Using Ptilochronology to Investigate Cross-seasonal Effects of Condition on Winter Social
Traits in a Migratory Sparrow

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Abstract

Within populations, traits vary between individuals due to differences in genetic, nutritional, and environmental condition. Genetic differences between individuals can lead to differences in intrinsic body condition and traits while differential access to environmental resources, such as food, can also lead to differences in body condition such as nutritional health. Some traits are more dependent on nutritional condition while others are more controlled by genetic influence. Ptilochronology is a method for determining the growth rate of feathers from feathers that have completed their growth based on distance between feather bars that indicate daily growth. Previous studies have examined the degree to which feather grown rates reflect condition-dependence at the time of feather growth. However, ptilochronology has yet to be used to determine cross-seasonal effects of condition on traits that function at a later time in a bird's life, such as plumage traits that are used in the following season from which they are grown. Here we show that feather growth rate in golden-crowned sparrows, an index of fall-molt conditions, have significant cross-seasonal influences on the color intensity of their black crown feathers in winter plumage. In contrast, we found that an index of genetic variation of individuals does not correlate with growth rate of feathers, which suggests feather growth rate in golden-crowned sparrows may be condition-dependent rather than a reflection of genetic differences among individuals. We found no other correlations between tail feather growth rate and other important winter traits. Our findings suggest that different winter social traits are influenced by different proximate mechanisms.

Keywords: social trait variation, condition-dependence, nutrition, feather growth rate, golden-crowned sparrow

Introduction

Understanding the causes and consequences of trait variation among individuals is a fundamental issue in evolutionary biology. Most traits vary between individuals in a population, and this trait variation can reflect the physiological and/or environmental conditions of individuals (King and Murphy 1985). In some cases, variation in individual condition or quality depends on the individual's access to environmental resources such as food (King and Murphy 1985). For example, nutritional condition in the loggerhead shrike (*Lanius ludovicianus*) depends on the density of perching spaces within a territory, individuals with few hunting perches suffer from lowered nutritional conditions when compared to individuals defending territories with richer densities of hunting perches (Yosef and Grubb 1992). Multiple studies have explored how the condition of birds and their environment are reflected in intraspecific variation in traits between individuals within the same flock. Low nutritional conditions in white-throated sparrow (*Zonotrichia albicollis*) juveniles lead to significantly reduced total body mass as adults, which suggests individuals metabolize muscle and lower total body mass to balance energy demands during poor conditions (Cristol et al. 2001).

The effect of nutritional condition on traits can play other roles in a bird's life, such as shaping intraspecific variable traits that affect aspects of fitness or reproductive success. For example, Zebra finches (*Taeniopygia guttata*) with poor nutrition early in life exhibit higher mortality rates later in life, as well as plumage abnormalities as compared to individuals with better nutritional conditions early in life (Birkhead et al. 1999). The pre-migration body condition in greater snow geese (*Chen caerulescens*) affects intraspecific variation in behavior and reproductive success; birds with a better pre-migration body condition reached optimal combinations of lay date and clutch size earlier than individuals in poor condition (Bêty et al. 2003). Nest initiation date and body condition have been shown to covary with reproductive and survival components of fitness (Blums et al. 2005). Previous studies showing that body mass and mortality rate correlate with nutritional condition suggest that body mass and mortality rate can act as proxies for general aspects of condition in individuals (Cristol et al. 2001; Birkhead et al. 1999). Other studies have shown that condition affect traits related to other aspects of fitness,

such as the behavioral timing of breeding and clutch sizes in snow geese (Bêty et al. 2003). Although these studies have successfully demonstrated certain traits can act as indices of condition, other influential factors like population, season, and sex make it difficult to use any one trait as a single universal morphometric measure of condition (Labocha and Hayes 2012). Given this, it is important to select traits known to accurately reflect aspects of condition being tested.

Bird plumage is an unusual trait in relation to condition because feathers are grown during a specific molt season but can then have important effects in a bird's life for an extended period of time past their growth period, generally a full season until the next molt. Many studies have demonstrated that the condition of a bird during a molt season affects the quality of feathers produced during that molt because energy and nutrients are expended to maintain a complete complement of body and flight feathers. For example, reduced feather growth and plumage abnormalities were exhibited by individuals under nutritional stress to compensate for the nutritional demands of other activities in compensatory mechanisms (Grubb 1989; King and Murphy 1985; Yosef and Grubb 1992; Cristol et al. 2001). These effects on plumage quality can then affect flight efficiency, thermoregulation, and a variety of signaling consequences, including sexual and social signals.

