* = 0.04, IQR = 0.071, Fission: *Md* = 0.35, IQR = 0.2, Fusion: *Md* = 0.12, IQR = 0.093).

Figure 3.5:

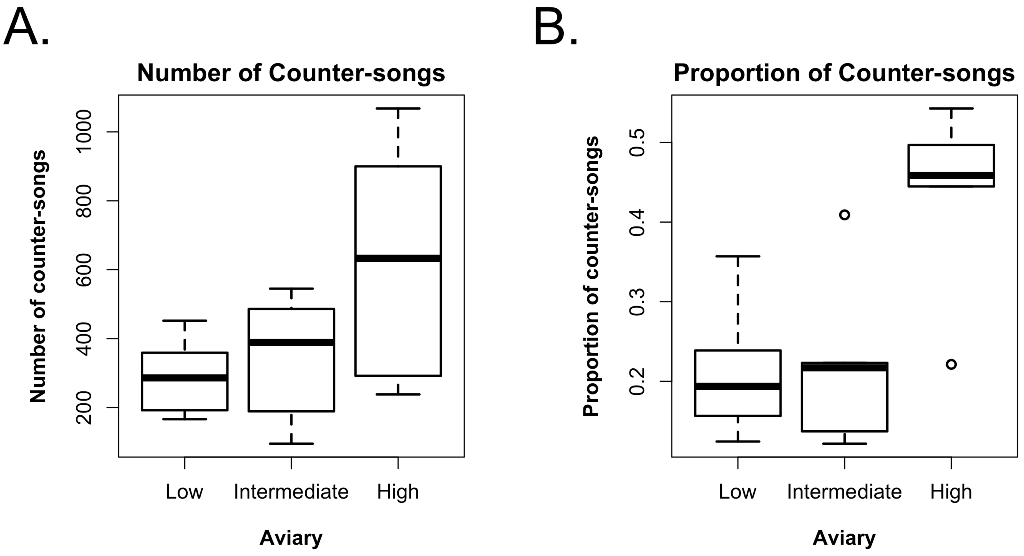


Figure 3.5: Number (A.) and proportion (B.) of songs within counter-singing matches between the three spring aviaries. Boxes represent interquartile ranges with the median in the middle represented by a bold line, whiskers represent the range of the highest and lowest values that are within a range of 1.5 times the interquartile range, open circles indicate data points that are outside this range.

Figure 3.6:

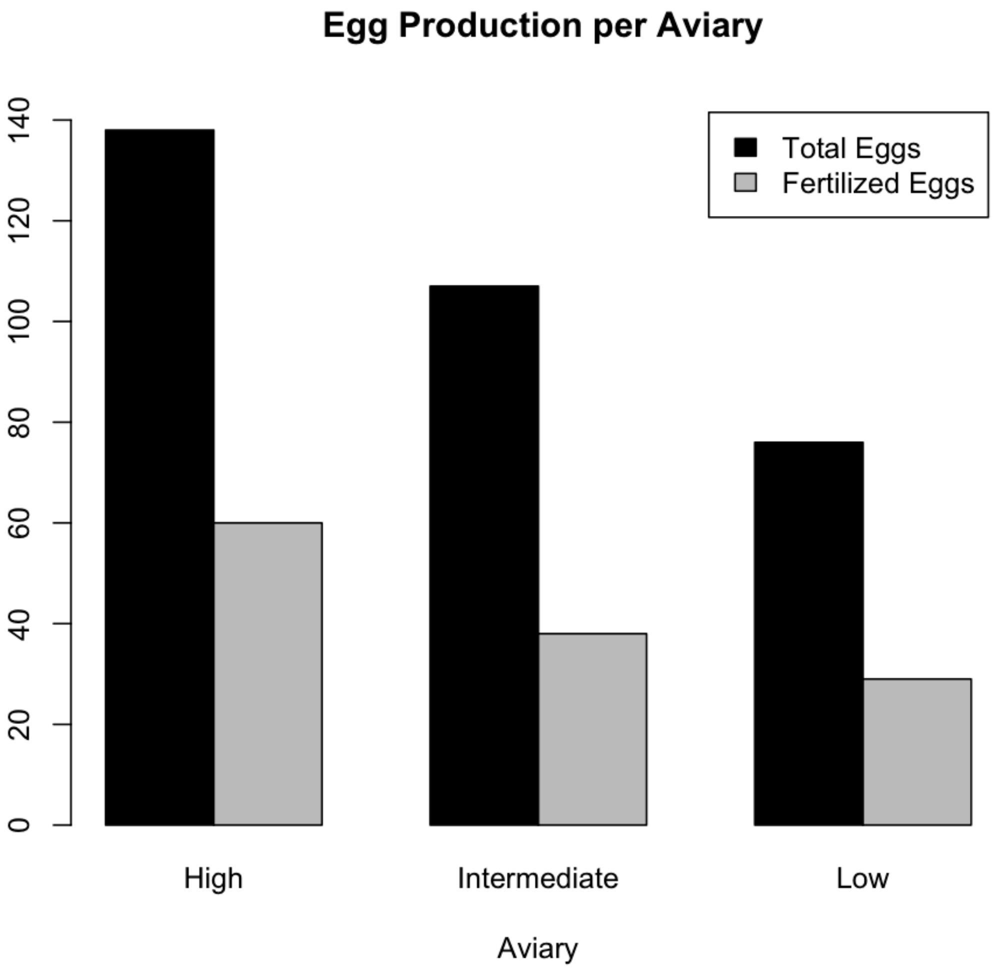


Figure 3.6: Number of total and fertilized eggs laid in each aviary during spring 2010.

Table 3.2

Head-down	Baseline-Fission	Fission-Fusion	Baseline-Fusion
Female	0.81***	0.89***	0.76**
Male	0.64**	0.81***	0.68**

Table 3.2 Spearman's rho correlations in the rates of head-downs for males and females over the three periods of the social perturbation experiment. Significant correlations are noted with asterisks. *: $P < 0.05$, **: $P < 0.005$, ***: $P < 0.0005$

Table 3.3

Sex	Degree	Baseline	Fission	Fusion
Female	Initiated	0.58 *	0.80 ***	0.76 ***
	Received	0.62 *	0.58 *	0.60 **
Males	Initiated	0.41	0.44	0.14
	Received	- 0.18	0.18	- 0.07

Table 3.3: Spearman's correlations between the rates of head-downs and social approaches for males and females over the three periods of the social perturbation experiment. Significant correlations are noted with asterisks. *: $P < 0.05$, **: $P < 0.005$, ***: $P < 0.0005$

Table 3.4

	Total song	Undirected	Directed	Counter-singing
Low	10 107 (*Md* =1 496, IQR = 1766)	1 818 (*Md* = 291, IQR = 262)	8 289 (*Md* =1 162, IQR = 1498)	1 741 *(Md* = 286, IQR = 151)
Intermediate	10 608 (*Md* =1 946, IQR =1467)	2 494 (*Md* = 439, IQR = 106)	8 114 (*Md* =1 377, IQR = 1426)	2 093 (*Md* = 389, IQR = 227)
High	8 836 (*Md* =1 423, IQR = 1791)	953 (*Md* = 125, IQR = 158)	7 883(*Md* =1 151, IQR =1710)	3 131 (*Md* = 633, IQR = 608)

Table 3.4: Number of total, undirected, directed and counter-songs within each spring aviary.

Chapter four: Social niches and the development of courtship skills in juvenile females

4.1 Introduction:

The last chapter showed how autumn social niches and affiliative skills were able to predict later reproductive performance and courtship behavior within adult birds. This chapter will investigate how early social niches and head-downs within juveniles predict the development of their courtship behavior. Across most species of birds little is known about a juvenile's social relationships, and how differences in early experience shape later behavioral outcomes. Within primates and birds, individuals possess ritualized affiliative behaviors that facilitate close interaction with others while mitigating aggressive tendencies. These ritualized behaviors reflect, and help to define, an individual's social niche. The use of affiliative behavior may be of particular importance during early life, where individuals need to initiate interactions with many novel, and potentially aggressive, conspecifics. Thus, consistent differences in the ability to utilize affiliative behaviors may create the contexts where individuals can engage others in close social interaction, while minimizing the risk of agonistic encounters. This chapter covers one study, where the frequency and consistency of both social approach displays are used to define the qualities of a juvenile's social niche. I then look at how these niches reflect a juvenile's use of affiliative behaviors within the fall, and how both of these social attributes predict later courtship behavior during a juvenile's first breeding season.

The last chapter established the head-down as a significant aspect of an adult's social behavior during the fall. Breeding season flocks composed of adults who initiated more head-downs during the fall exhibited higher rates of egg production and courtship behavior the following spring (Kohn et al. 2013c). The head-down is the only behavior that brings cowbirds into close proximity for extended periods of time, and studies have shown that repeated use of the display has an appeasing influence (Robertson & Norman 1976; Scott & Grumstrup-Scott 1983; Selander & LaRue 1961). Like other affiliative displays, such as grooming in primates and allopreening in other birds, head-downs are commonly reciprocated with cowbirds responding to another's display with a head-down. Consequently, individuals who initiate more head-downs during the fall will have more experience in close social interactions in contrast to individuals who initiate fewer head-downs. While the head-down display has been observed in juvenile cowbirds, it has not been systematically studied, and little is currently known about its consistency and relationship to courtship skills in this age group. In the current study, I manipulate group size and composition to see if juveniles exhibit predictable patterns of head-down displays and social niches in response to flock changes.

The ability to form and sustain strong pair bonds with preferred mates is often essential for successful reproduction. While female behavior is an essential component of adult courtship and reproduction (King et al. 2003; West & King 1988), little is known about the early variation in juvenile female courtship behavior. Females, who do not sing, use a chatter vocalization throughout the breeding season. These chatter vocalizations are individually distinct (Burnell & Rothstein 1994), and have been shown to attract both male and female attention (Dufty 1982). Females often respond to male song with a chatter, and these response chatters are assumed to indicate a preference for specific males' songs (Freed-Brown & White 2009). Females with a higher proportion of response to undirected chatters will use their chatter more selectively to communicate mate preferences. By attracting and reinforcing the attention of specific males, chatter vocalizations may aid females in the formation and maintenance of the pair-bonds necessary for successful reproduction.

Cowbirds are primarily a monogamous species and maintaining pair-bonds is often essential for successful reproduction (Yokel 1986). While juveniles are not successful when compared with adults (White et al. 2002c), they often engage in courtship behavior during their first breeding season. Courtship skills acquired as a juvenile may aid an individual's reproductive success when they become reproductively active as adults (White et al. 2007). Thus, in this study I considered a female's paired status, the number of songs received and response chatters, as well as the proportion of response chatters to undirected chatters as measures of early courtship skills. I hypothesize that robust variation in head-down displays will emerge during their first fall, and that higher head-down rates during the fall will predict better courtship behavior during their first breeding season. In particular, I expect female head-down rates to correlate with paired status, songs received and number of response chatters. While in males, I expected head-down rates to correlate with the number of directed songs and counter-singing matches.

4.2 Methods:

Subjects: All birds were originally captured in Philadelphia County, Pennsylvania and housed in aviaries in Monroe County, Indiana. All subjects were *Molothrus ater ater*. For this study I used 12 juvenile females and 12 juvenile males. All birds were juveniles, and at the beginning of the study ranged in age from 55 to 75 days old with an average age of 73 days, and were housed together for one month prior to the present study. Cowbirds without access to adults during the first year are not sexually competent in their first breeding season (White et al. 2002c). Each bird was marked with uniquely coloured leg bands to allow for individual recognition. All birds were provided daily with a diet of vitamin treated water (Aquavite Nutritional Research), red and white millet, canary seed and a modified Bronx Zoo diet for blackbirds.

Aviaries: I used three aviaries that were visually isolated and substantially acoustically attenuated from each other, each with identical dimensions (9.1 x 21.4 x 3.4 meters). Environmental conditions were similar throughout all aviaries with shrubs, trees, grass, covered feeding stations and access to indoor enclosures. All aviaries allowed birds to be exposed to ambient climatic conditions, wild cowbirds, and the sight of predators.

Data collection: During the fall 2010, I recorded both male and female social approach and head-down displays. An approach was scored when one individual approached another individual with any part of its body within a radius of 30cm. A head-down was scored when an individual maintained a low crouched position with its head pointed downwards so that the back of the head and neck are positioned in close proximity, if not touching, a neighboring individual for at least one second. Head-downs were either initiated, when one individual initiated a head-down to a conspecific who was not in the head-down posture, or reciprocated, when an individual responded to another's head-down posture with a reciprocal display. The identity of the individuals initiating and receiving an approach or head-down was recorded for each interaction.

During the breeding season, I recorded both male and female courtship behavior, focusing on the vocal behavior of both males and females. For male courtship behavior, I recorded the number of female and male directed songs, and the number of songs within counter-singing matches. A counter-singing match occurs when a male reciprocates a directed song within 15 seconds after receiving a song from a neighboring male. For females, I recorded the number of songs each female received from males and the number of female chatter vocalizations. Female chatter vocalizations were either response or undirected chatters based on their temporal proximity to male song. Response chatters occur when a female responds to a directed male song with chatter vocalization within a one second time window. Undirected chatter vocalizations occur when the females performs a chatter vocalization outside of singing contexts. Throughout the study, I utilized a scan-sampling procedure: behaviors were recorded, as they were observed, using voice recognition technology. When used in combination with voice recognition technology scan-sampling can accurately acquire a more comprehensive dataset than focal sampling. Fall behavior was recorded in blocks of 7-minute scan sampling periods and breeding season behaviors were recorded in blocks of 15-minute scan sampling periods. All observations were conducted between 07:00-10:30AM when cowbirds are most active and were counterbalanced, so each observer took the same number of scan-sampling blocks in each aviary at the same time of day. All work was conducted under ABS guidelines and approved by the Institutional Care and Use Committee of Indiana University (08-018).

Juvenile fall social behavior:

Stage one: Baseline period. From September 7th to October 11th, 2010, three observers conducted daily observations in Aviary 1, each recording approaches and head-downs, collecting a total of 165 seven-minute observation blocks.

Stage two: Fission Period. On October 13th, I separated birds into Aviary 1 and Aviary 2 based on their frequency of approaches during the Baseline period, so that both flocks contained individuals with a similar range of approaches. Both aviaries contained 12 cowbirds including 6 males and 6 females. From October 13th to October 24th, three observers conducted daily counterbalanced observations recording approaches and head-downs, and collected a total of 195 seven-minute observation blocks (98 blocks in Aviary 1, 97 blocks in Aviary 2).

Stage three: Fusion Period. On October 27th, all birds were moved into Aviary 1. From October 27th to November 6th, three observers conducted daily observations recording approaches and head-downs, and collected a total of 166 seven-minute observation blocks.

Stage four: Throughout the breeding season from May 1st to June 9th three observers conducted daily observations recording male song and female chatter vocalizations, and recorded a total of 252 fifteen-minute observation blocks.

Analysis: Due to small sample sizes and non-normality of data I primarily used non-parametric statistics. I used Friedman tests and Wilcoxon signed rank tests to see if the rates of head-down displays differed across periods during the fall. To investigate sex differences in the number of head-downs, and if males or females exhibited any significant sex preference in the head-downs they initiated or reciprocated I used Wilcoxon signed rank tests. During the fusion period, I tested if individuals preferentially interacted with their flock-mates from the fission period. Unseparated individuals were conspecifics that shared the same aviary during the fission period, whereas separated individuals were housed in the alternate aviary during the fission period. Wilcoxon signed rank tests were used to see if individuals preferentially approached and head-downed with unseparated in contrast to separated individuals. To look at the contextual generality of head-down behavior across periods I used Spearman's correlations to see if individuals maintained significantly comparable rank-ordered rates of initiated and reciprocated head-down displays across the periods during the fall. To see if the head-down rates reflected social approach behavior, I used Spearman's correlations to look at the relationship between approaches received and approaches initiated with the number of head-downs within each period.

To examine which fall social behaviors were predictors of courtship behavior during the spring, I used Generalized Linear Models (GLM) with a quasi-poisson distribution and a log link function. I used a model simplification procedure where a maximal model was simplified through stepwise elimination of non-significant variables. Log-likelihood tests were used for model comparisons during simplification, with a minimal adequate model defined when model comparisons exhibited a significant loss in the residual deviance with the removal of any remaining explanatory factors (Crawley 2005). I conducted four different GLMs for the females using the number of songs received, the total number of chatter vocalizations, and the number of undirected and response chatter vocalizations as the dependent variables. For males I ran four different GLMs looking at the number of total, female and male directed song, and the number of songs within counter-singing matches as the dependent variables. In all models, the explanatory variables were the number of head-downs performed (both initiated and reciprocated), approaches initiated and approaches received across the fall data collection period. I conducted an individual generalized linear regression with a binomial error distribution to investigate the relationship between fall head-down rates and the proportion of response chatters. All post-hoc tests included Spearman's correlations to look at the strength of the relationship between the explanatory variables and the dependent variables for each model.

