

Sexual Selection and Plumage in the Polymorphic White-throated Sparrow

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ABSTRACT

Feather coloration has been known to be connected with sexual selection for many years. It also provides an opportunity to study evolution, focusing on sexual selection and natural selection. Plumage is affected by both of these forces and the equilibrium is where these forces balance. The white-throated sparrow gives us a unique opportunity to observe the effects of the different strengths of these forces within a species. First, I established that there were differences in plumage characteristics between the morphs and sexes. White males had the brightest white and darkest black feathers. White females and tan males were the next brightest, with tan females having the dullest white and lightest black head stripes. Using plumage characteristics I was able to predict the morph/sex class of the bird significantly more than by chance.

With the exact differences between each morph/sex class now known, I looked at the relationship between fitness and plumage. White males with higher overall contrast (brighter white, darker black) were more successful than duller white males. This was attributed to the males displaying their quality to females. Duller tan males however, were more successful than brighter tan males. With duller plumage, they may reduce predation on their nest while they are feeding their offspring. The differences in reproductive strategy changed the relative strength of natural and sexual selection between the morphs. Observing this interaction in this system will let us judge the relative strength of these forces in other systems.

PREFACE

This thesis is the work of 3 years at Indiana State University and in the beautiful Adirondacks of New York. Over this time I have worked with hundreds of white-throated sparrows and come to know more than a few in great detail. Hiking in the Adirondacks allowed me to experience nature in a way not many others get to. Each bird I worked with seemed unique, both in the hand and while watching us from afar. While I know they often did not appreciate being studied I am thankful for the things they have taught me, about themselves, about birds, and about nature in general. Hopefully this thesis will contribute to our understanding of signals in the bird world and inspire others to pick up the standard and delve even deeper into the mysterious world of the birds.

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CHAPTER 1

SEXUAL SELECTION, PLUMAGE, AND THE WHITE-THROATED SPARROW

Introduction

Feather coloration has been well documented as a sexually selected signal of male quality, with females often preferring to mate with more brightly colored males, and more brightly colored males having higher reproductive success (Hill 1991, 2002; Safran & McGraw 2004; Safran et al. 2005). Brightly colored males have also been shown to have higher extra-pair mating success (Yezerinac & Weatherhead 1997). Despite these patterns, there are many other studies that suggest that dull plumage is advantageous to males if it signals status and/or allows for crypsis (Tuttle 1993; Houtman & Falls 1994; Karubian et al. 2008). Given this alternate evidence, it has been difficult to tease apart the adaptive significance of plumage cues. It would be useful to study these signals in a single species that varies greatly in plumage and is subject to a variety of selective pressures. Polymorphic species often vary greatly in plumage such as the barn owl (*Tyto alba*) (Roulin et al. 2004a), red-footed boobies (*Sula sula*) (Le Corre 1999) and ruffs (*Philomachus pugnax*) (Lank et al. 1995; Jukema & Piersma 2006). Coloration within these morphs can follow a continuous distribution, as in the tawny owl (*Strix aluco*) (Brommer et al. 2005) or there can be discrete differences between the morphs (with very little difference in coloration within one morph)

as in Gouldian finches (*Erythura gouldiae*) (Pryke & Griffith 2007). These plumage polymorphisms are also often correlated with differing reproductive strategies (Lank et al. 1995; Roulin et al. 2003; Jukema & Piersma 2006 but see Roulin et al. 2004b) which may go hand in hand with different selective pressures on each morph. Territorial males may be selected to display bright plumage advertising their quality or fighting ability (Pryke & Griffith 2006). Less aggressive males, such as satellite males and female mimics in lekking ruffs, may be selected to have duller plumage to reduce aggression and increase the chances for mating opportunities (Tuttle 1993; Houtman & Falls 1994; Lank et al. 1995; Jukema & Piersma 2006). The white-throated sparrow (*Zonotrichia albicollis*) however has the advantage of having genetically determined morphs that occur in both sexes with different reproductive strategies, allowing natural selection and sexual selection to both play roles in determining the evolution of plumage in the two morphs (Lowther 1961; Tuttle 1993, 2003).