For non-breeding birds, plumage can serve as signals of fighting ability, or badges of status. The Status Signaling Hypothesis explains some cases of intraspecific variation in plumage occurring in winter flocking birds that compete for resources in dominance hierarchies (Rohwer 1982). Rohwer (1982) showed that Harris sparrows (*Zonotrichia querula*) signal high social status with conspicuous plumage, which he called badges of status. This conspicuous plumage acts as a signal of fighting ability that is communicated to others in a flock (Rohwer 1982). However, it is unknown if this plumage variation reflects differences in condition among individuals.

Ptilochronology explores the relationship between feather growth rate and body condition by determining whether feather growth rates correlate with the nutritional condition during the period of feather growth. Multiple studies have demonstrated variation in feather growth rate does reliability indicate a bird's condition at the time of feather growth (Cristol et al. 2001;

Grubb 1989; Grubb 1991; Yosef and Grubb. 1992). Because plumage is replaced during the pre-basic molt in late summer and autumn for most boreal and temperate zone birds, feathers grown during these molts carry a record of nutritional status for each individual that can be assessed any time before the next molt, generally 6-8 months apart (Grubb 1989; Grubb 1991). Many studies have used ptilochronology to determine the effects of reduced nutritional conditions on the growth rate of feathers in many avian taxa. Several experimental studies have confirmed that feather growth rate correlates with diet (assumed to reflect condition). For example, Carolina chickadees (*Poecile carolinensis*) given poor calorie/protein diets exhibited significantly slower feather growth rates than compared to birds given ad-libitum diets (Grubb 1991). Another study used enriched and reduced diets on white-throated sparrows (*Zonotrichia albicollis*) to determine the effects of nutrition on feather growth rate (Cristol et al. 2001). Sparrows on subsistence diets exhibited significant reductions in feather growth rate and total body mass compared to sparrows on ad-libitum diets (Cristol et al. 2001).. These studies suggest that ptilochronology is a reliable method that can use feathers as reliable indices of a bird's nutritional health during the time the feather was grown. Because a bird's condition affects the quality of feathers grown during a molt, conditions leading up to, and during, the fall molt may influence the quality of feathers grown after the molt, which could have large implications for important plumage-based traits during the winter.

In this study, we examined whether feather growth rate, a potential indicator of condition for an individual in early fall, has a cross-seasonal connection with golden-crowned sparrow (*Zonotrichia atricapilla*) social, morphological, and genetic traits known to be important in their winter societies. Golden-crowned sparrows are migratory passerine birds that breed in Alaska and northern Canada and winter in western North America (Norment et al. 1998). In winter, they form large stable social communities comprised of smaller short-term foraging flocks of birds with varying degrees of flexibility in their composition. Community membership is influenced by a preference to flock with the same birds from year to year, and is not just a result of shared home ranges (Shizuka et al. 2014). Golden-crowned sparrow individuals exhibit badges of status (gold and black patches of plumage located on their head) which correlate strongly with an individual's dominant and/or subordinate behavior during contests over food (Chaine et al.

2011). The relative size difference in gold patches between dyads of birds influences whether an interaction will escalate to aggression, and the relative color intensity of the black patch plays a strong role in the outcome of aggressive interactions (Chaine et al. 2013). For birds two years and older, the size each patch on an individual's crown appears to be fairly consistent throughout life (Lyon et al. unpub. data); yearling birds tend to have uniformly dull crown plumage (Colwell 1999). In addition to varying in plumage and dominance, sparrows also vary in body size and genetic measures of heterozygosity (Arnberg 2014)

We used ptilochronology to analyze feather growth rates (during the fall molt) between individuals in our population to compare with winter traits of interest (body size, sex, heterozygosity, dominance score, and color/area of status signals). Our goal was to determine if conditions during the fall molt had cross-seasonal effects on important traits used in the winter. A secondary goal was to determine if the genetic condition of individuals (mean heterozygosity) influences their feather growth rate in the fall molt.

