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DEMOGRAPHIC AND SOCIAL INFLUENCES ON THE WINTER ECOLOGY OF A MIGRATORY SONGBIRD, THE GOLDEN-CROWNED SPARROW (*ZONOTRICHIA ATRICAPILLA*)

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Abstract

Demographic and social influences on the winter ecology of a migratory songbird, the golden-crowned sparrow (*Zonotrichia atricapilla*)

Theadora A. Block

Social groups can range from cohesive and stable to fluid and temporary, with many variations of the two. Social structure can effect selection pressures on individuals, and in turn, feedback from how social groups are organized can affect selection on different traits and behaviors. Here, I focus on group organization and how individual traits may correlate with sociality, and ultimately, survivorship. The research here ties together multiple threads to understand how individual traits connect to each other to shed light on how stable groups are organized, and which traits are most important to help maintain this structure over time.

In Chapter 1, I ask if golden-crowned sparrows have consistent behavior within a season and over multiple years, and if this consistent behavior correlates with behavior in the field and several morphological traits. I found that the sparrows do have consistent behaviors in short-term captivity, yet these are independent of the traits measured here, and may connect with other factors such as predation response or foraging methods. For Chapter 2, I quantified individual sociality using social network measures and asked if dominance, plumage badges of status, sex, age, or mass could predict a sparrows' social measures. I found that older and smaller birds had more connections. Chapter 3 links the previous chapters as I determined which behaviors and traits affected survivorship over ten years. Higher dominance increased survivorship, while older birds had lower survivorship. However, survivorship only decreased in the oldest age classes, showing evidence of senescence. Chapter 4 builds on Chapter 2, and used GPS tracking to discover if golden-crowned sparrows which were in the same winter communities bred in the same area. I discovered that sparrows in the same social community went to separate breeding locations, showing long-term social memory across migration.

This thesis demonstrates that age, size and dominance are important aspects in social behavior and survival. Older individuals had more connections, and in conjunction with previous research, had stronger connections over years. This shows that older individuals can play a keystone role in maintaining cohesiveness of social communities over time.

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Introduction

Interactions between individuals are an essential part of any social animals' life, and different types of interactions between individuals scale up to form the larger social groups (Pinter-Wollman et al. 2014; Silk et al. 2014). Which animals interact builds the basis of social groups through patterns of association, and the types of interactions, such as cooperative or aggressive, additionally shape the relationships between animals (Hinde 1976; Aureli et al. 2008). Indeed, understanding the drivers of individual interactions can help us understand patterns of social group organization on a larger scale (Wilson et al. 2012; Snijders and Naguib 2017). In species with complex societies and social relationships, understanding how individuals interact within groups, and what traits correlate with types of social behavior, is integral to deepen understanding of animal social behavior (Wey et al. 2008, Cantor et al. 2021). This body of work investigates how the behavior and morphology of individuals influence different aspects of sociality and ultimately survivorship in a migratory sparrow.

When seeking to understand animal societies, two broad-scale questions arise: why groups form in the first place and how they are organized. First, for groups to form, individuals would need to have increased fitness advantages as part of a group over being solitary (Alexander 1974). Research on small birds in winter has provided a fundamental understanding of why living in groups, particularly those comprised of non-kin, can be advantageous (Lima 1986; Houston et al. 1993; McNamara et al.

1994). Known as the Small Bird in Winter Theory, the focus is on the non-breeding season because the main impetus is for individuals to survive winter and deal with the trade-offs of foraging versus predation risk (Lima 1986; Houston et al. 1993; McNamara et al. 1994). Group living can provide many advantages, such as protection from predation and finding resources (Caraco et al. 1980; Davies et al. 2012). Because more individuals are watching for predators while in a flock, each individual can spend more time focusing on foraging (Lima 1987). Significant amounts of research has been dedicated to why groups form, and the finer nuances of group organization have emerged as a topic of interest in the last few decades (Aureli et al. 2008, Wey et al. 2008).

To begin to address the second question, how groups are organized, understanding the types of organization ranges from quantifying population metrics, such as the size and stability of groups, to the patterns of association between individuals (Krause et al. 2009; Krause et al. 2015). Animal societies can be classified by their degree of fission-fusion dynamics, which is how cohesive groups are and how individual membership changes over time (Aureli et al. 2008). Groups can range from strongly cohesive with stable membership to flexible groups with potentially fluid sub-groups within (Aureli et al. 2008). Resource distribution and habitat quality can drive where animals aggregate and general organization, but individual behavioral preferences also fundamentally shape group organization (Alexander 1974; Chapman et al. 1995; He et al. 2019). Indeed, resource density and distribution accounted for less than half of the variation in group size in spider monkeys and chimpanzees (Chapman et al. 1995). Social network analysis allows researchers to uncover patterns at different scales, from patterns of individual association to overall groups (Krause et al. 2015). Network analysis is a powerful tool to quantify patterns, but it does not necessarily explain them. Asking if well-understood traits such as dominance, age, or sex correlate with patterns of sociality helps us understand what may drive these patterns.

Here, I researched behavioral variation, how it connects to patterns of sociality, and what traits impact fitness. I studied a population of small, migratory birds, golden-crowned sparrows (*Zonotrichia atricapilla*), at their overwintering site at the University of California Santa Cruz (UCSC) Arboretum (Figure 1). These sparrows live in the UCSC Arboretum from September to April and breed in Alaska and western Canada. Previous research in this golden-crowned sparrow system provides a unique opportunity to study social interactions and behavior in stable groups in a wintering migratory bird. Golden-crowned sparrows live in non-kin groups in the winter, forming social connections that can last for years (Shizuka et al. 2014; Arnberg et al. 2015). Within these groups, plumage patches act as badges of status which signal dominance (Chaine et al. 2011; Chaine et al. 2013). Golden-crowned sparrows have stable communities (Shizuka et al. 2014), and I focused on individual-level behavior and sociality to learn what traits may predict patterns of individual social association. I measured several aspects of behavior: personality, sociality, and dominance, along with morphological measures such as plumage badge size, body size, mass, sex, and age. These behaviors and morphology are all potentially salient to the golden-crowned sparrows' social system. This dissertation discovers which ones are the most consequential in terms of correlations across different behaviors and survivorship.

In **Chapter 1**, I studied how individual behavior in captivity connects to morphological traits and dominance in the field. I focused on animal personality, or behaviors that are consistent within an individual over time and among different contexts, yet vary among individuals (Dingemanse et al. 2004; Bell 2007). Personality behaviors can be heritable and have been linked to many essential aspects of animal's lives, such as dominance, foraging, and survival (Dingemanse et al. 2004; Dingemanse and Réale 2005; Biro and Stamps 2008; Hall et al. 2015; Stein et al. 2016; Bubac et al. 2018). Alternative life-history strategies demonstrate behaviors that can be consistent over time, such as individuals using different foraging techniques to minimize competition (Barta and Giraldeau 1998). Animal personalities show parallels to alternative life-history strategies and may reflect an individual's life-history strategy; for example, individuals that reach maturity earlier may also take more risks and have more exploratory personalities (Stamps 2007; Wolf et al. 2007). Connecting personality to behaviors in the field and traits such as sex and size could show if personality mirrors life-history traits (Réale et al. 2010). I determined whether golden-crowned sparrows have consistent behaviors within and across years and if other life-history traits correlated with these consistent behaviors. I measured behavioral traits over three years, corresponding to a golden-crowned sparrow's expected lifespan, to understand whether personality was apparent within a year or whether personality varied with age or potential life-history strategy.

In **Chapter 2**, I investigated which aspects of behavior and morphology correlate with an individual's sociality. Previous research in this study system revealed that golden-crowned sparrows have stable communities with fission-fusion flocks within and primarily associate with other members of their community (Shizuka et al. 2014). These associations can last for years, and if a bird returns to an overwintering site, it most likely returns to the same community (Shizuka et al. 2014). I used social network analysis to determine individual patterns of association and overall community membership. I calculated three measures of sociality to quantify how individuals interacted—if they socialized with many individuals, how strong those connections were within a community, and how many close associates they had. I asked how several different golden-crowned sparrow characteristics (personality, age, mass, sex, dominance, and badge size) correlate with their sociality. Learning which traits predict an individual's sociality helps us understand the potential drivers of social organization in different species, and how those traits may effect social organization in different systems (Cantor et al. 2021).

In Chapters 1 and 2, I explored how behavior and morphology connect to sociality and personality. **Chapter 3** ties these two chapters together by examining ten years of data to learn which traits correlate with annual survival from winter to winter. Annual survival can be a significant component of fitness and influences everything from life-history evolution to social behavior (Promislow and Harvey

1990, Healy et al. 2019). Discovering which traits may affect annual survival is critical in understanding the selection pressures on both social and morphological traits in this study system. One trait I focused on, dominance, has been found to correlate with increased annual survival in other species of birds (Fretwell 1969; Kikkawa 1980; Desrochers et al. 1988; Koivula and Orell 1988; Piper and Wiley 1990). I measured social dominance, plumage badges of status, body size, age, and sex to investigate which of these traits predicted annual survival.

Chapter 4 arose from wanting to discover if the tight-knit communities and social connections present in winter continued through the annual cycle to the breeding grounds. It can be challenging to study migratory birds across their winter and summer seasonal locations (Sherry and Holmes 1996; Norris et al. 2004; Norris and Marra 2007). With the advent of new technology, we used Global Positioning System (GPS) tags to track golden-crowned sparrows from their wintering grounds through their migration paths to their breeding grounds. I used the comprehensive social data from our winter grounds to determine if birds from the same winter community migrate to similar summer areas or if summer communities are independent of winter communities.

Figure 1. On the left, a golden-crowned sparrow at the UCSC Arboretum (photo by Theadora A. Block). On the right, a display of the crown variation present in golden-crowned sparrows during winter (photo by Bruce E. Lyon).

Chapter 1

A migratory sparrow has personality in winter that is independent of other traits

Abstract

Small birds in winter face difficult trade-offs between predation risk and foraging, and alternate life-history strategies may be one way of managing these trade-offs. Animal personality shows similarities with alternative life-history strategies, and examining personality through the lens of life-history provides valuable insights. In winter, golden-crowned sparrows *(Zonotrichia atricapilla*), a small migratory bird, have a complex social system with high site-fidelity, long-term social associations between individuals, and competition mediated by badges of status. We asked if golden-crowned sparrows show personalities during winter, if these personalities were consistent over three years, and whether they linked to social and morphological traits. We found that golden-crowned sparrows have highly repeatable behaviours constituting personalities within one season and over time for up to three years. These sparrows live for around 2-3 years, so this covers most of their lifespan. While long-term repeatability was present, it varied considerably among different behaviours and timespans, and the length of time did not predict how repeatability changed. For all three years of the study, two movement-based aspects of sparrow personality were independent of the traits we measured (dominance, badges of status, size, and age). However, non-song vocalization behaviour (a repeatable part of personality) correlated with wing length and gold badge size in some years. Because personality did not strongly link to the social traits we measured, sparrow personality could represent a separate axis of variation that might predict other winter life-history parameters such as foraging, predation response, or survival.

Keywords: badge of status; birds; golden-crowned sparrow; life-history; personality; repeatability; social dominance; vocalization; winter ecology

Introduction

One of the main life-history trade-offs that animals face in winter is between foraging and survival (McNamara and Houston 1987; McNamara et al. 1994). Small birds, in particular, face many difficulties surviving winter conditions due to challenges of keeping warm combined with limited fat reserves—they must forage to avoid starvation, but in doing so, they increase the risk of predation (Lima 1986; Houston et al. 1993; McNamara et al. 1994). Known as the small-bird-in-winter paradigm (Roth et al. 2006), this was proposed as one reason why birds form groups in winter (Caraco et al. 1980). Forming groups can protect individuals from predation so that birds can spend more time foraging and less time scanning for predators (Lima 1987) despite increased competition for resources within groups. The trade-off between foraging and predation can manifest on multiple levels, from general selection pressures on decisions like when to forage or join a group to how individuals respond to risk, and can lead to a variety of optimal solutions.

Alternative life-history strategies have been studied mostly in the context of reproduction (Dominey 1984; Lyon and Eadie 2008; Taborsky et al. 2008), but there is some evidence that alternative life-history strategies occur in other parts of the life cycle. In wintering pied wagtails (*Motacilla alba*), some birds defend territories while others live in flocks (Davies 1976). Other examples of alternative non-breeding strategies have been found in partial migration tactics, which have been shown in pied avocets (*Recurvirostra avosetta*) and European robins (*Erithacus rubecula*) (Adriaensen and Dhont 1990; Chambon et al. 2019).

Considerable variation seen in social traits during the non-breeding season could be indicative of alternative strategies. For birds that form social groups in winter, competition between individuals for access to food can be mediated by signals of status or social recognition (Chaine et al. 2018). Previous studies suggest that variation in social dominance signaled by badges of status could favor alternative foraging strategies, such as producers versus scroungers (Barta and Giraldeau 1998) or sheep and shepherds (Rohwer and Ewald 1981). For example, Harris' sparrows (*Zonotrichia querula*) flock in winter and use variation in the size of their black chest patches (Rohwer 1975) as badges of status that predict an individual's dominance. Rohwer and Ewald (1981) further theorized that this variation in plumage and social dominance in Harris' sparrows could reflect alternative winter strategies with trade-offs between dominance and food-finding.

In many ways, animal personalities can mirror the patterns of alternative life-history strategies (Stamps 2007; Wolf et al. 2007; Réale et al. 2010). Behaviours associated with alternative life-history strategies are often consistent within individuals but differ across individuals (Brockmann 2001), and animal "personalities" also consist of specific behaviours that vary among individuals but are consistent for a given individual (e.g., boldness, exploration, neophobia). If dominant and subordinate individuals use different foraging mechanisms like producers versus scroungers, dominant individuals may be bolder in general, so dominance would potentially correlate with a bold-shy axis of personality. Indeed, personality types have been found to correlate with foraging and survival (Dingemanse et al. 2004; Cote et al. 2008; Patrick and Weimerskirch 2014; Bubac et al. 2018) and other life-history traits such as growth or the timing of reproduction (Niemelä et al. 2011; Montiglio et al. 2014; Hall et al. 2015).

The interplay between personality, dominance, and foraging strategy can vary within the same species. For example, in captivity, shy barnacle geese (*Branta leucopsis*) acted as scroungers and bold geese as producers, but personality did not correlate with dominance (Kurvers et al. 2009). In contrast, in the wild, less dominant geese (smaller and younger) were more explorative and acted as producers, while dominants (larger and older) would then displace them at the feeding sites (Stahl et al. 2001). Life history traits and strategies may also vary with age and sex, both of which can be correlated with personality (Biro and Stamps 2008; Johnson et al. 2017; Dammhahn et al. 2018). Connecting personality to other traits such as dominance, age, sex, and morphology can reveal if, and how, personality may be part of a winter alternative strategy.

By definition, personalities are behaviors that are consistent over time, but we currently do not have expectations for how long personalities should be stable. In theory, personality could be stable for a particular season, for one or multiple years, or over the animals' entire life. While it is important to determine the consistency of behavior over shorter time frames, we also need to measure the stability of these behaviors over longer periods of an animal's lifespan. If personality is a component of life-history strategies, then the timespan of the particular tactics an individual adopts should determine the timespan of stable personalities. For example, if the life-history tactic is age-dependent, personality should reflect those changes and we might expect to see consistent behaviors varying across age class. Alternatively, if the life-history tactics are fixed for life, personality should also be consistent across all years. Finally, if life-history tactics change across years, e.g. based on condition, personality should track these changes accordingly.

Despite clear links between personality and fitness in some study systems (Dingemanse et al. 2004; Dingemanse and Réale 2005; Biro and Stamps 2008; Hall et al. 2015; Stein et al. 2016; Bubac et al. 2018; Costanzo et al. 2018), personality is usually measured in captive conditions that are removed from the life-history contexts in which it is favored. Therefore, it is necessary to understand the relevance of the experimentally determined personalities by linking them to important behavioural and ecological aspects of an animal's life in the wild (Dingemanse et al. 2004; Archard and Braithwaite 2010; Carter et al. 2013).

We examine the occurrence and consistency of personality traits in a migratory bird, the golden-crowned sparrow (*Zonotrichia atricapilla*), during winter. We investigate whether personality correlates with behaviours and social traits that could be part of alternative winter social strategies such as producers versus scroungers (Barta and Giraldeau 1998). Golden-crowned sparrows vary widely in several traits that are likely important to survival, such as plumage and dominance. Golden-crowned sparrows have plumage crown patches with two outer black stripes that flank a central gold patch. Experiments confirm that the variable black and gold crown patches function as badges of status that determine social dominance in contests over food (Chaine et al. 2011; Chaine et al. 2013). However, whether the birds pay attention to the badges depends on social context: unfamiliar sparrows rely mostly on the badges of status to settle contests while familiar birds can rely on individual recognition (Chaine et al. 2018).

Golden-crowned sparrows live in highly stable, complex winter social groups (Shizuka et al. 2014), and individuals within these groups vary in social measures that could also potentially reflect different wintering strategies. The sparrows form flocks during winter and forage in fission-fusion groups, and these flocks are subsets of larger communities of 3-17 birds (Shizuka et al. 2014). These communities have organized social structure due to social preferences among individual birds; social structure is not an incidental byproduct of overlapping space use. Overall, communities are relatively stable, and if a sparrow returns to the wintering ground across winters, it nearly always returns to the same community (Shizuka et al. 2014).

As part of this remarkable fidelity, some sparrows socialize with the same individuals in the same area for multiple years (Shizuka et al. 2014). Theory suggests that stable social systems such as those seen in golden-crowned sparrows are particularly amenable for the evolution of personality (Wolf and Weissing 2010; Wolf and Krause 2014).

Migratory birds face different challenges compared to residents (Mettke-Hofmann et al. 2005), and much of the bird personality research is on resident year-round species (van Oers and Naguib 2013). The migratory aspect of the sparrow's lives emphasizes the importance of studying their behaviours over multiple years, as they deal with both social stability within a season and significant social changes and turnover over years (Shizuka et al. 2014). The social and geographical differences that come with breeding and wintering in different areas could mean that personality and other traits shift over time due to these seasonal changes. If migrant birds have stable personality types year-round, there could be tradeoffs in fitness between seasons. For example, if bolder birds had higher reproductive success during the summer, they might face a trade-off with lower survival during winter.

Here, we ask if golden-crowned sparrows show personalities in winter, and if so, whether personality correlates with social and morphological traits. If personality correlates with one or more of the key social traits we assess, it could reflect the occurrence of alternative winter life-history strategies in these birds. To address this, we ask three questions. First, do golden-crowned sparrows have experimentally-determined repeatable behaviours (personality traits) within one season? Second, if so, are these behaviours repeatable across multiple years? Third, does personality correlate with dominance, badge of status, age, or size?

Methods

Field Methods

We studied wintering golden-crowned sparrows at the University of California Santa Cruz Arboretum. These migratory sparrows breed in Alaska and western Canada and are on the wintering grounds from late September through the end of April. We gathered all field data and ran aviary trials during three winter seasons. Season 1 spanned September 2014–May 2015, Season 2 spanned September 2015–May 2016, and Season 3 spanned September 2016–May 2017. Subsequently, we will refer to each field season by the year in which it began: 2014, 2015, and 2016.

We caught golden-crowned sparrows with baited Potter traps and mist nets. Each captured bird was banded with a USFWS metal band and a unique combination of color bands to enable individual identification in the field. For all birds (new unbanded and returning banded individuals), we measured body mass (g), length of the tarsus (mm), culmen (mm), and flattened wing cord (mm), and collected a blood sample from the ulnar vein for sexing. Birds were sexed by amplifying the CHD gene on the Z and W sex chromosomes (Griffiths et al. 1998) following methods described in Chaine et al. (2011).

Personality Trials

We conducted behavioural trials during banding sessions after the birds were banded and before they were measured to minimize handling time (Block et al., 2020). We kept birds in bird bags in a quiet environment and started the trials by the order in which we caught the birds. In each assessment, the bird was placed in one of two 1.2 meter^3 outdoor aviaries in a natural, shaded environment and video recorded for five minutes with no observer present. Each cage had woodchips covering the ground, chicken wire walls with mosquito mesh covering the internal sides, and four natural wooden perches fixed on each corner of the cage floor. From the videos, we extracted the following eight behaviours that have been shown to be relevant in other avian studies (Dingemanse 2002; Dingemanse et al. 2004; van Oers 2004; Kluen et al. 2012): the number of quadrants used, number of perches used, perch bouts (number of times birds hopped onto a perch), number of perch turns (a 180° rotation on a perch), number of flights, latency to land after release into the cage, number of non-song vocalizations (call notes), and the number of hops in two minutes. All measures from the video were counted over five minutes, except for the number of hops, which were counted over two minutes (timing began one minute after we released the bird into the cage to give birds time to acclimate to the new environment). We also measured two additional behaviours with an *escape test* and a *bag test*. For the escape test, we placed each bird in a cardboard box (22.86 cm by 31.12 cm by 24.13 cm) with a small door (12.7 cm by 12.7 cm) opened after one minute of acclimation to the box environment (Sasaki et al. 2018). We positioned the box on the ground outdoors near vegetation, with the small door opening on ground level. An observer hidden behind the box opened the door and timed how long the bird took to leave the box (in seconds); the test was capped at 300 seconds. The bag test was conducted before we banded the bird. The bird was placed in a cloth bird bag, hung on a clothesline, and video recorded for one minute with no observer present (Montiglio et al. 2012). Later, the number of times the bird moved distinctly in the bag over one minute was counted from the video recording. Two observers extracted a set of the same videos to calibrate counts, and then they extracted all video data. The observers were blind to the sex, age, and social status of the birds. We performed personality trials for the following numbers of individuals per year: 2014, $N = 148$; 2015, $N = 143$; 2016, $N = 100$. No trials were conducted after March 1.

On a subset of birds ($N = 25$), we conducted repeated trials at least one month after the initial trial within the 2014 season to first identify which behaviors we would consider 'personality.' We measured the repeatability of the ten extracted behaviours (detailed above) and retained all behaviours with repeatability >25%. This revealed six repeatable behaviors which we then used as a measure of personality for all three seasons. To ask which traits correlated with personality, we condensed the six behaviors in a Principal Component Analysis (PCA) to form a composite measure of a birds' personality.

Potential Correlates with Personality

We measured several social and morphological traits, described in the sections below, to determine if personality correlates with other golden-crowned sparrow winter traits (Block et al., 2020). All of these morphological traits are stable within a winter season. Badge size (size of a plumage patch) does not change as birds do not molt their plumage feathers in the winter season; they start molting their badges shortly before leaving on spring migration and after we have finished collecting data on April 1 (Norment et al. 2020). Mass is also consistent both within-year and across-years (Author unpublished data), similar to other passerines during winter (Broggi et al. 2009).

Age

We characterized an individual's age as one of two standard avian age class categories: hatch-year (HY), which refers to birds in their first year of life, and after hatch-year (AHY), any age after year one. Previously banded birds are necessarily AHY, but ambiguity in age exists for unbanded birds captured for the first time. To estimate age classes of newly captured birds, we used a modified version of Colwell's (1999) method to determine age class using rank scores for crown plumage. The size of the crown patches can increase over an individual's lifetime, but there is often a large change between the HY and AHY, and all HY birds have relatively smaller and duller plumage patches. Crown features are an imperfect indicator of age, but plumage nonetheless improves the accuracy of ageing over the assumption that all unbanded birds are HY birds.