As the explanatory variables were inter-correlated I used variance inflation factors (VIF) to assess multicollinearity. A variance inflation factor greater than 10 is used to indicate potential multicollinearity, which makes model interpretation difficult (Chatterjee & Hadi 2013). I calculated VIFs for both the saturated models and for each resulting model during model simplification. In none of our presented models did the VIFs for any factor exceed 10.

I considered a female to be in a pair bond with a male when the songs of that particular male accounted for 75% of the songs she received, and when she was one of the top two females a male sang to. To look at the influence of fall social behavior on consort status during the breeding season I used Wilcoxon rank sum tests. Specifically, Wilcoxon rank sum tests were used to see if consorted females exhibited higher rates of social approach or head-down displays during the fall than un-consorted females.

4.3 Results:

Fall head-down displays: I observed a total of 1,289 head-down displays during the fall (Mdn = 39.0, IQR = 4875), including 640 female to female, 106 female to male, 194 male to female, and 349 male to male head-down displays. Females were more likely to initiate head-down displays with other females than males ($W = 78$, $P < 0.001$), whereas males did not exhibit any significant sex bias ($W = 19$, $P = 0.13$). Overall the rates of head-downs were significantly higher in the fusion period than during the baseline period ($W = 25$, $P = 0.007$). Our Kruskal test showed a significant effect of period on both male ($H^2 = 16.9$, $df = 2$, $P = 0.0002$) and female ($H^2 = 7.2$, $df = 2$, $P = 0.03$) head-down rates. Post hoc analysis demonstrated that females displayed significantly higher rates of head-downs during the fusion period in contrast to the baseline period ($W = 25$, $P = 0.007$). For males the rates of head-downs were significantly higher during the fusion period in contrast to the baseline ($W = 6$, P = 0.0001) and fission periods ($W = 24$, $P = 0.006$).

During the fusion period, individuals initiated a higher proportion of head-downs and approaches towards unseparated individuals from the same fission flock in contrast to individuals from the alternative flock. Both females and males almost exclusively approached unseparated individuals (females: $W = 144$, $P < 0.0001$; males: $W = 127$, $P = 0.002$), and preferentially directed head-downs towards unseparated conspecifics (females: $W = 113.5$, $P < 0.0005$; males: $W = 133$, $P = 0.0005$). Females who approached other individuals more often also initiated more head-downs, while males who received more approaches consistently initiated more head-downs (Table 4.2).

I uncovered no significant sex difference between the numbers of head-down displays initiated ($U = 86.5$, $P = 0.41$, females = 509, males = 381) or reciprocated ($U = 85$, $P = 0.47$, females = 240, males = 159) across the fall. Across all periods during the fall, females maintained the same rank ordered distributions in the rates of head-down displays initiated, whereas male head-downs initiated remained correlated across the baseline to fission periods (Table 4.1). I observed no consistent relationships for the rates of head-downs reciprocated across social periods for both males and females.

Female songs received and fall head-down displays: I recorded a total number of 1 770 songs to females (*Mdn* = 38, *IQR* = 246). Our model showed a significant effect of head-downs ($T = 2.701$, $P = 0.02$) on the number of songs a female received during spring. Post hoc correlations found a significant correlation between head-downs and number of songs received (*rho* = 0.68, $P = 0.02$), but not between approaches initiated (*rho* = 0.38, $P = 0.22$) or approaches received (*rho* = 0.40, P = 0.20, Fig 4.1). Female head-down to other females (*rho* = 0.71, $P = 0.01$) correlated with the number of songs they received, but not their head-downs initiated towards males (*rho* = 0.21, $P = 0.49$).

Chatter vocalizations and fall head-down displays: From May 1st to June 9th I recorded a total of 1 239 (*Mdn* = 23.0, *IQR* = 190.3) chatter vocalizations, including 539 (*Mdn* = 11.50, *IQR* = 56.5) response chatters and 700 (*Mdn* = 11.34, *IQR* = 102.5) undirected chatters. Our models predicting the total amount of chatter vocalizations and undirected chatter vocalizations found no significant effects. The model predicting the number of response chatters uncovered a significant main effect of head-downs ($T = 2.310$, $P = 0.04$). Our post hoc correlations uncovered a significant positive relationship between the number of head-downs initiated and number of response chatters (*rho* = 0.59, $P = 0.04$), but no significant correlation was observed between the number of approaches initiated (*rho* = 0.37, $P = 0.23$) or the number of approaches received (*rho* = 0.20, $P = 0.51$) and the number of response chatters. Female head-downs to other females (*rho* = 0.57, $P = 0.05$) correlated with the number of response chatters, but not their head-downs initiated towards males (*rho* = 0.34, $P = 0.28$).

Further analysis looking at the proportion of response chatters to undirected chatters revealed a significant relationship between all head-down rates in the fall and the proportion of response chatters. The proportion of response chatters was significantly correlated with head-downs (binomial regression: $T = 7.79$, $P < 0.001$, *rho* = 0.92, $P < 0.0001$). Therefore, cowbirds that engaged in more head-down displays during the fall had a higher proportion of response chatters to undirected chatters (Fig 4.2).

Pair Bonds: Females that formed a pair bond ($N = 8$) initiated more head-downs during the fall than females who did not ($N = 4$, $W = 4$, $P = 0.05$), but did not differ either in the number of approaches they initiated ($W = 6$, $P = 0.10$) or received ($W = 14.5$, $P = 0.86$, Fig 4.1). During the spring, consorting females also received more songs ($W = 1$, $P = 0.008$) and produced more response chatters ($W = 0.5$, $P = 0.01$) than females who were not in a pair bond.

Male singing behavior and fall behavior: I recorded a total of 5,140 songs (*Mdn* =223.5, *IQR* = 628.5) during the breeding season including 1,770 female directed songs (*Mdn* = 38, *IQR* = 246), 2,407 male directed songs (*Mdn* = 50.5, *IQR* = 289.3) and 963 undirected songs (*Mdn* = 70.5, *IQR* = 98.25). In total, males had 1,122 songs (*Mdn* = 19.5, *IQR* = 172.25) within counter-singing matches. Our GLMs showed no significant effects of approaches initiated, approaches received or head-downs on the proportion of songs to males, females and within counter-singing matches. Further analysis revealed no significant correlations between any fall social behaviors and either the frequency or proportion of singing behavior in the spring.

4.4 Discussion:

This study investigated the early behavioral correlates of courtship skills in naïve juvenile brown-headed cowbirds. In particular, I aimed to uncover if juvenile cowbirds, without access to adults, exhibit robust patterns of social behavior in the fall, and if these patterns predict courtship skills months later during their first breeding season. The rate and selectivity of head-down displays changed across the fall, with individuals engaging in more head-down displays with more unseparated individuals when they were reunited into a large flock. Nonetheless, I discovered that juvenile female head-down rates were correlated across changes in social contexts. The ability to maintain comparable levels of social interaction across contexts and over time may shape the expression and ontogeny of later social behavior. I showed that variation in fall head-downs also predicted the courtship performance of the juvenile females during the following breeding season. Females who initiated more head-downs were more likely to receive songs from males, respond to songs with a response chatter, and maintain pair bonds with preferred mates. In contrast, while males also initiated more head-down displays when reunited, the lack of significant correlations in juvenile male head-down rates suggests that the ability to initiate close interactions depends more on the current context than on consistent individual differences. Furthermore, male head-down rates did not predict courtship performance during the breeding season.

The head-down is unique, as it is the only behavior that allows two cowbirds to remain in close proximity for extended periods of time. While the exact functional benefits of the display are debated (Ortega 1998; Scott & Grumstrup-Scott 1983), numerous studies have shown that repeated use of head-down displays decreases inter-individual distances (Stevenson 1969), facilitates group cohesion, and appeases agonistic tendencies (Robertson & Norman 1976; Scott & Grumstrup-Scott 1983; Selander & LaRue 1961). While previous studies have demonstrated the presence of head-downs in wild juveniles (Lowther & Rothstein 1980b), here I demonstrate that juvenile head-down use is extensive, reciprocal, selective, and exhibits substantial individual variability.

In adult females the number of approaches a female both received and initiated correlated with their head-down rates. In this chapter I discovered that divergent aspects of a juvenile's social niche across the sexes reflected their head-down usage. For juvenile females the number of approaches they initiated towards others was correlated with their head-down rates, while in males the number of approaches received correlated with higher head-down rates. As males may approach other individuals to displace them (Rothstein et al. 1986), males who are approached more often may use the head-down to avoid being displaced and sustain close contact with others. As such a correlation was not observed in adult males, higher head-downing individuals may become more competent in engaging others, and over time become more dominant themselves, although this needs further study. For juvenile females, approaching others could elicit more aggressive responses from more dominant males, and therefore more sociable females may be more likely to use the head-down display. As females segregate from males early on, it is possible that more attractive females may not need to employ more head-downs as other females are primarily approaching them.

The predictability of head-downs across changes in group size and composition demonstrates that juvenile females vary in how they interact. By initiating more head-downs with more individuals some females will have more experience in close social interaction in comparison to others. In the fall, cowbirds converge into large roosting and feeding aggregations and must manage close interactions with a diversity of conspecifics. As shown in previous chapters and studies, an individual's interaction patterns and preferences during the fall can have a significant influence on their later reproductive performance (Freeberg 1997; Freeberg 1998; Freeberg et al. 1999; Kohn et al. 2011; Kohn et al. 2013a, b; Kohn et al. 2013c). In particular, close interaction with females during fall may expose individuals to cues regarding the quality of male song displays (Gros-Louis et al. 2003), and shape later mate preferences (West et al. 2006). During the spring, cowbirds focus on courtship and sustaining pair bonds with preferred mates (Friedmann 1929; Ortega 1998). Juvenile females who initiated more head-downs with females in fall received more song during the spring and used more response chatters. The attentiveness to social cues required for cowbird courtship may select for individuals who can initiate and sustain close interactions. Females who are more tolerant of another's proximity will have more opportunities to assess song and respond with a response chatter, and this may ultimately result in the formation of strong pair bond. While more work needs to be done to explore the developmental mechanisms linking early social attributes and reproduction, our findings demonstrate that robust variation in fall affiliative displays predicts the ontogenesis of courtship skills in birds in their first year.

4.5 Figures and Tables:

Figure 4.1:

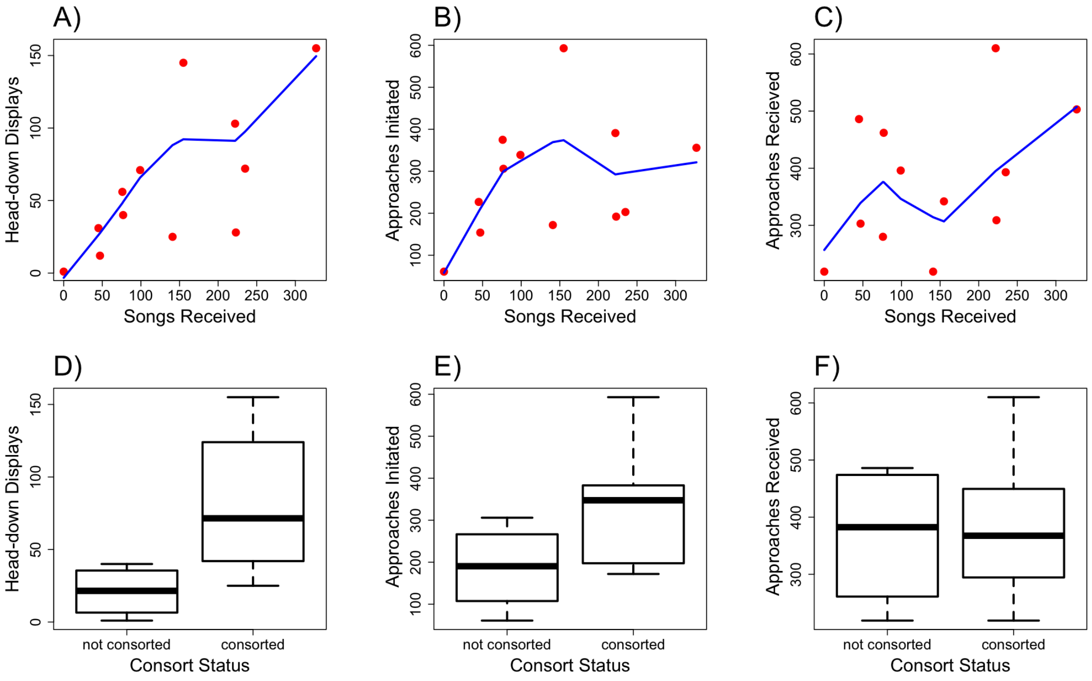


Figure 4.1: The top row looks at the relationship between the number of fall head-down displays (A), number of approaches initiated (B) and number of approaches received (C) and the number of songs received during the breeding season. The lines represent non-parametric lowess regressions to illustrate the relationship between the two variables. The bottom row looks at the relationship between the number of fall head-down displays (D), number of approaches initiated (E) and number of approaches received (F) during the fall and whether a female was in a consortship or not. Boxes represent interquartile ranges with the median in the middle represented by a bold line, whiskers represent the range of the highest and lowest values that are within a range of 1.5 times the interquartile range, Dots indicate data points that are outside this range.

Figure 4.2:

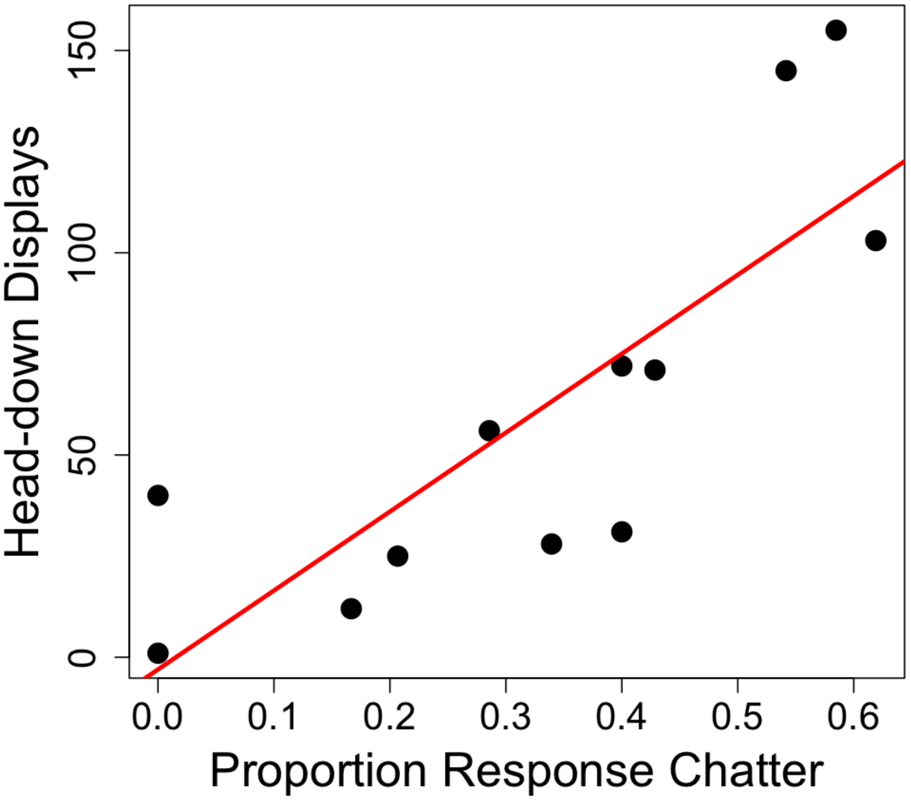


Figure 4.2: Relationship between head-down rates during the fall, and the proportion of response chatters in the spring. Regression lines are plotted to illustrate the strength and direction of the relationship.

Table 4.1.

Sex	**Baseline-Fission**	**Baseline-Fission**	**Fission-Fusion**	**Fusion-Baseline**
Female	Initiated	0.87**	0.84*	0.71*
	Reciprocated	0.77**	0.45	0.34
Males	Initiated	0.72*	0.23	0.38
	Reciprocated	0.01	0.69*	0.08

Table 4.1. Spearman's correlations for the head-down rates that were initiated or reciprocated across the fall social perturbations. *P<0.05, **P<0.01, ***P<0.001.

Table 4.2.

Sex		**Baseline**	**Fission**	**Fusion**
Female	AI-HD	0.73**	0.62*	0.91***
	AR-HD	0.25	0.5	0.59*
Males	AI-HD	0.47	0.16	0.77**
	AR-HD	0.76 **	0.57*	0.67*

Table 4.2. Spearman's correlations between the number of approaches initiated (AI), or the number of approaches received (AR) with the number of head-down displays (HD) within the baseline, fission, and fusion periods. *P<0.05, **P<0.01, ***

Fifth Chapter: Courtship skills and reproductive performance in adult females.

5.1 Introduction:

The last chapter showed how early differences in a female's affiliative behavior was able to predict the development of courtship behavior during their first breeding season. In particular it demonstrated that juvenile females who initiated more head-downs during autumn responded to a higher proportion of male songs using chatter vocalizations during their first breeding season. This chapter will look at the reproductive and social correlates of the chatter vocalization within adults. In particular I am interested in whether the adult chatter vocalization remains repeatable across years, and if variation in how females use their chatter corresponds with their paired status and the number of egg produced.