Methods

Study site and capture of birds

We studied feather samples collected from golden-crowned sparrows in a winter study population at the University of California Santa Cruz Arboretum. Golden-crowned sparrows arrive at this wintering ground around October and depart in April, returning to breeding grounds in Alaska and northern Canada (Arnberg et al. 2015). We caught birds with Potter-style traps and mist nets baited with millet seed. Trapping and banding is approved by the UCSC IACUC, the US Banding Office and the California Department of Fish and Wildlife. For each captured bird, we recorded standard body size measurements (mass, flattened wing chord, tarsus, and beak length), plucked the right fifth (R5) rectrix feather for growth bar analysis, and took a small quantity of blood (ca. 20 μL) from the ulnar vein for genetic analysis. Birds captured for the first time were given an aluminum band with a unique number and a unique combination of up to three nylon color bands for identification of individual birds in the field.

We targeted feather samples from our long-term database, selecting feathers from two field seasons where we had particularly detailed information: the 2009 and 2010 seasons (year

denotes the fall of the season, so the 2009 season would continue on into the spring of 2010). In part, we chose these two seasons because genetic data have been previously analyzed for these seasons (Arnberg 2014; Arnberg et al. 2015, including the heterozygosity data we include here).

Processing and photographing feather samples

Growth bars appear as cross-bands on feathers which correlate with 24-hour periods of growth (Grubb 1989). A full growth bar is characterized by one dark bar created by feather growth during the day and one light bar, made by feather growth during the night (Grubb 1989; Figure 1). The coloration is derived from melanin pigment which is integrated into the keratin

Figure 1. Photo of a feather with visible growth bars as alternating dark and light horizontal bands.

matrix of the feather during growth. I photographed feathers on a dark blue background angled against light so the alternating dark and light bands of the growth bars were visible. A millimeter scale-bar ruler, used to determine actual size, and an identification sticker with the band number of the bird the feather was from was included in each photo (Figure 1). I used Play-Doh to hold the feather in optimal position to display the growth bars. I photographed the feathers using an

iPhone 6 camera, and used a Fiber-Lite Model 190 Fiber Optic Illuminator as a light source to make the bars visible. I positioned each feather parallel to the ruler and on the same plane as the ruler to maximize accuracy when using the pixel counts on the ruler to determine the actual distance between sequential feather bars. I took multiple photos of each feather and selected the clearest photo to analyze.

Once I had photos of feathers, I adopted similar digital manipulations of photos described in previous ptilochronology studies which further improve the ease of working with growth bars. To do this, I adjusted the contrast and color balance images in Adobe Photoshop to improve growth bar clarity and magnified each image by 200-250% to improve growth bar measurement accuracy (Frasz et al. 2014; Grubb 1989). When necessary, I applied a black and white filter to some photos to improve the contrast between light and dark bars, which improved overall visibility of growth bars and measurements.

Measuring growth bars and calculating average daily growth rates

Once the contrast and color of each photo was adjusted to produce clear growth bars, I used the Photoshop line tool to record the length of 5 growth bars in terms of pixel count (5 to 10 bars is ideal; Grubb 1989), measuring distance along the central rachis perpendicular to the bars. Each measurement was taken in the same location of each feather from the left edge of one dark bar to the left edge of the 6th adjacent dark bar for accuracy and consistency. This number was divided by 5 to produce an average growth bar length (in pixels) for each feather. This calculated average represents daily feather growth since one full growth bar corresponds to one 24-hour period of growth (Grubb 1989).

Calibration of ruler and determining actual size of growth bars

For each photo, I calibrated the scale bar millimeter ruler to pixels to obtain a conversion factor for pixels to millimeters. To do this, I recorded the length (in pixels) of 20 millimeters with the photoshop line tool, and divided that number by 20 to obtain a conversion factor for pixels to millimeters for each photo. I then divided the average growth bar length of each feather

with the corresponding conversion factor to that feather to convert the previously calculated average growth bar lengths from pixels to millimeters. The ending number is the calculated average length of one growth bar in scale bar millimeters. This calculated average length of one growth bar is the number I use to represent the feather growth rate for each bird.

Estimating repeatability of the feather growth measures

Before measuring our whole sample set, we conducted a blind test to determine the repeatability of our measurement methodology. We were unsure about the accuracy of estimating feather growth rate because it can be tricky to see individual bars on some feathers and we wanted to be sure that our method was consistent. The first test consisted of two measurements with each of 20 feathers. We wanted the repeatability to not only take into account error involved in assessing the same photograph, but also variation among photographs. Accordingly, the second set of measurements was done on a second set of photographs taken two weeks apart from the first round. To make the assessment blind to the identity of the birds, the second test round used the same feathers in the first set but with concealed IDs in the form of numbered envelopes of the birds (numbered 1 through 20 with no correlation to the order of the first test and numbered by a different person who assessed the feather growth).