The white-throated sparrow (WTSP) is a common multi-brooded passerine that breeds in the northern U.S. and Canada between May and August. The morphs are determined genetically and associated with differences plumage and reproductive strategy (Lowther 1961; Thorneycroft 1966, 1975; Tuttle 1993, 2003). With these differing strategies, there is a greater variety of selective pressures acting in a variety of directions in this species than on others without morphs. The two morphs are determined by the presence of a complex rearrangement of chromosome 2 (Thorneycroft 1966, 1975; Thomas et al. 2008; Romanov et al. 2009). Birds of the white morph can be identified by the white stripes in their lores, while the tan morph birds have tan lores. Birds of the white morph are heterozygous for the rearrangement ($2^m/2$) while birds of the tan morph are homozygous for the absence of the rearrangement ($2/2$) (Thorneycroft 1966, 1975; Thomas et al. 2008). The reproductive

strategies of the two morphs also differ significantly. White birds are more promiscuous, seeking out extra pair copulations at the cost of giving lower parental care to their offspring (Tuttle 2003). Tan males guard their mates much more and give more parental care to their offspring (Tuttle 2003; Knapton & Falls 1983). Both morphs mate disassortively: white males pair with tan females and tan males with white females (Lowther 1961). This mating pattern appears to be maintained by mate choice. Studies have shown that males of both morphs prefer white females and that females of both morphs prefer tan males (Tuttle 1993; Houtman & Falls 1994). This leads to the two preferred types (tan males and white females) pairing together and leaving the other types (white males and tan females) to pair together. Dissortative pairing occurs in nature more than 97% of the time (Tuttle 2003). The pair types also segregate themselves spatially, with the tan males occupying territories that are located in more forested and less populated areas and the white males settling in the more densely populated boggy areas where they have a greater opportunity for extra-pair copulations (Formica et al. 2004, Formica & Tuttle 2009).

While the behavioral differences between the two morphs have been well documented, the most obvious difference between the morphs, their plumage, has not been fully quantified in wild birds until now. Most previous studies of WTSP plumage have mainly used qualitative analyses (e.g. Munsell system), museum specimens, or focused simply on brightness and not other measures of color (Lowther 1961; Vardy 1971; Atkinson & Ralph 1980; Watt 1986). These studies have also been from the point of view of the experimenter, not the birds themselves, which does not include the UV portion of the feather coloration. In this thesis I will fill in these gaps in our knowledge by conducting a study that quantitatively analyzes the differences between the plumage of each morphs, including the

UV reflectance. In chapter 2, I examine what the specific differences are between the morphs, sexes, and each morph/sex class and determine if an overall signal is used for discriminating between the morph/sex classes. This analysis is an essential first step before analyzing the function of plumage variation. In chapter 3, I examine the relationship between plumage and fitness, gaining an understanding of the differing effects of sexual selection and natural selection on the plumage of birds with different reproductive strategies. White males that are promiscuous may have very different selective pressures on their behavior and plumage than the other morph/sex classes that are less promiscuous. Sexual selection could affect their plumage to display their quality or advertise their presence to other males and females. Natural selection could act to increase the degree of crypsis of each morph/sex class to dissuade predation on the adults and their nests. The strength of these forces may be different in each morph/sex class, leading to equilibrium at different places for each plumage characteristic in each morph/sex class.

Using this method, the entire appearance of the bird may now be combined into one measure. With this new measure of overall appearance, studies can more easily correlate plumage with other factors such as fitness and health and may be more biologically relevant as an overall signal. In chapter 3, I analyze the relationship between an overall plumage signal and fitness and attempt to explain why the differences in plumage evolved. I show that selection on the plumage of males to show their quality to their females may be counteracted by natural selection, and that different selection regimes are present in the different morphs. The characteristics of the plumage of females are mostly under natural selection but may be confounded by the presence of sexual selection on genes shared with males (the rearranged 2nd chromosome).