Badges of status

To measure the plumage traits that function as badges of status, we took digital photographs of birds' crowns (photos focused on the top of the head, level with a ruler for size reference) during banding and extracted the size of the black and gold patches (mm^2). We used Adobe Photoshop to isolate each color patch and converted the number of pixels to mm^2 using a standardized method from Chaine et al. (2011).

Dominance assay

We determined social dominance by observing interactions between birds over access to seed at regular pre-baited feeding stations. We observed social interactions from at least 10 meters away and counted the interactions following methods from Chaine et al. (2011): fight, supplant, chase, and avoid. Fights occurred when birds made physical contact, while supplants occurred when one bird rapidly replaced another at the seed pile. During chases, the bird that initiated the chase was considered the winner, while the bird that fled was the loser. Avoidance took place when a subordinate waited nearby but did not approach a bird feeding at the pile. We recognized this as a dominance interaction because the converse does not happen: dominant birds do not wait for a subordinate to leave the food, but rather chase or supplant them. We only included interactions with a clear winner and loser and used these data to calculate dominance scores (Elo rating; see Statistical Methods). We used dominance data from before April 1 of each season to calculate Elo ratings. After April, birds begin molting their crown plumage to prepare for migration to the breeding grounds, and their behaviour may alter due to changing physiology. We calculated dominance for the following numbers of individuals per year: 2014, N = 91; 2015, N = 94; 2016, N = 61.

Ethical Note

All methods were approved by the UCSC IACUC, the committee for animal research welfare and ethical treatment (Animal Welfare Permit Number Lyonb1808 to B. Lyon). All research and bird handling complied with Federal and California State regulations under permits to B. Lyon. All bird capturing and handling was done in good weather conditions (dry, not too cold). We minimized stress by keeping birds in single bird bags and handled birds as little as required. All personality trials were conducted between 800 hours and 1400 hours. Birds were kept for the minimum amount of time necessary to perform the personality trials and banding, generally released no longer than 2 hours after capture. Personality trials occurred by the order in which birds were caught, so any impact of stress should be random rather than producing any particular response pattern. We monitored birds for stress, looking for well-known signs such as crown feather erection or lack of responsiveness. All birds appeared to suffer no lasting stress after release and were seen behaving normally in the field afterward.

Statistical Methods

We calculated repeatability for the experimentally-measured behaviours across different time scales: within-season (within-year) and across multiple seasons (across-year). Following Nakagawa and Schielzeth (2010), we used the *rptR* package (version 0.9.22) to calculate all repeatability measures (Nakagawa and Schielzeth

2010; Stoffel et al. 2017). We report link-scale repeatability values, confidence intervals were calculated via bootstrapping (1000 iterations), and we report likelihood ratio test (LTR) P-values. Link-scale repeatability measures the consistency of an individual's behaviour relative to variation among all individuals in the population (Nakagawa and Schielzeth 2010). All numeric fixed effects in the models were scaled and zero-centered.

For our within-year repeatability calculations, we used repeated trials within 2014. We included single trials (i.e. birds measured just once) in the models along with the repeated trials (N = 25 repeats, N = 125 total), as this represents the amount of variation for all birds sampled that year (Nakagawa and Schielzeth 2010). Within-year repeatability modeling had individual identity as a random effect in Poisson distributed generalized linear mixed-models (GLMMs). We could not estimate repeatabilities for perch bouts and number of quadrants because models did not converge. Hence, we did not include these two behaviours in Figure 1.

We used within-year repeatability measures to determine which behaviors to include in our estimate of personality. As we only wanted to focus on consistent behaviors, we selected repeatable behaviors (R > 0.25) to then integrate into a PCA using all years of data. For any individuals with multiple trials within a season, we used only the first trial to avoid violating any assumptions of PCA that are skewed with repeated trials (Budaev 2010; Dingemanse and Wright 2020). We retained principal components (PCs) with an eigen score >1. All PC scores were scaled and zero-centered. We used the global loading scores to calculate individual PC scores for the duplicate trials in 2014. PCA analysis was conducted in the base R stats package using Singular Value Decomposition without rotation (R Core Team 2019). We found three PCs, but the number of vocalizations was the main component loading for PC 3, so we used the raw data instead of PC 3 (see details in Results and Table A1-A2).

We calculated across-year repeatability for personality behaviors following the same procedure as within-year repeatability. We included all single trials when calculating the repeatability to account for all variation present in the sampled population. We analyzed repeatability over four time periods: 2014 to 2015 ($N = 35$ repeats, $N = 148$ total), 2015 to 2016 ($N = 14$ repeats, $N = 118$ total), 2014 and 2016 ($N = 14$ repeats, $N = 169$ total), and birds present in all three years ($N = 9$ repeats, $N = 195$ total). We considered these four time period contrasts as each time scale provides a better understanding of how consistent the behaviours were over time, and whether any consistency depended on the specific years analyzed. Some of the time periods showed zero percent repeatabilities for several behaviours, but as was the case for some within-year repeatabilities, these are not true zeros; rather, the models did not converge (Figure 2).

To see if repeatability changed over time and across different years, we ran separate models for the three components of personality (PC 1, PC 2, and vocalizations). Each model included all years of data and had the repeatability of each response variable with time since first trial as a fixed effect and individual identity as a random effect. We used linear mixed models to predict PC 1 and 2, while the vocalization model was a Poisson GLMM ($N = 249$ total, $N = 195$ unique individuals). Time since first trial was in units of years: zero, one or two. Therefore, for an individual tested only in 2014, the value would be zero; if a bird was tested in 2014, 2015, and 2016, it would be zero in 2014, one in 2015, and two in 2016.

We determined each bird's dominance score via Elo rating. Elo rating calculates dominance scores based on the sequence of observed interactions between dyads, and awards points based on winning or losing the interaction. The amount of points awarded depends on the probability of each individual winning the interaction—e.g. an individual with a high score has a higher probability of winning an interaction against an individual with a low score and so gains fewer points than if an individual with a low score wins an interaction against a high-scoring individual. Each individual started with a baseline score of 1000. The parameter k, which determines the speed of points changing after each interaction, was set to 100. We followed methods from (Neumann and Kulik 2014) and calculated dominance scores with the *EloRating* package (version 0.46.11).

To investigate connections between personality and other social and morphological traits, we determined whether personality correlated with black and gold crown size, wing length, dominance score, sex, and age class. We made models for several time periods, first examining global patterns (all three years combined), then looking at individual years. We had included the day of the year as a factor but it had no effect, so we removed it from the models. Sample sizes for individual models are smaller than the total sample of birds because we did not have all measurements for all birds, so using all factors in the same model decreased the sample size due to non-overlapping data. The final sample sizes in the global personality correlation models were $N = 144$ total samples and $N = 114$ unique individuals, and by year; 2014: $N = 60$, 2015: $N = 42$, and 2016: $N = 42$. For the global models including all years, we used linear mixed effect models (package *lme4*, version 1.2-21) with individual identity as a random effect and the previous factors listed as fixed effects for personality PC's (Bates et al. 2014). We did not include year as a random effect as it accounted for almost no variation in the multi-year models. Reported R^2 values for all mixed effect models are marginal R^2, which show how much variation the fixed-effects account for in the model (Nakagawa and Schielzeth 2012). Vocalizations were modeled similarly to the other PC's, but with Poisson GLMMs. In separate models by year, we did not include individual as a random effect as we used one personality trial for each bird. We used linear models for the PC models in each year separately and reported adjusted R^2. We used GLMMs with Poisson distributions for vocalizations and report Nagelkerke's R^2. All non-categorical fixed effects were scaled and zero-centered in the models. We checked all models for heteroscedasticity by visual inspection and ensured that models had low collinearity by measuring variance inflation factors (VIF calculated with the *car* package, version 3.0-3), where VIF values were less than five for all models (Fox and Weisberg 2019). For all 2015 models, VIF values were elevated, so we removed the factor with the largest VIF value, wing length (for correlation matrices, see Table A3). After this removal, the model collinearity decreased, and all VIF values were less than five.

All statistical analysis was performed in R version 3.6.2 (Block et al. 2020; R Core Team 2019).

Results

Within-year repeatability (2014)

Six of the ten behaviours we measured in 2014 had >25% within-season repeatability (Figure 1). We used these six repeatable behaviours to define personality behaviors for golden-crowned sparrows for all years. These behaviours included hops, vocalizations, perch turns, perch bouts, escape test, and bag test. While these behaviours had high repeatability estimates, the confidence intervals were large so only three were statistically significant. The large confidence intervals are due to the limited sample size combined with non-normal distributions, which can be problematic for using bootstrapping to construct confidence intervals accurately. Additionally, bootstrapped confidence intervals are larger than more traditional conversions to Fisher's Z as those tend to underestimate the degree of confidence (Nakagawa and Schielzeth 2010). Hence, we mostly focus on the magnitude of the repeatability.

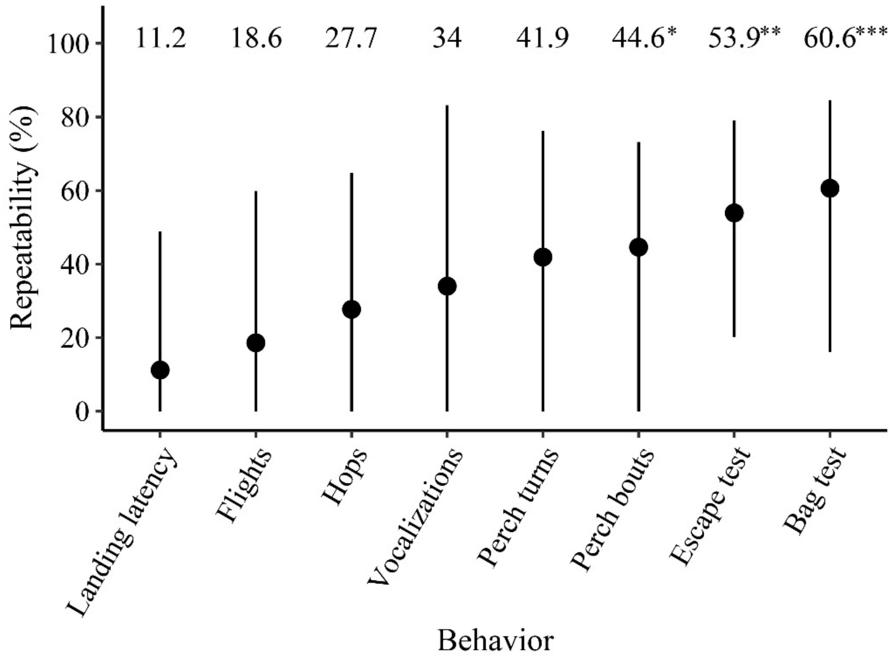


Figure 1. Within-year repeatability of golden-crowned sparrow behaviours during the 2014–2015 season. We dropped two behaviours, landing latency and flights, and used the six most repeatable behaviours (>25%) in a PCA to define golden-crowned sparrow personality. Error bars show 95% confidence intervals. Asterisks indicate the following LRT P-values: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Principal component summary of personality traits

We found three main principal components, which explained 75% of the variation: PC 1, an activity axis, PC 2, an escape response axis, and PC 3, a vocalization axis. PC 1 accounted for 39% of the overall variation in the behaviours we measured, PC 2 explained 19% of the variation, and PC 3 17% (Appendix Table A1). Principal Component one summarized movement and activity with the primary factor loadings of perch bouts, perch turns, and hops (Appendix Table A2). A higher PC 1 score represented increased activity and movement. Principal Component two's main factor loadings were escape time and bag test: as escape time increased, bag movements decreased. With a higher PC 2 score, the sparrows tended to stay still and stay put, while a lower PC 2 score meant that birds escaped the box more quickly and were more active in the bag (Table A2). Principal Component three was mainly comprised of how many times a bird vocalized (Table A2). As a single factor was the main factor loading, we used the raw vocalization behaviour for analysis instead of PC 3.

Across-year repeatability

We found that the individual behaviours and the three PCA behavioral measures were repeatable across years (Figure 2). We examined four different across-year comparisons: 2014–2015, 2015–2016, 2014–2015–2016, and 2014 and 2016 (i.e., no data from 2015). The comparisons thus include three different combinations of two seasons of samples (two with a two-year span and one with a three-year span) and one comparison with three years of samples. Some behaviours that were highly repeatable within one season showed both lower and higher repeatabilities over longer periods (Figure 2). Interestingly, the degree of repeatability within a season was unrelated to a behaviours' repeatability across years. For example, the bag test score was the most highly repeatable behaviour within one season (60.2%), yet never had similarly high across-year repeatability values (all time contrasts had <42% repeatability). Some of the other behaviour time-contrasts also had repeatability that varied considerably—e.g., vocalizations, which leapt from 32.8% in 2014–2015 to 79.5% in 2015–2016 (Figure 2).

We analyzed whether the length of time (in years) since the first trial affected repeatability. The amount of time from the first behavioural trial had no effect on repeatability, so the length of time between measurements did not influence behavioural consistency (PC 1: $\beta = 0.04$, $P = 0.76$, $R^2 = 0$, PC 2: $\beta = 0.09$, $P = 0.38$, $R^2 = 0.003$, Vocalizations: $\beta = 1.01$, $P = 0.96$, $R^2 = 0$). Additionally, time since the first trial accounted for very little to none of the variation in the models (see R^2 values above).

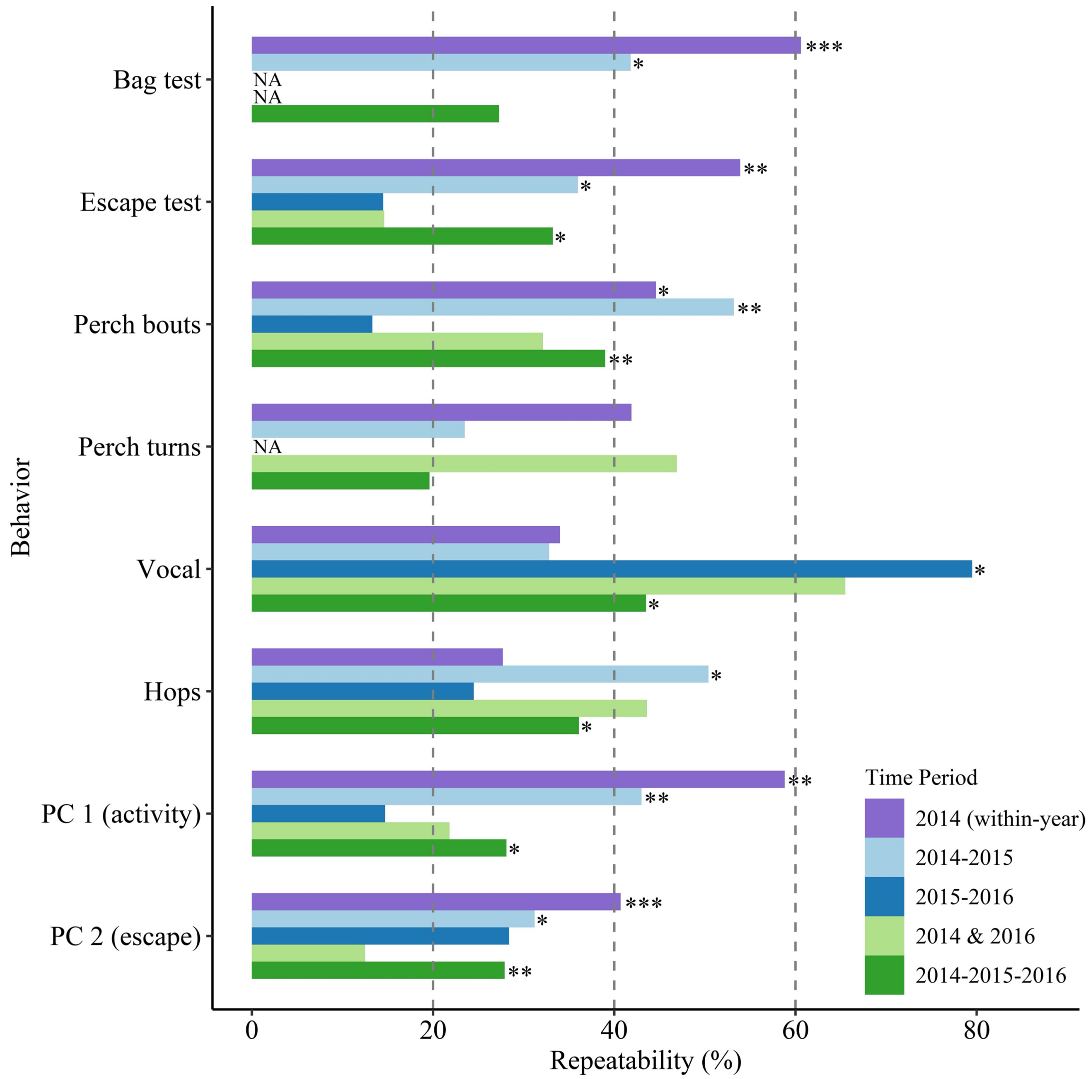


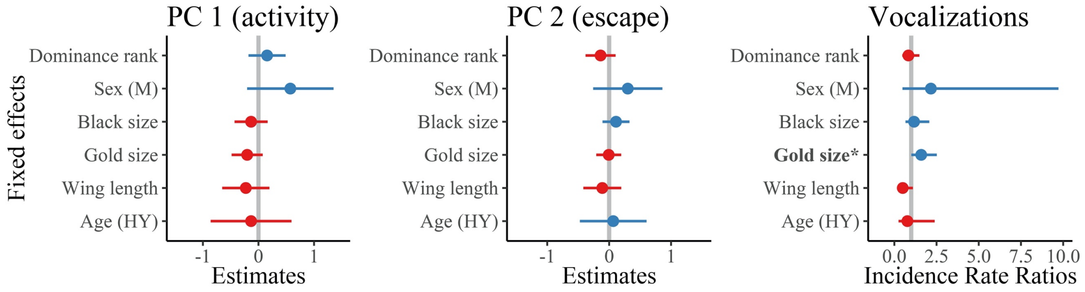
Figure 2. A comparison for the repeatability of behaviours covering within-year (2014) and across multiple years. For the long-term repeatability, we show all pairwise combinations of years. This comprises both raw behaviours (only considering behaviours with initial repeatability >25%) and PC 1 (activity axis) and PC 2 (escape axis). An NA indicates that repeatability estimates were not obtained because models with those behaviours failed to converge. Statistically significant repeatable behaviours are denoted by: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Personality correlates

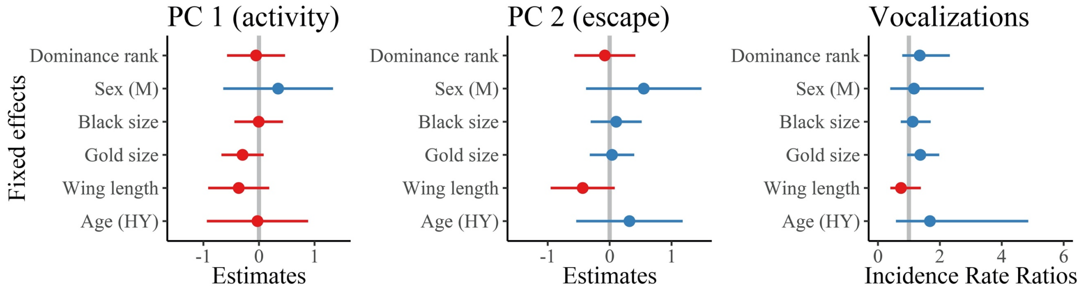
No traits correlated with PC 1 or PC 2 when examining all years together (PC 1: $R^2 = 0.042$, PC 2: $R^2 = 0.025$; Fig. 3a). Gold badge size increased somewhat with vocalizations, but this was a weak correlation as reflected in the low R^2 value ($\beta = 0.47$, SE = 0.23, $P = 0.05$, $R^2 = 0.056$; Fig. 3a). Given the considerable variation in the consistency of behaviours between years, we also examined each year separately. Similar to the global model, no traits correlated with personality in 2014 (PC 1: $R^2 = 0.033$; PC 2: $R^2 = 0$; vocalizations: $R^2 = 0.16$; Fig. 3b). In 2015, vocalizations increased with gold badge size ($\beta = 0.70$, SE = 0.27, $P = 0.010$, $R^2 = 0.416$; Fig. 3c), but none of the traits correlated with PC 1 or PC 2 (PC 1: $R^2 = 0$; PC 2: $R^2 = 0$; Fig. 3c). In 2016, males were more active than females (PC 1: $\beta = 2.12$, SE = 0.93, $P = 0.029$, $R^2 = 0.059$; Fig. 3d), and birds with longer wings vocalized less (vocalizations: $\beta = -1.03$, SE = 0.33, $P = 0.002$, $R^2 = 0.52$; Fig. 3D). However, in 2016 the model for PC 1 explained very little of the variation (low R^2), so we do not consider sex to be important in explaining the PC 1 axis of the birds' personalities.

Figure 3. Results from models showing the relationships between personality axes and other traits for all years: (A) 2014, 2015, 2016; (B) 2014; (C) 2015; (D) 2016. Blue indicates positive correlations (circles right of the horizontal line), and red indicates negative correlations (circles left of the horizontal line). Circles show the location of effect size values, and lines show 95% confidence intervals. Incidence rate ratios are back-transformed estimates to compare effect sizes to PC 1 (activity) and PC 2 (escape), as vocalization models were in a Poisson distribution. Statistically significant values as indicated: * $P<0.05$ ** $P<0.01$ *** $P<0.001$.

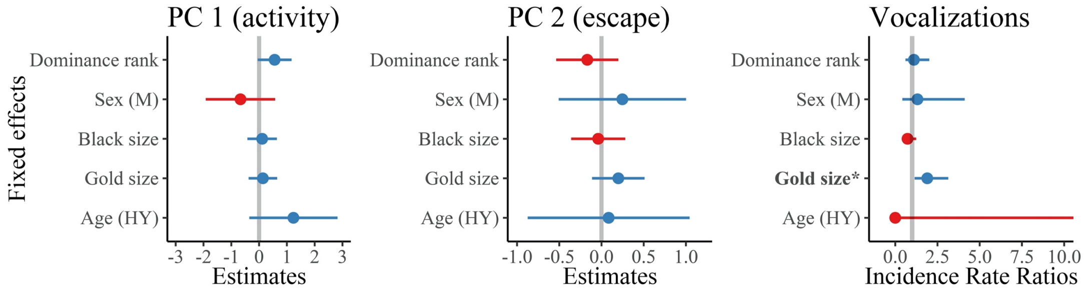
A. Global (2014, 2015, 2016)



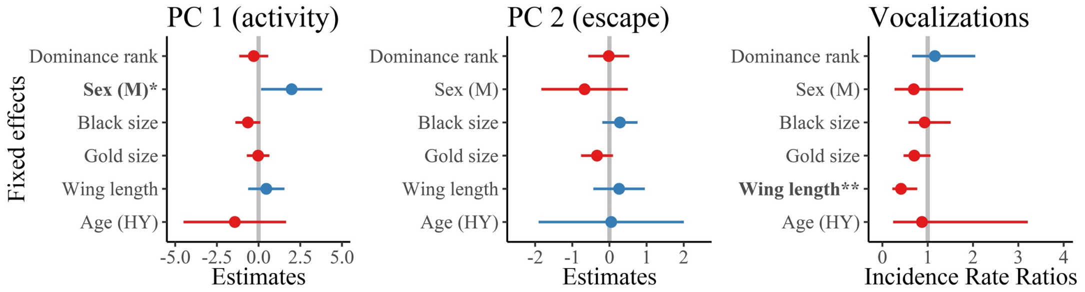
B. 2014



C. 2015



D. 2016



Discussion

Our experiments revealed that golden-crowned sparrows have highly repeatable behaviours—i.e., personalities—within a winter season. These behaviours also showed varying degrees of consistency over multiple years. However, these personalities did not show any strong correlations with dominance score, sex, or age, contrary to expectation if personality were connected to winter alternative behavioural strategies. Thus, these behavioural traits may represent a separate axis of variation among individuals important in migratory birds' winter ecology.