After determining repeatability with the first two measures I measured the feathers again in a third test round in a similar fashion to the second test set. I refined my approach in the third set of measures by using black and white filters on any problematic feathers from the first two rounds (problematic being defined as feathers with large differences between the first and second measures. I then measured all feathers using this adjusted approach in the third set of measures to see if the adjusted measurement approach increase repeatability relative to the first estimate.

Measuring plumage patch size and color

I used crown patch size data collected by a previous study that correlate with the birds in my sample size from the 2009 and 2010 seasons (Chaine et al. 2011). Size data was collected by photographing the top of the head of birds with a size standard to scale images. Adobe Photoshop was used to isolate both black and gold patch areas on the crown. The color of the

crown patches were measured using an Ocean Optics USB2000 spectrometer (fitted with a tip that restricted movement to a standard 2 mm squared diameter area at a 45 degree angle; Andersson *&* Prager 2006**;** Chaine & Lyon 2008) and a PX-2 pulsed xenon light source (Chaine et al. 2011). Three measurements for each gold and black patch were taken for each bird and the spectrometer was standardized using light and dark standards between measurements (Chaine et al. 2011). For both colors, we measured color as the total brightness—the total reflectance in the range of wavelength of interest (Montgomerie 2006).

Determining social dominance

I also used dominance data from the previous study that correlates with the birds in my sample size from the 2009 and 2010 season (Chaine et al. 2011). This data was collected by scoring the outcome of behavioral interactions between dyads of birds at a seed pile. Two types of behavior that reflect social dominance were observed by Chaine et al. (2011): aggression and avoidance. Aggressive behavior was scored when an individual fought, chased, or lunged at another bird. Aggressive interactions always yielded seed pile access to the dominant bird, and some of these interactions occurred away from the food dish. Avoidance behavior was scored when an individual showed no signs of challenging another bird for food or perching space. Birds expressing avoidance behavior generally perch away from resources and do not approach them. This subordinate behavior has also been observed in other studies (Watt 1986). The scored outcomes of these behavioral interactions were analyzed by Nina Arnberg (2014) to obtain a David's score as a measure of average social dominance index. This score is the average percentage an individual succeeds in interactions with each of its group members (Gammell et al. 2003), as the dominance score for each of our birds.

Collection of genetic data

I use multi-locus heterozygosity measures from individual golden-crowned sparrows calculated by Nina Arnberg (2014) using fourteen microsatellite primers. Thirteen of the primers were originally optimized for white-crowned sparrows (Poesel et al. 2009) and one of the primers was originally optimized for golden-winged warblers (*Vermivora chrysoptera*) (Stenzler

et al. 2004). Heterozygosity was measured using mean d^2, a measure of the stepwise difference in microsatellite repeats between the games that formed an individual which is estimated from two alleles each individual has at a locus (Coulson et al. 1998). Then for all loci analyzed in individuals, the squared distance between the two alleles within a locus was averaged. I used these calculated means of heterozygosity in 60 of the sparrows in my sample size of 74 birds because I used the 2009 and 2010 season as my sample size for measuring growth bars.

Statistical analyses

Our study has 72 individual samples, 48 from the 2009 season and 24 from the 2010 season. However, 12 birds are represented in both years, so that the sample includes 60 unique individual birds. Because we had measures of some of the same individuals in two different years, we use mixed models to determine if feather growth rate (fixed effect) was correlated with the traits of interest, excluding mean heterozygosity, controlling for the repeated measures from the same individuals by including individual bird as a random effect.

To determine if mean heterozygosity influences feather growth rate in the fall, we used a linear regression analysis between mean heterozygosity, as the independent variable, and feather growth rate, as the dependent variable. Because 12 birds were represented in both years, we excluded the growth values for the repeated birds from their second year (the 2010 season) to give us a sample size of 60 unique individual birds. All our analyses were done in JMP Pro (Version 14).

Results

Variation and repeatability of feather growth measures

Our ptilochronological approach revealed there is variation in feather growth rate between golden-crowned sparrow individuals (Figure 2). We then determined that this variation reflects true variation among individuals as is not simply measurement error. Our measurements of 20 feathers, measured from different photographs and blind to the identity of individual birds, revealed that our measures of feather growth are highly repeatable. Repeatability was very high in our first assessment (R = 0.85, P < 0.0001) and was improved somewhat after fine-tuning the

measurement approach based on investigation of problematic measures in the first assessment (repeatability in the second improved assessment, R = 0.90, P < 0.0001). These results confirm we can reliably measure feather growth rates from photographs of feathers.