At the conclusion of this thesis, I will have shown significant differences among the morph/sex classes of the white-throated sparrow, summarized these differences in one measure of overall appearance, correlated this measure with fitness, and determine what signals are sent by what plumage patches and why selection would have favored these signals over other signal types in each morph/sex class. These plumage signals and sexual selection that created these differences could help to maintain the polymorphism in the population. Plumage is a phenotypic marker of the genotype of a bird, and also an indicator of its future behavior (). Females can be aware then of the genetics of her mate as well as the level of parental care he will provide and choose the best match for her, which is usually the tan male. Males exhibit a preference for white females, possibly due to their territorial behaviors or they may signal their quality with their plumage, creating the disassortative mating system that maintains the polymorphism in the population. The differences in plumage are thus very important to maintaining this polymorphism in the population.

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CHAPTER 2

DISCRIMINATING CLASSES OF THE WHITE-THROATED SPARROW BY THE SPECTRAL ANALYSIS OF PLUMAGE

Introduction

Intraspecific differences in plumage color and other characteristics are thought to have evolved through both natural and sexual selection and to serve a variety of communication functions. Many species use plumage to attract and keep mates, blend into their environment, or a combination of both (Hill 1991, 2002; Safran & McGraw 2004; Gotmark 1993). Mate attraction can be achieved by incurring a handicap (Darwin 1871), such as increased pigmentation, either melanin (Safran & McGraw 2004) or carotenoid (Hill 1991) or increased feather size or symmetry (Møller 1988, 1993, 1994; Pryke & Andersson 2005) that imposes a cost on the individual with the ornament (Evans & Thomas 1992; Pryke & Andersson 2005; Clark & Dudley 2009). Only high quality individuals can incur this cost and are then preferred as mates (Darwin 1871). Plumage however also has natural selection acting on it as well as sexual selection. To determine the interaction of these two selective forces, it would be useful to have a species with similar natural selective forces, but deal with separate sexual selective pressures. In addition, plumage ornaments can come in many forms. A species with multiple types of ornaments as well may give us an idea about which

ornament types could be signals under different selective pressures. These requirements are present in the white-throated sparrow (*Zonotrichia albicollis*).

The two morphs of the white-throated sparrow (WTSP) including their behavioral differences, from the aggression levels of the morphs, sex ratios of the different pairs, and habitat use have been well studied, leading to discoveries about their alternative reproductive strategies and their consequences on fitness (Knapton & Falls 1983; Kopachena & Falls 1991, 1993; Tuttle 1993, 2003; Formica et al. 2004; Korody 2006, Tuttle et al. 2006; Tuttle et al. 2010). However, the most obvious difference between the morphs, their visual difference, has not been well studied, although they are usually distinguished visually (Figure 1) no specific differences have been quantified in their breeding plumage to this point. Winter plumage has been examined (Piper & Wiley 1989) but there are fewer obvious differences in plumage at that time. Signals relevant to reproduction are also more likely to be sent while in breeding plumage and not in winter plumage. We also do not know what kind of signal, if any, the plumage differences convey. Plumage in the WTSP serves as a visual marker of its genotype and phenotype, with white males being more promiscuous and tan males being more parental and morph being determined by the presence of a rearranged 2nd chromosome, with white being heterozygous for the rearrangement and tans being homozygous without the rearranged chromosome (Lowther 1961; Thorneycroft 1966, 1975; Tuttle 1993, 2003; Thomas et al. 2008; Romanov et al. 2009).

The plumage differences of the morphs must also be apparent to the birds themselves, as the morphs mate disassortatively, requiring them to distinguish the morph of their mate (Lowther 1961; Houtman & Falls 1994; Tuttle 2003). The morph of other individuals must be assessed as well, as a white male may present a higher threat to another male's fitness than

a tan male would (Formica & Tuttle 2009). Discriminating the sexes of the same morph is essential as well to decide to court a female or defend against another male. Crown plumage is molted just before the breeding season, whereas back and belly plumage are not. This suggests that crown plumage plays an important role in reproduction.