Two of the PC axes that resulted from condensing the top six most repeatable behaviours are similar to those found in other animal personality studies. Our first PC axis (PC 1), termed the ‘activity axis,' describes the movement level in the cage, which we considered to represent exploratory behaviour. Exploratory behaviours often align on a fast-slow exploration continuum, and they have been found to relate to foraging (Verbeek et al. 1994; Kurvers et al. 2009; Aplin et al. 2014; Patrick and Weimerskirch 2014; Tan et al. 2018) and risk-taking (van Oers et al. 2004; Garamszegi et al. 2008; Dammhahn and Almeling 2012; Cole and Quinn 2014). Our second PC axis (PC 2) summarizes escape response, with measures from the bag and escape tests correlating strongly. Both of these variables could be viewed in the context of predation risk; birds that escape more quickly or show more movements in the bird bags may be more reactive and quicker to flee from predators. Escape response could also be tied to a stress-response—birds with different personalities respond differently to stress and predation (and often the two are intertwined). This escape response could be seen as boldness and fall along the ‘shy-bold’ continuum, a common spectrum of individual differences in animal behaviour across taxa. Additionally, escape response has been found to correlate with a genetic polymorphism in blue tits (*Cyanistes caeruleus*), suggesting a genetic basis (Kluen et al. 2012). The axes of fast-slow and shy-bold can correlate with each other (e.g., exploration and neophobia), forming 'behavioural types’ in some systems (David et al. 2011; Montiglio et al. 2012; Hall et al. 2015). However, as these behaviours were on orthogonal PC axes, they were clearly not correlated similar to other studies (Herborn et al. 2010; David et al. 2011; Favati et al. 2014).

For vocalizations, we used the raw data rather than a PC axis because the third PC axis (PC 3) consisted mostly of the number of non-song vocalizations during cage exploration. Studies rarely include non-song vocalizations in personality assays, but we found they were sufficiently repeatable within-year to meet our criteria for personality behaviour. One other study examined vocalizations in the non-breeding season and found that black-capped chickadees (*Poecile atricapillus*) had repeatable songs and vocalizations which correlated with exploration in response to a stressful situation, but not during a control assessment (Guillette and Sturdy 2011). More studies have focused on song response during breeding; for example, more exploratory great tits responded differently to simulated territory intrusions than non-explorative, and the direction of response varied in different populations (Amy et al. 2010; Naguib et al. 2010; Jacobs et al. 2014). Vocalizations during winter can serve different functions than for territory defense and mate attraction (Sorensen et al.

2016). Golden-crowned sparrow non-song winter vocalizations could have several functions: maintaining contact and cohesion within a flock, establishing social dominance, or functioning as alarm calls. If calls are used as warnings, we may be detecting vocalizations as individually consistent responses to a stressful situation, whether that is being in a new environment like a cage, or needing to escape from a predator.

Our study was unusual for the length of time over which we assessed personality, as we measured behaviour repeatability both within a year and up to three years. Golden-crowned sparrows live for approximately 2-3 years (Norment et al. 2020), so measuring repeatability over three years covers most of their lifespan. Less than 10% of previous studies examined repeatability over more than one year (Bell et al. 2009). The high repeatabilities we observed within years indicate stable personalities in golden-crowned sparrows within a single winter season. Similar patterns of high within-year (or shorter-term) repeatability are common in personality studies (Sih et al. 2004; Bell 2007; Sih et al. 2015). However, sparrow personalities were often repeatable for up to three years and, importantly, the strength of repeatability measures were unrelated to the time between the first and second assessments. The fact that repeatabilities did not diminish with time interval is surprising as multiple studies have found that consistency tends to decrease over longer periods for many behaviours (see Bell et al. 2009 for a review). Additionally, the time span over which repeatability is maintained can vary substantially among behaviors (Bell et al. 2009). For example, David et al. (2012) found that exploratory behaviour in captive zebra finches (*Taeniopygia guttata*) was repeatable over both short (~1 week) and moderate (~ 7 month) timespans, but struggling behaviour was only repeatable over the short-term.

On average, golden-crowned sparrows have consistent personality traits during winter for much of their lives, but the variability present across years indicates that personality behaviors may change in response to external factors such as the physical or social environment. For instance, the behavior assessed with the bag test showed very high within-season repeatability with lower repeatability over multiple years, which could reflect changes due to years having different environmental pressures. In some species, individuals' personalities change depending on the season (Carter et al. 2012), while individuals' in other species react to changes in the environment (Herborn et al. 2014; Nicolaus et al. 2016) or social situations (Marchetti and Drent 2000; van Oers et al. 2005). One mechanism for behavioral plasticity is personality types varying in their response to environmental factors. For example, more exploratory individuals could have more plastic responses (Dall et al. 2004; Dingemanse et al. 2010; Sih et al. 2015). In our study, the magnitude of repeatability varied across years and behaviours, so personality behaviours could be changing in reaction to external factors. Some may be responding to year-to-year changes in the environment, while others could be responding to predation pressure or climate. This pattern of behavioural change is similar to the pattern of plumage trait changes in lark buntings (*Calamospiza melanocorys*), where male traits can change asynchronously across years, potentially due to a combination of local and broad factors (Chaine and

Lyon 2015). One puzzling pattern of change was that several behaviours had higher consistency across years than within a season. We do not have a biological explanation for this, and it could be an artifact of different sample sizes across time scales.

Altering external conditions could differentially affect the fitness of individuals based on their personality or experience level (Dammhahn and Almeling 2012). For example, in North American red squirrels (*Tamiasciurus hudsonicus*), the associations between different personality traits and lifetime offspring production for males depended on whether or not they experienced a year with a strong resource pulse (Haines et al. 2020). Recognizing behavioural changes over time and contexts will help us make sense of the temporal patterns of consistency versus flexibility. Indeed, understanding how personality and/or fitness payoffs change over time can help future studies shed more light on how selection maintains personalities (Dingemanse and de Goede 2004; Dingemanse et al. 2012; Mathot et al. 2012; Sih et al. 2015).

We focused on personality in the context of sociality as previous research suggested that sparrows might have alternative wintering strategies related to dominance and plumage badges of status (Rohwer and Ewald 1981; Chaine et al. 2011; Chaine et al. 2013). However, our study did not provide support for this idea based on the personality traits we measured. Neither activity (PC 1) nor escape behaviour (PC 2) correlated with any social or morphological traits we measured. Although the vocalization axis did increase with gold badge size in 2015 and decrease with wing length in 2016, that these patterns were limited to single years suggest that they are not robust. While we also observed a weak relationship between vocalizations and gold badge size in the global model, this pattern was driven by the 2015 relationship. Thus, the three axes of personality we identified, seem to be independent of variation in morphology or traits related to dominance.

In golden-crowned sparrows, the mechanism for dominance can change depending on the social context, which may require more flexible behavioural responses (Chaine et al. 2018), potentially explaining the lack of correlation between personality and dominance. Personality has correlated with dominance in a number of species (Dingemanse and de Goede 2004; Kurvers et al. 2009; David et al. 2011), but the patterns of correlation vary across species, even closely related ones. For example, personality predicted dominance in mountain chickadees (*Poecile gambeli*) (Fox et al. 2009), but not in black-capped chickadees (Devost et al. 2016). One possible explanation for the variable connection between personality and dominance is that the patterns and mechanisms of social dominance likely depend on the specific details of social organization. Both dominance and social organization varies among species and can even change within species across space and time.

A valuable next step is determining whether personality traits in winter could be relevant to other contexts necessary for winter survival that we did not assess, such as foraging, risk-response, or other environmental factors. The small-bird-in-winter paradigm (Roth et al 2006) stresses the critical importance of the trade-off between survival and foraging in winter (Lima 1986; McNamara and Houston 1987; Houston et al. 1993). Bird-eating raptors are common at our study site and are likely important drivers of the sparrows' winter ecology and behaviour. While the small-bird-in-winter paradigm focuses on group size and foraging behaviour as key aspects of survival, variation among individuals in these trade-offs could select for variation in how the individuals react to foraging and predation situations that might be aligned with personality traits such as boldness. Along with different risk-responses, personality measures have predicted variation in foraging behaviour (Wilson and Coleman 1993; Wilson and McLaughlin 2007; Kurvers et al. 2009). For example, black-browed albatross (*Thalassarche melanophris*) individuals varied in foraging patterns based on personality type, and personality correlated with reproductive success in some years depending on the quality and availability of food (Patrick and Weimerskirch 2014). The trade-offs between survival and foraging in winter could be a factor maintaining adaptive variation in individual behaviour.

Conclusion

Golden-crowned sparrows have personality traits in winter, but these consistent behaviors are independent of the morphological and social traits we measured. We did not find evidence connecting personality to stable alternative winter strategies, as the degree of repeatability varied across years. Whether birds are migratory or resident could have a considerable impact on the links between personality and other traits, and selection on personalities in migratory birds may occur during the breeding season, rather than in winter. Not only are migrants undergoing seasonal change but also large geographic change. Therefore, migrant bird behaviors may face different selection pressures than resident bird behaviors. Golden-crowned sparrow personality traits may be under selection during breeding season, or in other winter contexts like foraging or predation avoidance.

Chapter 2

Older individuals help maintain distinct community structures in a flocking bird

Abstract

Social connections are a key part of a gregarious animal's life. Individual interactions are the basis of groups and scale up to create the social environment. The social environment can have many effects, from increasing an individual's fitness to increasing disease spread. There can be large amounts of variation in how individuals within a social group interact, and learning which traits correlate with individual social patterns can help us understand what drives social organization within groups. Here, we study the golden-crowned sparrow (*Zonotrichia atricapilla*), a migratory bird that forms social groups in the winter, in order to assess the behavioral and morphological traits that predict individual social network measures. Previous work in this system found that the sparrows have dominance relationships and distinct groups, and when they return to their wintering site, they almost always return to the same group and associate with the same individuals. Consistent with prior research, the sparrows in this study continued to have discrete groups in each year. Further, our study found that social positions were repeatable over time, older and smaller birds had more connections and social position was independent of dominance, sex, and personality. As birds return to the same wintering site, they not only grow stronger associations with the same individuals but increase the number of connections over time. Older birds have experience in the environment and can exploit known resources and transmit this information to newer community members. Additionally, older birds could gain benefits from more connections by gaining access to information about new resources. We show how older animals likely play an essential role in maintaining community structure over time due to their increasing connections across years.

Keywords: age, animal groups, communities, dominance, golden-crowned sparrow, personality, repeatability, social network measures, social organization, social position

Introduction

Individual interactions form the basis for how groups are organized (Alexander 1974; Hinde 1976). Conversely, the structure of social groups can have effects on individuals' fitness, and the feedback between social structure and individual traits can shape selection on both (Kohn 2017; Snijders and Naguib 2017; Cantor et al. 2021). We have long known that ecological factors such as resource distribution and predation risk can drive social structure (Alexander 1974; Lima 1987; Chapman et al. 1995; Hatchwell 2009). Further examining social groups at a finer scale, the level of individual social interactions, deepens our understanding of social organization as we learn what individual traits may correlate with sociality (Pinter-Wollman et al. 2014; Silk et al. 2014).

Individuals can differ in the way they socialize and, as a result, their relationships in groups can vary widely (Hinde 1976; Aureli et al. 2008). These differences in an individual's social behavior, or an individual's social position, are the result of interactions with others (Wilson et al. 2012). These interactions can be direct and indirect, and the dynamics of the social environment are based on individual interactions which can, in turn, be influenced by feedback from the social environment (Krause et al. 2010; Pinter-Wollman et al. 2014). An individual's social preferences can shape overall group structure. For example, great tits (*Parsus major*) grouped by age and with a relatively even sex ratio, and juvenile females formed larger groups while adult males were in smaller ones (Farine et al. 2015). Differences in how bold and shy three-spined stickleback (*Gasterosteus aculaeatus*) associated shaped their groups, as shy fish had stronger connections and preferred to shoal in smaller groups, and bold fish associated more evenly with group members (Pike et al. 2008). These cases indicate how variation in social behavior may depend on certain characteristics and traits.

An organism's life-history patterns can integrally shape social connections (Shizuka and Johnson 2019). Traits that affect an individual's life-history strategy, such as dominance, sex, size, or age, may explain the variability typically observed in social associations. Finding correlations between phenotypic traits and social position can explain some of the variation found in different social behaviors within a species (Whitehead 2008). Attributes like dominance and sex may affect sociality and life history patterns—for example, in baboons (*Papio cynocephalus*), adult females that are more socially dominant can reproduce earlier (Alberts 2018). Sex can also shape types of sociality, as found in many cetacean societies where community structure is often centered around lineages of close female relatives (Rendell et al. 2019).

A key question is if dominance determines group organization. For example, age could influence how individuals group together, and dominance contests could happen within those groups. Conversely, dominance interactions could form the basis for association patterns based on how dominants and subordinates interact and whether these interactions are aggressive or cooperative (de Waal 1986). Rohwer (1975) proposed several theories for different interactions between dominant and subordinate individuals, where badges of status or status signals indicate dominance. In the first scenario, 'likes-will-fight' whereby dominance contests are more likely among similarly ranked animals. In the second 'despotic' scenario, dominant individuals typically face down subordinates (Rohwer 1975). Dominance and badges of status can influence an individual's patterns of social interaction, as shown in the despotic-interactions in Harris' sparrows (*Zonotrichia querula*), and in a study that showed plumage ornamentation in male house finches (*Haemorhous mexicanus*) influenced how frequently they changed social groups (Rohwer 1975; Oh and Badyaev 2010).

Animal personality shows particular promise for connecting with variation found in individual sociality (Krause et al. 2010). Studies of animal personality, or consistent behaviors within an individual over contexts and time, focus on why individual behavior may be consistent yet vary within the population (Bell 2007).

How an individual interacts with others may be influenced by its personality, and personality and sociality could be under similar selective pressures in the social environment (Krause et al. 2010). Different personality types could occupy certain social positions, and both social position and personality have been found to be consistent and, in some cases, heritable (van Oers et al. 2004; Lea et al. 2010). Correlations have been found between personality and sociality in a number of taxa such as birds, fishes, and mammals (Pike et al. 2008; Croft et al. 2009; Aplin et al. 2013; Chock et al. 2017; Alberts 2018).

Social network analysis is a powerful tool to quantify and explore individual social relationships, and it does so by measuring interactions between individuals (Krause et al. 2009). Network measures of social position are extremely useful to quantify social patterns, but they do not necessarily explain them. Finding patterns where well-understood traits correlate with variation in individual sociality can help us understand why individual sociality varies in the first place. Traits like dominance, personality, sex, or age may correlate with social network measures and focus on what drives social structure. For example, female brown-headed cowbirds (*Molothrus ater*) preferred to associate with known females (Kohn et al. 2015). In contrast, males brown-headed cowbirds changed between associating with familiar males and interacting with new ones, suggesting that female social preferences help maintain group stability (Kohn et al. 2015). Social network analysis allows for examining animal personalities in the context of the whole population, such as if animals with similar personalities group together (Krause et al. 2010; Aplin et al. 2013). Some social network measures can be consistent within individuals over time and contexts (Jacoby et al. 2014; Blaszczyk 2018; Plaza et al. 2020). However, few studies have connected consistent network measures to traditional personality measures (see Blumstein et al. 2012, Aplin et al. 2013, Aplin et al. 2015). It is worth noting that even when finding links between social position and other traits, it can be challenging to understand the direction of causality as factors that affect grouping patterns could also affect behaviors like dominance or personality.

Here we ask if behavioral and morphological traits in migratory golden-crowned sparrows (*Zonotrichia atricapilla*) correlate with an individual's social network measures. Golden-crowned sparrows form foraging flocks in the winter (Shizuka et al. 2014). Previous research discovered that these birds have fission-fusion flock dynamics that derive from stable communities of 10–30 birds with high site fidelity across winters (Shizuka et al. 2014). Additionally, these communities are based on individual preference for social partners more than simply the result of overlapping space use (Shizuka et al. 2014). When sparrows return to the study site, they almost always return to the same community and form associations with the same birds, unrelated to kinship (Shizuka et al. 2014; Arnberg et al. 2015). As birds return across multiple seasons, they become more central parts of their communities (Shizuka et al. 2014), so we might expect to find that older birds have stronger associations and potentially more social connections as well.

Golden-crowned sparrows have several social and morphological traits that vary among individuals that could drive their social patterns. The sparrows have dominance relationships where badges of status can determine the outcomes of contests over food (Chaine et al. 2011). The badges consist of a central gold plumage patch on the top of a sparrow's head (the 'crown') surrounded by two black stripes. The size of these plumage patches varies considerably in winter, in contrast to low variation during the summer (Chaine et al. 2011). Each patch independently influences dominance, in somewhat different ways, confirming that each patch functions independently as a badge of status (Chaine et al. 2011; Chaine et al. 2013). The social situation determines how these badges are used: experimentally manipulating badges affected the outcome of contests among unfamiliar birds that had not previously interacted but had no effect on familiar birds' competitive interactions from the same social group (Chaine et al. 2018). Golden-crowned sparrows also have personalities that are repeatable for up to three years, which spans much of their life, and these personalities were independent of dominance and badge size (Block et al. in press). Additionally, sparrows that engaged in dominance contests at feeders (such as chases or fights) tended to flock together (Shizuka et al. in prep). One way dominance could influence association patterns is if dominant individuals interact with more birds than subordinates to maintain their dominance status, hence having more connections.

The multiple complex and variable aspects of the sparrows' social lives leads us to ask how dominance and other traits may connect to individual sociality. Our first question is how an individual bird's traits may correlate with its social position. Second, we ask if birds with similar personalities flock together. Third, we ask if individual social position is consistent over time. We assessed the relationship between several key traits—age, badge size, dominance score, mass, personality, sex—and individual-level social network measures. To address these questions, we used several social network measures: the number of associations (degree), the strength of these associations within a community (within-community strength), and the number of close associates (effective degree).

Methods

Field Methods

We studied a wintering population of golden-crowned sparrows at the University of California Santa Cruz (UCSC) Arboretum. In this long-term study (started in 2003), we study the sparrows during their non-breeding season from September through the end of April. As each field season covers two calendar years, we refer to the season by the year it starts. This study includes three field seasons: 2014, 2015, and 2016. We caught 285 unique sparrows over three seasons with baited Potter traps and mist nets. Each bird was given a USFWS metal band and a set of unique color bands to enable individual identification in the field. During banding, we measured body mass (g), tarsus length (mm), culmen size (mm), flattened wing cord (mm), and collected a blood sample from the ulnar vein for sexing. We followed methods from Chaine et al. (2011), and birds were sexed by amplifying the CHD gene on the Z and W sex chromosomes (Griffiths et al. 1998). To measure the plumage traits that function as badges of status, we took digital photographs of the sparrows' crowns and extracted the size of the black and gold patches (mm^2) using techniques established by Chaine et al. (2011).

We gathered two types of data from field observations: flocking data and dominance data. Throughout the season, we observed which individuals flocked together in short-term flocks and the location of each flock (using a photo grid map with $10m^2$ cells) and used these flocking observations to construct social networks. Golden-crowned sparrows form fission-fusion flocks that are subsets of larger communities (Shizuka et al. 2014). We gathered data on free-ranging flocks and did not bait feeding stations during flock observations. On separate days, we collected dominance data at long term feeding stations baited with millet seed on the ground to attract sparrows. We scored interactions between individuals at these food piles and based the winner and loser of dyads on fights, chases, supplants, and avoidance, following methods from Chaine et al. (2011).

Behavioral trials for personality traits took place in outdoor aviaries (1.3 $meter^3$) along with a 'bag test' and an 'escape test.' The bag test was done before banding: each bird was placed in a bird bag, videotaped for one minute, and observers later counted the number of times a bird moved distinctly in the bag in the video (Montiglio et al. 2012). Each five-minute aviary trial was videotaped with no observer present and the following behaviors were extracted afterwards: number of 180° turns on a perch (perch turns), number of times a bird used a perch (perch bouts), and number of hops in two minutes. The escape test occurred after the aviary trial and measured how long the bird took to escape from a cardboard box. Each bird was placed in a box (22.86cm by 31.12cm by 24.13cm) with a door (12.7cm by 12.7cm) on the ground, and a hidden observer opened the door after the bird acclimated to the box for one minute (Sasaki et al. 2018). For further detail about personality tests and results, see in Block et al. (in press).

This research was done under UCSC IACUC approval (Animal Welfare Permit Number Lyonb1808 to B. Lyon) plus state and federal permits to B. Lyon for all bird capturing and handling.

Statistical methods

We calculated birds' personality scores by distilling five repeatable behaviors (hops, perch turns, perch bouts, escape test, and bag test) into two main Principal Components (PCs) using Principal Components Analysis (Block et al. in press). All behaviors had > 25% repeatability within one field season (Block et al. in press). Personality PC 1 mainly represented hops, perch turns, and perch bouts, and a higher PC 1 showed higher levels of activity. Personality PC 2 represented the escape and bag tests. Individuals with a faster escape time were more active in the bag test, so birds with a larger PC 2 score had a quicker escape response (Block et al. in press).

Dominance was measured with Elo rating, which is a sequential method of calculating dominance scores for individuals (Neumann et al. 2011; Sánchez-Tójar et al. 2017). We calculated individual bird's Elo scores with data up to March 30, via the package *AniDom* (Farine and Sánchez-Tójar 2019). Each bird started with an initial score of zero, and wins and loses were calculated from fights, chases, supplants, and avoids. The scores were evaluated in the order of the date when they occurred, and the parameter K (set to 200) determined how quickly the scores changed after each encounter. We had dominance scores for 195 unique birds with the following numbers of individuals in each year—2014 $N = 111$; 2015 $N = 119$; 2016 $N = 74$.

We built a social network for each season of golden-crowned sparrow flocking data following the methods from Shizuka et al. (2014). We used flocking data from September through March 30; in April, closer to migration, the sparrows change their behavior and social interactions. We excluded birds first banded in a given year and any individuals seen less than three times to avoid transient birds. We built the networks using the *asnipe* (Farine 2013) and *igraph* (Csardi and Nepusz 2006) R packages. Every network is made up of 'nodes,' or individuals, and 'edges,' the lines connecting pairs of individuals (Croft et al. 2008; Krause et al. 2015). Here, edges are weighted by how frequently a pair of birds are seen together, based on a Simple-ratio index that corrects for each bird's total sightings (Cairns and Schwager 1987). The Simple-ratio index ranges from zero to one, where zero means birds were never seen together, and one means that birds were together each time they were sighted (Cairns and Schwager 1987). We used the 'netcarto' function from *rnetcarto* (Doulcier and Stouffer 2015) with a simulated annealing method for determining community structure, assigning nodes to communities, and measuring within-community node strength (z-score: Guimerá and Amaral 2005). Modularity measures how discretely a network is grouped into communities. Communities are best partitioned when the highest proportions of edges fall within a community rather than between individuals in different groups (Clauset et al. 2004). Hence, group partitioning is most accurate with a maximum modularity.