Within cowbirds and other species the social niches individuals construct will change across the seasons. During non-reproductive periods individuals engage a wider diversity of conspecifics, whereas during reproductive periods individuals may focus their interactions towards preferred mates. In many vertebrates successful pair bonds require sustained periods of social interaction, and the exchange of ritualized "courtship" displays (Wickler 1980). While courtship has traditionally been limited to the periods before pair-formation, it is increasingly apparent that courtship displays within a pair continue well after formation, and contribute to the strength of the pair bond (Wachtmeister 2001). Many studies have suggested that the strength of the pair bonds contributes to increased reproductive output (Coulson 1966) by stimulating the endocrine systems needed for reproduction (Brockway 1967; Oliveira 2004). Thus, how individuals initiate and respond to both potential and established mates may influence their ability to successfully reproduce (Emery et al. 2007; Wachtmeister 2001).

The interactions within a pair may have a significant influence on reproductive output. As the coordinated exchange of courtship displays can change reproductive physiology, variation in courtship behavior may be a significant influence on individual fitness. For instance, in ring doves (*Streptopelia risoria*), the presence of a preferred male song stimulates the females to use 'coo' vocalizations (Lott & Lehrman 1967). In turn, the coo vocalizations themselves stimulate ovarian development (Cheng 1992; Cheng et al. 1998). While the influence of courtship signals on reproductive physiology is well known, less is known about the reproductive consequences of individual differences in courtship behavior. Consistent differences in courtship behavior may provide qualitatively different amount of social stimulation during critical breeding periods, influencing individual variation in reproductive output.

Across many species females utilize vocalizations in response to male courtship displays: e.g., red winged blackbirds, *Agelaius phoeniceus* (Beletsky 1982), grasshopper sparrows, *Ammodramus savannarum* (Smith 1959), dunnocks, *Prunella modularis* (Langmore & Davies 1997), and all duetting species (Hall 2004, 2009). The individually distinct chatter vocalization used by female cowbirds (Burnell & Rothstein 1994), may signal a preference for a specific male. For instance, females exposed to playbacks of songs with response chatters preferred these songs in contrast to females who were only exposed to playbacks of the song alone (Freed-Brown & White 2009). As the chatter is used throughout the breeding period it may reflect the strength of the pair-bond between individuals, and be used to both attract and reinforce male attention. Playbacks of chatters have been shown to attract attention from both males and females in the wild (Dufty 1982; Snyder-Mackler & White 2011). Recent studies have uncovered that lesioned females who were less likely to maintain a pair bond, were also significantly less selective in which songs elicited a chatter vocalization (Maguire et al. 2013). These studies suggest that females use chatters to modulate and reinforce their attractiveness to specific males, and in turn shape the strength of their pair bond during the breeding season.

The first aim of this study was to investigate whether differences in female courtship displays remain equivalent across time, with some females consistently responding to more songs using chatters than others across breeding seasons. Individual differences in female song preferences have been known for quite some time. For example, some females are less selective in their song preferences, and are more likely to go into a copulatory posture in response to wide diversity of different songs (Hamilton et al. 1997; Hamilton et al. 1998). As shown in previous chapters consistent individual differences in social preference are important aspects of fall social niches (Kohn et al. 2011). As the focus shifts from interactions within a flock to interaction within a pair, the social niche during the breeding season may primarily reflect the characteristics of the pair bond. Therefore, consistent individual differences in the frequency of chatter vocalizations within the selective foundation of a pair-bond may be an important aspect of the female social niche by attracting and reinforcing approaches from preferred males.

Our second aim was to uncover whether variation in responsiveness reflects a female's reproductive output. Previously it had been shown that female cowbirds tend to lay more eggs when housed with males that engage in higher rates of courtship displays (White et al. 2010b). Nonetheless, few studies have shown that consistent differences in a females vocal behavior correspond with higher rates of egg output. As females who consistently engage in more interactions in autumn produce more eggs during the breeding season (Kohn et al. 2013a), females who engage in more interactions during the breeding season may have more opportunities to develop a strong pair bond, and therefore exhibit higher reproductive output. As both strong pair bonds (Coulson 1966), and vocal behavior (Cheng et al. 1998) can influence egg production in birds, I predicted that female cowbirds who consistently used more response chatters would be more likely to sustain a pair bond, and exhibit higher rates of egg production than less responsive females.

5.2 Methods:

Subjects: All birds were originally captured in Philadelphia County, Pennsylvania and Monroe County, Indiana and housed in aviaries in Monroe County, Indiana. All subjects were *Molothrus ater ater*. Previous studies have shown no differences in song or social behavior between the Philadelphia and Indiana populations (King & West 1990). For this study I used 28 females including 21 adult (after second year by 2012) and 7 subadult (second year by 2012) females. I also used 28 males including 24 adult males and 4 subadult males. Birds ranged in age from 2 to 13 years old with an average age of 4.9 years. All birds had been used in previous studies, and were housed in large flocks prior to the beginning of this study. Each bird was marked with uniquely colored leg bands to allow for individual recognition. All birds were provided daily with a diet of vitamin treated water (Aquavite Nutritional Research), red and white millet, canary seed and a modified Bronx Zoo diet for blackbirds.

Aviaries: I used a single aviary complex that consisted of 4 subsections each with identical dimensions (9.1 x 21.4 x 3.4 meters), one small subsection (11 x 3 x 3.4 meters), and three indoor enclosures described in detail within Smith et al. (2002). The large size of the aviary provides each cowbird with significant degrees of freedom to either engage or avoid interaction with conspecifics. Each large subsection of the aviary contained a covered feeding station and water bowls. Environmental conditions were similar throughout the entire aviary with shrubs, trees, and grass that allowed individuals to both forage and hide. All birds were exposed to ambient climatic conditions, wild cowbirds, and the occasional sight of predators.

Data collection:

Behavioral observations: Throughout the study, I utilized a scan-sampling procedure: the entire flock was scanned and behaviors were recorded as they were observed (Martin & Bateson 1986). During scan sampling all behaviors were recorded using voice recognition technology described in detail by White, King & Duncan (White et al. 2002a). When used in combination with voice recognition technology scan-sampling can accurately acquire a more comprehensive dataset than focal sampling (White & Smith 2007). All observations were conducted between 07:00-10:30 AM when cowbirds are most active and were counterbalanced, so each observer took the same number of scan-sampling blocks in each aviary every day.

From 9 June to 8 July 2011, and from 1 May to 8 June 2012, I recorded courtship behavior, focusing on the vocal and approach behavior of both males and females. Throughout the study courtship behavior was recorded during 15-minute scan sampling blocks. For females, I recorded the number of songs each female received from males, and the number of female chatter vocalizations. Female chatter vocalizations were either response or solitary chatters. Response chatters occur when a female responds to a directed male song with chatter vocalization within a one second time window. Solitary chatter vocalizations occur when the females performs a chatter vocalization alone, and outside of singing contexts. For male courtship behavior, I recorded the number of female and male directed songs. Copulations were also recorded in order to assess a female's paired status (see below). During the pre-breeding season from 18 March to 23 April in 2012 I also recorded approach behavior in separate 7-minute observation blocks. Here an approach was scored when one individual approached another individual with any part of its body within a radius of 30cm.

Egg Collection: From 1 May to 8 June I recorded the number of eggs each female laid. Six decoy nests were installed in each of the 4 large subsections of the aviary complex. Each nest was mounted on a forked perch attached to a backboard that contained a video camera, and was installed on posts or bushes within the aviary. All nests were supplied with yogurt-covered raisins as decoy eggs. A decoy egg was added every day to each nest until the nest contained three decoy eggs. Each day all nests were checked for the presence of cowbird eggs laid during the morning. After 8 days in one area each nest was moved to a different location within the aviary, all nesting material was replaced, and the nest was treated as a new. All nests were video monitored to determine the identity of laying females by using Geovision software (Geovision Inc. 2008, 9235 Research Drive, Irvine, CA, USA) on Dell Vostro 230 computers running a 32-bit Windows 7 operating system. All work was conducted under ASAB/ABS guidelines and approved by the Institutional Care and Use Committee of Indiana University (08-018).

Procedure:

Year 1: Spring 2011: From 9 June to 8 July three observers collected a total of 240 observation blocks recording courtship behavior.

Year 2: Spring 2012: In the pre-breeding season from 18 March to 23 April three observers collected a total of 40 blocks recording approach behavior, and 164 blocks recording courtship behavior. During the breeding season from 1 May to 8 June, three observers collected a total of 360 observational blocks recording courtship behavior. All decoy nest units were installed on 1 May and used to record the number of eggs laid until the end of the breeding season on 8 June.

Analysis:

Repeatability of chatter vocalizations: To document the repeatability of chatter across years, I used one-way intraclass correlation coefficients on the rate of each female's solitary and response chatters per observation block across 2011 and 2012. Intraclass correlation coefficients estimate the proportion of behavioral variance that is due to differences between individuals. To assess the rank ordered consistency in the individual tendency to chatter, I used Spearman's correlations on the rate of both solitary and response chatters across 9 June to 10 July 2011 to 1 May – 8 June 2012.

All further analysis was conducted on the data recorded during spring 2012.

Chatters and Pair Bond Status: I considered a female to be paired if she received at least 100 songs and 70% of the songs she received came from a single male, with whom she exclusively copulated from 1 May to 8 June 2012. Furthermore, this female also had to be within the top two highest-ranking females sung to by the male. Thus, paired females maintained a selective relationship with a single male throughout the length of the breeding season, whereas unpaired females did not. I used Mann Whitney U-tests to look at the differences in the proportion of songs that a female responded to with a chatter, and the number of songs a female received, the number of eggs laid between paired and unpaired females.

Factors shaping Egg Production: To investigate how variation in spring behavior predicted a female's reproductive output I performed a series of multiple regressions with a permutation test (lmp function in the lmPerm package) using an exact permutation method (Anderson 2001). Three models were preformed; one that included all females, one that included only paired females, and another that included only unpaired females. The dependent factor in each model was the number of eggs each female laid. The explanatory factors included in all models were the rate of songs received, rate per observation block of solitary chatters, rate per observation block of the approaches initiated during the pre-breeding season, proportion of songs received with chatters (number of response chatters/ total number of songs), and an individuals age-class (first or second year birds). The paired model contained an additional explanatory factor that captured the stability of individual's pair bonds across 2011 to 2012 (same-male or different-male), and the model for all females contained an additional explanatory factor that included their pared status (paired or unpaired).

I simplified all models through the selection of terms based on minimizing the Akaike's information criteria (AIC). If removal of factor increased the AIC value, then that explanatory factor remained in the model. A minimal model was defined when the removal of any remaining non-significant explanatory factors increased the AIC value. Variable selection was done using both drop1 and stepAIC functions in R (R Development Core Team 2012) with identical results. As some explanatory factors were inter-correlated, I used variance inflation factors to assess the multicollinearity of main effects. A variance inflation factor greater than 10 is used to indicate potential multicollinearity, which makes model interpretation difficult (Chatterjee & Hadi 2013). In none of our presented models did the VIFs for any main effects exceed 2.5. Post hoc analysis was conducted using Spearman's correlations on continuous explanatory factors, and Wilcoxon rank sum test for categorical explanatory factors. Confidence intervals for Spearman's coefficients were calculated using resampling techniques.

5.3 Results:

Repeatability of chatters across years: Across years, females were predictable in their propensity use both solitary and response chatters. In 2011, I observed a total of 4,152 chatters including 1,272 response chatters (*Mdn* = 28.5) and 2,880 solitary chatters (*Mdn* = 28). During the breeding season in 2012, I observed a total of 6,830 chatters, including 2,339 response chatters (*Mdn* = 27), and 4,491 solitary chatters (*Mdn* = 36). The rate of response chatters and solitary chatters was repeatable across both years (Table 5.1). Females were also consistent in how they used their chatter in relation to others, as the rate of response and solitary chatters were correlated across both years (Table 5.1).

Paired status: From 1 May to 8 June in 2012, I recorded 5,091 songs to females, with a median of 177.5 songs per female. A total of 14 birds were in pairs during 2012, and of those only 6 individuals maintained the same pair-bond from 2011 to 2012. Paired females received more songs than unpaired females (*Mdn* 1 = 242, *Mdn* 2 = 62, Mann-Whitney *U* test: $U = 44.5$, $N_1 = 14$, $N_2 = 14$, $P = 0.0003$), responded to a higher proportion those song with response chatters (*Mdn* 1 = 0.60, *Mdn* 2 = 0.05, $U = 14$, $N_1 = 14$, $N_2 = 14$, P = 0.0001, Fig 5.1), and had higher rates of solitary chatters (*Mdn* 1 = 0.03, *Mdn* 2 = 0.55, $U = 17$, $N_1 = 14$, $N_2 = 14$, P = 0.0002).

Response chatters were used very selectively, and were primarily directed towards a single male across the breeding season. For each female, I rank ordered the number of response chatters to each male and calculated the proportion of response chatters in response to each male’s songs. The top male accounted for the majority of the female’s response chatters (*Mdn* = 0.90), and in paired females the top male was always the female’s mate.

Egg production across all individuals: I identified the laying female for 93 eggs with 69 eggs laid by paired females and 24 eggs laid by unpaired females. Our best model for all females was significant ($F(2,25)= 26.62$, $P < 0.0001$) and explained 65% of the variance. This model included both proportion response chatter ($Coef = 15.08$, $P < 0.0001$) and an individuals paired status ($Coef = 1.67$, $P = 0.02$). Females who responded to a higher proportion of songs received with response chatters laid more eggs than other females ($rho = 0.77$, $N = 28$, $P < 0.0001$, 95% CI = 0.54 – 0.92, Figure 5.1), and paired females produced significantly more eggs in contrast to unpaired females ($Mdn\ 1 = 3.00$, $Mdn\ 2 = 0.05$, $U = 145$, $N_1 = 14$, $N_2 = 14$, $P = 0.03$).

All other factors were removed from the model during simplification. I identified 72 eggs from adult females and 21 eggs from sub-adult females. Age did not influence the number of eggs produced as there was no significant difference in the number of eggs produced by sub-adults in contrast to adults ($Mdn\ 1 = 2.00$, $Mdn\ 2 = 0.05$, $N_1 = 21$, $N_2 = 7$, $U = 88$, $P = 0.45$). The number of songs received was also removed from the final model, and there was no significant relationship between songs received and the number of eggs produced across all females.

Egg production within Paired Females: As paired status was an important predictor of eggs produced I conducted two further models to assess the factors shaping egg production within both paired and unpaired females. Our best model for paired females was significant ($F(5,8)= 5.68$, $P = 0.02$) and explained 64% of the variance. The proportion or response chatters was the only significant factor in the model, and I uncovered a significant positive correlation between the numbers of eggs laid and proportion chatter (*rho* = 0.72, $N = 14$, $P = 0.004$, 95% CI = 0.34 – 0.92). While the stability of an individual's pair bond across years remained in the model, it did not significantly influence the number of eggs an individual laid. Females who maintained the same pair-bond across 2011 to 2012 did not produce significantly more eggs (*Mdn* 1 = 2.6, *Mdn* 2 = 5.00, $U = 14.5$, $N_1 = 8$, $N_2 = 6$, P = 0.24) or have significantly higher proportion of response chatters (*Mdn* 1 = 0.59, *Mdn* 2 = 0.64, $U = 20$, $N_1 = 8$, $N_2 = 6$, P = 0.65) than females who changed their paired males. While the rate of undirected chatters and songs received remained in the paired model (Table 2), there was no significant relationship between the rate of undirected chatters and the number of eggs produced (*rho* = 0.43, $N = 14$, $P = 0.13$, 95% CI = -0.08 – 0.82), or the number of songs an individual received (*rho* = -0.07, $N = 14$, $P = 0.82$, 95% CI = -0.56 – 0.49).

Egg production within unpaired females: Our best model for unpaired females was significant ($F(2,11) = 103.5$, P < 0.0001) and explained 94% of the variance. The proportion of response chatters was the only significant factor in the model, and I found a significant positive correlation between proportion of response chatters and the number of eggs produced (*rho* = 0.84, $N = 14$, $P = 0.0002$, 95% CI = 0.64 – 0.93, Figure 3). The rate of undirected chatters remained in the unpaired model (Table 2), and was also positively correlated with the number of eggs the female produced (*rho* = 0.66, $N = 14$, $P = 0.009$, 95% CI = 0.31 – 0.87).

5.4 Discussion:

In this chapter I investigated how individual differences in courtship behavior shaped reproductive performance in female brown-headed cowbirds. In birds, female vocal signals can attract potential mates (Langmore et al. 1996), shape reproductive physiology (Lehrman 1959; Oliveira 2004), facilitate pair bonding (Beletsky 1982; Yasukawa 1989) and coordinate breeding activities (Hall 2009). I hypothesized that female cowbirds who consistently had higher rates of chattering would be more likely to sustain a pair-bond, and exhibit higher rates of reproductive output. Our results confirmed our initial hypothesis, as individual variation in chatters was consistent over time, and reflected both paired status and the number of eggs produced. This suggests that female vocal behavior, by modulating and reinforcing interaction with males, may have reproductive consequences, and therefore be shaped through sexual or social selective pressures.