For these reasons, I predicted that there are significant differences between the morphs and between each morph/sex class (white male (WM)/ tan male (TM)/ white female (WF)/ tan female (TF)) that the birds are reacting to. I also predicted that these differences would be signals between the classes to help with discrimination and possibly used to indicate condition or quality. Most sexually dimorphic species only have to discriminate between males and females, without the added complexity of the morphs. This added complexity may push the limits of the abilities of these birds and give us information on the capabilities of birds for discrimination of the characteristics of other individuals. By determining what the differences are between each morph/sex class we can better understand the variation between the morphs that may be a basis for selection and give us more insight into their unique mating system. Quantifying the differences between the classes will allow analysis of how plumage interacts with the fitness of these birds. This would lead to an understanding of how selection acts on the plumage of these birds and why it resulted in different plumage for each class.

Methods

Feather Analysis

Feathers were collected from 107 adult white-throated sparrows (*Zonotrichia albicollis*) during the breeding season (May-August) at the Cranberry Lake Biological

Station (44°15'N; 74°48'W) in the Adirondacks of New York for the summers of 2006-2009. The site has >32 hectares of forest, pond, and bog where the birds breed naturally. The birds were captured using passive mist netting as well as song playback on their breeding territories. Feathers were sampled from the median crown stripe (MCS), lateral crown stripe (LCS), superciliaries (Scil), throat, back and belly from each adult bird (Figure 2). At least 3 feathers from each patch were taken but most patches had at least 5 feathers sampled. Some birds did not have all patches sampled or had fewer than 3 feathers for a patch and were excluded from the analysis of that particular patch (N = 6). The feathers were refrigerated and stored in the dark in 1.5ml centrifuge tubes until spectral analysis was conducted in order to prevent pigment degradation. At the time of feather collection, other standard morphological measurements were taken as well as a blood sample. Birds were weighed using a Pesola spring balance (± 0.25 g). Tarsus length was measured using a digital sliding caliper (± 0.01 mm). All birds were given a unique combination of colored plastic bands as well as a unique Fish and Wildlife band to prevent unknowingly resampling the same bird.

Before analysis, the feathers were taped down onto blank index cards using clear tape, overlapping the feathers to recreate how they occur naturally on the bird. Reflectance data were then collected on these patches using the USB2000+ Miniature Fiber Optic Spectrometer (Ocean Optics, Dunedin, FL) with Spectrasuite software (Ocean Optics, Dunedin, FL). The probe was vertically placed 2.5mm from the surface of the feather on the card. Three measurements for each patch were taken from the exposed, colored part of the feather. The probe was replaced before each measurement to sample the variation within a patch. The data were then analyzed using the CLR program (v1.05) developed by Dr. Robert Montgomerie of Queens University (2008). This scored each feather patch for hue, saturation

and brightness; where hue is the actual color displayed by the feather, saturation is the amount of the color pigment, and brightness is how much light the feather reflects for any given wavelength or range of wavelengths. A wavelength range of 300-700nm was used in this study. The equations used by the CLR program can be found in Appendix 1. The scores from the three measurements for each patch were averaged for each bird.

Sex and Morph Identification

Adults were sexed using cloacal protuberance/brood patch differentiation and morphed using visual characteristics. Morph was determined using the criteria of Lowther (1961) and Piper & Wiley (1989). Morph identification in the field has been confirmed genetically for other individuals with 100% accuracy.

Age Determination

The age of each bird was determined by the number of years it was spotted alive after initial banding. All unbanded adults were classified as 1 year old at capture unless there was reason to believe it had been seen previously (i.e. distinct song) but not banded. Age classes of the birds were created classifying all birds 2 years old or older into one class and those birds only seen for 1 year into another class. Age classes were created to increase the sample size of birds older than 1 year that had feathers collected.