We calculated three social network centrality measures to quantify individual social patterns: degree, within-community node strength, and effective degree. Degree is the number of direct connections to other individuals (Wey et al. 2008). Within-community node strength (hereafter called ‘within-community strength’) focuses on individuals within one community, sums all edge weights for each individual, then normalizes the score (Guimerá and Amaral 2005; Doulcier and Stouffer 2015). Each score is normalized by the distribution of scores in the community, so results are comparable between birds in different communities (Guimerá and Amaral 2005). Effective degree is a metric proposed by McDonald and Hobson (2018), which reveals how many others an individual associates with strongly. It also takes into account the variance in the strength of associations (edge weights) for an individual, so if all the edge weights are identical, effective degree would have the same value as degree (McDonald and Hobson 2018). For example, if an individual associated with 10 others but spent most of its time with one other individual, its effective degree would be close to one. If an individual associated with 10 others relatively equally, its effective degree would be closer to 10. We determined social network measures for 157 unique birds, with the following numbers of individuals each year: 2014 $N = 79$; 2015 $N = 85$; 2016 $N = 67$.

We built linear mixed-effects models (package *lme4*) to evaluate which behavioral and morphological variables correlated with degree, within-community strength, and effective degree (Bates et al. 2015). We asked if dominance, badge size, personality, age, and sex correlated with the three centrality measures in a global analysis of all three years of data, as well as analyses of each year separately. In the global models, we assigned individual and year as random effects, except for the edge strength global model, where we removed year as it accounted for almost no variation as a random effect. We report marginal R^2 for the global models, which estimates the variance explained by fixed effects (Nakagawa and Schielzeth 2012). Globally, we had a sample size of 129 birds with 106 unique individuals (all repeated birds were across-year returnees). We had the following numbers of individual birds each year: 2014 $N = 48$; 2015 $N = 41$; 2016 $N = 40$. Each model includes only individuals with complete sampling of the factors included. All models were checked for heteroscedasticity (by visual inspection), and all variables in the models had variance inflation factors less than five, ensuring low collinearity.

We also asked if associations between individuals were assorted based on personality. We used the package *assortnet* to calculate assortment scores, which measure a correlation between an individual's phenotype and those of its associates (Farine 2016). Positive assortment values mean that more similar personality scores group together, while negative assortment values tend not to clump together. To measure if the assortment values were significant, we compared the empirical assortment score against a null distribution based on node-label permutations. To conduct the node-label permutations, we kept the observed network and randomly resampled the personality scores without replacement. Then, we recalculated the assortment value with personalities randomized in the network. We iterated this process 10,000 times to generate a null model distribution. We calculated the proportion of times the random assortment value was greater than or equal to the actual assortment value to get *P*-values.

To be able compare the stability of social metrics with personality, we tested the consistency of individual social metrics. We measured the repeatability of individual social network metrics with linear mixed-effect models in the *rptR* package (Nakagawa and Schielzeth 2010; Stoffel et al. 2017). We had *N* = 74 birds with repeated trials; some birds had network measures across two years and some across all three years of data. We included individual and year as random effects. The social networks had different numbers of birds each year, so including year controlled for this variation. Within-community strength was normalized by the size of the community, so this measure was already comparable across years. We used link-scale repeatability, which measured how consistent individuals were compared with the distribution of variability in the other individuals present. All individual network measures were included in this analysis to calculate the variance most accurately. We report *P*-values from likelihood-ratio testing (LRT) and confidence intervals from bootstrapping (1000 permutations).

All statistical analysis was performed in R version 4.0.2 (R Core Team 2020).

Results

In all three years, the golden-crowned sparrows were organized into several distinct communities within each social network. While most animal social networks are non-random, the types of structures within populations can vary widely, with different levels of stability present (Aureli et al. 2008; Papageorgiou and Farine 2021). The sparrows formed four communities in 2014 and 2015, and three in 2016 (Figure 1). We had 79 birds in the 2014 network with the following numbers of birds in each community: 7, 20, 21, 31). For the 2015 network, we had 85 individuals (community breakdown: 14, 22, 23, 26). In 2016, there were 67 birds in the network (community breakdown: 18, 24, 25). Individuals varied in their social interactions; for example, degree ranged from three to 61 (mean 33.4, SD 12.9; Figure 1). We found maximum modularity, Q_{max}, for the social networks in each year: 2014 $Q_{max} = 0.45$; 2015 $Q_{max} = 0.46$; 2016 $Q_{max} = 0.37$. These were similar to modularity values reported in Shizuka et al. (2014) for three other years (2009-2011), which were all significantly different from null modularity values generated from simulations with randomized flocks.

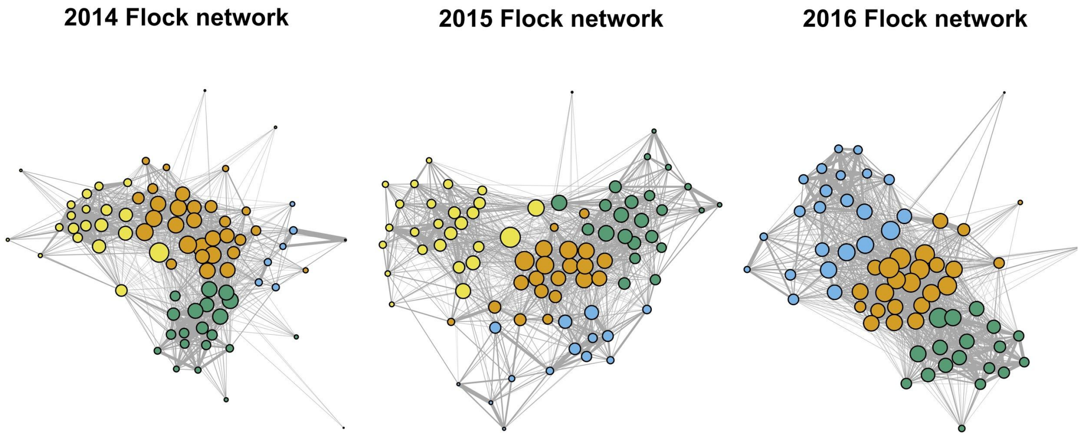
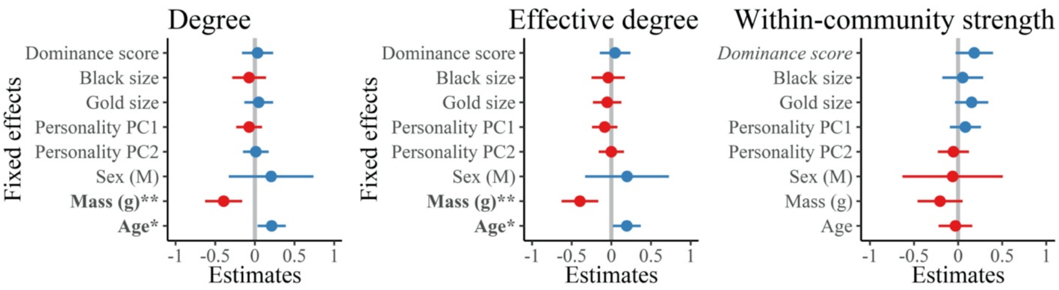


Figure 1. Golden-crowned sparrow social networks for each year of the study, with each community of birds shown in a different color. A circle represents an individual bird, and the size is weighted by degree, displaying a wide range of variation. Lines connecting individuals are the weighted edges, so wider lines show stronger associations. Node placement is not spatially explicit but based on a force-directed layout from the igraph package where nodes are closer together when they are more strongly associated.

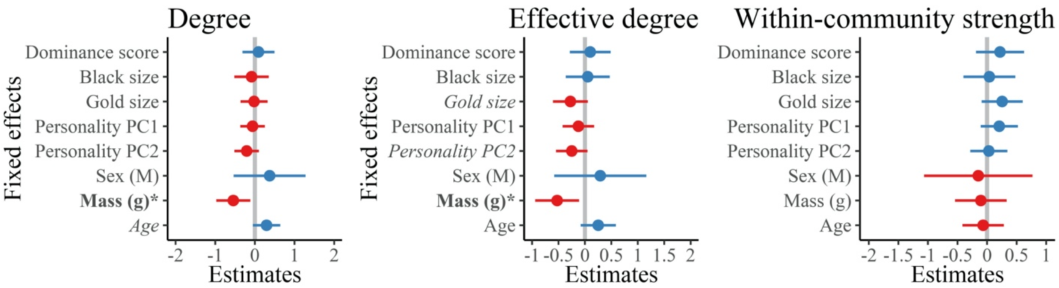
In our global (all years) correlations with centrality social measures, degree increased with age ($t = 2.32$, $P = 0.02$) but decreased with mass ($t = -3.28$, $P = 0.001$; $R^2 = 0.11$; Figure 2A). Similar to degree, birds with larger effective degrees had smaller masses ($t = -3.35$, $P = 0.001$) and were older ($t = 2.17$, $P = 0.03$; $R^2 = 0.12$; Appendix 2 Table S1). Within-community strength did not correlate with any factors, but it showed a tendency to increase with dominance ($t = 1.70$, $P = 0.09$; $R^2 = 0.07$).

The analysis of individual years showed some variation not present in the global model (Figure 2). Smaller birds had larger degrees and effective degrees in 2014 and 2015 (Appendix 2 Table S2, S3). No traits predicted within-community strength in any year (Figure 2, Appendix 2 Table S2-S4). In 2016, no factors correlated with degree ($R^2 = 0$), effective degree ($R^2 = 0$), or within-community strength ($R^2 = 0.05$), and the factors accounted for very little of the overall variation in each social network measure (Appendix 2 Table S3). The effect of age on degree and effective degree was detected in the global model but was not present in the analysis for each year (Figure 2).

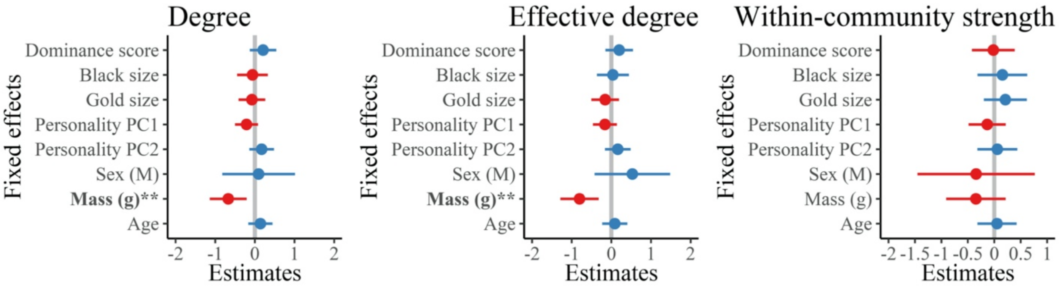
A. Global (2014, 2015, 2016)



B. 2014



C. 2015



D. 2016

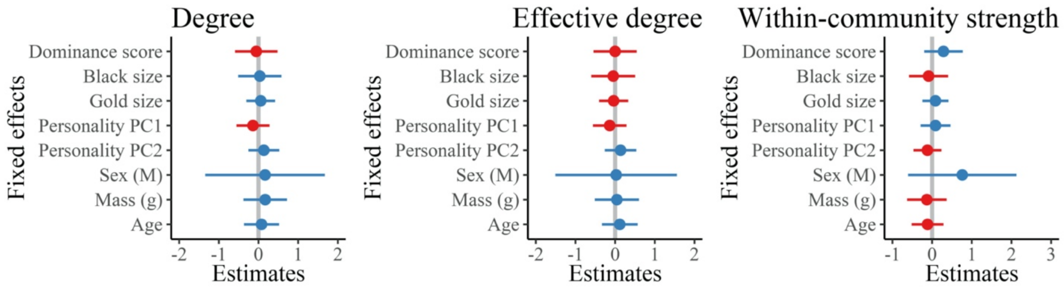


Figure 2. Plots for individual social network measures showing the effect sizes of traits for all social network measures in the following years: (A) Global (2014, 2015, 2016), (B) 2014, (C) 2015, and (D) 2016. Blue values right of the central line show positive correlations, and red values left of the central line show negative correlations, bars are 95% confidence intervals, and all effect sizes are normalized. Any significant correlations have bold labels, italics indicates a trend, and levels of significances are show by asterisks: * P < 0.05, ** P <0.01, *** P <0.001.

In two of the years, sparrow communities assorted partially by personality, so birds with more similar personality scores were more likely to be seen together (Figure 3). Personality PC 2 had positive assortment in 2015 (assortment value = 0.073, $P = 0.048$; expected mean = -0.024 ± 0.001; Figure 3B) and personality PC 1 showed positive assortment in 2016 (assortment value = 0.013, $P = 0.03$, expected mean = -0.024 ± 0.0007; Figure 3C).

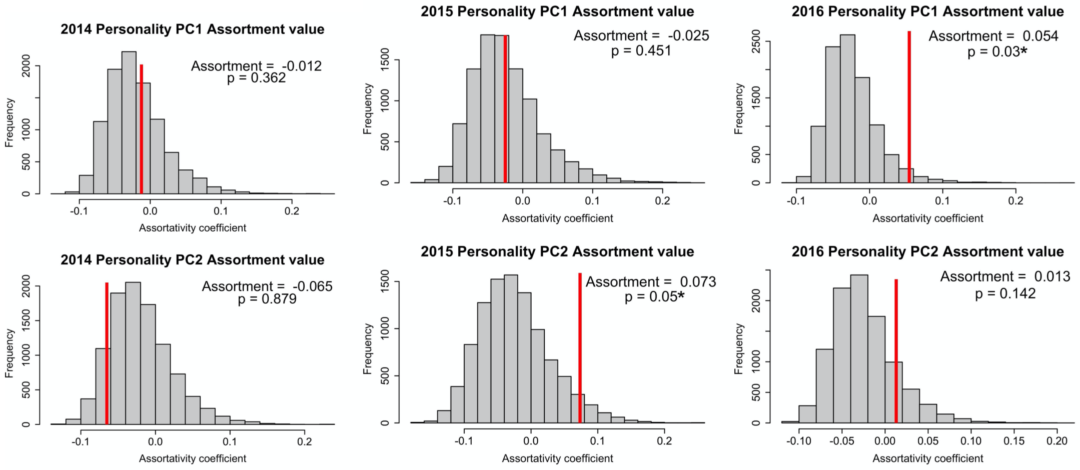


Figure 3. Null and observed personality assortment values for personality PC 1 (top row) and PC 2 (bottom row) each year. The vertical red line marks the observed assortment value for each personality measure each year, while the histogram shows a null distribution of expected assortment values when personality score is randomized within each community. Personality assortment values measure how similar an individual's personality is to that of its associates. A positive value means that more similar personality types group together.

All three social network metrics for individual birds were significantly repeatable over the three year time span of the study. The two degree measures were strongly repeatable, while the repeatability of within-community strength was more modest (Figure 4).

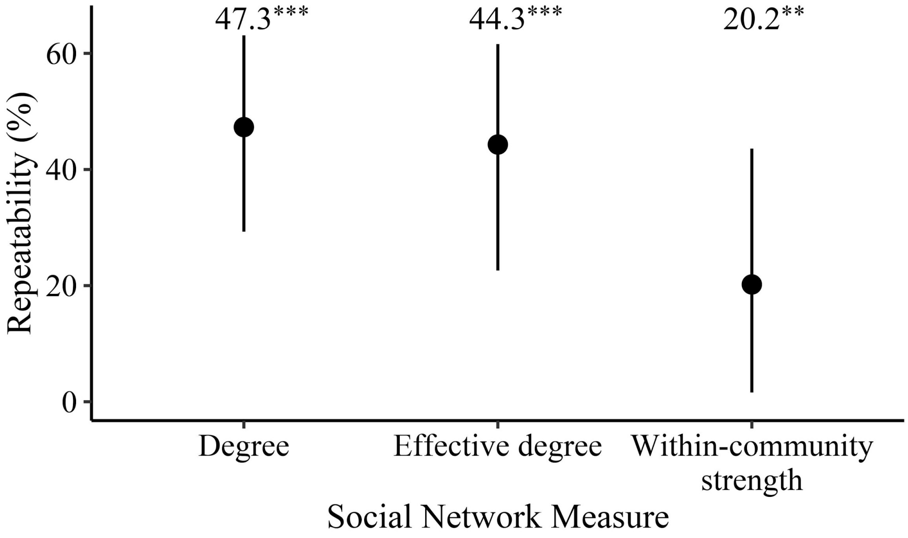


Figure 4. Repeatabilities for individual social network measures over the three year span. P-values are denoted by: P < 0.05 = **, P < 0.001 = ***.

Discussion

Discovering which individual traits correlate with sociality helps us understand how traits may drive social interactions between individuals and overall group organization. We found that overall, a golden-crowned sparrow's age and size correlated with the number and evenness of its social connections, but not the strength of the relationships within a community. Of the traits we measured, only morphological features correlated with social position, and social position was repeatable over three years. It was surprising to find that neither dominance nor personality was linked to social position, so it appears that sparrow associations are shaped by other factors, even though social preference shapes their groups (Shizuka et al. 2014).

Social network analysis of our study population showed three to four communities each year. These results mirror those of Shizuka et al. (2014), who studied golden-crowned sparrow social networks at the same study site in previous years and initially uncovered the social groups' cohesiveness and continuity. Finding fission-fusion dynamics within stable communities which lasted over time was surprising, and Shizuka et al. (2014) were one of the first to find evidence of such social stability over time in a wintering migratory bird. We found similar levels of how distinct the communities were from each other (measured as maximum modularity), showing the sparrow populations have these distinct communities over long periods of time (Shizuka et al. studied 2010-2012, we studied 2014-2016). The 2014 and 2015 modularities were 0.45-0.46, agreeing with Shizuka et al. (2014) who found modularities ranged 0.43-0.49 over three previous years (2010-2012). The 2016 communities were somewhat less discreet, as the social network modularity (0.37) was lower than all other years measured in this system, and this may result in breaking down the relationship between sociality and other traits.

Morphology and social position

An animal's experience develops with age, and this knowledge could help maintain group structure if associations continue across years. Age and/or lifespan can relate to social position in different ways; for example, more connected yellow baboon females lived longer than less connected females (Archie et al. 2014), and older female Barbary macaques (*Macaca sylvanus*) had fewer associates (Sosa 2016). In our study, age correlated positively with how many connections (degree and effective degree) golden-crowned sparrows had but not with the overall strength of those connections in their communities. Shizuka et al. (2014) found that age correlated with a different aspect of social position: birds that returned across years developed stronger bonds within their communities. Golden-crowned sparrows almost always returned to the same communities and associated with the same individuals each winter (Shizuka et al. 2014), even though birds in the same community bred in highly disparate locations (Block et al. submitted). Multiple lines of evidence point towards older individuals being critical to keep community structure stable over time as individuals: return to the same communities and connect with the same individuals (Shizuka et al. 2014), remember these connections across time (Block et al. submitted), and increase the number of connections with age. If older birds only kept the same connections, communities would not be stable as there are large amount of turnover each year (Shizuka et al. 2014). But, by remembering connections and making new connections, older individuals likely help new birds integrate into the communities, enabling the continuation of communities beyond individual life spans.

Along with age, size can also be a factor in determining grouping patterns. For example, in cichlids (*Neolamprologus pulcher*), males grouped with females depending on size and personality type (Schürch et al. 2010), and Trinidadian guppies (*Poecilia reticulata*) assorted by body size depending on external predation risk (Hasenjager and Dugatkin 2017). We found that smaller golden-crowned sparrows had more connections, and mass consistently predicted degree and effective degree both globally and by year. Even though female sparrows are generally smaller than males (unpublished data), mass was a predictor rather than sex, as both sexes showed large amounts of variation in degree and effective degree. Smaller birds may suffer various disadvantages due to their size, such as lower dominance scores and lower abilities to store fat without increasing predation risk (Lima 1986; Witter and Cuthill 1993; Pravosudov et al. 1999). Having larger numbers of connections could be one way of offsetting some of these disadvantages by increasing the flow of information about foraging options and accessing food patches more quickly. For example, in three different species of small birds (family *Paridae*) an individual's number of connections in a social network was positively correlated with a greater likelihood of finding and foraging at new food patches (Aplin et al. 2012). Smaller golden-crowned sparrows tend to be more subordinate (Chaine et al. 2011) and may be at a disadvantage when accessing food resources; having larger numbers of social connections could increase their food finding or other beneficial sources of information.

Behavior and social position

For animals with discrete communities, patterns of dominance may change within versus between those communities. For example, in determining the outcome of dominance contests, golden-crowned sparrows use badges of status between unfamiliar birds and individual recognition with familiar flockmates (Chaine et al. 2011; Chaine et al. 2013; Chaine et al. 2018). As the social situation can change if badges of status are used, dominance and/or badges could have been expected to correlate with either within- or between-group social network measures. Hence, we examined within-community strength, measured within groups, and degree and effective degree, which included all of an individual's associations both within and between communities. However, we found no correlation between dominance or badges of status with the network measures we investigated. Shizuka et al. (in prep) found that most dominance contests occurred between birds that flocked together, so dominance relationships occur within sparrow groups. Yet, dominance did not predict an individuals' social network measures. By distinguishing within- and among-group interactions to consider how dominance and badges change depending on the social circumstances, our results indicate that both dominance and badges of status are independent of social flocking associations.

Examining the years separately revealed year to year variation in which traits correlated with social position. We also find year to year variation in other aspects of social behavior in golden-crowned sparrows. For example, how badges of status predicted dominance changed over time—the black patches correlated with dominance scores most years, while the gold badges only occasionally correlated with dominance (Shizuka et al. in prep). Additionally, in several years (but a minority), sparrows assorted by gold badge size (Shizuka et al. in prep). One potential explanation for the lack of correlates with social metrics in 2016 is that this was a year where communities were less clearly defined (lower modularity value). Perhaps factors like age and mass only correlate with social measures when groups are more structured and distinct from one another. The reasons why community structure changed in the first place are not clear, but one possibility is that this reflects an increased turnover of individuals (Shizuka and Johnson 2019). When individuals in networks die or disperse, their social connections are removed, which changes how the remaining individuals interact (Aureli et al. 2008; Shizuka and Johnson 2019). Similarly, new individuals joining a social group creates new connections (Shizuka and Johnson 2019). Years with more turnover could result in looser groups and less population structure, potentially leading to the observed lack of correlations between social metrics and age and size. However, as we excluded any birds first joining the network (due to sampling bias), we would not have directly picked up on newcomers' effects.

If personality type influences how individuals interact, we would expect to see consistent social network positions. Golden-crowned sparrows had repeatable social positions, similar to those found in great tits, house sparrows (*Passer domesticus*), small spotted catsharks *(Scyliorhinus canicular)*, and wild vervet monkeys (*Chlorocebus pygerythrus*) (Jacoby et al. 2014; Aplin et al. 2015; Blaszczyk 2018; Plaza et al. 2020). However, few studies have looked for a link between known consistent social network positions and experimentally-determined personality traits (but see Blumstein et al. 2012, Aplin et al. 2013, Alin et al. 2015). The personality traits we measured here were determined in a cage environment with high short- and long-term repeatability. In great tits, with similarly determined personalities, faster explorers were more central and had larger numbers of associations (Aplin et al. 2013, Snijders et al. 2014). However, we found no correlation between sociality and personality. This is in line with Block et al. (in press), who found that personality was independent of dominance, badge size, age, and sex. The evidence here further indicates that personality is a separate axis of variation from social behavior.