Female cowbirds exhibited consistent individual differences in the use of their chatter vocalization, with some females being more likely to respond to song using chatters than others. In the previous chapter I demonstrated that a juvenile female's social interaction patterns during the fall was a significant predictor of the proportion of chatters that were used in response to males. Across breeding seasons the male composition remained consistent, and therefore the current design could not rule out that differences in male quality shaped the repeatability of chatter across breeding seasons. Further studies have since show that females maintain equivalent rates of chatters even after they are moved to a new flock with novel males within a breeding season. In these studies the number of undirected ($rho = 0.68$ $P = 0.01$) and response ($rho = 0.79$ $P = 0.002$) chatter vocalizations remained significantly correlated across the introduction into a new flock. This finding further suggests that it is not just the presence of specific males that causes a female to begin chattering, but rather that females exhibit reliable variation in how they use their chatter across contexts with different males. Thus the chatter vocalization may be a more specialized expression of a general social phenotype, one that seeks to attract, initiate, and sustain close social interaction with others.

Chatters were the strongest predictor of a female's reproductive output. In each of our models the response chatters had a significant influence on the number of eggs produced. Females who were more responsive to male song with chatters overall produced more eggs than other females. Similar findings have been observed in red winged blackbirds where females who had a successful nest were more likely to answer male songs with a chit vocalization (Yasukawa 1989). Even outside a pair-bond, more vocal females sustained higher rates of egg production than less vocal females. While unpaired females were less likely to use chatters than paired females, the individual variation in both the proportion of response chatters, and the rate of solitary chatters, were both positively correlated with the number of eggs laid. In many mammals such as brown rats, *Rattus norvegicus* (Matochik et al. 1992), grey mouse lemurs, *Microcebus murinus* (Buesching et al. 1998), and Barbary Macaques (Engelhardt et al. 2012) female vocalizations often reflect reproductive status. To our knowledge this is the first demonstration that individual variation in vocal behavior within female birds reflects their reproductive output.

By possessing a signal that reflects their reproductive status, consistently more vocal cowbirds may be better able to attract and maintain attention from preferred males. Across many birds female vocal signals are used to attract and reinforce male courtship. In alpine accentors (*Prunella collaris)* females use complex songs in order to attract mates

(Langmore et al. 1996), and the calls of female whitethroats (*Sylvia communis)* both attract males and shape their courtship behavior (Balsby & Dabelsteen 2002). In cowbirds, female responses to male vocalizations are commonly used to assess the quality and attractiveness of male signals (West & King 1988). As females exclusively copulated with their paired males, chatters are a reliable signal of female preferences, and used to reinforce bonds with specific males. Chatters are also individually distinct (Burnell & Rothstein 1994), and their selective use may facilitate the identification needed to sustain a social bond (Beletsky 1982; Smith 1994). Female cowbirds with lesions to their HVC area are not selective in their response chatters, and chatter in response to nearly all song playbacks, regardless of quality (Maguire et al. 2013). As a result these lesioned females were unable to sustain a pair bond, and were courted by a larger number of males. Thus, a female's own courtship behavior might contribute to a pair's success by consistently attracting the attention of preferred males, leading to the maintenance of pair bonds over time.

Differences in social interaction patterns and preferences will guide the ontogeny of social skills, and ultimately shape reproductive success (Taborsky et al. 2012). The results of the last two chapters suggest that how females use their chatter may constitute a social skill, with females who reliably use chatters to attract and reinforce male attention gaining higher rates of reproductive output. The individual differences in early social interaction patterns may facilitate the closer contact needed to learn the consequences of chatter usage. More sociable individuals, may also be more willing to use chatters in order to attract attention from others. In adulthood, chatters will facilitate access to preferred mates, and potentially be used in competition with other females for access to higher reproductive status. These studies suggests that early social niches influence the ontogeny of courtship skills, and that selection may act on different social niches to produce the diversity of social behaviors observed across populations and species (Capitanio 2010; Mason 1978).

5.5 Figures and Tables:

Figure 5.1:

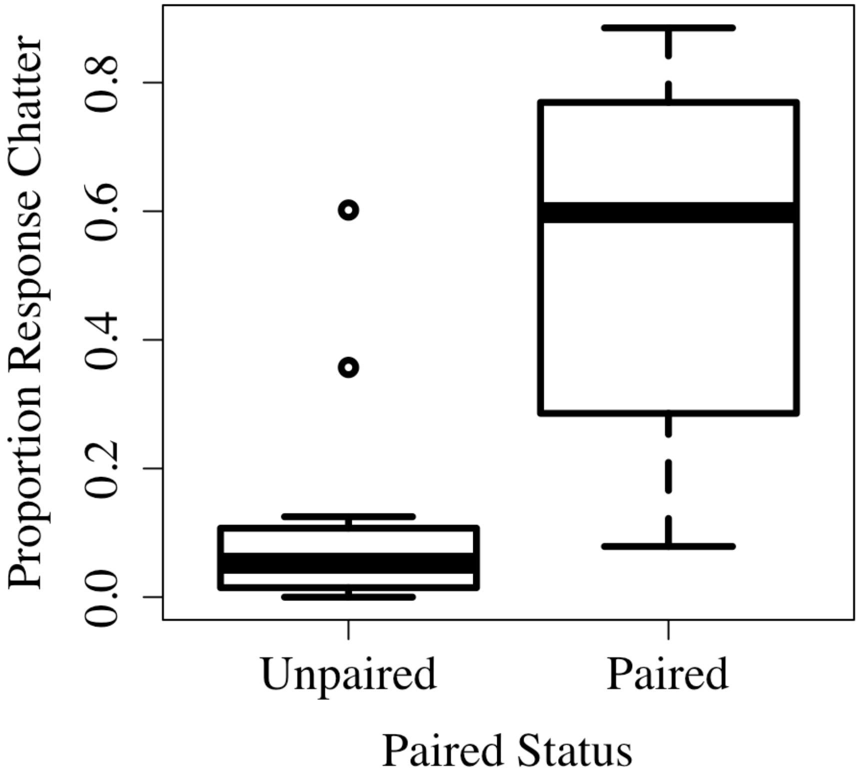


Figure 5.1: The proportion of response chatter vocalization based on an individuals paired status. Boxes represent interquartile ranges with the median in the middle represented by a bold line, whiskers represent the range of the highest and lowest values that are within a range of 1.5 times the interquartile range. Dots indicate data points that are outside this range.

Figure 5.2

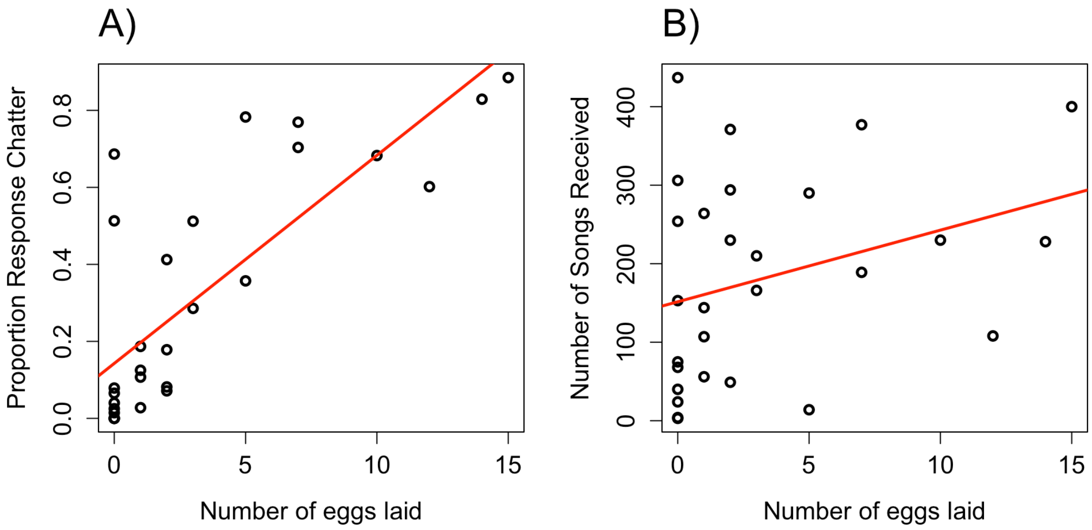


Figure 5.2: Scatterplots for the number of eggs laid and A) the proportion of songs with response chatters, B) the number of songs an individual received. Regression lines are plotted to illustrate the strength and direction of the relationship.

Table 5.1:

	Coef	Standard error	Z Value	P value
Proportion Chatter	4.999	0.60	8.345	$p < 0.00001$***
Pair bond Status	-0.608	0.64	-1.604	$p = 0.108$
Songs received	-0.003	0.002	-1.988	$p = 0.0468$*

Table 5.1: Results of the generalized linear model that tested which factors best predicted the number of eggs an individual produced ($N = 93$). Proportion Chatter is the number of response chatters divided by the total number of songs she received. Pair bond status reflected if a female was paired or unpaired, and songs received was the number of songs each female received from males. *$P < 0.05$, *** $P < 0.0001$

Chapter Six: General Discussion

Phenotypic variation – its developmental origins and evolutionary consequences – has always been a central theme within both biology and psychology. In this dissertation, I presented a series of studies that highlight how the construction of social niches may have evolutionary potential by predicting reproductive performance. In particular, both adult and juvenile females exhibited significant preferences to approach familiar females, thus constructing reliable sub-groups. Within these sub-groups, females maintained specialized social niches, as individual differences in their sociability and social preferences remained repeatable across contexts and over years. These niches predicted egg production in adults, as well as the ontogeny of female competence. Competent juvenile females, who were more likely to initiate head-downs during the fall and sustain a pair-bond using chatters in their first breeding season, predictably occupied more sociable niches. As chatters are correlates of adult egg output, individuals who construct more sociable niches may ultimately exhibit higher reproductive success. Together, these results suggest that early social niche construction may be an important factor in the evolution of social behavior.

Traditionally, evolutionary theorists have regarded developmental variation as noise around an optimal population mean. The conjoining of Mendelian genetics with Darwinism meant that only behavioral variation caused by genetic variation has evolutionary potential, as only such variation can be transmitted to further generations. Thus, evolution acts solely on genes, with organisms and their phenotypes having little influence over evolutionary processes. Nonetheless, epigenetic research has shown the complicated and contextual nature of gene expression, and demonstrated that the "information" in an individual's DNA reflects the state of the developing organism and its behavior. Genes don't lead evolution, organisms do. The assumption that evolution acts solely on the genes has created a world of conflicts between parents and offspring, altruists and selfishness, individuals and groups, senders and deceivers. These conflicts may be resolved by considering evolution as acting on developing organisms who require a whole range of experiences – some cooperative, some conflicting – in order to become competent. Studies within animal behavior should expand their focus beyond the mechanisms of genetic transfer, such as copulations, mate choice, and sperm competition, to an emphasis on the ontogeny of competent social skills across a wide range of modalities that ultimately influence the ability to successfully reproduce.

Cowbirds require direct social interaction for the ontogeny of basic social and reproductive skills. For example, juvenile male cowbirds raised without adult male interaction develop deficient courtship behavior (White et al. 2002c), and juvenile males exposed to more sociable females display more aggressive tendencies and more directed song (King et al. 2003). Female cowbirds copy mate preferences by attending to other female song responses (Freed-Brown et al. 2006), and direct female-female interaction is necessary for acquiring local song preferences (West et al. 2006). Most social interaction in cowbirds requires close proximity as song degrades over short distances (King et al. 1981), and important communicative cues, such as wing-strokes, can only be observed in close proximity (West & King 1988; White et al. 2007). Our findings suggest that variation in social niches, by exposing individuals to different levels of social stimulation, may have consequences for the development of later reproductive skills.

The social niche across development:

Across social life there are benefits to being predictable. Predictable differences in behavior may be essential for the emergence of complex social systems where individuals interact and form social relationships for long time periods. Knowing who to interact with, and how to interact with them, requires some level of consistency over time. For example, if an aggressive individual suddenly becomes affiliative, only to randomly switch to being aggressive again, it may be difficult to learn how to engage that individual. Recently, both models and empirical studies have suggested that increased social responsiveness, or the ability to select individuals to interact with, may foster the emergence of predictable individual differences in behavior (Wolf et al. 2008). Nonetheless, most studies have not considered how such differences arise within an individual's lifespan, and whether one should expect to see significant variation in predictability across different sexes and ages. Within this dissertation the first challenge was identifying the existence of predictable social niches within a semi-naturalistic flock. The second challenge was investigating the within-flock contexts where these different social niches develop.

Predictable differences in how individuals approach and interact with others have been observed across a wide diversity of different species. These differences often develop in response to prior social conditions, and may have a significant influence over their status and perfomance within the group (Capitanio 2010; Mason 1978). For instance, more impulsive juvenile rhesus macaques (*Macaca mulatta*) approached others frequently and obtained higher social status in adulthood (Box 1999), while more sociable rhesus macaques exhibit more appropriate behavioral responses to video playbacks of conspecific behaviors (Capitanio 2002). Aggressive male water-striders (*Aquarius remigis*) elicit withdrawal responses from females and reduce reproductive opportunities for the whole group (Sih & Watters 2005). Sapolsky & Share (2004) discovered that the removal of aggressive males from baboon (*Papio anubia*) troops resulted in the emergence and maintenance of a more pacific dynamic. While many of these studies did not explicitly aim to measure an individual's social niche, they do suggests that predictable social differences will both constrain and facilitate access to beneficial social resources.

The neural and physiological foundations of predictable differences in social behavior are well known. All vertebrates, from fish (Thompson & Walton 2004) to humans (Heinrichs & Domes 2008), use homologous nonapeptide neurohormones to control the expression of social approach behavior. In birds, the nonapeptide hormone mesotocin modulates their tendency to approach others (Goodson et al. 2009; Goodson & Kingsbury 2011). The selectivity of approach tendencies is also related to basic neural structures and processes. In prairie voles, (*Microtus ochrogaster*) individual variation in oxytocin systems shapes the selectivity of mate choice decisions (Williams et al. 1994). Similarly, female cowbirds who are selective in their responsiveness to male song exhibit a denser lMAN (a brain region associated with song perception in females and song expression in males) in contrast to less selective females (Hamilton et al. 1997). While conserved neural systems may play a role in structuring an individual's social behavior, such systems are often highly responsive to changes within the social environment (Curley et al. 2011; Tanaka et al. 2010). Understanding how such systems both influence and respond to an individual's social niche may provide valuable insights.

The social niche specialization hypothesis proposes that differences in social behavior should emerge when individuals have repeated interactions with known conspecifics. The natural history of many species would seem to support such a view, as parents often go to extreme lengths to assure that individuals have access to a predictable early environment. Ungulates often give birth and raise offspring in smaller groups outside the main group, and mammals of all kinds construct burrows, dens, and nests to raise offspring in a protected environment with reliable interaction from family members. While these environments may assure that individuals acquire the species-typical behavioral repertoires needed to survive, they may also foster the emergence of between-individual differences in those repertoires. Thus, the context of development may both assure survival and generate variation, two processes necessary for evolution to proceed.

Cowbirds, because of their brood parasitism, seem to be an exception to that rule, as their early environment is far more heterogeneous in comparison to other bird species. Most social development in cowbirds may therefore begin after they integrate into flocks as fledglings. Once integrated, male and female cowbirds construct very different social niches. On average females significantly and consistently expressed stronger social preferences in comparison to males. Females preferred to engage other familiar females, whereas males tended to engage a broader range of different conspecifcs. Such homophily was consistently expressed across a female’s lifespan, as significant familiarity and sex preferences were observed in flocks of juveniles and adults (Kohn et al. 2011; Kohn et al. 2013b). These results suggest that females may actively construct a more predictable social environment by seeking out repeated associations with similar individuals.

Although research on social niche specialization is fairly recent, studies have shown conflicting results regarding the role of repeated interactions in generating behavioral consistency. For instance, individuals in groups of familiar social spiders (*Stegodyphus mimosarum*) exhibited higher levels of behavioral consistency than spiders housed with unfamiliar conspecifics (Laskowski & Pruitt 2014). Other studies in Sticklebacks (*Gasterosteus aculeatus*) and Meerkats (*Suricata suricatta*) did not find evidence that repeated interactions shaped behavioral consistency (Carter et al. 2014; Laskowski & Bell 2014). However, in these studies the existence of significant social preferences within the group was not measured. Even in static groups, where social composition remains consistent, individuals may distribute their interactions randomly. Random interaction patterns may make it hard for individuals to access the predictable social experiences needed to differentiate their behavior from others, even within smaller groups. Furthermore, if changes in context outside the group cause individuals to shift whom they interact with, then individuals may actively avoid repeated interactions with conspecifics. Within more homogenous social networks it may be unclear if individuals are familiar with all members, or if individuals simply interact with others randomly. However, if the within-group networks are biased by social preferences, one can be more certain that individuals experience repeated interactions. Without understanding the social preferences within the group, it may be more difficult to know if the presence or lack of behavioral consistency is influenced by repeated social interaction.

Significant familiarity preferences mean that individuals will experience a more predictable social environment. If such preferences change when group size and composition shifts, then such predictability may only be maintained while groups are static.