Figure 2. Distribution of feather growth bar lengths showing the degree of variation of feather growth rate between individuals.
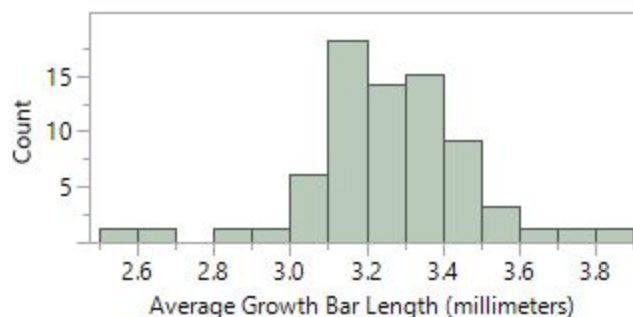
Correlations between growth rate and traits of interest

Among the eight traits we analyzed, feather growth rate was correlated with the color intensity of an individual's black crown patch (Table 1). Interestingly, the correlation between the size of this same patch (black crown patch) and feather growth rate was marginally significant (Table 1). There were no significant relationships between feather growth rate and any of our other physical or social traits (Table 1).

Table 1. Result of Mixed Models that examine the relation between feather growth rate and several social traits. A separate model was run for each trait, with feather growth rate as a fixed effect and bird identity as a random effect.

Trait	Estimate	Std error	t	P
Black patch size	57.58	32.6	1.77	0.083
Gold patch size	14.59	18.7	0.78	0.44
Black patch color	-15.41	6.4	-2.39	0.021
Gold patch color	-10.50	14.0	-0.75	0.46
Dominance score	19.82	16.5	1.2	0.24
PCA body size	4.01	17.9	0.22	0.82
Body mass residual	-2.14	21.4	-0.1	0.92

There was also no significant correlation between mean heterozygosity and feather growth rate (Table 2).

Table 2. Result of linear regression of feather growth rate on genetic heterozygosity.

Estimate	Std. error	t	P
-0.21	0.27	-0.79	0.43

Discussion

The repeatability study shows that converting growth bar values from pixels to millimeters was a reliable way to measure growth bars between different photos, taken at different times, for the same feather. There is also variation in estimated feather growth bar lengths between individual golden-crowned sparrows, which suggests there are differences in fall-molt feather growth rates between birds because growth bar length is determined by feather growth rate (Grubb 1991; Grubb 1989). Other studies found that, like feather growth rate,

variation in other important traits are also condition-dependent (Birkhead et al. 1999; Bêty et al. 2003; Blums et al. 2005). These condition-dependent traits should positively correlate with feather growth rates because feather growth rate reflects the nutritional condition of a bird. Our results show a positive correlation in one important winter trait, the color intensity of black plumage, of golden-crowned sparrows to their fall molt feather growth rate. The crown patch is produced at the same time of year—fall molt—as the tail feathers whose growth rate we measured. The correlation between the two feather traits suggests the black plumage patch in golden-crowned sparrow social badges has some degree of cross-seasonal condition-dependence to conditions during, and leading up to, the fall molt. It is suggestive that the one other measure of this same black plumage trait, patch size, showed a suggestive correlation with tail feather growth rate. Our other tests suggest there is no cross-seasonal effect of condition on other important winter traits , including gold patch size/color, dominance score, body size, and relative body mass. Additionally, our genetic test results suggest mean heterozygosity has no significant effect on fall molt feather growth rates.

Our detection of intra-population variation in feather growth bar sizes is of interest because it suggests golden-crowned sparrow individuals experience differential feather growth rates during their fall molt. Because feather growth rate and body nutritional condition have been strongly correlated in several avian taxa (Grubb 1989; Grubb 1991; Cristol et al. 2001) our results suggest there is likely to be intra-population variation in an aspect of body condition or nutritional state during the fall molt, and that this variation affects the features of some plumage traits. Additionally, a previous ptilochronology study showed condition-dependent feather growth rates in a close relative of the golden-crowned sparrow, the white-throated sparrow (*Zonotrichia albicolis*) (Cristol et al. 2001). Individuals were caught and assigned different diets; some birds were given ad-libitum diets and others were given subsistence diets. Original feather lengths and growth bar lengths did not differ between high and low quality diet groups at the start of the study. Feathers were plucked from each bird to induce the growth of new feathers. Birds on subsistence diets grew shorter induced feathers, with shorter growth bars, than birds given ad-libitum diets. Cristol et al. (2001) concluded that protein and calorie-restricted diets can cause slowed feather growth rate in white-throated sparrows. This corroborates the idea of the

slowed feather growth rate we observed in golden-crowned sparrows being due to compromised nutritional conditions during the time which those feathers were grown in the fall.