Interactions between individuals form the basis of social groups (Hinde 1976). Personality types have been shown to influence animal grouping patterns, such as in studies of great tits (Aplin et al. 2013), common degu (*Octodon degus*; Chock et al. 2017), three-spined stickleback (Pike et al. 2008), and cichlids (Schürch et al. 2010). For example, Trinidadian guppies assorted by personality type and shy fish had more and stronger connections than bold fish (Croft et al. 2009). Here, golden-crowned sparrows with similar escape responses (personality PC 2) were more likely to be in a community together in 2015, and birds with similar activity levels (personality PC 1) grouped together in 2016. However, the lack of consistent assortment in either axis of personality showed that personality is likely not a stable driver of group organization in golden-crowned sparrows. This fits with the lack of correlation between personality and sociality. Similarly, Block et al. (in press) found that golden-crowned sparrow personality traits were independent of other social traits like dominance and badges of status. However, an alternate option is that personality assortment may vary year to year due to external factors like predation risk or population density. For example, personality types in great tits were found to be under fluctuating selection, as faster explorers had higher survival probabilities in lower population density, while slower explorers did better in high population density (Nicolaus et al. 2016). The changing social environment was shown to have survival consequences, and if some personality types do better in some years, this could be a potential reason for why individuals assorted by personality in some years and not others. Additionally, reducing risk of predation is not only a dominant reason why individuals form groups (Lima 1987; Davies et al. 2012), but changing levels of predation risk can also affect fine-scale social structure (Hasenjager and Dugatkin 2017). Captive guppies not only grouped by personality type in captivity, but they also changed the strength of social associations and how they assorted depending on the level of predation risk in the environment (Hasenjager and Dugatkin 2017). Animals may group with similar personality types under certain conditions, yet the cause of group assortment may not predict the nuances of how an individual associates within the group. We suggest that a valuable future direction is to investigate how animals in the wild may group by similar behaviors, such as personality, and to determine whether such grouping patterns are contingent on particular conditions such as level of predation risk, resource availability or population density.

Conclusions

In golden-crowned sparrows, morphological traits correlated with social network measures while behavioral traits did not. Of the behaviors we studied, individual patterns of sociality (e.g., the strength and number of connections) were not predicted by dominance and personality. Consistent behaviors were similarly independent of social network measures in yellow-bellied marmots (*Marmota flaviventris*) where repeatable aggression in a cage was separate from social network measures of aggression in the field (Blumstein et al. 2012). Even though golden-crowned sparrows that engaged in dominance contests at feeders were also ones that flocked together (Shizuka et al. in prep), how the birds associated within groups appeared separate from dominance relationships.

The ecological knowledge of older animals can be critical to maintaining group structure (Brent et al. 2015). Sparrow communities are driven by social preference more than just use of space, and individual sparrows accumulate more and stronger connections with each additional year (Shizuka et al. 2014). The sparrow communities are remarkably stable over time considering the large turnover present across years (30-50%; Shizuka et al. 2014). As older and smaller birds tended to be more central players in their communities, experienced birds likely play an important role in maintaining the continuity of the groups over time. In addition to the effects of long-term social memory strengthening associations over years, the birds accumulate more connections over time which helps maintain the continuity of social groups. Older returning sparrows have experience in the given environment and can exploit known resources for food and protection from predation. The older birds could transmit this information to younger, newer members of the community. In addition, because older birds have more connections, they can benefit from receiving information about new resources; information flow is a central part of group living and can provide many benefits, such as increased access to food (Aplin et al. 2012). A future direction is to determine how older, more central individuals influence the flow of information about resources and predation risk. Here, we found that older individuals could be key in maintaining the structure of social communities over time.

Chapter 3

Age and winter dominance predict annual survival in a migratory bird

Abstract

Annual survival is an important component of fitness, and traits that influence annual survival are expected to be under natural selection. While many studies of annual survival in migratory birds have focused on traits measured in the breeding season, relatively few studies to date have investigated winter traits that affect annual survival. We studied how traits measured on wintering grounds affected annual survival across winters in a small migratory bird, the golden-crowned sparrow (*Zonotrichia atricapilla*). These sparrows form flocks in the winter, and these flocking relationships can last for years. Along with these flock relationships, golden-crowned sparrows have dominance relationships and use plumage badges of status (freshly molted prior to each winter) to determine their dominance in different contexts. In theory, dominance can have many potential advantages, such as increased access to food and other resources, which may affect survival. We ask if dominance, age, or other morphological traits predict survival to the following year. Combining all years of data, we found that dominance and age predicted survival to the next year, where more dominant birds had higher survival, and older birds were less likely to survive. However, separate year-to-year survival analyses showed that different traits predicted annual survival in different years, and several morphological traits predicted annual survival along with dominance and age. However, dominance and morphological traits showed no consistent relationship predicting survival, rather, varying in most years. The decline in survival in the oldest age classes is consistent with senescence. Detecting senescence was possible through our long-term study with large numbers of birds and a sample of unusually long-lived individuals. Overall, we found that badges of status and sex did not affect annual survival, while size and dominance may have periodic effects that may reflect fluctuating selection.

Keywords: badge of status, flocks, golden-crowned sparrows, migration, senescence

Introduction

Annual survival can strongly influence fitness, driving everything from life-history evolution to social behavior (Promislow and Harvey 1990, Healy et al. 2019). Survival rates can determine the timing of key life-history events such as the onset of reproduction or the onset of senescence (Holmes and Austad 1995). For example, early growth rates can be driven by predation (Reznick et al. 1990; Martin 2015), and low adult mortality may be a prerequisite for cooperative breeding in birds (Arnold and Owens 1998). Survival is affected by both extrinsic factors like predation and internal factors like senescence, the latter evidenced by increasing physiological decline (Rockwell et al. 1993; Ricklefs 2000). In birds, where populations often experience relatively steady rates of mortality through adult life (Promislow 1991), it is important to evaluate whether survival is random or if certain traits link to increased survival. In fact, theory suggests that in longer-lived organisms, variation in survival can have stronger effects on fitness than reproductive output (Saether and Bakke 2000; Crone 2001).

Connecting annual survival with different traits helps identify the origins of selection pressures on those traits and, eventually, their evolutionary dynamics. When seeking to correlate annual survival to traits, it is important to consider how selection acts on traits and how it may change in different seasons. Further, some traits are expressed within a particular season, and selection could act both within that season and on traits present year-round. Many migratory animals spend the majority of their lives in the non-breeding season (Marra et al. 2015), yet selection on the wintering traits of migratory birds is not well understood, with more research on reproductive traits such as clutch size, the timing of breeding, and mate choice (Arnold and Owens 1998). Focusing on selection only during the breeding season can result in missing out on potentially significant selective factors that affect large portions of migratory animals' lives (Marra et al. 2015). Additionally, what happens during the winter season can have strong carry-over to the breeding season (Norris et al. 2004; Norris and Marra 2007). For example, more dominant American redstarts (*Setophaga ruticilla*) from higher-quality winter territories had higher reproductive success the following summer (Norris et al. 2004). However, the nature of migration makes it challenging to study seasonal interactions in many migratory birds. Examining neglected parts of the annual cycle helps us piece together how selection may act in different seasons.

Social dominance can have a critical impact on the survival of small birds that flock in winter (Desrochers et al. 1988; Koivula and Orell 1988; Lahti 1998). During winter, small birds must balance the tradeoff between foraging and predation, and forming groups is one way of balancing this risk (Lima 1986; Lima 1987; Houston et al. 1993). While groups can be advantageous overall, they also come with increased competition (Caraco et al. 1980), and dominance ranks and/or signals of status may be mechanisms for decreasing conflict within a group (Smith and Price 1973; Rohwer 1975; Rohwer and Ewald 1981). Dominance can potentially affect survival by increasing access to resources like food and shelter (Drews 1993). For example, more dominant black-capped chickadees (*Poecile atricapillus*) and willow tits (*Poecile montanus*) have higher over-winter survival than subordinates (Desrochers et al. 1988; Koivula and Orell 1988). Investigating how dominance may predict survival can reveal if dominance or subordinance is advantageous in a particular system and how the strategies may result in different fitness payoffs.

How traits affect survival can change across environments and time, potentially leading to variation in strength and/or direction of selection on traits (Siepielski et al. 2009). For example, in Darwin's finches (*Geospiza sp.*), selection oscillated on beak shape and body size and changed with extreme environmental conditions (Grant and Grant 2002). In addition to variation in selection caused by changing environments, selection can also change with an individual's age. While birds have long been cited as an example of relatively constant adult mortality rates unrelated to age (Deevey 1947; Pinder et al. 1978), large-scale, longitudinal studies are increasingly picking up evidence of senescence (Promislow 1991; Nussey et al. 2008; Bouwhuis et al. 2012). Hence, we may expect to find lower survival rates in the oldest birds.

Here, we investigate whether social and morphological traits, some only expressed on the wintering grounds, correlate with annual survival across winters in a migratory songbird, the golden-crowned sparrow *(Zonotrichia atricapilla*). Golden-crowned sparrows vary considerably across seasons both in plumage features and social behaviors—they form breeding pairs in the summer, with minor plumage variation, and then form flocks on their wintering grounds where there is considerable plumage variation among individuals (Chaine et al. 2011; Shizuka et al. 2014; Norment et al. 2021). Golden-crowned sparrows, true to their name, have a gold plumage patch on the top of their heads (the ‘crown’) surrounded by two black stripes. In summer, both males and females have bold, relatively monomorphic appearances, but in winter, there is a wide range of variation in both color and size of their crowns. During winter, golden-crowned sparrows live in flocks with complex social dynamics, consistent group membership, and relationships with other individuals in their group that can last for years (Shizuka et al. 2014). The sparrows have high site fidelity, and if they return to the study site, they almost always rejoin the same social group (Shizuka et al. 2014). Interestingly, while relatives are present in the population, the affiliations among individuals are not predicted by kinship (Arnberg et al. 2015). Golden-crowned sparrows have dominance relationships within these groups, and their crown plumage serves as badges of status in some social contexts (Chaine et al. 2011; Chaine et al. 2013). Specifically, the plumage badges are decisive in interactions with unfamiliar individuals, while individual recognition is important among the familiar individuals within the stable social groups (Chaine et al. 2018).

Our prior research on the significance of traits and social organization in golden-crowned sparrows allows us to focus on several traits that could feasibly influence fitness through their effects on survival (Chaine et al. 2011; Chaine et al. 2013; Shizuka et al. 2014; Chaine et al. 2018). Sandercock and Jaramillo (2002) previously investigated annual survival during winter in golden-crowned sparrows. They found an average survival rate (42%) similar to other migrant and resident sparrows species at their nearby study site in central California and higher survival amongst adults than first-year birds. With our long-term demographic and social data, we go further to connect winter annual survival to individual variation in golden-crowned sparrow winter traits. We studied golden-crowned sparrows at an established long-term field site and applied a decade of survival data to assess year-to-year relationships between traits and survival. We ask if traits measured in a given winter season—dominance, plumage badges of status, age, sex, or size—predict survival to the following winter. We use two main approaches. First, we grouped all years of data together for a long-term, global analysis. A large, multi-year dataset may be essential for uncovering long-term survival trends. Second, we examined survival in separate year-to-year comparisons, as we know that some sparrow traits change over time (such as plumage size), and the direction of selection on traits can change across time as well (Gibbs and Grant 1987; Siepielski et al. 2009).

Methods

Study background

We studied a population of golden-crowned sparrows at their wintering site in the University of California Santa Cruz (UCSC) Arboretum. The sparrows winter at the Arboretum from September through April, after which they migrate to their northern breeding sites in Alaska and Canada. As each winter field season spanned two calendar years, we refer to the season by the year in which it started. Every winter, we conducted three types of surveys: banding, flocking, and dominance.

We regularly banded birds throughout the season, trapping them mostly with baited potter-traps and more rarely with mist nets. We gave each bird a USFWS metal band and a unique combination of color bands to identify individuals in the field from a distance. During banding, we took the following measurements for each bird: culmen (mm), tarsus (mm), flattened wing chord (mm), mass (g), and a photo of the top of each bird's head for measuring plumage badges. We used Adobe Photoshop to extract the area of black and gold (in mm^2) on the top of their heads, following standardized methods from Chaine et al. (2011). We also took a small blood sample from the ulnar vein to sex the birds genetically by amplifying the CHD gene on the Z and W chromosomes (Griffiths et al. 1998), following methods described in Chaine et al. (2011).

To collect flocking data, observers identified banded birds in the field and recorded the identities of all banded sparrows present, along with the time and location. Location is based on a photographic map of gridded cells ($10m^2$) of the Arboretum (Shizuka et al. 2014). Dominance data were collected on different days than flocking data, and we observed dominance interactions at long-established fixed feeding stations, baited with millet on those days. Observers scored interactions between banded birds at these stations and recorded the winner and loser of each interaction based on the following behaviors: fight, chase, supplant, and avoid, from methods originating in Chaine et al. (2011). In the aggressive interactions of fight, chase, or supplant, the winner initiated the behavior, and the loser vacated the immediate area. An avoidance interaction was scored when the loser waited for access to the seed pile while it was occupied by the winner. Individual dominance scores were calculated from the wins and losses of each interaction.

We used census data to determine which birds were present (alive) and conversely which were not observed (likely dead). We censused which birds were recorded in the arboretum from a combination of banding, flocking, and dominance sightings. We then filtered these data to determine which birds were present to account for any potential band reading errors by observers in the field. A bird was considered present if caught during banding or if the band combination was seen more than three times in the combined dominance and flocking data. We analyzed data covering ten years, from 2009 to 2018. A total of 575 birds were confirmed present over these ten years. Of these, only 14 birds (2.4% of total) 'skipped a year'—

i.e., were seen in one year, not detected the following year, then seen again in subsequent years. The low number of birds which skipped a year indicates that the risk of failing to detect a bird that was actually alive was very low. Since birds identified as skipping a year were known to be alive based on returning in the future, in the year they skipped they, either went to a different wintering location, or they were present at our site, but we failed to detect them. Since they were alive in the year which they skipped, we counted them as present for the skipped year in data analyses. Because of our high confidence in detecting birds if present, we used models with logistic regression to identify traits that predict survival.

The golden-crowned sparrows at our field site have a biased sex ratio: females comprised 66% of the 431 birds we sexed with genetic methods. The duration of residency in the population ranged from 0–7 years, where zero indicates a bird initially banded in that season. Not all birds banded for the first time are in their first year of life, but 'band age,' or years since first banding, is a good proxy for age and serves as an index of residency time in the population.

Statistical Methods

All the traits we measured are stable within a year, and body size measurements should be relatively stable across years, while dominance and plumage can change. Golden-crowned sparrows have stable crown plumage within each season as they do not molt crown plumage until shortly before migration at the end of

April (Norment et al. 2021). Plumage size can change across years, especially from the first year to later years (Colwell 1999).

To ensure that we were not missing effects of traits on survival due to measurement error or changes in size over time, we measured the repeatability of culmen, mass, tarsus, and wing length within and across years using the rptR package. The confidence intervals were calculated via bootstrapping (1000 iterations), and we report likelihood-ratio test P-values (Nakagawa and Schielzeth 2010; Stoffel et al. 2017). We found that wing length, tarsus length, and mass were all repeatable measures across years, and within-year repeatability was very similar to across year despite having a much smaller sample size (Appendix 3 Figure S1). However, culmen had low repeatability both within a year and across years (R_{within} = 41%, CI = 0-72%, $P = 0.03$; R_{across} = 44%, CI = 34-54%, $P < 0.001$), which we attribute mostly to measurement error rather than substantial changes across years. Due to this variability, we omitted culmen from our final models.

We estimated dominance scores for individuals using Elo rating, which calculates individual dominance scores based on the sequence of observed dominance interactions (Neumann et al. 2011; Sánchez-Tójar et al. 2017). We calculated an individual’s dominance score with the package AniDom (Farine and Sánchez-Tójar 2019), using data from the start of dominance data collection to a cutoff date of March 30 each year, as the birds’ behaviors can change when migration approaches. The magnitude of awarded points was based on the probability of an individual winning or losing dominance interactions. Each bird started with an initial score of zero and the parameter K (set to 200) specified how quickly points changed after each interaction. Dominance scores were scaled within each year.

We investigated the relationship between survival and behavioral and morphological traits using logistic models with a binomial distribution (package lme4; Bates et al. 2015). For birds with multiple measures of the same morphology within a single year, we used the mean of the measurements. We were unable to have all factors in one larger model due to reductions in sample size that resulted from incomplete sampling of all variables for all birds. Hence, we arranged the explanatory variables into three groups which both maximized the sample size and made sense biologically. Using survival as the response variable, we ran three different model types that varied with respect to the explanatory variables examined: model A—dominance and age; model B—age, black badge size, gold badge size, tarsus, wing length, and mass; and model C—sex. We included age as an interaction term with dominance in model A and with black plumage size in model B, since dominance and plumage can change with age.

We first ran models A and B for all years of data (global models) with individual and year as random effects. All variables in model A and B were zero-centered and scaled. The global model for dominance and age did not include data for 2009 and 2013 because we did not have dominance data for those years. We use marginal R^2 for models with both random and fixed effects, as marginal R^2 estimates the variance accounted for by fixed effects, while conditional R^2 estimates the variance accounted for by random and fixed effects (Nakagawa and Schielzeth 2012).

Since survival could vary among specific years, we then used these same three model types to examine survival for each specific, adjacent year-pair. We used model selection (MuMin package) with Akaike Information Criterion (AIC) for model B and chose the top model to determine which factors best fit the data (Barton 2018). Model B in 2013 had black and gold badge size with no other morphological measurements, so we did not use model selection in this particular instance. We report Tjur's R^2 for each model, a pseudo-R^2 (ranging from 0-1) which estimates the amount of variance accounted for by the fixed effects of logistic models in an approximation of standard R^2 (Tjur 2009). All models with multiple factors had VIF scores less than five, so while measurements of the birds can be correlated, there were no issues with autocorrelation within the models. We transformed all effect sizes (ß) from the logistic regression into odds ratios ($e^{ß}$) to be more easily interpreted. In an odds ratio, for every unit of x, y increases the same amount; an odds ratio >1 means a positive likelihood and an odds ratio of <1 means a negative likelihood.

We performed all analysis in R version 4.0.2 (R Core Team 2020).

All research was done with UCSC IACUC research permits (Animal Welfare Permit Number Lyonb1808 to B. Lyon) and with federal and state permits to B. Lyon.

Results

The golden-crowned sparrows had an average return rate of 50%, ranging from 36%-63% (Figure 1).

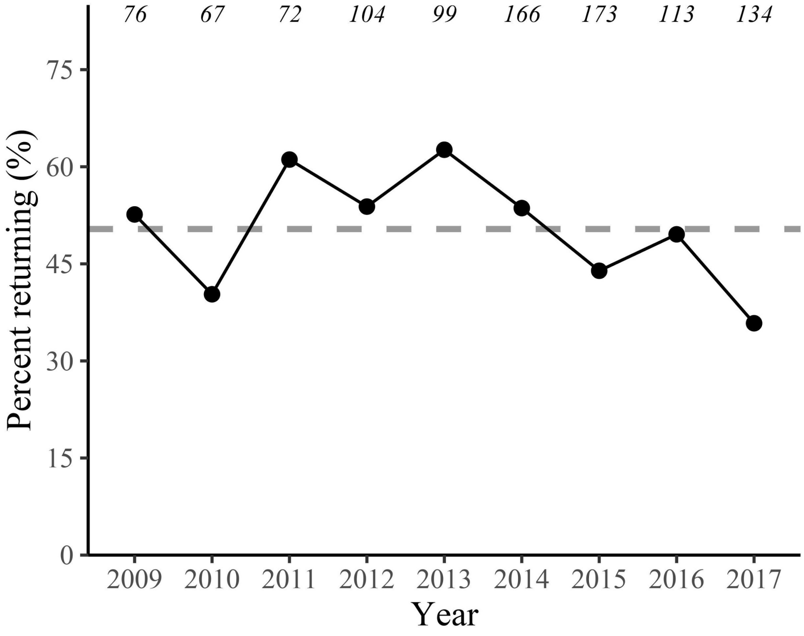


Figure 1. Return rates for golden-crowned sparrows at the UCSC Arboretum. The dashed line shows the average return rate, and numbers in italics show the total number of birds in each year. Points indicate the percentage of birds returning in the following year. E.g. In 2009, there were 76 confirmed individuals with 53% returning in 2010.

For model A, dominance and age predicted survival in all years combined (Table 1A; Figure 2). More dominant birds were more likely to survive to the next year (*Odds ratio* = 1.24, CI = 1.01-1.51, p = 0.04), while older birds were less likely to survive to the following year (*Odds ratio* = 0.81, CI = 0.68-0.98, p = 0.03). We see that the proportion of birds surviving to the next year for each age class decreases at band age four (Figure 3). However, these patterns were not consistent in separate year analyses. More dominant birds were more likely to survive from 2010-2011 (*Odds ratio* = 3.32, CI = 1.05-10.49, p = 0.04) and older birds had decreased survival from 2016-2017 (*Odds ratio* = 0.55, CI = 0.30-1.00, p = 0.05; Table 2).

In the age and morphology models, model B, no traits predicted survival when analyzing all years together (Table 1B; Figure 2). In the separate year-to-year analysis for model B, traits predicted survivorship in two out of nine years (Table 3). Heavier birds were more likely to survive in 2011-2012 (*Odds ratio* = 2.27, CI = 1.09-4.70, p = 0.03) and 2016-2017 (*Odds ratio* = 2.32, CI = 1.36-3.94, p = 0.002). Age was in the top model for five years yet only significantly predicted lower survival in 2016-2017 (*Odds ratio* = 0.50, CI = 0.27-0.91, p = 0.002) and showed a non-significant trend in 2017-2018 (*Odds ratio* = 0.46, CI = 0.20-1.02, p = 0.06). Interestingly, birds with smaller tarsus lengths showed trends towards higher survival in 2012-2013 (*Odds ratio* = 0.61, CI = 0.36-1.03, p = 0.07) and 2014-2015 *(Odds ratio* = 0.71, CI = 0.49-1.09, p = 0.06).

In model C, sex did not predict year-to-year survival for all years combined (Table 1C). In separate year-to-year analysis, sex showed a trend towards males having higher survival in 2011-2012 (*Odds ratio* = 3.25, CI = 0.90-11.70, p = 0.07) and 2014-2015 (*Odds ratio* = 1.81, CI = 0.95-3.47, p = 0.07; Table 4). However, this was not a strong pattern and showed considerable variation among years with changing directional effects (while all non-significant, some years indicated males had a higher likelihood of surviving and some years females).

In separate year-to-year analysis, we found that three out of nine years had traits influencing the likelihood of birds surviving to the following year. In two of the years, morphology was a significant predictor, and in one year, dominance and age were. While birds with larger masses were more likely to survive in two years, in two other years birds with smaller tarsus lengths trended towards a higher survival probability.

Table 1. Three global models combine data from all years to determine if features in a given year predict an individual's survival to the following year. Letters correspond to the three model types: A (age, dominance), B (age, morphology), and C (sex).

A.

	Survival to next year		
Predictors	*Odds Ratios*	*CI*	*p*
Intercept	1.18	0.90 – 1.54	0.235
Dominance	1.26	1.03 – 1.54	**0.025**
Age	0.81	0.67 – 0.98	**0.026**
Age*Dominance	1.04	0.88 – 1.22	0.680
Random Effects			
σ^2	3.29		
$\tau_{00\ ID}$	0.00		
$\tau_{00\ year}$	0.06		
N_{ID}	312		
N_{year}	7		
Observations	501		
Marginal R^2 / Conditional R^2	0.023 / NA		

C.