Statistical Analysis

Statistical Analysis was conducted using JMP (v. 4.0) and SPSS (v. 16.0). The sample sizes were 107 birds (42 white males (WM), 16 white females (WF), 32 tan males (TM), 17

tan females (TF)). ANOVAs, t-tests, and discriminant function analysis were performed using SPSS v 16.0. Each patch was analyzed separately for this analysis. The average of the three measurements for brightness/saturation/hue for each patch on each bird was used to create a model for predicting the morph/sex class of an individual. A chi squared test was then performed on the predicted and actual group memberships. Correlations were performed in JMP v 4.0 to find the relationships between the patches.

Brightness was found to be the most common difference between the morph/sex classes, so the analysis was focused on this area. A principle component analysis was conducted using SPSS v. 16.0 to combine all of the measurements of crown brightness into one variable that could be associated with fitness. These methods have been used to determine sexually selected signals in other species such as the barn swallow (Safran & McGraw 2004). The first principle component (“overall contrast”) was extracted with the brightness of the MCS (0.845), superciliaries (0.854), and throat (0.845) loading positively on the axis, with LCS brightness (-0.403) loading negatively on the axis. A bird with a high overall contrast score had bright MCS, superciliaries, and throat with a dark LCS, creating a high level of overall contrast on the head of the bird. Overall contrast scores for each bird were then correlated with fitness characteristics using JMP v4.0. An additional discriminant function analysis was performed on the overall contrast scores to determine if there were signals for discriminating the morph/sex classes present when combining all of the patches into one variable.

Results

Pigments

Almost all patches sampled were pigmented with melanins exhibiting the characteristic melanin reflectance spectrum of slowly increasing reflectance over all wavelengths (Figure 3: Prota 1992; Riley 1997). The yellow superciliaries displayed the characteristic absorption in the blue-green range (430-500nm) thereby exhibiting a peak in the yellow wavelengths, this is indicative of a carotenoid pigment (Figure 4: Britten et al. 1995; Keyser & Hill 1999). Repeatability of each patch was calculated for each morph/sex class using the method outlined in Lessells & Boag (1987) and the brightness measurements for each patch except for the back was found to be repeatable (Back $r = 0.42$, Belly $r = 0.81$, LCS $r = 0.77$, MCS $r = 0.90$, Scil $r = 0.84$, Throat $r = 0.82$) (Table 2.1).

Discrimination of Morph/Sex Classes

Plumage variables were compared using multiple one-way ANOVAs to determine whether there were significant differences between the morph/sex classes (Table 2.2). The frequency of brightness scores was also plotted for each plumage patch and each morph/sex class. The data were graphed and show clear distinctions between at least some of the classes for most plumage patches (Figures 5-10).

Brightness, hue, and saturation scores from the six different patches were separately used to predict the morph/sex class for the bird in a discriminant function analysis. Three discriminant functions were calculated for each patch (Table 2.3). The combined functions for each patch were significant with $p < 0.05$ except for the back patch ($p = 0.121$). Using these predictors, each of the head feathers (LCS, MCS, Scil, Throat) predicted the class of the bird

approximately 50% of the time, whereas the back and belly feathers did were correct approximately 40% of the time (Table 2.4). The predicted group membership was compared with the actual group membership and it was found that the model was statistically significant in predicting the class for all feather patches (Back: $p=0.018$, Cramers $V=0.307$; Belly: $p=0.020$, Cramers $V=0.306$; LCS: $p<0.001$, Cramers $V=0.584$; MCS: $p<0.001$, Cramers $V=0.713$; Scil: $p<0.001$, Cramers $V=0.789$; Throat: $p<0.001$, Cramers $V=0.757$). The effect sizes (Cramers V) differed for the head and body feathers though, with the head feathers having large effect sizes (Cramers V range 0.584-0.789) and the body feathers having small effect sizes (Cramers V range 0.306-0.307). Effect sizes (Cramers V) show the strength of a relationship between variables and the size of the differences between groups which indicates more than just significance levels.