There are interesting implications from the positive correlation between black plumage color intensity and feather growth rate. Other ptilochronology studies demonstrated that condition-dependent traits positively correlate with feather growth rate and reflect nutritional condition. Our observed positive relationship between black color intensity in the winter plumage and fall feather growth rates implies there is some cross seasonal condition-dependence in the color intensity of melanin-based plumage. This suggestion is supported by past literature suggesting melanin-based plumage traits are condition-dependent and not just under genetic control (Griffith et al. 2006). Other studies also found similar trends between nutritional condition and melanin deposition in feathers. For example, Eurasian kestrels (*Falco tinnunculus*) display reduced black bands on their tail feathers when they have a poor nutritional condition (Piault et al. 2012). Kestrel nestlings also show a positive correlation between melanin-based coloration and rich territories and/or high quality providing parents (Fargallo et al. 2007). There is also a positive relationship between food supply and melanization in northern flickers (*Colaptes auratus*) (Musgrove and Wiebe. 2016). The suggestive correlation between the black patch size and feather growth rate is also interesting because the size and color of this melanin based trait may be influenced by the same (or similar) metabolic pathways. Musgrove and Wiebe (2016) found that it was the amount of melanin deposited in northern flicker (*Colaptes auratus*) plumage and not the arrangement or pattern of black plumage that correlated positively to nutritional condition. This could explain why we found a weaker correlation between black patch size and nutritional condition when compared to black color intensity.

The metabolic pathways involved in incorporating melanin into black plumage are entirely different than pathways involved in the incorporation of carotenoids into gold plumage (Griffith et al. 2006), which could explain why we did not see similar condition-dependence in gold plumage traits the sparrows. Melanin can be synthesized by amino acids in the body whereas birds cannot synthesize carotenoids de novo but instead must get them from their diet. Additionally, only a small amount of carotenoids are considered essential for the production of colors used in carotenoid-based signaling (Furr and Clark 1997). Our wintering population of

sparrows may have had a high enough dietary intake of carotenoid pigments to maintain uninhibited levels of gold plumage growth during the fall molt whereas inter- and intraspecific temporal and spatial differences in access to dietary amino acids and proteins could have caused enough nutritional stress in some individuals to reduce the amount of melanin deposition during the fall molt. This is speculation because we do not have data on the birds' condition during their fall molt. Melanin-based plumage trait and condition dependent trends are seen in many other birds, and our results suggest the same trend in golden-crowned sparrows.

Other important traits we analyzed such as body size and dominance had no correlation with feather growth rate during the fall molt. This suggests these other important winter traits are not cross-seasonally affected by conditions during the fall molt, otherwise, we would have detected positive correlations between these traits and fall molt feather growth rates. Our negative results with respect to body size are supported by the extensive literature showing that body size is a highly heritable trait (Silva et al. 2017; Santure et al. 2013, 2015; Bérénos et al. 2015). Additionally, the use of body size as a proxy for body condition in general has been controversial due to a wide array of metabolic compensatory mechanisms that may influence body size in a wide array of taxa (King and Murphy. 1985).

It is also interesting that we found no correlation between fall nutritional condition and dominance scores during the winter months, particularly since we did find correlations between fall nutritional condition and the black crown plumage. Black crown plumage has previously been shown to plays a strong role in the outcome of aggressive contests during foraging in this species, and hence is used as a badge of status (Chaine et al. 2011). A recent study demonstrated that golden-crowned sparrow badges of status may play a stronger role in dominance interactions between strangers rather than familiar flockmates, and that familiar flock mates recognize each other regardless of manipulations to their crowns, based more on individual recognition (Chaine et al. 2018). The dominance interactions used in this study involved familiar birds from the same social communities. If there is a weak relationship between plumage and dominance within social groups, this could explain why our results suggest a condition-dependence in crown blackness but not dominance.

Acknowledgements

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