	Survival to next year		
Predictors	*Odds Ratios*	*CI*	*p*
Intercept	0.21	0.14 – 0.33	**<0.001**
Sex (M)	1.12	0.94 – 1.35	0.205
Random Effects			
σ^2	3.29		
$\tau_{00\ ID}$	0.12		
$\tau_{00\ year}$	0.38		
ICC	0.13		
N_{year}	9		
N_{ID}	431		
Marginal R^2 / Conditional R^2	0.001 / 0.132		

B.

	Survival to next year		
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.96	0.76 – 1.21	0.723
Age	1.03	0.83 – 1.28	0.781
Black size	0.98	0.80 – 1.21	0.874
Gold size	0.93	0.77 – 1.13	0.470
Wing	1.16	0.95 – 1.43	0.148
Tarsus	0.88	0.73 – 1.06	0.169
Mass (g)	1.15	0.93 – 1.43	0.185
Age*Black size	0.99	0.84 – 1.18	0.951
Random Effects			
σ^2	3.29		
$\tau_{00\ ID}$	0.00		
$\tau_{00\ year}$	0.04		
ICC	0.01		
N_{ID}	439		
N_{year}	8		
Observations	587		
Marginal R^2 / Conditional R^2	0.015 / 0.027		

Table 2. Results for separate year-to-year models showing whether age and dominance predicted survival to the following year (Model A). The year category indicates the year traits were measured to survival the following year. The odds ratios are greater than one (positive effect sizes) for age and dominance. There were no dominance data for 2009 and 2013. We display all factors with $P < 0.1$.

Year	**Age*Dominance**					
	Factor	*Odds ratio*	*CI*	*P*	*N*	R^2
2009-2010	NA					
2010-2011	Dominance	3.32	1.05 – 10.49	**0.04**	33	0.18
2011-2012	Age*Dominance	0.48	0.21 – 1.09	*0.08*	46	0.09
2012-2013					67	0.03
2013-2014	NA					
2014-2015					107	0.002
2015-2016					115	0.04
2016-2017	Age	0.55	0.30 – 1.00	**0.05**	73	0.06
2017-2018					60	0.02

Table 3. Results for models run for separate year-to-year models examining whether age and morphological traits predicted survival to the following year (Model B). 'Top model' shows which traits were selected from the full model after model selection based on AIC criteria. Asterisks show an interaction term, and bolded values highlight significant traits in the top models and P-values. 'AIC full' shows the AIC for all traits in each full model. 'AIC top' shows the AIC for the top model, whether that was null (no traits) or with the traits in the top model. We ran analyses on the top model for each year and show the odds ratio (e^{β}) for each factor in the top model. P-values are indicated as: * = $P < 0.05$, ** = $P < 0.01$, and text in italics shows $P < 0.08$. 'Year' shows each separate year-to-year model; the traits in year one predict the survival to year two. We report Tjur's R^2. † 2013 morphology model only includes black and gold badge size and we did not use model selection; neither badge was significant.

Year	**Age*Black size + Gold size + Mass + Tarsus + Wing**												
	Top model	*AIC (full)*	*N (full)*	*AIC (top)*	*N (top)*	R^2	*Black* e^{β}	*Gold* e^{β}	*Mass* e^{β}	*Tarsus* e^{β}	*Wing* e^{β}	*Age* e^{β}	*Age* Black* e^{β}
2009-10	NA	72.85	43	61.6									
2010-11	Gold size	72.38	45	68.13	49	0.06		0.6					
2011-12	Age*black + **mass**	78.33	56	77.47	64	0.15	2.05		**2.27***			0.73	0.59
2012-13	*Tarsus*	68.01	42	101 .49	74	0.05				*0.61*			
2013-14	NA	54.15	36										
2014-15	Age + *tarsus* + wing	182.2	130	201.38	145	0.04				*0.71*	1.32	1.29	
2015-16	Age*black + gold	148.99	104	149.86	106	0.06	0.68	1.38				1.39	1.6
2016-17	**Age + mass**	94.67	67	115.77	90	0.16			**2.32****			**0.5***	
2017-18	Age + black	132.95	98	126.88	98	0.05	*1.61*					*1.61*	

Table 4. Results for each separate year-to-year analysis that investigate whether sex predicts survival (Model C). Here, we use females as the control level so all values show males in contrast to females; males had a trend toward higher survival in 2011 and 2014. We use Tjur's R^2 to estimate variance accounted for by the model.

Year	**Sex**				
	Odds ratio	*CI*	*P*	*N*	R^2
2009-2010	0.61			65	0.01
2010-2011	1.64			45	0.01
2011-2012	3.25	0.90 – 11.70	*0.07*	57	0.06
2012-2013	0.61			67	0.01
2013-2014	0.52			80	0.02
2014-2015	1.81	0.95 – 3.47	*0.07*	162	0.02
2015-2016	0.79			150	0.003
2016-2017	1.54			104	0.01
2017-2018	1.18			94	0.001

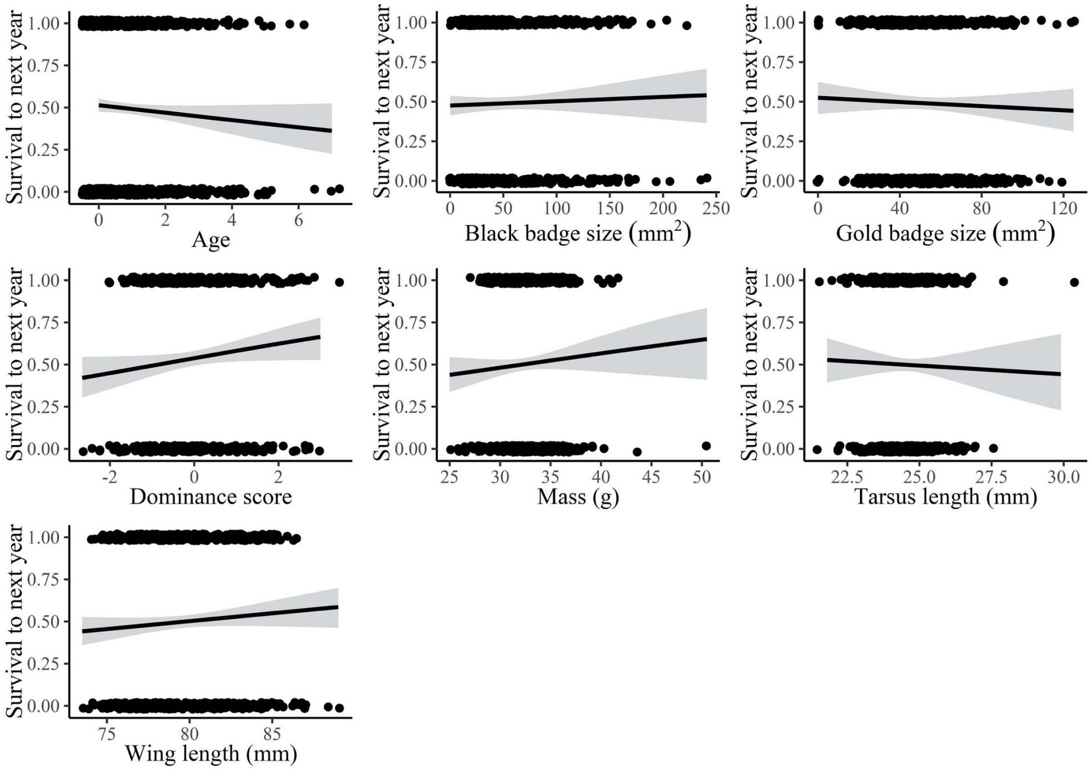


Figure 2. Raw data showing how traits correlate with survival to the next year for all years of data combined. Data points are survival to the next year (alive = 1, dead = 0) in relation to the trait values for individual birds. Age and dominance were the two traits to predict survival to the following year. Lines show the probability plot of surviving as predicted by a binomial model, and shaded grey areas shows 95% confidence intervals.

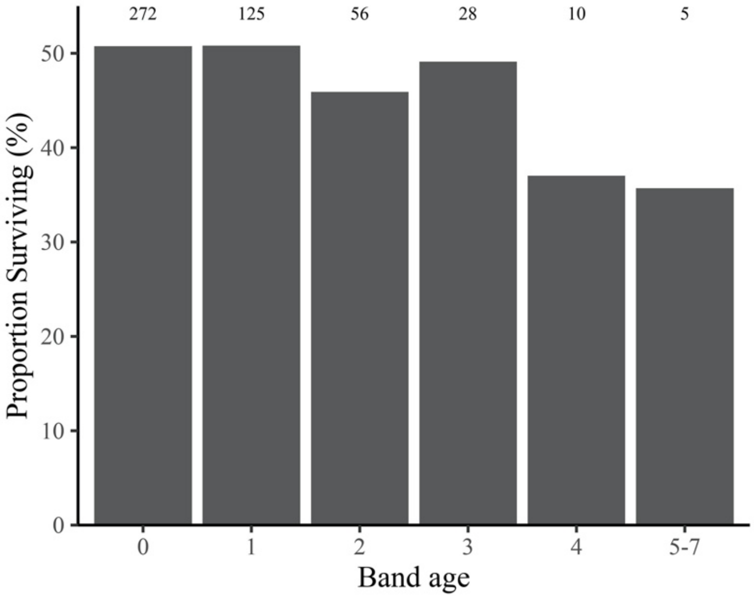


Figure 3. For each age category, the proportion of birds surviving to the next year is shown. Bars are labeled with the sample sizes of the birds surviving to the next year. As fewer birds returned each year to deal with the decreasing sample size we combined the proportion surviving from band ages five through seven. Birds band age four and up show a decreased proportion of survivors than previous age classes.

Discussion

Our research focused on a decade of banding and census data to determine which traits correlated with survival in golden-crowned sparrows. Along with banding data, we used frequent censuses in the field to determine if birds were present each season after their initial capture, with multiple censuses during most weeks of each season. With this intensive census effort, if a bird was alive in a given season we were almost certain to detect its presence; only 2.4% of the birds went undetected for a season and then were confirmed alive during a later year. Over the ten-year study we found that more dominant birds, measured through behavioral interactions, had higher year-to-year survival. Older birds had lower survival indicating an age-related decline in survival that is consistent with senescence. In the separate year-to-year analyses, we found that various traits predicted survival to the following year, but these traits differed across years.

Traits predicting survival

Dominance has been linked specifically to increased over-winter survival in several other species of small flocking birds, such as black-capped chickadees (Desrochers et al. 1988), willow tits (Koivula and Orell 1988), silvereyes (*Zosterops lateralis chlorocephalus*) (Kikkawa 1980), dark-eyed juncos (*Junco hymalis*) (Fretwell 1969), and white-throated sparrows (*Zonotrichia albicollis*) (Piper and Wiley 1990). In all cases, however, it is difficult to disentangle correlation from causation. For example, dominant individuals could have higher annual survival due to benefits that come from dominance, but it is also possible that higher quality individuals, with higher survival, tend to be more dominant (Eberhard 1975). Although our global model revealed an effect of dominance on survival, in our individual year-to-year analyses, dominance predicted survival in only one year, showing that dominant birds do not always have a clear survival advantage. The effect of dominance could be somewhat subtle in most years and only be revealed with a long-term dataset and large sample size. This pattern could reflect the influence of dominance on survival within the winter season, but since we assessed annual survival, it could also be the result of carryover effects across different seasons, including migration or breeding. It is worth noting that initial evidence found that golden-crowned sparrows from the UCSC Arboretum all breed in very different places (hundreds of kilometers away from each other; Block et al. in submission), so dominance benefits from winter may carry through the year as birds experience different potential pressures in different environmental locations. Alternatively, the global pattern could be driven by one year in which dominance was particularly advantageous and strongly affected survival rates. For example, the conditions that cause dominance to affect survival could vary and be infrequent, such as a sporadic environmental stressor in the nonbreeding season.

No morphological traits correlated with survival in our global analysis, but mass correlated with increased survival in two years in the individual year analyses. Mass can reflect structural size, but in species that store fat, mass can vary considerably among and even within individuals, depending on the environmental conditions that favor fat storage. Daily fat reserves can be important for winter survival in some species, but the link between variation in fat stores and survival can also depend on the environmental conditions (Piper and Wiley 1990; Clark and Ekman 1995). For example, in great tits (*Parsus major*), fat stores do not correlate with survival when conditions are good and food is abundant (Gosler 1996). In golden-crowned sparrows, we assessed fat stores during banding with a commonly used rank scoring system (Mueller and Berger 1966; Dunn 2003), but we rarely see much fat deposited during the winter season (Lyon et al. unpubl.); this could reflect access to plentiful resources during most of the winter season, as storing fat can come with costs (Hurly 1992; Witter and Cuthill 1993). Given that the sparrows store little fat and that an individuals' mass is repeatable across years, we suggest that mass likely represents structural body size in the sparrows. While larger mass was correlated with higher survival in two years, there was no evidence that other measures of large structural size were linked with higher survival. In fact, in two different years, smaller legs (tarsus size) showed suggestive, though non-significant, correlations with higher survival. One explanation for these conflicting size patterns could be that there is weak oscillating selection on size. Other extreme environmental conditions with large mortality events can result in strong fluctuating selection on size, for example, smaller bodied Darwin's finches survived better following heavy rain years, where larger finches had higher survival in drought years (Gibbs and Grant 1987). In our study, more subtle patterns of survival may result in opposing directional selection on bird body size even without drastic mortality events.

Both size and dominance in golden-crowned sparrows could be subjected to fluctuating selection pressures from ecological factors such as variations in population density, food abundance, and other non-random causes of mortality (Siepielski et al. 2009; Bassar et al. 2013). Further, some selection is not seen until extreme mortality events (Grant and Grant 2002; Siepielski and Benkman 2007), so the variable patterns we observed could be due to slight environmental changes that result in weaker selection. However, we also note that while changes in directional selection are quite common and the strength of the selection on traits can vary (Siepielski et al. 2009), random error may also increase the amount of variance found in traits under weak selection (Morrissey and Hadfield 2012). Hence, we do not discount the possibility that, in general, the sparrows may have relatively stable lives without much selection on morphology.

Implications of age structure

While early studies supported the idea that birds had relatively stable rates of adult mortality (Deevey 1947; Pinder et al. 1978), our results add to a growing body of work from long-term studies supporting senescence, i.e., decreasing rates of survival with older age (Rockwell et al. 1993; Bouwhuis et al. 2012; Class and Brommer 2016). Visual inspection of the age-dependent survival rates suggest that survival rates decline starting in birds five years and older. Long-term data are necessary for detecting senescence, especially in wild populations, because extrinsic mortality means that only a small fraction of the population lives to the ages where senescence can be detected (Nussey et al. 2008). Additionally, large sample sizes are needed to have confidence that the reduced survival of these older individuals is significantly lower than that of earlier age classes (Nussey et al. 2008); this statistical power issue is illustrated with our study. Ten years of data revealed the decline of survival with age in a global analysis with good sample size, but we only found an age effect in one specific year-to-year analysis, 2016. Interestingly, this year happened to include two of the oldest birds we have ever detected; both birds were at least eight years old. Senescence is thought to be driven, in part, by weak selection against genes with deleterious effects that occur only in later age classes because so few individuals live long enough to suffer the fitness consequences of these genes

(Williams 1957; Charlesworth 2000). With extrinsic mortality, very few individuals live to relatively old age classes, and the magnitude of extrinsic mortality can shape the timing of senescence (Promislow and Harvey 1990). In our study, only 4.6% of the 575 individuals we followed survived to at least year five ('band age' 4), the first year where annual survival dropped relative to younger age classes, and only 1.6% lived to at least year 6 (Figure 3).

Survival and seasonal carryover

Our average survival rate of 50% fits well within general survival rates for North American passerines. For example, Karr et al. (1990) found an average survival rate of 52% for eight North American passerines, and Johnston et al. (1997) found an average of 53% for 30 North American passerines. One previous study conducted a detailed investigation of annual survival rates specifically for golden-crowned sparrows: Sandercock and Jaramillo (2002) found rates of 42% for returning adults compared to our finding of 50%. Sandercock and Jaramillo (2002) used mark-recapture models to estimate survival rates for golden-crowned sparrows over 13 years in a study site 53 km from our location in central California. They used age-structured models to account for differences between the first and sequential captures, and found evidence that first year birds had lower survival than older age classes. We posit several reasons why our survival rates might have been higher both for first year birds and adults. First, we used 'band age' (year since first capture and banding) rather than absolute age to categorize birds. Hence, if there is a mix of first-year and older birds in our sample of first-captured birds, this could obscure a lower survival rate for the yearling age-class. Second, we used many field surveys throughout the season to resight birds with individually-unique colored leg bands, which allowed us to track survival without recapturing individuals. Last, our study site may be unusual in the amount of food and high-quality habitat. Golden-crowned sparrows are omnivorous, and mostly eat plant material, buds, flowers and nectar, seeds, with some arthropods (Norment et al. 2021). Our study site is an Arboretum that is frequently watered and maintained with an abundance of plants that bloom during winter with high nectar content (*Grevillea and Banksia spp.*), as well as grass, seeds, and invertebrates. The rich food resources at our site could, in part, explain our higher survival rates compared to those reported by Sandercock and Jaramillo (2002).

It is important to keep in mind differences between over-winter survival and annual survival, which includes potential carryover effects from one part of the annual cycle to the next. Over-winter survival of small, non-migratory birds has been connected to several traits, such as dominance, sex, and age (e.g. Lahti 1998), but few studies connect these traits to annual survival. Here, we found that winter dominance has a strong enough effect to correlate with increased annual survival. Increased annual survival could derive from different parts of the annual cycle and is therefore a challenge to disentangle the specific mechanism and season where mortality is affected (Norris et al. 2004; Rockwell et al. 2016). First, traits in winter could mostly affect over-winter survival. Food and habitat often affect survival during a season and food additions increased over-winter survival in black-capped chickadees (Desrochers et al. 1988), and young song sparrows (*Melospiza melodia*) (Smith et al. 1980). Second, benefits from over-winter survival could bring positive carryover effects to the next parts of the annual cycle, such as migration and breeding season (Norris and Marra 2007). For example, Louisiana waterthrushes (*Parkesia motacilla*) that arrived on their wintering grounds with low stressors obtained higher quality territories, better over-winter body condition, and consequently had increased annual return rates (Latta et al. 2016). Thirdly, advantageous traits and behaviours during one season could correlate with another, for instance, black-tailed godwits in higher-quality breeding areas had higher-quality wintering areas (*Limosa limosa islandica*), reflecting that some individuals have year-round advantages and potential higher fitness (Gunnarsson et al. 2005). An important next step is to measure how overwinter survival might differ from annual survival and discover if seasonal traits like dominance are mostly beneficial in one season or throughout the year.

Conclusions

Predation avoidance and food finding are central tenets for the survival of small birds which form flocks in winter (Caraco et al. 1980). As evidenced here, and in other species, more dominant individuals can often have more access to resources and higher survival (Fretwell 1969; Kikkawa 1980; Desrochers et al. 1988; Koivula and Orell 1988; Piper and Wiley 1990). While dominance can decide the outcome of interactions between individuals in flocks, many of the interactions between flock mates are cooperative (Clark and Mangel 1984). Social connections and communities are hugely important for social animals and can have many benefits (Alberts 2018). Indeed, individuals can gain information about food sources through social connections, which may play a pivotal role in gaining resources and increasing survival (Aplin et al. 2012). For example, in mammals, North American red squirrels (*Tamiasciurus hudsonicus*) with familiar neighbors had increased survival and reproductive success (Siracusa et al. 2021). Golden-crowned sparrows have strong social associations across years (Shizuka et al. 2014), and we suggest that future research investigate how winter social ties may affect annual survival.

We found that winter dominance has a strong enough benefit to increase annual survival. Additionally, only the oldest age classes of golden-crowned sparrows experience lower survival, showing evidence of senescence. Golden-crowned sparrows' badges of status predict dominance, but not perfectly, and these badges are used reliably between strangers (Chaine et al. 2011, Chaine et al. 2013). But, familiar birds show signs of individual recognition beyond the badges of status (Chaine et al. 2018). The fact that dominance predicts survival and badges of status does not shows a potential mismatch between benefits from badges and dominance, and this brings up the question: are badges of status are an honest signal? While dominance did not predict survival in each individual year, we never saw a negative cost of dominance. Hence, it appears that dominance in this system can be neutral or beneficial, and subordinance is not an alternative life-history strategy with similar or cycling survival payoffs.

Chapter 4

Social migratory connectivity: do birds that socialize in winter breed together?

Abstract

Researching complete life cycles of migratory animals is essential for understanding conservation and population dynamics. Many studies focus on the breeding season, but surviving winter is equally important and living in groups during winter can play a vital role. Social connections within groups could provide many benefits, and it is often unknown how social connections change across seasons in migratory animals. Here, we focus on social connections in a migratory bird, and ask whether social connections in winter continue during breeding. Golden-crowned sparrows have distinct, stable winter communities which include both winter site and group fidelity across years: birds almost always rejoin the same social community each year. If these birds have social connectivity across migration, we would expect that individuals that associate in winter would also associate together on their breeding grounds. Our small-scale GPS tagging study combined with intensive social behavior data revealed that sparrows in the same tightly-knit winter community migrated to highly disparate locations during summer, showing that social connections in winter do not continue in summer. This suggests that the birds have entirely separate social structures across seasons, and that long-term social memories allows them to reform stable groups each winter.

Keywords: animal communities, migration, non-breeding season, social carryover, social networks, winter groups

Introduction

The study of migratory connectivity seeks to understand the degree to which breeding and non-breeding populations of migratory animals go to similar locations, generally focusing on migratory patterns of populations across broad regions (Webster et al. 2002; Norris and Marra 2007). Understanding these migration patterns and can be vital to conservation and uncovering population dynamics (Sherry and Holmes 1996; Webster et al. 2002; Faaborg et al. 2010; Norris et al. 2004; Marra et al. 2015; Dunn et al. 2019). For example, both golden-winged warblers (*Vermivora chrysoptera*) and Swainson's thrushes (*Catharus ustulatus)* have strong migratory connectivity at the level of populations and their populations declines are linked to specific areas across seasons (Kramer et al. 2018; Humple et al. 2020). However, migratory connectivity could potentially operate on a finer scale if individual-level social connections between migratory animals persist from nonbreeding to breeding seasons. If present, social migratory connectivity could fundamentally affect our understanding of how social relationships form and are maintained across seasons in migratory animals in ways that cannot be understood by only observing them in one part of the year. For example, do the effects of social relationships in one season carry over to affect social relationships in another season? Such carry-over effects are seen in year-resident birds such as great tits (*Parsus major*), where connections in winter predict associations in the breeding season, and in blue tits (*Cyanistes caeruleus*) where social connections in winter predicted nesting proximity and even increased extra-pair paternity (Firth and Sheldon 2016; Beck et al. 2020). In theory, such social carry-over effects could exist in migratory birds as well, but this ideas is rarely tested. In one remarkable case, the migratory European bee-eaters (*Merops apiaster*) maintain cohesive social relationships across seasons by migrating together (Dhanjal-Adams et al. 2018). Some other social relationships have been shown to be maintained across years in migratory birds (e.g., 'dear-enemy' effects among territorial neighbors in breeding season: Godard 1991; flock mate relationships in winter: Shizuka et al. 2014), but we currently do not know if these represent carry-over effects of social relationships that were established in other seasons.