As many, if not most, groups exhibit some level of fission and fusion, the average social preferences would need to be robust across these changes to maintain repeated interactions. Here I demonstrated that female cowbirds expressed significant familiarity and sex preferences across a series of introductions with novel conspecifics, thus constructing robust sub-groups. While males did exhibit significant social preferences within one introduction, these were not consistently expressed across subsequent introductions. Consequently, males were not able to construct robust sub-groups. These results suggest that consistent familiarity preferences are important in providing individuals with a predictable social environment.

By preferentially associating with familiar individuals, females will be facing a different developmental context than males. Such assortment is commonly seen in many social mammals, where females remain within a natal female group, and juvenile males disperse to join other males (Ruckstuhl & Neuhaus 2005). Early differences in activity between the sexes may generate behavioral incompatibility that fosters the differential assortment between the sexes. Juvenile male cowbirds tend to exhibit more aggressive and social exploratory behaviors than females. As a result, females may initially separate from males in order to avoid aggressive interactions. Nonetheless, an individual's sex may not be the only factor predicting behavioral compatibility, as females also prefer to engage familiar cowbirds. Stable groups of familiar individuals often exhibit better behavioral coordination during predation, and are able to exchange information more efficiently than groups of unfamiliar individuals (Croft et al. 2009; Dyer et al. 2008). Familiarity may also lower aggression within the group (Marler 1976), allowing for closer interactions, and more opportunities for social learning (Swaney et al. 2001). By forming familiar female sub-groups, females may create the proximal social ecologies necessary to differentiate and sustain their niche from others.

Female social niches were consistent. Across almost every study, measures of female sociability and social preferences remained both repeatable and correlated. For both juveniles and adults, individual consistency was expressed across varying timescales from changes in social composition within a season, to changes over seasons and years. Such consistency, coupled with the females' ability to sustain familiar sub-groups, suggests that repeated interactions between known females is related to the emergence of specialized social niches. In contrast to females, male niches are substantially more plastic. Male sociability and social preferences tended not to be significantly correlated across contexts. In fact, adult males with the strongest familiarity preferences exhibited the largest proportional increase in interaction with unfamiliar conspecifics when conditions changed. While some aspects of adult males' sociability, mainly the number of approaches initiated, were correlated across contexts in some studies, the strength of these correlations were always below that of females, and disappeared across longer timescales. Thus, males were unable to construct specialized social niches.

The consistency of a female's social niche was reliably coupled with their ability to access repeated interaction with familiar conspecifics within the flock. Consequently, our results do support the core assumption of the social niche specialization hypothesis. Additional studies, such as the formation of female groups where all individuals are equally novel, will be conducted in order to confirm the importance of familiarity preferences for the consistency of both juvenile and adult niches. If females maintain consistent patterns of sociability within a flock of entirely novel females, than familiarity preferences are not responsible for consistent social niches. However, if individuals change their sociability, than familiarity preferences may be necessary in order to maintain individual consistency. While such results may provide additional support for niche specialization, they do not inform us about the processes within the sub-groups that cause individuals to construct different niches.

Aspects of female-female interaction may facilitate the development of specialized social niches. During the breeding season female cowbirds will compete with other females for access to better nests, and potentially over access to males. Nonetheless, during autumn, females rarely engage in any competition, but use social cues from other females in order to communicate and learn the mate preferences of conspecifics. The dynamics of communication in stable groups may seek to differentiate individuals into information “providers” and “recipients”. Many of the cues advertising mate preferences during the fall, such as wing-strokes, are very subtle, and may only be accessed by maintaining close proximity to other females. Some females may function as “information” providers, by interacting and providing many cues about their mate preferences, whereas other females may become recipients, and rely on the cues of others in order to avoid competing over similar mates. Analogous differences may be present in the producer and scrounger dynamics seen in many social foraging species (Giraldeau & Caraco 2000; Kurvers et al. 2009). While additional work needs to be conducted, the communicative dynamics between females may facilitate the development of consistent differences in sociability by selecting for different communicative roles.

Aspects of male-male behavior may facilitate the development of plastic niches. Throughout the year males tend to form dominance relationships with other individuals. Dominance relationships are defined by their asymmetrical qualities, with some individuals being displaced, and others being the displacers. Networks exemplified by these relationships may be very stable when groups are static, but as soon as individuals leave or enter a group the web of relationships may change. For instance, when individuals leave these networks they create “power vacuums ”, and remaining individuals compete in order to access their status. If new individuals enter into the group it may create conflict over their dominance status, and eventually reorder all the dominance relationships. Small changes may therefore have cascading influences across the entire network, and individuals must change their social behavior to adapt to new conditions. Under such conditions it may be difficult for individuals to maintain a specialized niche, as their relationship with familiar conspecifics will change across fission-fusion processes.

Unlike males, females do not seem to exhibit dominance relationships during the fall. Therefore, female networks may be considerably more stable in contrast to males as individuals leaving the network will not create power vacuums, and individuals entering the network may not introduce new competition. Thus, the introduction or removal of individuals from the females’ sub-group may not have cascading influences on another’s relationships, resulting in more consistent differences across time. The different social challenges faced by males and females may require substantially different skill sets when navigating interaction with others. As social interaction is essential for successfully survival and reproduction in cowbirds, different social niches may prepare individuals to face these challenges by shaping the development of relevant social skills.

Complex sociality requires social competence:

In the last section I discussed sex differences in social niches. Whereas females formed selective, specialized niches, males formed diverse, plastic niches over time. This section will discuss the social skills that are both a cause of, and consequence of, these different niches. By skill I mean adaptive variation in the ability to initiate and respond to the presence of others based on the available social information (Taborsky et al. 2012; Taborsky & Oliveira 2012). Individuals with different skills will employ different behavioral responses, with different consequences for their performance within the group. Competent individuals with "good" social skills will be able to successfully interact across a broad range of social contexts, by constructing the social relationships needed to access information quicker, attract and reinforce attention from preferred mates, and successfully compete with others. Therefore, it is commonly assumed that competence will ultimately reflect fitness. One way to assess competence is to look at an individual's performance across different sets of ecologically relevant social challenges. By looking at individual performance across these challenges in relation to the niches they occupy, I may uncover the interrelationship between the position within the group and the ontogeny of competence.

The challenges cowbirds face across the fall and breeding seasons are substantially different. During the fall, cowbird flocks experience fission-fusion processes where individuals must respond to a continually changing social composition. Here, the ability to interact with a wide diversity of conspecifics, while avoiding aggression, may be important for integrating into new social conditions. During the breeding season, individuals focus their attention toward competing with others, courting potential mates, and reinforcing established pair bonds. Competent individuals may possess the skills necessary to engage in a wide diversity of different interactions, from courting and maintaining pair bonds during the breeding season, to integrating into changing conditions in fall flocks.

It is often assumed that social competence will ultimately shape an individual's ability to survive and reproduce. Therefore, it is commonly accepted that some individuals will have "good" social skills, allowing them to obtain better fitness, whereas others may have "bad" social skills. The reality of social life means that things are never this dichotomous. There is a diversity of alternative strategies that individuals can use when interacting with others, and different strategies may be successful across different timescales and contexts. For example, studies of frequency-dependent selection have shown that the social composition of groups will select for different behavioral traits. There may not be one optimal way to engage others within the flock, but rather a diverse range of competences that reflects the different niches individuals occupy. Whereas individuals with highly sociable niches may develop better skills to navigate interactions with others, and enjoy higher reproductive success, they may also face increased competition that may limit their ability to sustain higher reproduction across longer timescales. In turn less sociable individuals may actively avoid competition and enjoy moderate reproductive performance across long timescales. Further research will focus on the potential trade-offs of different social niches, and investigate the mechanisms sustaining variation in social niches.

In the third chapter of this dissertation I demonstrated how specialized social niches were able to predict reproductive output in female cowbirds. Females who engaged in more interaction with more individuals exhibited increased egg production during the breeding season. Additional studies have also shown that within non-separated flocks, variation in fall sociability correlates with egg output the next year (Kohn, unpublished data). Thus, it seems that the pressures of social life may select for individuals who can consistently and frequently interact with a wide diversity of individuals. In the second chapter I split up breeding season flocks into high, intermediate, and low conditions based on the number of times they both approached, and were approached by, conspecifics. Within the high flock I observed a strong correlation between individual sociability and egg output. No significant correlation was observed in the intermediate and low flocks. The conditions within the high flocks will create increased pressure to interact more often, with more conspecifics, than other flocks. More sociable individuals within these flocks may have comparatively higher rates of reproductive output as they are better suited to meet the increased social demands of these flocks. If more sociable cowbirds then facilitate the development of high sociability within their offspring, directional selection may result in increased sociability in the population over time.

While the exact mechanisms linking differences in sociability to reproductive behavior are unknown, our results do demonstrate that sociability predicts higher rates of reproductive output in females. It is widely accepted that the ability to sustain a successful pair bond is necessary for securing higher fitness across many bird species (Sa´nchez-Macouzet et al. 2014). Individuals within a pair bond exhibit higher rates of reproductive output, and differences in a pair's behavioral coordination may influence the endocrine systems shaping egg production. Thus, developing better skills to both initiate and reinforce pair bonds may be an important mechanism in securing higher reproductive output. If the existence of specialized social niches shapes the development of social behavior across a wide range of modalities, from flocking with others in the fall, to securing stable pair bonds during the breeding season, I should see a relationship between fall niches and egg production. The next step was to explore if early differences in sociability predict the ability to initiate and maintain pair bonds with preferred mates during a juveniles first breeding season.

Courtship is a social skill for reproduction:

Courtship is a prelude to successful reproduction. In most vertebrates, courtship requires the ability to initiate and respond appropriately to another's behavior using specific behavioral displays. While courtship displays have traditionally been restricted to the period where individuals assess potential mates, such displays are often exchanged within established pairs, and contribute to the strength and maintenance of the pair bond (Beletsky 1982; Ce´zilly et al. 2000; Coulson 1966; Darley 1978; Emery et al. 2007; Wachtmeister 2001; Wickler 1980). Thus, variation in courtship displays may reflect an individual's ability to both attract and sustain the attention of a preferred mate. The exchange of displays within a pair may also influence a female's reproductive output. Work by Lehrman (Lehrman 1959; Lott & Lehrman 1967) and others (Brockway 1965, 1967) have shown that the presence of visual and acoustic stimuli from paired males can stimulate the release of luteinizing hormone. A female's own courtship signals can also stimulate her reproductive physiology. Within ringdoves, females use a coo vocalization in response to male calls. This coo vocalization stimulates follicular development, and females who coo more often may have higher rates of reproductive output over time

(Cheng 1992; Cheng et al. 1998). Thus, variation in courtship behavior is a social skill that may have a direct influence over an individual’s reproductive output through its relationship with reproductive physiology.

In the fifth chapter I discussed how the frequency of a female's vocal responsiveness was able to predict her egg production within the breeding season. Adult females who engaged in more chatter vocalizations were more likely to sustain a pair bond, and laid eggs at higher rates than others. Furthermore, variation in an adult female’s ability to use the chatter was repeatable across years, and across interactions with novel males (Kohn et al. Submitted). Consistent variation in a female’s courtship signals was positively related with her reproductive performance, and this was largely independent of the specific males being courted. Traditional theories of sexual selection have often considered females to be passive recipients of courtship signals from males. Here the female’s aim is to choose the highest “quality” male based on the characteristics of their courtship display. However, it is increasingly becoming apparent that it is not only the choice of partner, but also the dynamics within the pair bond that have an important influence over the reproductive success for both males and females (Emery et al. 2007; Huxley 1923; Wachtmeister 2001). In many vertebrates, partner compatibility and coordination is important in maintaining the pair bond, and its associated benefits in terms of mate guarding, vigilance and parental care. Thus, thus the ability to attract and reinforce attention from preferred males may be a widespread, albeit under-researched, social skill that shapes a female’s reproductive performance.

During the spring chatter vocalizations facilitate social interaction with mates during important reproductive periods (Burnell & Rothstein 1994). It has been widely known that the chatter is an effective means of attracting attention from both males and females (Dufty 1982). Individuals who use chatters more often may spend more time engaging in social interaction. I therefore expected that more sociable females would be more likely to use chatters during their first breeding season, thus providing a link between early social niches and spring reproductive output in adulthood. In chapter four I uncovered that consistent variation in juvenile chatter usage reflected the rate of head-down displays initiated during an individual's first fall. Therefore, females who engaged in higher rates of close social interaction during non-breeding periods were able to effectively use a vocal signal as a means of attracting preferred males and maintaining a pair bond. As chatters are robust across time and partners in adulthood, early differences in social interaction patterns during the first breeding season may guide the development of differences in courtship behavior that extend well into adulthood.

The ability to perform successfully across an array of different contexts is a defining aspect of social competence. The hallmark of male competence during the breeding season has been their ability to counter-sing with other males and compete for access to females. As male social niches did not remain consistent over the fall, I did not observe any significant correlations between their niche and later counter singing abilities. However, I did uncover that counter-singing reflected a male's ability to initiate head-downs towards others. In the second study of chapter two, males were distributed into a high, intermediate, and low breeding season flocks based on the amount of head-downs initiated during the fall. While the amount of singing did not differ between the flocks, males in the high flock exhibited a higher proportion of songs within counter-singing matches. Thus, males in the low and intermediate flocks were less likely to reciprocate a directed song, suggesting they did not possess the appropriate responses to a vital courtship signal.

Across both males and females, variation in spring social skills reflected the use of fall head-down displays. While it is widely accepted that vocal behavior during the breeding season is a social skill for reproduction, less is known about the skills individuals use during non-reproductive periods. This may be because it is harder to assess if a behavior has beneficial consequences to the organism, as they are not directly related to their ability to successfully reproduce. In the next section I will explore why social skills during the breeding season are predicted by head-down rates during the fall. In particular, I will show how head-downs may be an efficient way to manage close interactions, facilitate access to social learning opportunities, and aid in social integration.

Head-downs as a social skill for integration:

Within both male and female cowbirds, variation in autumnal head-downs reflected courtship behavior during the breeding season. As head-down displays disappear at the beginning of spring, they cannot directly shape cowbird courtship and pair formation. Nonetheless, consistent patterns of head-downs across the fall could expose individuals to closer social interactions, and provide opportunities to learn the appropriate responses to another's behavior. Head-downs may serve as a "gateway" to learning how to engage a wide diversity of conspecifics, a key ingredient when both courting potential mates, and integrating into new flocks.

Social integration reflects the ability to interact with a broad range of conspecifics within the group. Often integration is used to describe how individuals enter into novel groups, but it can also describe differences in the within-group social dynamics. Groups where individuals are highly integrated will exhibit a more homogenous network structure, and display lower incidences of aggression. Integration is like the “social glue” that keeps groups cohesive in contrast to aggressive, agonistic and dominance related behaviors that decrease cohesion, and discourage further interaction. As cohesive groups often confer more benefits to individuals in terms of learning opportunities, and protection from predators, individuals may actively seek to integrate into groups, and maintain their integrated status when conditions change. Behaviors used during integration should be affiliative, facilitate close proximity while lowering aggression, and be used widely across an array of different individuals. All these qualities are reflected in the cowbird’s head-down display (Scott & Grumstrup-Scott 1983).

Affiliative behaviors, by sustaining close proximity, can be essential for integration into new groups, as well as reinforcing and forming new social relationships (de Waal & Tyack 2002). Often affiliative behavior exhibits a higher degree of “ritualization” in order to increase the effective communication of non-aggressive “intent”. The risks of using a more ambiguous behavior when approaching others closely may result in aggression if it is misinterpreted. Examples of affiliative displays include allopreening within birds and primates (Lewis et al. 2007; Sinha 1998; Webber 1983), greeting displays in social mammals (Smith et al. 2011), bared teeth displays within primates (Goldenthal et al. 1981), lipsmacking and grunting in baboons (Cheney et al. 1986; Cheney & Seyfarth 1995; Cheney & Seyfarth 1997; Palombit et al. 1999), reconciliatory behaviors (de Waal & Johanowicz 1993) as well as head-down and nodding displays across many species of birds (Emery et al. 2007; Morris 1956; Selander & LaRue 1961). Variation in the use of such displays will shape an individual's ability to engage others in close proximity, and thus play a role in their integration into established groups.

The head-down is the only behavior in the cowbird's repertoire that brings individuals into close proximity, often touching, and sustains that proximity for an extended length of time (Scott & Grumstrup-Scott 1983). The development of the head-down occurs very early in cowbirds, as complete reciprocated displays have been observed at 42 days after hatching (Miller, unpublished data). Upon fledging the first challenge juvenile cowbirds face is integrating into flocks of unrelated conspecifics. Juveniles are more indiscriminate in who they initiate head-down displays toward, readily using head-downs to initiate interaction with both conspecifics, as well as members of other species (Lowther & Rothstein 1980b). The first reports of the display thought it was an adaptation to appease potential host species (Selander & LaRue 1961). While the reciprocated nature of the display means that juveniles will receive species-specific responses, the appeasing influence may also allow juveniles to sustain social contact for longer periods of time. Across many species, close interaction with others may have lasting consequences for an individual's ability to integrate inside the group as adults. Guinea pigs raised in large colonies showed attenuated stress responses to social stimulation when grouped with unfamiliar individuals, while those raised with a single female did not (Sachser 1993).