After determining there were differences between the morph/sex classes, each morph and sex were compared. T-tests were performed on all patches between the morphs, and significant ($p<0.05$) differences were found between the morphs in all head feathers brightness but not the body feathers (LCS: $t=-2.960$, $df=103$, $p=0.004$; MCS: $t=8.305$, $df=103$, $p<0.001$; Scil: $t=11.587$, $df=104$, $p<0.001$; Throat: $t=9.843$, $df=103$, $p<0.001$, Belly: $t=0.086$, $df=103$, $p=0.932$, Back: $t=1.698$, $df=104$, $p=0.092$). In the morph analysis, sexes were grouped together to determine the effects of the presence of the rearranged 2nd chromosome on plumage. When looking for differences between the sexes, we first split it by morph and then analyzed the data. T-tests showed that in white birds, the sexes differ only in the brightness of their MCS ($t=4.990$, $df=55$, $p<0.001$), whereas in tan birds, the difference between the sexes is in the brightness of the LCS ($t=-3.468$, $df=46$, $p=0.001$) (Table 2.5).

While there were differences between the morph/sex classes, this analysis was done without examining the relationship between patches. Each patch was analyzed individually, but the correlations between patches could reveal signals as well. This was done by correlating the brightness of each patch with all other patches. Linear regression was used and all relationships reported are linear. For tan males, the brightness of the LCS was negatively correlated with the brightness of the MCS ($F_{1,28}=3.63$, $r^2=0.11$, $p=0.069$), brightness of the superciliaries ($F_{1,28}=5.837$, $r^2=0.17$, $p=0.023$), and brightness of the throat ($F_{1,28}=3.30$, $r^2=0.10$, $p=0.079$), while positively correlated with the brightness of the back ($F_{1,28}=17.517$, $r^2=0.38$, $p<0.001$) and brightness of the belly ($F_{1,28}=0.0062$, $r^2=0.24$, $p=0.006$). For white males, the brightness of the LCS was negatively correlated with the brightness of the MCS ($F_{1,37}=11.87$, $r^2=0.24$, $p=0.001$), brightness of the superciliaries ($F_{1,37}=5.888$, $r^2=0.14$, $p=0.02$), and brightness of the throat ($F_{1,37}=4.97$, $r^2=0.12$, $p=0.03$), while positively correlated with the brightness of the back ($F_{1,38}=32.699$, $r^2=0.46$, $p<0.001$) but not correlated with the brightness of the belly ($F_{1,37}=0.388$, $r^2=0.01$, $p=0.53$). These correlations in brightness between patches were only present in males, where females had no significant correlations between the patches (all $p>0.05$) (Table 2.6). No significant pattern of correlations between patches were found in males or females for hue or saturation.

Overall contrast discrimination

Discriminant function analysis conducted on the principle component analysis scores for brightness of the head feathers correctly classified the morph/sex class in 56% of cases (Table 2.6), which is significantly higher than chance ($\chi^2=66$, $df=9$, $p<0.001$). This was not

an improvement over the average 54.9% correctly classified using each head plumage patch separately.

Individual Variation within the Morphs

The initial spectra also demonstrated that there is individual variation within each morph/sex class for each patch. An example of such variation is shown in Figure 11 with the superciliaries of all white males sampled. This variation was not correlated with the age of the bird (years) or with its age class ($p > 0.05$).