Long-term research on golden-crowned sparrows gives us a sufficiently nuanced understanding of their winter ecology and sociality to test whether social connectivity is maintained across seasons. Golden-crowned sparrows (*Zonotrichia atricapilla*) are small migratory birds that live in complex societies during winter. Specifically, they winter in relatively stable communities with high site fidelity across years, and associations are based on social preference more than overlapping space use (Shizuka et al. 2014). Birds that return to the winter site almost always return to the same social community and tend to increase the strength of their associations with other individuals present (Shizuka et al. 2014). While there are related individuals in the population at the wintering grounds, kin does not predict patterns of association (Arnberg et al. 2015). This raises questions about how sociality may change across seasons, and if migration and breeding location could connect the birds' social patterns across seasons. Evidence from other species suggests that young animals make social connections with neighbors early in life; for example, captive barnacle geese (*Branta leucopsis*) formed connections early in life and showed these preferences into adulthood (Kurvers et al. 2013) and across seasons (Kurvers et al. 2020). Currently, we know that golden-crowned sparrows have broad-scale migratory connectivity, as birds wintering in coastal California tended to go to coastal areas in Alaska while more inland birds went to inland areas in the north to breed (Seavy et al. 2012; Cormier et al. 2016).

Here, we ask if golden-crowned sparrows have social migratory connectivity, defined as social connections between migratory animals from nonbreeding to breeding season. We investigate whether individuals with close social ties during winter go to the same breeding grounds. Two patterns are possible: 1) golden-crowned sparrows from the same winter social communities could breed in close proximity, or, 2) winter associations may be entirely unconnected to breeding locations and associations. The first pattern would reveal that the sparrows maintain social connections year-round and strongly suggest that associations during the breeding season and first migration may be critical for establishing and maintaining the close winter social associations we observe in these birds during winter. The second pattern would be equally interesting as it would reveal that these birds have a strong capacity to remember individuals and have long social memories to reform stable communities each winter.

Understanding social migratory connectivity requires precise geographic locations and detailed information about social interactions. We used archival Global Positioning System (GPS) tags to study golden-crowned sparrow social migratory connectivity. GPS tags light enough to use on small birds are a relatively new technology, and few songbirds have this sort of precise location data across seasons (see: Hallworth and Marra 2015; Fraser et al. 2018; Cooper and Marra 2020; Humple et al. 2020). GPS tags open up opportunities to discover exact migration paths and breeding locations. This technology gives us the geographic resolution to answer questions about how social connections change across seasons. While we report a small sample size, we have detailed data on individual social interactions prior to migration and follow birds from the same winter social group. In addition, the suggestive patterns we observed motivate novel questions about the relationships we might expect between migration departure dates, duration of migration, and time spent on summer breeding grounds.

Methods

Golden-crowned sparrows arrive at our field site at the University of California Santa Cruz (UCSC) Arboretum around the end of September. They form winter flocks and remain at the study site until April/May, when they leave for their breeding grounds in northern Canada and Alaska. Our study focused on the migratory patterns of individual golden-crowned sparrows after observing the birds for at least one season on their wintering ground.

We programmed the GPS locators (PinPoint 10 Swift GPS tags, Lotek Wireless) to take up to 100 locations. The length of time a tag took to read satellite signals at each point affected how long the battery life lasted, and tags were expected to record around 75-80 points. These locations are precise GPS coordinates, accurate to within 10 m (Figure 3), which gave us the precision to see if birds not only bred nearby each other, but if they had neighboring territories (golden-crowned sparrow breeding territories are approximately 0.86 hectares, D.S. unpublished data). We programmed the tags to take points along the birds' migration paths and points on the breeding ground to establish the exact location of breeding territories. The tags took points every two to five days, depending on our estimations of when the birds might be on migration versus established on the breeding grounds.

In the spring of 2017, we attached 30 archival PinPoint 10 Swift GPS tags to previously banded golden-crowned sparrows that had been at the Arboretum for at least several months prior or had returned from previous years. In the spring of 2018, we attached 40 GPS tags to a different sample of sparrows who met the same criteria. After attaching the GPS tags, we monitored sparrows in the field, ensuring that birds maintained their normal behavior and were able to move, fly, and feed unhindered.

Archival GPS tags must be recovered to retrieve the data, so we depended on the tagged birds returning to the UCSC Arboretum after the breeding season. Despite deploying a reasonable number of tags, we only obtained adequate data from four birds over two field seasons due to several unanticipated obstacles. From 30 GPS tags in 2017, we recovered five the next field season. The low return rate of tags was due to problems with the GPS harness attachment, as at least four to six birds lost their harnesses before migration, and of seven previously tagged birds which returned, two had lost their tags after leaving the winter site. Of the five that returned with tags, two tags malfunctioned and gathered incomplete data (8 and 15 locations respectively, all before the birds left California), leaving us with data for three birds. From 40 tags attached to sparrows in 2018, we recovered one tag. In 2018, a substantial portion of our study site was destroyed to make a parking lot (0.54 ha) within a month of tag-deployment, in the precise location where we had focused our tagging effort. Additionally, during fall migration in 2018, multiple large fires along the California coast may have interfered with birds returning. These two factors in 2018 likely resulted in the very low return rates of tagged birds in the fall. The four GPS tags with full data collection gathered 75 points for bird 77968, 68 points for bird 81319, 85 points for 81324, and 49 points for 19388.

We used the GPS data to determine the location of the golden-crowned sparrows' breeding territories by searching for highly localized clumps of more than five GPS points at the furthest northern location of a bird's migration route. The breeding locations for all four birds had a high density of GPS points over a small area (< 0.4 km^2), and we used these locations to determine the start and end date of the time each sparrow spent on its putative breeding territory. We determined the average breeding territory location by calculating a centroid location from the clustered points using the package *geosphere* (Hijmans 2019). To calculate the distance of spring migration, we used the great-circle-distance between two points from the Vincenty ellipsoid method (Hijmans 2019). We exclude two outlier GPS points during the breeding season (one for bird 77968, one for bird 81324) that were deemed erroneous due to their extreme distance from other points clumped on the breeding grounds (327 and 615 km away) and reduced number of satellites for the GPS fixes (3 satellites, compared to 5 or more for most other points).

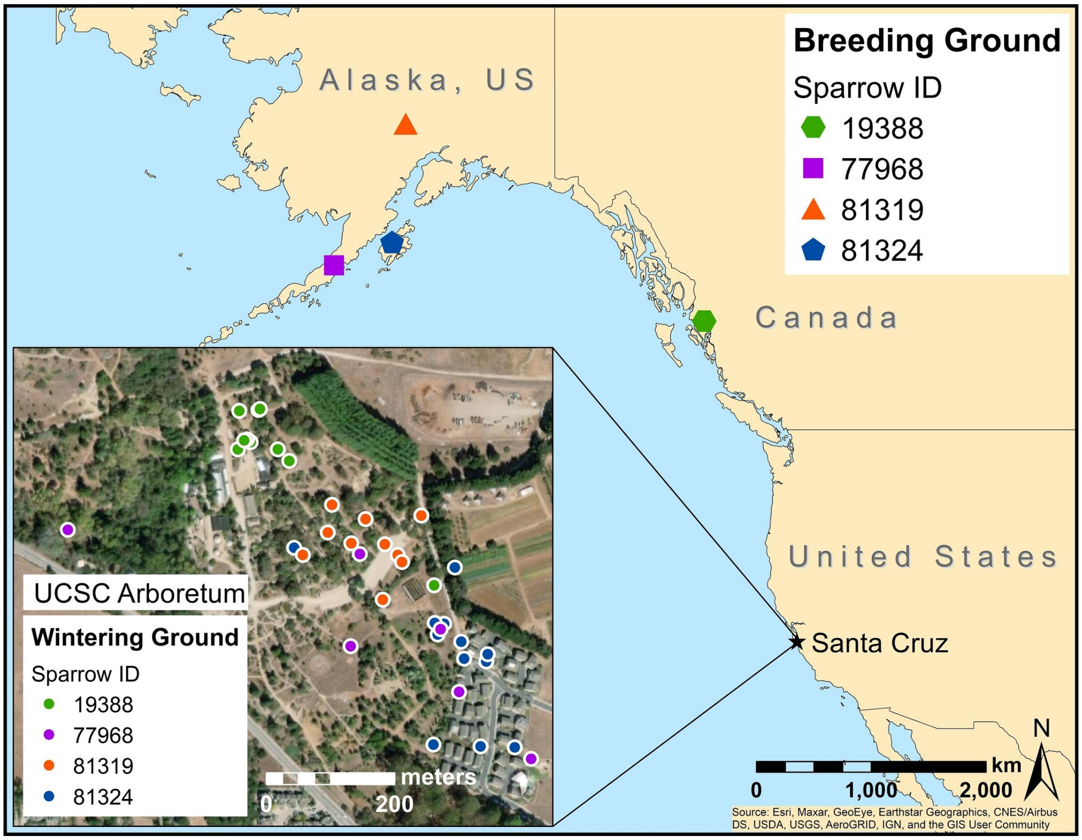
As part of an ongoing study, we gathered morphological and behavioral data from golden-crowned sparrows during their non-breeding season at the UCSC Arboretum. We caught, measured, and banded the sparrows, and collected a blood sample from the ulnar vein to sex individuals (Chaine et al. 2011; Griffiths et al. 1998). During banding, each bird received a numbered metal band and color bands with unique color combination to be identifiable in the field. We found which birds flocked together with frequent censuses throughout the winter season and build social networks following methods from Shizuka et al. (2014). We modified these methods to include all birds, regardless of age (Shizuka et al. (2014) excluded birds from the social network analysis if they were banded for the first time that season). Our network analysis incorporated all birds seen more than five times in the field that season, including birds that were initially banded that year. We only used flocking data from before April 1 of each year, as later in the season closer to migration, community structure can decrease. From the flocking data, we built undirected social networks with the R package *igraph* (Csardi and Nepusz 2006). The network is made up of individuals (‘nodes’), which are connected by lines (‘edges’) (Croft et al. 2008; Krause et al. 2015). We weighted edges by how often birds are seen together with a correction for how many times each bird is seen in total, called the Simple-ratio index (Cairns and Schwager 1987). The simple-ratio index ranges from zero to one; if one bird is never seen without the other bird, they are connected by edge value of one, if they are rarely seen together, the value is closer to zero (Cairns and Schwager 1987). We determined bird community membership with a simulated annealing algorithm from the package *rnetcarto* (Doulcier and Stouffer 2015). We used a social network measure for individuals called within-community node strength (z-scores from Guimerá and Amaral 2005; hereafter called within-community strength) with the package *rnetcarto* and normalized scores (Doulcier and Stouffer 2015). Within-community strength takes the sum of all edge weights a bird has to other individuals within its own community, then these scores are normalized using a Z-score based on the distribution of association strengths within the community so values are comparable for individuals in different communities and years. For example, a bird that associates with numerous individuals in its community would have a higher within-community strength, as well as if a bird is seen frequently with a smaller number of individuals in its community.

All analysis was performed in R version 4.0.2 (R Core Team 2020), and maps were made in ArcMap version 10.7.1. We made a live migration track map, available in the online Supplementary Material, using the R package *moveVis* (Schwalb Willmann et al. 2020).

All methods complied with Federal and California State regulations under permits to B. Lyon and were approved by the UCSC Institute for Animal Care and Concern (IACUC; Animal Welfare Permit Number Lyonb1808 to B. Lyon).

Results

All four of the tagged birds that yielded usable data had summer locations distant from each other, with the closest 698 km apart and the most distant 1837 km apart (Figure 1). The three birds in 2017, all from the same tight-knit winter social group, had very distant breeding territories, so we found no evidence that winter community affected the proximity of summer breeding territories for these individuals. Note that the scale on which birds overlap during the winter is hundreds of meters, while in the summer, all sparrows were many hundreds of kilometers apart. Bird 19388, which we tracked in 2018, was also present on the wintering grounds at the Arboretum the previous year with the three other birds (2017), and it was in a separate social group from those three (Figure 2). The data from the GPS tags showed precise locations, with the ability to even see approximate potential nesting locations from the density of points in one location (Figure 3).



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1. Breeding (main map) and wintering (inset map) locations for each bird. Tag data for bird 19388 was from one year after (2018) the other three birds (2017), but all birds were present in winter 2017. Symbol representation of each point is not to scale, and breeding ground areas are vastly smaller than each symbol. The points shown at the UCSC Arboretum were from the GPS tags shortly before the birds left for spring migration, not the birds' home ranges for the winter season. Close to spring migration, winter community structure can begin to break down. To see the communities throughout winter from social network analysis, see Figure 2.

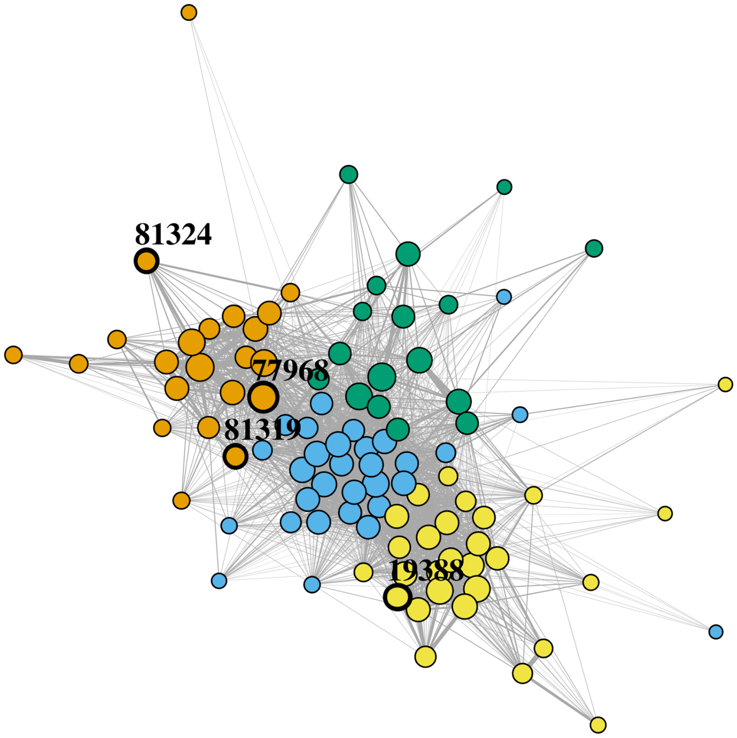


Figure 2. The visualized golden-crowned sparrow social network at the UCSC Arboretum for the winter of 2016–2017 (representation is not spatially explicit). We found four communities where each community is shown in a different color, and circles represent individual birds. The size of each circle is proportional to within-community strength, so larger circles show birds that have stronger associations with other birds in their communities. The thickness of the lines connecting individuals is proportional to how frequently birds associated with each other weighted by the times each bird was seen in total (a Simple-ratio index). The four individuals with GPS tag data are highlighted in black edging with their band ID's. Birds 81324, 77968, and 81319 have GPS data corresponding with this year, but GPS data for bird 19388 is from the following year (2018).

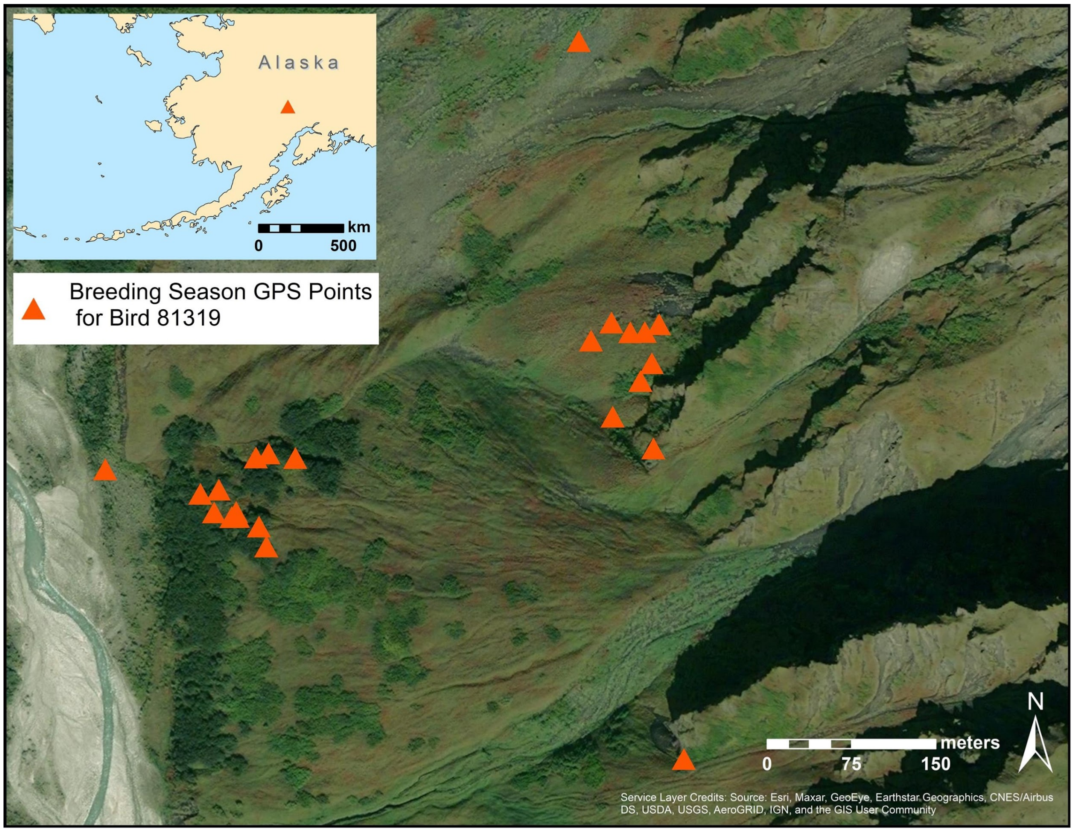


Figure 3. A map illustrating breeding season site occupancy and the level of resolution possible with GPS tags. Each triangle is a GPS point taken for bird 81319 on its summer breeding ground. The GPS points span June 21 to September 2, 2017, the birds' entire duration on its summer grounds. The two main clusters of points are sequential and could reflect a second nesting attempt, perhaps after nest depredation, or the adult's movement with fledglings away from the nest. We found a similar pattern with bird 19388.

The sparrows' spring migrations followed the same approximate coastal route, but the birds did not use the same routes or stopover spots (Figure 5). Bird 19388 migrated further inland than the others, up to 98 km inland in parts of central California (39.10146, -122.5892) and 180 km inland in south-western Canada (50.81969, -125.8825). As this was the only bird with GPS data in 2018, it is unclear if this difference is due to a year effect or general variation among birds' migration paths. The variation in spring migration duration appeared to originate from time spent at stopover sites rather than number of stopovers. Most of the GPS tags stopped recording points before birds had completed fall migration, but we have the complete fall migration record for bird 81324. Interestingly, this bird spent 36 days on fall migration, identical to the 36-day spring migration (Appendix 4 Table S1).

How quickly birds migrated made the difference in how long they spent on the breeding territory. Spring migration duration ranged from 32-62 days, nearly a two-fold difference. The sparrows departed for spring migration from the Arboretum within 12 days of each other, and fall migration departure was within seven days of each other (Appendix 4 Table S1). Due to such similar migration departure dates in both spring and fall, time on the breeding territory appeared to be constrained by the duration of spring migration (Figure 4). We might expect that a closer breeding location would allow the birds to get there more quickly. However, spring migration distance appeared unrelated to how many days it took the birds to migrate and even suggested a negative relationship (Figure 4).

The sparrows had a wide range of within-community strength scores, but within-community strength showed no pattern with migration duration or distance (Figure 4). Nonetheless, the limited sample size warrants caution on this interpretation.

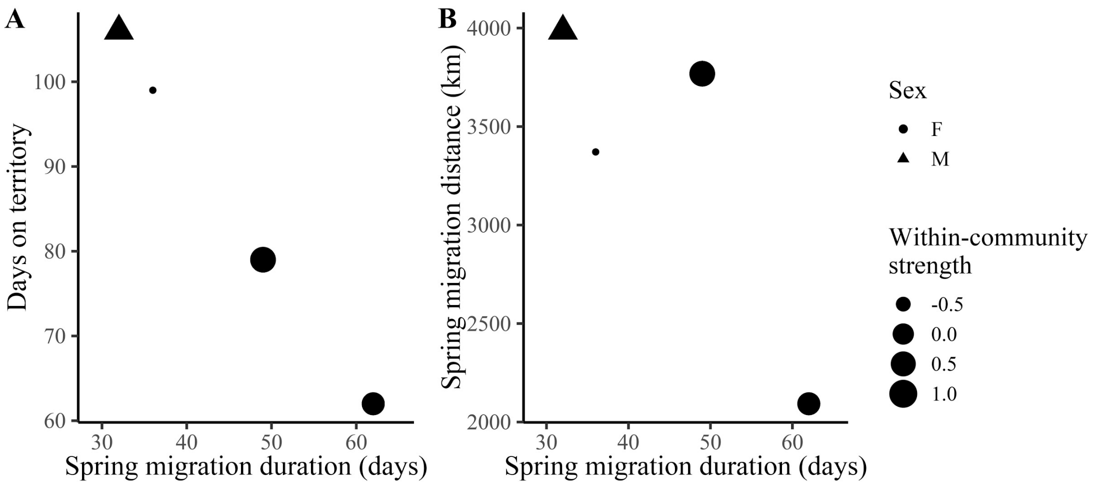


Figure 4. A. The number of days a bird spent on its breeding territory decreased with time spent on migration. **B.** Migratory distance appeared to have little to no relationship with how many days a bird spent on spring migration, and potentially hinted at a negative relationship. Point shape indicates sex and point size is weighted by within-community strength, or how strongly a bird associated with other individuals in its community.

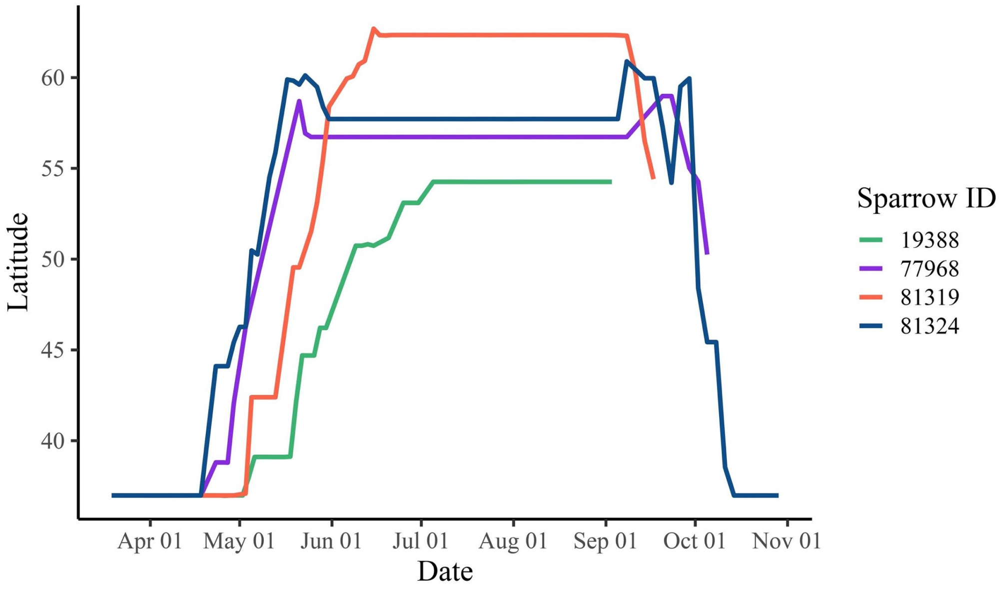


Figure 5. An increase in latitude from spring to fall of golden-crowned sparrows migrating north to their breeding territories illustrates the among-individual variation in the duration of migration and both the location and time on the breeding grounds.