Male zebra finches who were raised in larger mixed age / sex groups were more likely to be observed in close proximity to others as adults (Ruploh et al. 2014). Differences in the use of head-down displays as juveniles may shape the development of later behavior by facilitating close interactions with others during periods when social experiences are most critical to the development of later behavior.

While all integration requires the ability to engage conspecifics in close proximity, the risks of maintaining close proximity may differ across males and females, especially within fission-fusion societies. By constructing all female familiar sub-groups, females may resist integration into the larger group. However, more sociable females with low social preferences will have a higher probability of interacting with novel conspecifics in contrast to other females. Therefore, these more sociable females should possess the affiliative behaviors necessary for integrating into the larger group. Males, through their lack of social preferences, may have a significant influence over social integration. However, due to their dominance relationships, males may approach individuals in order to displace them, and therefore male sociability may not reflect their use of affiliative displays. In the studies presented here I found no significant relationship between male sociability and use of the affiliative head-down display.

The challenges of social integration begin during adolescence. Sex-based assortment patterns were much stronger for females within all juvenile flocks (Kohn et al. 2013a). Such patterns may make it more important for females to integrate into the familiar female sub-groups. Consequently, I observed that juvenile females preferentially initiated more head-downs towards other familiar females, and that their rate of head-down displays remained correlated across contexts (Kohn et al. 2013b). Juvenile males exhibited no significant sex bias in who they initiated head downs towards, and the rates of their head-down were not significantly consistent across group changes (Kohn et al. 2013b). While juvenile males may head-down in order to facilitate close interaction across a wide array of group members, juvenile females may consistently use their head-downs to facilitate integration within familiar females' sub-groups.

Social integration extends into adulthood. Previous studies have shown that the rate of head-downs increases during periods of social change, such as the addition or removal of individuals into the group (Rothstein 1980a; Rothstein 1980b). The fission-fusion nature of fall flocks means individuals are faced with a shifting landscape of both familiar and novel cowbirds, and adults may use the head-down in order to facilitate close interaction with a wide range of conspecifics. Unlike social approaches the use of the head-down display seems more egalitarian, with no consistent sex bias in either adult males or females. As such the head-down will be a useful skill for integrating oneself within the larger group and gaining the diverse social experiences necessary for later competent performance. Research has shown that male cowbirds who experience a more diverse social environment exhibit better courtship skills than individuals who experience a more limited social environment (Gersick et al. 2012; White et al. 2010a). While more work needs to be done to investigate the exact mechanisms whereby head-downs shape later courtship skills, the studies presented here suggest that head-downs are an important component of social integration within cowbird flocks.

In complex social groups it may be important to maximize one's social experiences in order to learn the skills to cope with the diverse challenges one will encounter across development. Competent individuals can interact successfully across a wide diversity of different challenges. Here I showed that a head-down display might be an important component in integrating into the changing fabric of fall flocks. Individual variation in the head down was consistent across contexts and reflected the characteristics of a female's social niche. Juveniles who were more sociable during their first fall were more likely to use head-down displays, and were also more likely to respond to song using chatters during their first breeding season. Thus, the qualities of an individual's early niche may foster the emergence of better courtship skills and overall social competence.

Social development as an evolutionary force:

This dissertation explored the extent and development of social competence within Brown-headed Cowbirds. Here I showed that early interaction patterns, within the first few weeks of independent life, are able to predict the development of courtship skills that as adults will result in higher reproductive performance. The Baldwin effect presumes that selection may favor individuals who can reliably and robustly acquire beneficial behavioral characteristics over ontogeny resulting in behavioral canalization over time. The pressures of social life may select for individuals who are adept and willing to engage others in close proximity to access the necessary experiences for their own social development. Thus, the social niche an individual constructs, by scaffolding the acquisition and expression of competent social behavior, may be an important locus on which selection can shape both the behavior of individuals, as well as the social properties of groups and populations.

Evolutionary processes generally need two main components, variation and selection. While the mechanisms governing selection have been well studied across many species, less is known about the processes that generate the variation needed for selection. Early differences in how individuals engage their environments, represented by their approach-withdrawal systems, may lead some individuals to learn the qualities of their environments quicker, and develop the skills needed for social interaction faster. If this ultimately results in higher reproductive success, then over time the approach-withdrawal systems reliably leading to higher competence may evolve.

This dissertation took a comparative approach, by investigating the commonalities and differences of the social niches across juvenile and adult cowbirds. Nonetheless, in order for a more comprehensive view of social niche construction over ontogeny, I need to follow an individual's social behavior in detail as they transition from naïve juveniles to competent adults. New studies using a novel RFID system will be able to track social approaches across every day of development and show how the qualities of an individual's niche shape the development of their behavior in real time. Further experiments using this technology will demonstrate how the interaction networks within stable and novel groups shapes the specialization or plasticity of an individual's niche as they develop.

While much is known about early development, where offspring are dependent on parents for their survival, less is known about juvenile and adolescent periods. Increasingly, research is showing how differences in social experience in juveniles shapes the development of adaptive behavioral traits (Kasumovic 2013). Despite this, the adolescent periods are often where individuals learn the relevant social skills to interact with other successfully. These skills may then have a positive feedback effect over development, where the niches an individual occupies facilitates the ontogeny of skills needed to maintain and differentiate their niches from other individuals. In order to fully understand the evolution of social behavior, in future research I will need to study the developmental factors shaping the competent social behavior within an individual’s lifetime.

References:

2005. SPSS, Inc. Chicago: SPSS, Inc.

Alberts, J. R. 1978. Huddling by rat pups: Group behavioral mechanisms of temperature regulation and energy conservation. *Journal of Comparative and Physiological Psychology*, **92**, 231-240.

Alberts, J. R. & Gubernick, D. J. 1983. Reciprocity and resource exchange: A symbiotic model of parent-offspring relations. In: *Symbiosis in parent-offspring interactions* (Ed. by L. A. Rosenblum & H. Moltz), pp. 7-44. New York: Plenum.

Alberts, J. R. & Cramer, C. P. 1988. Ecology and experience: Sources of means and meaning of developmental change. In: *Handbook of Behavioral Neurobiology* (Ed. by E. M. Blass), pp. 1-39. New York: Plenum.

Alberts, J. R. 2007. Huddling by rat pups: Ontogeny of individual and group behavior. *Developmental Psychobiology*, **49**, 22-32.

Anderson, M. J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 626-639.

Archie, E. A., Moss, C. J. & Alberts, S. C. 2011. Friends and relations: Kinship and the nature of female elephant social relationships. In: *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal* (Ed. by C. J. Moss, H. Croze & P. E. Lee), pp. 238-245. Chicago: University of Chicago Press.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K. E., Korstjens, A.

H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernández, G., Strier, K. B. & van Schaik, C. P. 2008. Fission-fusion dynamics. *Current Anthropology*, **49**, 627-654.

Baldwin, J. M. 1896. A new factor in evolution. *The American Naturalist*, **30**, 536-553.

Balsby, T., J. S. & Dabelsteen, T. 2002. Female behaviour affects male courtship in whitethroats *Sylvia communis*: an interactive experiment using visual and acoustic cues. *Animal Behaviour*, **63**, 251-257.

Bautista, A., García-Torres, E., Martínez-Gómez, M. & Hudson, R. 2008. Do newborn domestic rabbits Oryctolagus cuniculus compete for thermally advantageous positions in the litter huddle? *Behavioral Ecology and Sociobiology*, **62**, 331-339.

Beletsky, L. D. 1982. Aggressive and pair-bond maintenance songs of female red-winged blackbirds (*Agelaius phoeniceus)*. *Zeitschrift für Tierpsychologie*, **62**, 47-54.

Bergmüller, R. & Taborsky, M. 2010. Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, **25**, 504-511.

Bertin, A. & Richard-Yris, M. 2005. Mothering during early development influences subsequent emotional and social behaviour in Japanese quail. *Journal of Experimental Zoology*, **303A**, 792-801.

Blair, C., Peters, R. & Granger, D. 2004. Physiological and neuropsychological correlates of approach/withdrawal tendencies in preschool: Further examination of the behavioral inhibition system/behavioral activation system scales for young children. *Developmental Psychobiology*, **45**, 113-124.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, **161**, 1-28.

Bon, R. & Campan, R. 1996. Unexplained sexual segregation in polygamous ungulates: A defense of an ontogenetic approach. *Behavioural Processes*, **38**, 131-154.

Borgatti, S. P., Everett, M. G. & Freeman, L. C. 2002. *Ucinet for Windows: Software for Social Network Analysis.* Harvard, MA: Analytic Technologies.

Box, H. O. 1999. Temperament and socially mediated learning among primates. In: *Mammalian social learning: comparative and ecological perspectives* (Ed. by H. O. Box & K. R. Gibson), pp. 33-56. Cambridge, United Kingdom: Cambridge University Press.

Braaten, R. F. & Reynolds, K. 1999. Auditory preference for conspecific song in isolation-reared zebra finches. *Animal Behaviour*, **58**, 105-111.

Brockway, B. F. 1965. Stimulation of ovarian development and egg laying by male courtship vocalization in budgerigars (Melopsittacus undulatus). *Animal Behaviour*, **13**, 575–578.

Brockway, B. F. 1967. Social and experiential influences of nestbox-oriented behavior and gonadal activity of female budgerigars (*Melopsittacus undulatus* Shaw). *Behaviour*, **29**, 63-82.

Brodkin, E. S. 2007. BALB/c mice: Low sociability and other phenotypes that may be relevant to autism. *Behavioural Brain Research*, **176**, 53-65.

Buesching, C. D., Heistermann, M., Hodges, J. K. & Zimmermann, E. 1998. Multimodal oestrus advertisement in a small nocturnal prosimian, *Microcebus murinus*. *Folia Primatologica*, **69**, 295-308.

Burghardt, G. M. 2005. *The genesis of animal play: testing the limits*: MIT Press.

Burnell, K. & Rothstein, S. I. 1994. Variation in the structure of female brown-headed cowbird vocalizations and its relation to vocal function and development. *Condor*, **96**, 703-715.

Calhoun, J. B. 1962. Population density and social pathology. *Scientific American*, **206**, 139-150.

Capitanio, J. P. 2002. Sociability and responses to video playbacks in adult male rhesus monkeys (*Macaca mulatta*). *Primates*, **43**, 169-177.

Capitanio, J. P. 2010. Personality factors between and within species. In: *Macaque societies: A model for the study of social organization* (Ed. by B. Thierry, M. Singh & W. Kaumanns). Cambridge, United Kingdom: Cambridge University Press.

Carter, C. S., Lederhendler, I. I. & Kirkpatrick, B. 1999. *The Integrative Neurobiology of Affiliation*: Mit Press.

Carter, C. S., English, S. & Clutton-Brock, T. H. 2014. Cooperative personalities and social niche specialization in female meerkats. *Journal of Evolutionary Biology*, **27**, 815-825.

Ce´zilly, F., Pre´ault, M., Dubois, F., Faivre, B. & Patris, B. 2000. Pair-bonding in birds and the active role of females: acritical review of the empirical evidence. *Behavioural Processes*, **51**, 83-92.

Chatterjee, S. & Hadi, A. S. 2013. *Regression analysis by example*, 4th edn. New York: John Wiley & Sons.

Cheney, D. L., Seyfarth, R. M. & Smuts, B. 1986. Social relationships and social cognition in nonhuman primates. *Science*, **234**, 1361-1366.

Cheney, D. L. & Seyfarth, R. M. 1995. The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour*, **50**, 249-257.

Cheney, D. L. & Seyfarth, R. M. 1997. Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour*, **54**, 409-418.

Cheng, M. 1992. For whom does the dove coo? A case for the role of self-stimulation. *Animal Behaviour*, **43**, 1035-1042.

Cheng, M., Peng, J. P. & Johnson, P. 1998. Hypothalamic neurons preferentially respond to female nest coo stimulation: demonstration of direct acoustic stimulation of luteinizing hormone release. *Journal of Neuroscience*, **18**, 5477-5489.

Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*, 2nd ed. edn. Hillsdale, NJ: Erlbaum.

Cote, J., Dreiss, A. & Clobert, J. 2008. Social personality trait and fitness. *Proceedings of the Royal Society B*, **275**, 2851-2858.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B*, **365**, 4065-4076.

Coulson, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. *Journal of Animal Ecology*, **35**, 269-279.

Coussi-Korbel, S. & Fragaszy, D. M. 1995. On the relations between social dynamics and social learning. *Animal Behaviour*, **50**, 1441-1453.

Couzin, I. D. 2006. Behavioral ecology: social organization in fission–fusion societies. *Current Biology*, **16**, R169-R171.

Crawley, M. J. 2005. *Statistics: An introduction using R*. Chichester, UK: John Wiley & Sons.

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J. & James, R. 2009. Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, **63**, 1495-1503.

Curley, J. P., Jensen, C. L., Mashoodh, R. & Champagne, F. A. 2011. Social influences on neurobiology and behavior: epigenetic effects during development. *Psychoneuroendocrinology*, **36**, 352-371.

Darley, J. A. 1978. Pairing in captive brown-headed cowbirds (Molothrus ater). *Canadian Journal of Zoology*, **56**, 2249-2252.

David, M., Cézilly, F. & Giraldeau, L. 2011. Personality affects zebra finch feeding success in a producer–scrounger game. *Animal Behaviour*, **82**, 61-67.

Davidson, R. J. 2006. Toward a biology of personality and emotion. *Annals of the New York Academy of Sciences*, **935**, 191-207.

Dawkins, R. 1976. *The Selfish Gene*. New York: Oxford University Press.

de Waal, F. B. M. & Johanowicz, D. L. 1993. Modification of reconciliation behavior through social experience: An experiment with two Macaque Species. *Child Development*, **64**, 897-908.

de Waal, F. B. M. & Tyack, P. L. 2002. *Animal social complexity: Intelligence, culture and individualized societies*. Cambridge: Harvard Press.

Dingemanse, N. J., Kazem, A. J. N., Réale, D. & Wright, J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution*, **25**, 81-89.

Dolman, C. S., Templeton, J. & Lefebvre, L. 1996. Mode of foraging competition is realted to tutor preference in *Zenaida aurita*. *Journal of Comparative Psychology*, **110**, 45-54.

Dufty, A. M., Jr. 1982. Response of brown-headed cowbirds to simulated conspecific intruders. *Animal Behaviour*, **30**, 1043-1052.

Dufty, A. M., Jr. & Wingfield, J. C. 1986. Temporal patterns of circulating LH and steroid hormones in a brood parasite, the brown-headed cowbird, Molothrus ater. II Females. *J. Zool., Lond.*, **208**, 205-214.

Dyer, J. R. G., Croft, D. P., Morrell, L. J. & Krause, J. 2008. Shoal composition determine foraging success in the guppy. *Behavioral Ecology*, **20**, 165-171.

Elliot, A. J. & Thrash, T. M. 2010. Approach and avoidance temperment as basic dimensions of personality. *Journal of Personality*, **78**, 865-906.

Emery, N. J., Seed, A. M., von Bayern, A. M. P. & Clayton, N. S. 2007. Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B*, **362**, 489-505.

Engelhardt, A., Fischer, J., Neumann, C., Pfeifer, J.-B. & Heistermann, M. 2012. Information content of female copulation calls in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology*, **66**, 121-134.

Etkin, W. 1964. *Social behavior and organization among vertebrates*: University of Chicago Press.

Faust, K. & Skvoretz, J. 2002. Comparing networks across space and time, size and species. *Sociological Methodology*, **32**, 267-299.

Fernández-Juricic, E. & Kacelnik, A. 2004. Information transfer and gain in flocks: the effects of quality and quantity of social information at different neighbour distances. *Behavioral Ecology and Sociobiology*, **55**, 502-511.

Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. 2006. Policing stabilizes construction of social niches in primates. *Nature*, **439**, 426-429.

Flack, J. C., Hammerstein, P. & Krakauer, D. C. 2012. Robustness in Biological and Social Systems. In: *Evolution and the mechanisms of decision making* (Ed. by P. Hammerstein & J. R. Stevens). Cambridge, Ma: MIT Press.

Flynn, E. G., Laland, K. N., Kendal, R. L. & Kendal, J. R. 2013. Developmental niche construction. *Developmental Science*, **16**, 296-313.

Freeberg, T. M., King, A. P. & West, M. J. 1995. Social malleability in cowbirds (*Molothrus ater artemisiae*): Species and mate recognition in the first 2 years of life. *Journal of Comparative Psychology*, **109**, 357-367.

Freeberg, T. M. 1996. Assortative mating in captive cowbirds is predicted by social experience. *Animal Behaviour*, **52**, 1129-1142.

Freeberg, T. M. 1997. Cultural transmission of behaviors facilitating assortative courtship and mating in cowbirds (*Molothrus ater*) PhD., Indiana University.

Freeberg, T. M. 1998. The cultural transmission of courtship patterns in cowbirds, *Molothrus ater*. *Animal Behaviour*, **56**, 1063-1073.

Freeberg, T. M., Duncan, S. D., Kast, T. L. & Enstrom, D. A. 1999. Cultural influences on female mate choice: an experimental test in cowbirds, *Molothrus ater*. *Animal Behaviour*, **57**, 421-426.