Discussion

The golden-crowned sparrows we studied all used breeding grounds that were widely separated from each other, showing entirely different social connections on winter versus summer grounds. While space use and the physical environment can play a large role in helping determine social structures (He et al. 2019), social affiliations and preferences are a critical part of driving animal interactions within these groups (Papageorgiou and Farine 2021). Shizuka et al. (2014) established that golden-crowned sparrows maintain social connections across years, and that these social preferences are not just based on space use. This research in the same study system combined with our findings here indicates that these birds have long-term social relationships, and potentially long-term social memory. Other migratory birds have been shown to have social memory across years; for example, male hooded warblers (*Setophaga citrina*) recognized a few neighboring males' songs eight months later during the following breeding season (Godard 1991). While we have a limited sample size for the location of the sparrows' breeding territories, the social affiliations from the field are comprehensive, and if birds in the same winter community went to similar breeding grounds, we should have seen some indication with breeding locations closer to each other, rather than hundreds of kilometers apart.

The timing of the golden-crowned sparrows' migrations revealed some interesting suggestive patterns that could motivate future investigations. The sparrows did not appear to migrate together or use any of the same stopover sites despite being part of the same winter social community. The golden-crowned sparrows all departed for spring migration in a relatively small window of time (12 days), so arrival on the breeding grounds is potentially determined by the speed of migration and length of time spent at stopover sites. Speed of migration is subject to a many factors, whether environmental or based on individual behavior and flexibility; for example, the length of time spent at stop-over sites similarly determined how long migration took in Northern Wheatears (*Oenanthe oenanthe*) (Arlt et al. 2015). This contrasts with wood thrushes (*Hylocichla mustelina*), where the date left on spring migration correlated with the arrival date on the breeding grounds (Stanley et al. 2012). The phenology of migration can have many effects and repercussions on the success of the breeding season and fledging young, and causes on the variation of timing can be due to wind, weather, temperature, photoperiod, combinations of the above, along with some unknowns (Haest et al. 2020). Along with environmental factors, it could be necessary to consider individual variation in migration timing and how that effects the length of time on the breeding grounds, especially in species which have similar departure dates.

Golden-crowned sparrow winter communities are relatively stable yet also show some turnover (Shizuka et al. 2014). Communities continue over multiple years despite changing composition due to deaths and new individuals joining. How new birds integrate into these communities will be vital to our understanding of social group maintenance and stability over time (Shizuka et al. 2014; Shizuka and Johnson 2019). While we found no connection between winter social communities and summer locations, previous work in winter found genetic relatedness in the UCSC

Arboretum sparrow population, implying that some related individuals migrate from the breeding grounds to similar wintering areas. While kinship did not predict social group membership nor associations in 2010 and 2011, 16% and 20% of the sparrows respectively had first-order relatives (relatedness coefficient ≥ 0.5, such as a parent, offspring, or sibling) present in the population (Arnberg et al. 2015). Perhaps related juveniles migrate from a shared breeding ground to the same over-winter location in their first year, then migrate to different breeding grounds in the following years while keeping fidelity to their initial winter site. This pattern has been observed in migratory pied avocets (*Recurvirostra avosetta*) and greater flamingos (*Phoenicopterus roseus*), both of which show high fidelity to their first wintering site despite differing breeding sites (Sanz-Aguilar et al. 2012; Chambon et al. 2019). Hence, low natal breeding philopatry does not require low wintering site fidelity.

Conclusions

Understanding how animal social groups are organized and the consequences of individual interactions are central to behavioral studies (Svensson and Sheldon 1998). Individual interactions shape social groups, and different behavioral and morphological traits can drive these interactions (Snijders and Naguib 2017). There is feedback between individual traits and social organization: individual interactions scale up to build group organization, and overall group structure can, in turn, shape selection pressures and drive the evolution of certain traits (Aureli et al. 2008; Cantor et al. 2021). This dissertation focuses on how different aspects of animal sociality connect through animal personality, dominance, social behavior, and what traits affect individual survival. I studied how social behaviors co-occur with physical characteristics and how those connections might influence survivorship in a social, migratory bird during the non-breeding season.

In **Chapter 1**, I found that golden-crowned sparrows show consistent behaviors within and across seasons, constituting personalities. Personality traits did not show a pattern of decreased repeatability over time, contrary to many other studies of personality in different taxa where the repeatability of behaviors decrease over time (Bell et al. 2009). Personality behaviors did not correlate with the behaviors and morphologies I measured: dominance, badge size, age, wing length, and sex. Additionally, in Chapter 2, personality did not correlate with any social network measures. It was surprising that no factors here correlated with personality, as this is not in line with many other studies where personality correlated with sociality, dominance, age, sex, and size (Dingemanse and de Goede 2004; Kurvers et al. 2009; David et al. 2011; Class and Brommer 2012; Herborn et al. 2014). However, personality in this system appears to be an independent axis of variation, supported by results in Chapters 1 and 2. While personality did not drive social interactions, it could correlate with other factors not measured here, such as foraging and predation.

Uncovering which traits and behaviors correlate with social position is key to understanding potential drivers of individual sociality. Previous research has found links between social behaviors and everything from personality to age to dominance (Aplin et al. 2013; Farine et al. 2015; Oh and Badyaev 2010). My dissertation adds to this body of work and integrates many facets not often considered, such as comparing personality and dominance to social network position at the same time. Like personality, measures of sociality in golden-crowned sparrows were relatively consistent in an individual over time but did show development with age (**Chapter 2**). Even with the turn-over of group composition each year, individuals tended to maintain similar levels of interactions, such as how many individuals they associated with, which is comparable to consistent social positions found in other bids birds, sharks, and mammals (Jacoby et al. 2014; Aplin et al. 2015; Blaszczyk 2018; Plaza et al. 2020). While two of the three aspects of social position in golden-crowned sparrows, degree and effective degree, were moderately repeatable across years, within-community strength showed much lower consistency. Older and smaller individuals had more connections and also larger numbers of close connections.

Chapter 4 investigated if social connections between birds were present only in winter or maintained in the breeding season. While several obstacles arose in the field research that led to a very small sample size, I detected that individuals in the same social group do not breed in the same location. This shows evidence of long-term social memory, as Shizuka et al. (2014) established that birds return to the same communities across years, interact with the same individuals, and here (Chapter 4), birds in the same social group breed in different locations, hundreds of kilometers apart. Enduring social connections over time is an essential aspect of maintaining stable social structures, both here and likely in other species.

In **Chapter 3**, I examined annual survival from winter to winter, a critical timeframe that is frequently overlooked in studies of migratory birds. This chapter puts traits examined in previous chapters into a fitness context, and the results here provide concrete directions for further research. I found that dominance correlates with higher rates of year-to-year survival across ten years of data. More dominant individuals had higher probabilities of returning to the study site, suggesting that dominance in winter provides benefits that ultimately increase annual survival rates. Other studies have found that more dominant individuals have higher levels of over-winter survivorship (i.e., within a single winter season), but little research has investigated annual survival from winter to winter (Kikkawa 1980; Desrochers et al. 1988; Koivula and Orell 1988; Piper and Wiley 1990). Dominance did not correlate with personality in Chapter 1 nor the number of social connections in Chapter 2, yet interestingly proved crucial to survivorship. An important next step is to see if social network measures provide any survivorship benefits. Separate analyses of year-to-year survivorship revealed that dominance only correlated with survival in one year. Hence, dominance may only improve survival in particular circumstances, e.g., specific environmental conditions. Alternatively, the effects of dominance could be more subtle and only detected over extended time periods with larger sample sizes. I found that survival decreased with age, and this was only detected in the very oldest age classes, showing evidence of senescence. While birds are known for relatively steady rates of survival in adults (Deevey 1947; Pinder et al. 1978), it is possible to pick up signs of senescence with long-term data (Rockwell et al. 1993; Bouwhuis et al. 2012; Class and Brommer 2016).

Ultimately, life-history stages can shape individual behaviors as individuals gain experience over time, and the social environment can, in turn, have selective pressure on the evolution of life-history traits (Svensson and Sheldon 1998). Additionally, demography plays a pivotal role in shaping social groups (Shizuka and Johnson 2019). As individuals leave their group (e.g death or emigration), how the remaining individuals respond influences the group's stability, and how new members join the group alters behaviors and patterns of social interaction (Shizuka and Johnson 2019). Here, I sought to link demography and life-history in a social animal by focusing on how individual traits such as size and sex connect to social behavior and survival. I found that the sparrows' winter social interactions are not determined by personality and that dominance, age, and size are some of the most important factors in various measures of social behavior, and in turn, which birds are more likely to survive. Golden-crowned sparrows have a complex social system that the birds maintain over time yet is only present in a single season of the annual cycle, winter. Shizuka et al. (2014) established that golden-crowned sparrows have stable groups and association preferences that can last for years, motivating this research to investigate what behavioral and morphological traits determine individual social associations. The sparrows not only maintain social associations over time (Shizuka et al. 2014), but gain in the number of social connections with age (Chapter 2). Age, and likely experience, play a pivotal role in the golden-crowned sparrow system in maintaining social communities. Additionally, connecting annual survival with different traits is essential to learn which traits may be under selection. Certain traits may increase fitness at different times of year and have strong enough benefits to increase fitness in the following stages in the annual cycle. Prior studies have examined distinct elements of sociality, personality, dominance and fitness, for example, dominance and survival, or social position and age, or personality and badge of status (Fretwell 1969; Mateos-Gonzalez and Senar 2012; Sosa 2016). My dissertation integrates all of these factors into a comprehensive study of golden-crowned sparrow's social lives, morphology, and survivorship, presenting a more complete and integrated understanding of the interplay between sociality and survival in migratory birds.

Appendix 1

Supplementary Material for Chapter 1

Table S1. Eigenvalues for each Principal Component, showing percent variance and cumulative variance. PC 1, PC 2, and PC 3 were selected as they all have eigenvalues greater than one.

	Eigenvalue	Variance (%)	Cumulative Variance (%)
PC 1	2.337	38.947	38.946
PC 2	1.157	19.276	58.223
PC 3	1.005	16.742	74.965
PC 4	0.836	13.935	88.901
PC 5	0.515	8.590	97.491
PC 6	0.151	2.509	100

Table S2. Factor loadings for each trait in all Principal Components. Values over 0.5 are shown in bold for PC 1, PC 2, and PC 3, as these have the strongest influence on each PC.

	PC 1	**PC 2**	**PC 3**	PC 4	PC 5	PC 6
Hops	**0.527**	-0.029	-0.080	0.061	0.801	-0.265
Vocalizations	0.031	0.109	**-0.985**	0.037	-0.122	-0.012
Perch turns	**0.567**	0.161	0.107	-0.060	-0.545	-0.584
Perch bouts	**0.616**	0.082	0.034	-0.078	-0.140	0.766
Escape test	-0.060	**0.704**	0.096	0.699	0.037	0.047
Bag test	0.129	**-0.678**	-0.025	0.705	-0.162	0.012

Table S3. Correlation matrices for each year of data (2014, 2015, 2016) and all three years combined. Wing length correlated with all other traits strongly in 2015, so to avoid collinearity issues within the 2015 models, we removed wing length. We used Pearson-correlations and listwise-deletion for any missing values. All values in grey are non-significant, and P-values are indicated as: *P < 0.05, **P < 0.01, ***P < 0.001.

All years correlation matrix

	Dominance	*Black size*	*Gold size*	*Wing length*
Dominance				
Black size	0.45^{***}			
Gold size	0.20^{*}	0.33^{***}		
Wing length	0.51^{***}	0.50^{***}	0.40^{***}	

2014 Correlation matrix

	Dominance	*Black size*	*Gold size*	*Wing length*
Dominance				
Black size	0.61^{***}			
Gold size	0.30^{*}	0.40^{**}		
Wing length	0.43^{***}	0.32^{*}	0.39^{**}	

2015 Correlation matrix

	Dominance	*Black size*	*Gold size*	*Wing length*
Dominance				
Black size	0.37^{*}			
Gold size	0.18	0.41^{**}		

Wing length	0.48***	0.65***	0.58***	

2016 Correlation matrix

	Dominance	*Black size*	*Gold size*	*Wing length*
Dominance				
Black size	0.33*			
Gold size	0.10	0.17		
Wing length	0.70***	0.50***	0.27	

Appendix 2

Supplementary Material for Chapter 2

Table S1. Social network models of the data from all years: 2014, 2015, and 2016.

	Degree			**Effective Degree**			**Within-community strength**		
Predictors	*B*	*95% CI*	*P*	*B*	*95% CI*	*P*	*B*	*95% CI*	*P*
Intercept	35.12 ***	29.92 – 40.32	**<0.001**	20.72 ***	17.06 – 24.38	**<0.001**	0.20	-0.05 – 0.45	0.119
Dominance	0.43	-2.02 – 2.87	0.734	0.41	-1.28 – 2.10	0.631	0.17	-0.03 – 0.37	0.090
Black size	-0.87	-3.42 – 1.68	0.502	-0.34	-2.10 – 1.42	0.708	0.05	-0.16 – 0.26	0.660
Gold size	0.58	-1.60 – 2.77	0.600	-0.44	-1.95 – 1.07	0.567	0.14	-0.03 – 0.31	0.110
PC 1	-0.91	-2.95 – 1.13	0.384	-0.74	-2.14 – 0.67	0.304	0.08	-0.09 – 0.24	0.358
PC 2	0.15	-1.87 – 2.17	0.882	-0.00	-1.39 – 1.39	0.997	-0.05	-0.22 – 0.12	0.557
Sex (M)	2.51	-4.02 – 9.05	0.451	1.69	-2.83 – 6.22	0.463	-0.06	-0.58 – 0.47	0.832
Mass (g)	-4.66 **	-7.44 – -1.88	**0.001**	-3.28 ***	-5.20 – -1.36	**0.001**	-0.18	-0.41 – 0.05	0.117
Band Age	2.75 *	0.43 – 5.07	**0.020**	1.77 *	0.17 – 3.37	**0.030**	-0.03	-0.22 – 0.16	0.756
Random Effects									
σ^2	72.70			32.90			0.81		
τ_{00}	54.66_{band}			28.23_{band}			0.03_{band}		
	13.07_{year}			6.58_{year}					
N	106_{band}			106_{band}			106_{band}		
	3_{year}			3_{year}					
Observations	129			129			129		
Marginal R^2 / Conditional R^2	0.115 / 0.542			0.122 / 0.574			0.067 / 0.100		

* *$p<0.05$* ** *$p<0.01$* *** *$p<0.001$*

Table S2. Results from the social network models for 2014.

	Degree			**Effective Degree**			**Within-community strength**		
Predictors	*B*	*95% CI*	*P*	*B*	*95% CI*	*P*	*B*	*95% CI*	*P*
Intercept	33.17 ***	28.37 – 37.98	**<0.001**	18.47 ***	15.40 – 21.54	**<0.001**	0.36 *	0.04 – 0.69	**0.031**
Dominance	1.13	-3.87 – 6.14	0.649	0.83	-2.37 – 4.03	0.601	0.18	-0.16 – 0.52	0.283
Black size	-0.97	-6.03 – 4.08	0.699	0.42	-2.81 – 3.65	0.795	0.03	-0.31 – 0.37	0.858
Gold size	-0.24	-4.45 – 3.97	0.908	-2.24	-4.93 – 0.45	0.100	0.21	-0.08 – 0.50	0.146
PC 1	-0.69	-4.32 – 2.95	0.704	-0.96	-3.28 – 1.36	0.408	0.16	-0.08 – 0.41	0.192
PC 2	-2.52	-6.32 – 1.27	0.186	-2.03	-4.45 – 0.40	0.099	0.02	-0.23 – 0.28	0.849
Sex (M)	4.55	-6.55 – 15.66	0.412	2.36	-4.73 – 9.46	0.504	-0.12	-0.88 – 0.63	0.745
Mass (g)	-6.35 *	-11.38 – -1.31	**0.015**	-4.08 *	-7.29 – -0.86	**0.014**	-0.08	-0.42 – 0.26	0.629
Band Age	3.48	-0.61 – 7.57	0.093	1.98	-0.63 – 4.59	0.133	-0.05	-0.33 – 0.22	0.704
Observations	48			48			48		
R^2 / R^2 adjusted	0.181 / 0.013			0.243 / 0.088			0.161 / -0.011		

* *$p<0.05$* ** *$p<0.01$* *** *$p<0.001$*

Table S3. The results from social network models for 2015.

	Degree			**Effective Degree**			**Within-community strength**		
Predictors	*B*	*95% CI*	*P*	*B*	*95% CI*	*P*	*B*	*95% CI*	*P*
Intercept	31.52 ***	25.10 – 37.93	**<0.001**	17.25 ***	12.65 – 21.85	**<0.001**	0.24	-0.45 – 0.93	0.490
Dominance	2.82	-1.74 – 7.38	0.218	1.86	-1.41 – 5.13	0.256	-0.02	-0.51 – 0.47	0.930
Black size	-0.71	-5.30 – 3.88	0.755	0.32	-2.97 – 3.61	0.845	0.16	-0.33 – 0.66	0.509
Gold size	-0.84	-4.60 – 2.92	0.653	-1.20	-3.90 – 1.50	0.371	0.21	-0.20 – 0.62	0.302
PC 1	-2.79	-6.64 – 1.06	0.149	-1.48	-4.24 – 1.27	0.281	-0.16	-0.57 – 0.26	0.444
PC 2	1.97	-1.64 – 5.59	0.275	1.30	-1.29 – 3.89	0.315	0.06	-0.33 – 0.45	0.755
Sex (M)	1.11	-9.66 – 11.89	0.834	4.30	-3.43 – 12.02	0.266	-0.36	-1.52 – 0.80	0.534
Mass (g)	-7.38 **	-12.49 – -2.27	**0.006**	-6.09 **	-9.75 – -2.42	**0.002**	-0.34	-0.89 – 0.21	0.218
Band Age	1.77	-2.11 – 5.65	0.360	0.77	-2.01 – 3.55	0.579	0.06	-0.36 – 0.48	0.776
Observations	41			41			41		
R^2 / R^2 adjusted	0.437 / 0.297			0.393 / 0.241			0.176 / -0.030		

* *p<0.05* ** *p<0.01* *** *p<0.001*

Table S4. Results from the social network models for 2016.

	Degree			Effective Degree			Within-community strength		
Predictors	*B*	*95% CI*	*P*	*B*	*95% CI*	*P*	*B*	*95% CI*	*P*
Intercept	40.58 ***	33.93 – 47.23	**<0.001**	24.62 ***	19.33 – 29.92	**<0.001**	-0.04	-0.53 – 0.45	0.864
Dominance	-0.59	-6.27 – 5.08	0.832	-0.01	-4.53 – 4.51	0.996	0.25	-0.17 – 0.66	0.238
Black size	0.36	-5.48 – 6.21	0.900	-0.41	-5.06 – 4.25	0.860	-0.08	-0.51 – 0.35	0.717
Gold size	0.64	-3.44 – 4.72	0.751	-0.33	-3.58 – 2.92	0.836	0.08	-0.22 – 0.38	0.601
PC 1	-1.55	-6.17 – 3.08	0.500	-1.19	-4.87 – 2.49	0.516	0.08	-0.26 – 0.42	0.644
PC 2	1.65	-3.12 – 6.42	0.485	1.31	-2.49 – 5.11	0.486	-0.12	-0.47 – 0.23	0.501
Sex (M)	1.82	-14.75 – 18.39	0.824	0.22	-12.97 – 13.42	0.973	0.68	-0.54 – 1.89	0.265
Mass (g)	1.91	-4.29 – 8.11	0.535	0.39	-4.55 – 5.33	0.874	-0.12	-0.58 – 0.33	0.590
Band Age	0.98	-4.67 – 6.62	0.727	1.17	-3.33 – 5.66	0.601	-0.12	-0.53 – 0.30	0.564
Observations	40			40			40		
R^2 / R^2 adjusted	0.078 / -0.160			0.049 / -0.197			0.243 / 0.048		

* *p<0.05* ** *p<0.01* *** *p<0.001*

Appendix 3

Supplementary Material for Chapter 3

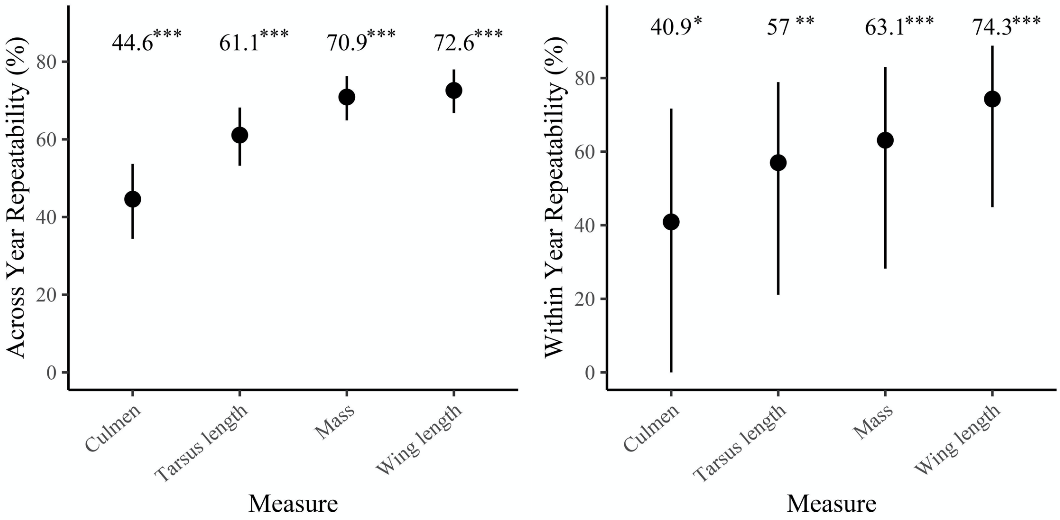


Figure S1. The repeatability for body size measurements for individual golden-crowned sparrows within and across years. Error bars are 95% confidence intervals. Confidence intervals for within year repeatability are much larger due to small sample size (*N* = 18-20), while sample size for across year is much larger (*N* = 210-235) so the bootstrapped confidence intervals are much more accurate. Significance is indicated by: * $P < 0.05$, ** $P < 0.01$, , *** $P < 0.001$.

Appendix 4

Supplementary Material for Chapter 4

Table S1. Migratory and breeding location parameters for four golden-crowned sparrows.

Bird ID	Year	Spring migration start date	Migration distance (km)	Days on spring migration	Dates on breeding territory	Days on territory	Average breeding location (lat, long)
77968	2017	23/4/17	3986	32	25/5/17 – 8/9/17	106	(56.72763, -158.2483)
81319	2017	3/5/17	3768	49	21/6/17 – 9/2/17	73	(62.34368, -152.7031)
81324	2017	23/4/17	3371	36	29/5/17 – 5/9/17	99	(57.71666, -153.7152)
19388	2018	4/5/18	2093	62	5/7/18 – 5/9/18*	62+	(54.25583, -129.2881)

*Indicates that this was not the start of fall migration but when the GPS tag stopped recording data.

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