Freeberg, T. M., King, A. P. & West, M. J. 2001. Cultural transmission of vocal traditions in cowbirds (Molothrus ater) influences courtship patterns and mate preferences. *Journal of Comparative Psychology*, **115**, 201-211.

Freeberg, T. M. & White, D. J. 2006. Social traditions and the maintenance and loss of geographic variation in mating patterns of brown-headed cowbirds. *International Journal of Comparative Psychology*, **19**, 206-222.

Freed-Brown, G. & White, D. J. 2009. Acoustic mate copying: female cowbirds attend to other females' vocalizations to modify their song preferences. *Proceedings of the Royal Society B*, **276**, 3319-3325.

Freed-Brown, S. G., King, A. P., Miller, J. L. & West, M. J. 2006. Uncovering sources of variation in female sociality: Implications for the development of social preferences in female cowbirds (Molothrus ater) *Behaviour*, **143**, 1293-1315.

Freeman, L. C. 1979. Centrality in social networks: Conceptual clarification. *Social Networks*, **1**, 215-239.

Friedmann, H. 1929. *The cowbirds: A study in the biology of social parasitism*. Springfield, Ill: C. C. Thomas.

Fushing, H., Jordà, Ò., Beisner, B. & McCowan, B. 2014. Computing systemic risk using multiple behavioral and keystone networks: The emergence of a crisis in primate societies and banks. *International Journal of Forecasting*, **30**, 797-806.

Garrett, K. L. & Molina, K. C. 2005. A field observation of the head-down display in the bronzed cowbird. *The Wilson Bulletin*, **117**, 410-412.

Gause, G. F. 1934. *The struggle for existence*. Baltimore MD: Williams & Wilkins.

Gersick, A. S., Snyder-Mackler, N. & White, D. J. 2012. Ontogeny of social skills: social complexity improves mating and competitive strategies in male brown-headed cowbirds. . *Animal Behaviour*, **83**, 1171-1177.

Gibbons, J. M., Lawrence, A. B. & Haskell, M. J. 2010. Measuring sociability in dairy cows. *Applied Animal Behaviour Science*, **122**, 84-91.

Gibson, J. J. 1966. *The senses considered as perceptual systems*. Boston: Houghton-Mifflin.

Giraldeau, L. A. & Caraco, T. 2000. *Social foraging theory*. Princeton: Princeton University Press.

Goldenthal, P., Johnston, R. E. & Kraut, R. E. 1981. Smiling, appeasement, and the silent bared-teeth display. *Ethology and Sociobiology*, **2**, 127-133.

Goodson, J. L., Schrock, S. E., Klatt, J. D., Kabelik, D. & Kingsbury, M. A. 2009. Mesotocin and nonapeptide receptors promote estrildid flocking behavior. *Science*, **325**, 862-866.

Goodson, J. L. & Kingsbury, M. A. 2011. Nonapeptides and the evolution of social group sizes in birds. *Frontiers in Neuroanatomy*, **5**.

Gottlieb, G. 1963. A naturalistic study of imprinting in wood ducklings (Aix sponsa). *Journal of Comparative and Physiological Psycholog*, **56**, 86.

Gottlieb, G. 1971. *Development of species identification in birds*. Chicago: University of Chicago Press.

Gottlieb, G. 1980. Development of species identification in ducklings: VI. Specific embryonic experience required to maintain species-typical perception in Peking ducklings. *Journal of Comparative and Physiological Psychology*, **94**, 579-587.

Gottlieb, G. 1992. *Individual development and evolution: The Genesis of Novel Behavior*. New York: Oxford University Press.

Gottlieb, G. 1993. Social induction of malleability in ducklings: Sensory basis and psychological mechanism. *Animal Behaviour*, **45**, 707-719.

Griffiths, S. W. & Magurran, A. E. 1998. Sex and schooling behaviour in the Trinidadian guppy. *Animal Behaviour*, **56**, 689-693.

Gros-Louis, J., White, D. J., King, A. P. & West, M. J. 2003. Female brown-headed cowbirds' (*Molothrus ater*) social assortment changes in response to male song: A potential source of public information. *Behavioral Ecology and Sociobiology*, **53**, 163-173.

Gros-Louis, J., White, D. J., King, A. P. & West, M. J. 2006. Do juvenile males affect adult males' reproductive success in brown-headed cowbirds (Molothrus ater)? *Behaviour*, **143**, 219-237.

Hall, M. L. 2004. A review of hypotheses of the function of avian duetting. *Behavioral Ecology and Sociobiology*, **55**, 415-430.

Hall, M. L. 2009. A review of vocal duetting in birds. *Advances in the Study of Behavior*, **40**, 67- 121.

Hamilton, K. S., King, A. P., Sengelaub, D. R. & West, M. J. 1997. A brain of her own: A neural correlate of song assessment in a female songbird. *Neurobiology of Learning and Memory*, **68**, 325-332.

Hamilton, K. S., King, A. P., Sengelaub, D. R. & West, M. J. 1998. Visual and song nuclei correlated with courtship skills in brown-headed cowbirds. *Animal Behaviour*, **56**, 973-982.

Hardin, G. 1960. The competitive exclusion principle. *Science*, **131**, 1292-1297.

Hassett, J. M., Rupp, H. A. & Wallen, K. 2010. Social segregation in male but not female yearling rhesus macaques. *American Journal of Primatology*, **72**, 87-92.

Heinrichs, M. & Domes, G. 2008. Neuropeptides and social behavior: Effects of oxytocin and vasopressin in humans. *Progress in Brain Research*, **170**, 337-350.

Henzi, S. P. & Barrett, L. 2007. Coexistence in female-bonded primate groups. *Advances in the Study of Behavior*, **37**, 43-82.

Hinde, R. A. 1976. Interactions, relationships and social structure. *Man*, **11**, 1-17.

Hood, K. E., Greenberg, G. & Tobach, E. 1995. *Behavioral development: concepts of approach/withdrawal and integrative levels*. New York: Garland.

Hunter, J. E. 1994. Further observations of head-down displays by brown-headed cowbirds. *Western Birds*, **25**, 63-65.

Hutchinson, G. E. 1957. Concluding remarks. In: *Cold Spring Harbor Symposia on Quantitative Biology*, pp. 415-427: Cold Spring Harbor Laboratory Press.

Huxley, J. S. 1923. Courtship Activities in the Red-throated Diver (Colymbus stellatus Pontopp.); together with a discussion of the Evolution of Courtship in Birds. *Journal of the Linnean Society (Zoology)*, **35**, 253-292.

Insel, T. R. & Young, L. J. 2001. The neurobiology of attachment. . *Nature Reviews Neuroscience*, **2**, 129-136.

Jablonka, E. & Lamb, M. E. 2005. *Evolution in four dimensions*. Cambridge: MIT press.

Jacklin, C. N. & Maccoby, E. E. 1978. Social behavior at thirty-three months in same-sex and mixed-sex dyads. *Child Development*, **49**, 557-569.

Jacoby, D. M. P., Busawon, D. S. & Sims, D. W. 2010. Sex and social networking: the influence of male presence on social structure of female shark groups. *Behavioral Ecology*, **21**, 808-818.

Johnston, T. D. & Gottlieb, G. 1985. Effects of social experience on visually imprinted maternal preferences in Peking ducklings. *Developmental Psychobiology*, **18**, 261-271.

Kasumovic, M. M. 2013. The multidimensional consequences of the juvenile environment: towards an integrative view of the adult phenotype. *Animal Behaviour*, **85**, 1049-1059.

King, A. P., West, M. J., Eastzer, D. H. & Staddon, J. E. R. 1981. An experimental investigation of the bioacoustics of cowbird song. *Behavioral Ecology and Sociobiology*, **9**, 211-217.

King, A. P. & West, M. J. 1987. The experience of experience: An exogenetic program for social competence. In: *Perspectives in ethology* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 153-182. New York: Plenum.

King, A. P. & West, M. J. 1990. Variation in species-typical behavior: A contemporary theme for comparative psychology. In: *Contemporary Issues in Comparative Psychology* (Ed. by D. A. Dewsbury), pp. 331-339. Sunderland, Massachusetts: Sinauer.

King, A. P., West, M. J. & Freeberg, T. M. 1996. Social experience affects the process and outcome of vocal ontogeny in two populations of cowbirds. *Journal of Comparative Psychology*, **110**, 276-285.

King, A. P. & West, M. J. 2002. Ontogeny of competence. In: *Conceptions of development* (Ed. by D. J. Lewkowicz & R. Lickliter), pp. 77-104. New York: Psychology Press.

King, A. P., White, D. J. & West, M. J. 2003. Female proximity stimulates development of male competition in juvenile brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour*, **66**, 817-828.

Kohn, G. M., King, A. P., Scherschel, L. L. & West, M. J. 2011. Social niches and sex assortment: uncovering the developmental ecology of brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour*, **82**, 1015-1022.

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R. & West, M. J. 2013a. In the company of cowbirds, *Molothrus ater ater*: Robust patterns of sociability predict reproductive performance. *Journal of Comparative Psychology*.

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R. & West, M. J. 2013b. Robust autumn social attributes predict spring courtship skills in juvenile female brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour*.

Kohn, G. M., King, A. P., Pott, U. & West, M. J. 2013c. Robust fall social displays predict spring reproductive behavior in Brown-headed Cowbirds (*Molothrus ater ater*). *Ethology*.

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R. & West, M. J. Submitted. Female vocal behavior reflects reproductive performance in Brown-headed Cowbirds (*Molothrus ater*). *Proceedings of the Royal Society B*.

Koski, S. E. 2011. Social personality traits in chimpanzees: Temporal stability and structure of behaviourally assessed personality traits in three captive populations. *Behavioral Ecology and Sociobiology*, **65**, 2161-2174.

Kralj-Fišer, S., Scheiber, I. B. R., Blejec, A., Moestl, E. & Kotrschal, K. 2007. Individualities in a flock of free-roaming greylag geese: Behavioral and physiological consistency over time and across situations. *Hormones and Behavior*, **51**, 239-248.

Krause, J., Lusseau, D. & James, R. 2009. Animal social networks: An introduction. *Behavioral Ecology and Sociobiology*, **63**, 967-973.

Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A. & Ydenberg, R. C. 2009. The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society B*, **277**, 601-608.

La Freniere, P., Strayer, F. F. & Gauthier, R. 1984. The emergence of same-sex affiliative preferences among preschool peers: A developmental/ethological perspective. *Child Development*,

55, 1958-1965.

Lachlan, R. F., Crooks, L. & Laland, K. 1998. Who follow whom? Shoaling preferences and social learning of foraging infomation in guppies. *Animal Behaviour*, **56**, 181-190.

Laland, K. & Sterelny, K. 2006. Perspective: seven reasons (not) to neglect niche construction. *Evolution*, **60**, 1751-1762.

Laland, K. N. & Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, **53**, 1161-1169.

Langmore, N. E., Davies, N. B., Hatchwell, B. J. & Hartley, I. R. 1996. Female song attracts males in the alpine accentor, *Prunella collaris*. *Proceedings of the Royal Society B*, **263**, 141-146.

Langmore, N. E. & Davies, N. B. 1997. Female dunnocks use vocalizations to compete for males. *Animal Behaviour*, **53**, 881-890.

Laskowski, K. L. & Bell, A. M. 2014. Strong personalities, not social niches, drive individual differences
in social behaviours in sticklebacks. *Animal Behaviour*, **90**.

Laskowski, K. L. & Pruitt, J. N. 2014. Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society B*, **281**, 20133166.

Lehrman, D. S. 1959. Hormonal responses to external stimuli in birds. *Ibis*, **101**, 478-496.

Lewis, S., Roberts, G., Harris, M. P., Prigmore, C. & Wanless, S. 2007. Fitness increases with partner and neighbour allopreening. *Biology Letters*, **3**, 386-389.

Lewontin, R. C. 1982. Organism and environment. In: *Learning, Development and Culture* (Ed. by E. C. Plotkin), pp. 151-170: Wiley.

Lewontin, R. C. 1983. The organism as the subject and object of evolution. *Scientia*, **118**, 65-82.

Lickliter, R. & Gottlieb, G. 1988. Social specificity: interaction with own species is necessary to foster species-specific maternal preference in ducklings. *Developmental Psychobiology*, **21**, 311-321.

Lott, D. & Lehrman, D. S. 1967. Exteroceptive stimulation of the reproductive system of the female ring dove (*Streptopelia risoria*) by the mate and by the colony milieu. *Animal Behaviour*, **15**, 433-437.

Lott, D. F. 1991. *Intraspecific variation in the social systems of wild vertebrates* Cambridge: Cambridge University Press.

Lowther, P. E. & Rothstein, S. I. 1980a. Head-down or "preening invitation" displays involving juvenile Brown-headed Cowbirds. *Condor*, **82**, 459-460.

Lowther, P. E. & Rothstein, S. I. 1980b. Head-down or "preening-invitation" displays involving juvenile brown-headed cowbirds. *Condor*, **82**, 459-460.

Lusseau, D. 2003. The emergent properties of a dolphin social network. *Proceedings of the Royal Society Series B*, **270**, 186-188.

Maguire, S. E., Schmidt, M. F. & White, D. J. 2013. Social brains in context: Lesions targeted to the song control system in female cowbirds affect their social network. *PLOS one*, **8**.

Marler, P. 1976. On animal aggression: The roles of strangeness and familiarity. *American Psychologist*, **31**, 239-246.

Martin, P. & Bateson, P. P. G. 1986. *Measuring behaviour: an introductory guide*. Cambridge: Cambridge University Press.

Mason, W. A. 1978. Ontogeny of Social Systems. In: *Recent Advances in Primatology* (Ed. by D. L. Chivers & J. Herbert), pp. 5-14. London: Academic Press.

Matochik, J. A., White, N. R. & Barfield, R. J. 1992. Variations in scent marking and ultrasonic vocalizations by Long-Evans rats across the estrous cycle. *Physiology & Behavior*, **51**, 783 - 786.

Mayr, E. 1974. Behavior programs and evolutionary strategies. *American Scientist*, **62**, 650-659.

McBride, G. 1971. Theories of animal spacing: The role of flight, fight and social distance. In: *Behavior and envrionment: The use of space by animals and men* (Ed. by A. H. Esser). New York: Plenum Press.

McBride, G. 1976. The study of social organizations. *Behaviour*, **59**, 96-115.

McPherson, J. M. & Smith-Lovin, L. 1987. Homophily in voluntary organizations: Status distance and the composition of face-to-face groups. *American sociological review*, **52**, 370-379.

Meaney, M. J. & Stewart, J. 1979. Envrionmental factors influencing the affiliative behavior of male and female rats (*Rattus norvegicus)*. *Animal Learning & Behavior*, **7**, 397-405.

Meaney, M. J. & Szyf, M. 2005. Environmental programming of stress responses through DNA methylation: life at the interface between a dynamic environment and a fixed genome. *Dialogues in Clinical Neuroscince*, **7**, 103-123.

Mills, A. D. & Faure, J. M. 2000. Ease of capture in lines of Japanese quail (*Coturnix japonica*) subjected to contrasting selection for fear or sociability. *Applied Animal Behaviour Science*, **69**, 125-134.

Montiglio, P. O., Ferrari, C. & Réale, D. 2013. Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B*, **368**, 20120343.

Morgan, C. L. 1896. On modification and variation. *Science*, **4**, 733-740.

Morris, D. 1956. The feather postures of birds and the problem of the origin of social signals. *Behaviour*, **9**, 75-113.

Nicolás, L., Martínez ‐ Gómez, M., Hudson, R. & Bautista, A. 2011. Littermate presence enhances motor development, weight gain and competitive ability in newborn and juvenile domestic rabbits. *Developmental Psychobiology*, **53**, 37-46.

O'Loghlen, A. L. & Rothstein, S. I. 2010. Multimodal signalling in a songbird: Male audiovisual displays vary significantly by social context in brown-headed cowbird. *Animal Behaviour*, **79**, 1285-1292.

Odling-Smee, F. J., Laland, K. N. & Feldman, M. W. 2003. *Niche construction: the neglected process in evolution*. Princeton, New Jersey: Princeton University Press.

Oliveira, R. F. 2004. Social modulation of androgens in vertebrates: Mechanisms and function. *Advances in the Study of Behavior*, **34**, 165-239.

Ortega, C. P. 1998. *Cowbirds and other brood parasites*. Tucson: The University of Arizona Press.

Osborn, H. F. 1896. Ontogenic and Phylogenic Variation. *Science*, **4**, 441-451.

Ottoni, E. B., de Resende, B. D. & Izar, P. 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal Cognition*, **8**, 215-219.

Palombit, R. A., Cheney, D. L. & Seyfarth, R. M. 1999. Male grunts as mediators of social interaction with females in wild chacma baboons (Papio cynocephalus ursinus). *Behaviour*, **136**, 221-242.

Payne, R. B. 1969. Giant cowbird solicits preening from man. *Auk*, **78**, 459-460.

Persuad, K. N. & Galef, B. G., Jr. 2003. Female Japanese quail aggregate to avoid sexual harassment by conspecific males: a possible cause of conspecific cueing. *Animal Behaviour*, **65**, 89-94.

Post, W. & Wiley, J. W. 1992. The head-down display in shiny cowbirds and its relation to dominace behavior. *Condor*, **94**, 999-1002.

Pratt, J. W. 1959. Remarks on zeros and ties in the Wilcoxon signed rank procedures. *American Statistical Association*, **54**, 655-667.

Pusey, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution*, **2**, 295-299.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Reyes-Meza, V., Hudson, R., Martínez-Gómez, M., Nicolás, L., Rödel, H. G. & Bautista, A. 2011. Possible contribution of position in the litter huddle to long-term differences in behavioral style in the domestic rabbit. *Physiology & Behavior*, **104**, 778-785.

Robertson, R. J. & Norman, R. F. 1976. Behavioral defenses to brood parasitism by potential hosts of the brown-headed cowbirds. *Condor*, **78**, 166-173.

Rothstein, S. I. 1977. The preening invitation or head-down display of parasitic cowbirds. I. Evidence for intraspecific occurrence. *Condor*, **79**, 13-23.

Rothstein, S. I. 1980a. The preening invitation or head-down display of parasitic cowbirds. 2. Experimental-analysis and evidence for behavioral mimicry. *Behaviour*, **75**, 148-184.

Rothstein, S. I. 1980b. The preening invitation or head-down display of parasitic cowbirds. II. Experimental analysis and evidence for behavioral mimicry. *Behaviour*, **75**, 148-184.

Rothstein, S. I., Yokel, D. A. & Fleischer, R. C. 1986. Social dominance, mating, and spacing systems, female fecundity and vocal dialects in captive and free-ranging brown-headed cowbirds. *Current Ornithology*, **3**, 127-185.

Ruckstuhl, K. E. & Neuhaus, P. 2005. *Sexual Segregation in Vertebrates*. Cambridge: University Press.

Ruckstuhl, K. E. 2007. Sexual segregation in vertebrates: proximate and ultimate causes. *Integrative and Comparative Biology*, **47**, 245-257.

Ruploh, T., Bischof, H. J. & von Engelhardt, N. 2014. Social experience during adolescence influences how male zebra finches (*Taeniopygia guttata*) group with conspecifics. *Behavioral Ecology and Sociobiology*, **68**, 537-549.

Sa´nchez-Macouzet, Rodrı´guez, C. & Drummond, H. 2014. Better stay together: pair bond duration increases individual fitness independent of age-related variation. *Proceedings of the Royal Society B*, **281**.

Sachser, N. 1993. The ability to arrange with conspecifics depends on social experiences around puberty. *Physiology & Behavior*, **53**, 539-544.

Saltz, J. B. & Foley, B. R. 2010. Natural Genetic Variation in Social Niche Construction: Social Effects of Aggression Drive Disruptive Sexual Selection in *Drosophila melanogaster*. *The American Naturalist*, **177**, 645-654.

Saltz, J. B. & Nuzhdin, S. V. 2014. Genetic variation in niche construction: implications for development and evolutionary genetics. *Trends in Ecology & Evolution*, **29**, 8-14.

Sapolsky, R. M. & Share, L. J. 2004. A Pacific Culture among Wild Baboons: Its Emergence and Transmission. *PLOS Biology*, **2**, 0534-0541.

Schneirla, T. C. 1965. Aspects of stimulation and organization in approach/withdrawal processes underlying vertebrate behavioral development. In: *Advances in the Study of Behavior* (Ed. by D. S. Lehrman, R. A. Hinde & E. Shaw), pp. 1-74. New York: Academic Press.

Schoener, T. W. & Cherrett, J. M. 1989. The ecological niche. *Ecological concepts: the contribution of ecology to an understanding of the natural world.*, 79-113.

Schradin, C. 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philosophical Transactions of the Royal Society B*, **368**, 20120346.

Schweitzer, C., Houdelier, C., Lumineau, S., Lévy, F. & Arnould, C. 2010. Social motivation does not go hand in hand with social bonding between two familiar Japanese quail chicks, *Coturnix japonica*. *Animal Behaviour*, **79**, 571-578.

Scott, D. M. & Ankney, C. D. 1983. The laying cycle of Brown-headed Cowbirds; passerine chickens? *Auk*, **100**, 583-592.

Scott, T. W. & Grumstrup-Scott, J. M. 1983. Why do Brown-headed Cowbirds perform the head-down display? *Auk*, **100**, 139-148.

Searcy, W. A. & Marler, P. 1987. Response of sparrows to songs of deaf and isolation-reared males: Further evidence for innate auditory templates. *Developmental Psychobiology*, **20**, 509-519.

Selander, R. K. & LaRue, C. J. 1961. Interspecific preening invitation display of parasitic cowbirds. *Auk*, **78**, 473-504.

Selander, R. K. 1964. Behavior of captive South American cowbirds. *Auk*, **81**, 394-402.

Sibbald, A. M., Elston, D. A., Smith, D. J. F. & Erhard, H. W. 2005. A method for assessing the relative sociability of individuals within groups: an example with grazing sheep. *Applied Animal Behaviour Science*, **91**, 57-73.

Sih, A. & Watters, J. V. 2005. The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, **142**, 1417-1431.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003a. Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231-1234.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003b. Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231-1234.

Silk, J. B. 2007. Social components of fitness in primate groups. *Science*, **317**, 1347-1351.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B*, **276**, 3099-3104.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010. Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. *Current Biology*, **20**, 1359-1361.

Sinha, A. 1998. Knowledge acquired and decisions made: triadic interactions during allogrooming in wild bonnet macaques, Macaca radiata. *Philosophical Transactions of the Royal Society of London B*, **353**, 619-631.

Smith, J. E., Powning, K. S., Dawes, S. E., Estrada, J. R., Hopper, A. L., Piotrowski, S. L. & Holekamp, K. E. 2011. Greetings promote cooperation and reinforce social bonds among spotted hyaenas. *Animal Behaviour*, **81**, 401-415.

Smith, R. L. 1959. The songs of the grasshopper sparrow. *The Wilson Bulletin*, **71**, 141-152.

Smith, V. A., King, A. P. & West, M. J. 2000. A role of her own: female cowbirds, Molothrus ater, influence the development and outcome of song learning. *Animal Behaviour*, **60**, 599-609.

Smith, V. A., King, A. P. & West, M. J. 2002. The context of social learning in brown headed cowbirds: Association patterns in a captive flock. *Animal Behaviour*, **63**, 23-35.

Smith, W. J. 1994. Animal duets: forcing a mate to be attentive. *Journal of Theoretical Biology*, **166**, 221-223.

Snyder-Mackler, N. & White, D. J. 2011. The developmental ecology of acoustic reactions: approaches to song playbacks by male cowbirds change across their first year of life. *Behaviour*, **148**, 747-764.

Stamps, J. & Groothuis, T. G. G. 2010. The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews*, **85**, 301-325.

Stevenson, M. 1969. Agonistic behavior in the cowbird *Molothrus ater* PhD Thesis, Kansas State University.

Stöwe, M., Bugnyar, T., Schloegl, C., Heinrich, B., Kotrschal, K. & Möstl, E. 2008. Corticosterone excretion patterns and affiliative behavior over development in ravens (*Corvus corax*). *Hormones and Behavior*, **53**, 208-216.

Strodl, M. A. & Schausberger, P. 2013. Social familiarity relaxes the constraints of limited attention and enhances reproduction of group ‐ living predatory mites. *Oikos*, **122**, 1217-1226.

Swaney, W., Kendal, J., Capon, H., Brown, C. & Laland, K. N. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, **62**, 591-598.

Székely, T., Moore, A. J. & Komdeur, J. 2010. *Social behaviour: genes, ecology and evolution*. Cambridge: Cambridge University Press.

Taborsky, B., Arnold, C., Junker, J. & Tschopp, A. 2012. The early social environment affects social competence in a cooperative breeder. *Animal Behaviour*, **83**, 1067-1074.

Taborsky, B. & Oliveira, R. F. 2012. Social competence: an evolutionary approach. *Trends in Ecology and Evolution*, **27**, 679-688.

Takeda, K. I., Sato, S. & Sugawara, K. 2003. Familiarity and group size affect emotional stress in Japanese Black heifers. *Applied Animal Behaviour Science*, **52**, 1-11.

Tanaka, K., Osako, Y. & Yuri, K. 2010. Juvenile social experience regulates central neuropeptides relevant to emotional and social behaviors. *Neuroscience*, **166**, 1036-1042.

Thompson, R. R. & Walton, J. C. 2004. Peptide effects on social behavior: effects of vasotocin and isotocin on social approach behavior in male goldfish (*Carassius auratus*). *Behavioral Neuroscience*, **118**, 620-626.

van Schaik, C. P. & van Noordwijk, M. A. 1988. Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour*, **105**, 77-98.

Wachtmeister, C.-A. 2001. Display in monogamous pairs: a review of emperical data and evolutionary explanations. *Animal Behaviour*, **61**, 861-868.

Waddington, C. F. 1962. *New patterns in genetics and development*. New York: Columbia University Press.

Waddington, C. H. 1940. *Organisers and genes*. Cambridge: Cambridge University Press.

Wasserman, S. & Faust, K. 1994. *Social Network Analysis*. Cambridge: Cambridge University Press.

Webber, T. A. 1983. Allopreening by brown-headed cowbirds. *Condor*, **85**, 249-250.

West, M., King, A. & Kohn, G. 2011. Developmental Ecology: Platform for designing a communication system. *Interaction Studies*, **2**.

West, M. J. & King, A. P. 1987. Settling nature and nurture into an ontogenetic niche. *Developmental Psychobiology*, **20**, 549-562.

West, M. J. & King, A. P. 1988. Female visual displays affect the development of male song in the cowbird. *Nature*, **334**, 244-246.

West, M. J., KIng, A. P. & Freeberg, T. M. 1998. Dual signaling during mating in Brown-headed Cowbirds (Molothrus ater; Family Emberizidae/Icterinae). *Ethology*, **104**, 250-267.

West, M. J., White, D. J. & King, A. P. 2002. Female brown-headed cowbirds' (*Molothrus ater)* organization and behaviour reflects male social dynamics. *Animal Behaviour*, **63**, 377-385.

West, M. J., King, A. P., White, D. J., Gros-Louis, J. & Freed-Brown, G. 2006. The development of local song preferences in female cowbirds (*Molothrus ater*): Flock living stimulates learning. *Ethology*, **112**, 1095-1107.

West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. Oxford: Oxford University Press.

White, D. J., King, A. P. & Duncan, S. D. 2002a. Voice recognition technology as a tool for behavioral research. *Behavioral Research Methods, Instrumentation, and Computers*, **34**, 1-5.

White, D. J., King, A. P. & West, M. J. 2002b. Plasticity in adult development: Experience with young males enhances mating competence in adult male cowbirds, *Molothrus ater*. *Behaviour*, **139**, 713-728.

White, D. J., King, A. P. & West, M. J. 2002c. Facultative development of courtship and communication in juvenile male cowbirds (*Molothrus ater*). *Behavioral Ecology*, **13**, 487-496.

White, D. J., Gros-Louis, J., King, A. P., Papakhian, M. & West, M. J. 2007. Constructing culture in cowbirds (*Molothrus ater*). *Journal of Comparative Psychology*, **121**, 113-123.

White, D. J. & Smith, V. A. 2007. Testing measures of animal social association by computer simulation. *Behaviour*, **144**, 1447-1468.

White, D. J., Gersick, A. S., Freed-Brown, G. & Snyder-Mackler, N. 2009. The ontogeny of social skills: experimental increases in social complexity enhance reproductive success in adult cowbirds *Animal Behaviour*, **79**, 385-390.

White, D. J., Gersick, A. S., Freed-Brown, G. & Snyder-Mackler, N. 2010a. The ontogeny of social skills: experimental increases in social complexity enhance reproductive success in adult cowbirds. *Animal Behaviour*, **79**, 385-390.

White, D. J., King, A. P., West, M. J., Gros-Louis, J. & Tuttle, E. M. 2010b. Effects of singing on copulation success and egg production in brown-headed cowbirds, *Molothrus ater*. *Behavioral Ecology*, **21**, 211-218.

Whitman, C. O. 1899. *Animal behavior*: Ginn & Company.

Wickler, W. 1980. Vocal dueting and the pair bond. I. Coyness and partner commitment. *Zeitschrift für Tierpsychologie*, **52**, 201-209.

Williams, J. R., Insel, T. R., Harbaug, C. R. & Carter, C. S. 1994. Oxytocin administered centrally faciliates formation of partner preference in female prairie voles (*Microtus ochrogaster*). *Journal of Neuroendocrinology*, **6**, 247-250.

Windle, M. 1995. The approach/withdrawal concept: Associations with salient constructs in contemporary theories of temperament and personality development. In: *Behavioral development: Concepts of approach/withdrawal and integrative levels* (Ed. by K. E. Hood, G. Greenberg & E. Tobach). New York, NY: Garland Publishing.

Wolf, M., van Doorn, G. S. & Weissing, F. J. 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, **105**, 15825-15830.

Yasukawa, K. 1989. The cost and benefits of a vocal signal: The nest-associated 'chit' of the female red-winged blackbird, *Agelaius phoeniceus*. *Animal Behaviour*, **38**, 866-874.

Yokel, D. A. 1986. Monogamy and brood parasitism: An unlikely pair. *Animal Behaviour*, **34**, 1348-1358.

CV

Gregory M. Kohn
Psychological and Brain Sciences, Indiana University-Bloomington
1101 E 10th St., Bloomington, IN, 47405
(845)-227-4056
gmkohn@indiana.edu

A. Education

2002- 2006, University of Montana, BS, Major: Zoology and Ecology

2006- 2009, Utrecht University. MS, Advisor: Simon Reader and Kees van Oers, Dissertation: Directed Social Learning in the Guppy (*Poecilia reticulate*), and 'The influence of food type on the early development of personality in a natural population of Great Tits (*Parus major*).

2009- 2015, Indiana University, PhD candidate, Psychological and Brain sciences

B. Teaching / Assistantships:

August 2010- December 2010: Instructor for P211 ("Methods in Experimental Psychology"). Here I taught two classes that explored methodological issues in psychology. I introduced students to basic experimental designs and statistical concepts from Student t-tests to bootstrapped resampling statistics.

March 2008- May 2008: Instructor for the "Behavioural Biology" and "Cognition and Behaviour" courses at Utrecht University in the Netherlands. Here I taught undergraduate lab courses that introduced undergraduates to behavioral research and lead lab sessions involving behavioral experiments with guppies (*Poecilia reticulata*).

June 2006- September 2006: Research Assistant at the Konrad Lorenz Research Center. Here I worked on hand raising corvids and performing behavioral and cognitive studies with both jackdaws (*Corvus monedula*) and carrion crows (*Corvus corone*). My project here looked at how the presence of familiar versus unfamiliar conspecifics influenced performance on a cognitive task, and fostered an interest in how social context shapes the expression of behavior.

C. Peer reviewed Publications:

West, M., King, A. & Kohn, G. (2011) Developmental Ecology: Platform for designing a communication system. Interaction Studies, 12, 350-370.

Kohn, G. M., King, A. P., Scherschel, L. L. & West, M. J. (2011) Social niches and sex assortment: uncovering the developmental ecology of brown-headed cowbirds, *Molothrus ater.* Animal Behaviour, 82, 1105-1022. http://dx.doi.org/10.1016/j.anbehav.2011.07.035

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R. & West, M. J. (2012) In the company of cowbirds, *Molothrus ater ater*: Robust patterns of sociability predict reproductive performance. Journal of Comparative Psychology. Published online first: http://psycnet.apa.org/doi/10.1037/a0029681

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R. & West, M. J. (2013) Robust fall social attributes predict spring courtship skills in juvenile female Brown-headed Cowbirds (*Molothrus ater*). Animal Behaviour.

Kohn, G. M., King, A. P., Pott, U. & West, M. J. (2013) Robust fall social displays predict spring reproductive behavior in Brown-headed Cowbirds (*Molothrus ater ater*). Ethology.

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R. & West, M. J. (submitted) Vocal behavior in female Brown-headed Cowbirds (*Molothrus ater*) reflects individual reproductive performance.

Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R. & West, M. J. (in revew) Sex differences in Familiarity Preferences within Fission-Fusion Brown-headed Cowbird (*Molothrus ater*) Flocks.

Kohn, G. M., Bruce, M., Reader, S. R. (in prep) Directed social learning from successful demonstrators in the guppy (*Poecilia reticulate*)

D. Selected Presentations:

- 2008 G. M. Kohn, S. Reader, M. Bruce, Directed social learning from successful demonstrators in the guppy (*Poecilla reticulate*), Poster presentation at the Netherlands society for behavioral biology

- 2011 G. M. Kohn, A. P King, L. L. Scherschel, M. J. West, Social niches and sex assortment: Uncovering the developmental ecology of brown headed cowbirds, Presentation at Behavior 2013

- 2011 G. M. Kohn, A. P King, L. L. Scherschel, M. J. West, Social niches and social context: Uncovering the developmental of sociability in brown headed cowbirds, Presentation at the Meeting for the International society for Developmental Psychobiology