Discussion

Differences were found between the morphs in all of the head plumage patches, suggesting it is a signal to distinguish between the morphs. The white morphs were brighter in the MCS, superciliaries and throat, but darker black in the LCS (Figure 12, Table 2.7). The signal may be involved in male-male competition where white males need to advertise their presence and condition due to occupying more densely populated areas (Formica 2004; Formica & Tuttle 2009). White females are also more involved in territory defense than tan females so their brighter plumage may be a reflection of this aspect of their behavior (Tuttle 2003). Tan males may not have evolved this specific signal because they generally have fewer neighbors to defend against (Formica 2004). The tan males also provide a larger proportion of the parental care than their white counterparts, and may thus have evolved cryptic plumage to help disguise themselves when they are at or traveling to their nest (Knapton & Falls 1983; Tuttle 2003). The difference may also simply be to distinguish between the morphs, since the morphs pair disassortatively, making the ability to distinguish

the morph of your mate important (Lowther 1961; Houtman & Falls 1994; Tuttle 2003). This may help prevent two white birds from pairing together, giving the chance that some offspring may be homozygous for the rearranged 2nd chromosome, which is hypothesized to be lethal because it has been rarely found in the population (Thornycroft 1975; Tuttle 2003; Romanov et al. 2009).

The nature of plumage differences between the sexes depends on the morph. In tan birds, males had a darker (black) LCS than females. However, in white birds, the males and females differed in the brightness of their MCS, with males being brighter (Table 2.7). Two patches signaling the difference between sexes in each morph is unique. These two signals may also suggest that there are different selective pressures on each morph creating these signals, and may be a result of their different reproductive strategies.

The discriminant function analysis for each plumage patch showed that the plumage characteristics in each morph/sex class are significantly different. Random chance would predict classifications of four classes correctly 25% of the time, and the percentage correctly classified using these predictors greatly exceeded that. Not surprisingly, the best predicting patch was the median crown stripe (MCS) with 61.9% correct since white males often have the brightest white MCS, followed by white females, with tan males and tan females similar in brightness (Figure 8, 11). Differences in the color of the MCS were where the original character used to determine the morphs (Thornycroft 1966, 1975). The visual analysis of plumage by humans is also limited to the visual spectrum and was how these birds were classified before (Piper & Wiley 1989). Birds however, can see UV light and this analysis includes that range to better determine the differences between the classes in a biologically relevant manner (reviewed in Rajchard 2009).

Morph/sex class prediction is much less effective when based on back or belly (~40%) feathers than when based on head feathers (~50%). This indicates that the head feathers are likely used in signaling the differences between the types, whereas back and belly feathers are used much less so and may have been influenced by bird condition or used in crypsis. Crown feathers are also molted in the spring, but back and belly feathers are not (Law 1929; Kuenzel & Helms 1974). The newer crown feathers would more likely be involved in reproduction because they are a reflection of condition at a much more recent time than the back and belly feathers.

The back and belly patches were not hypothesized to be used in signaling because they are not molted before the breeding season so there was not expected to be a difference between the groups. The ability to predict the morph/sex class of the birds at a greater rate than chance with these plumage patches however, means that there are differences between the morph/sex classes when all three variables (brightness, saturation and hue) are taken into account. The reason for these differences is unknown, but may be due to condition, the diversion of resources from pigmenting the body plumage to pigmenting the head for signaling or some other unknown constraint on plumage development.

While the use of the principle component scores for the discriminant function analysis did not improve the ability to classify the morph/sex classes, it was able to predict their class significantly more often than chance. Each morph/sex class must be different in their overall contrast for this to occur. When examining the raw data for the classification (Table 2.8), we can see that white males are predicted correctly the most (33/40 or 82.5%) and that white females and tan males were predicted correctly the least often (WF 6/14 or 43%: TM 3/30 or 23%). These two classes appeared to often be confused by the model, with the tan males also

being classified as tan females to a large extent. From this analysis it does not appear that the combination of patches creates a more effective signal for discriminating between the morph/sex classes than many of the individual patches do.

While a large amount of individual variation was observed in the data, this study showed that the groups can be distinguished from each other using plumage characteristics. The plumage characteristics could be the basis for the birds to determine the morph and/or sex of another individual. The variation within a morph/sex class indicates that there may be a basis for sexual selection to act on the plumage of these birds, and that it may act differently due to their different reproductive strategies. Figures 5-10 do not show the characteristics of being only dependent on genes, where there would likely be little variation around the mean, but show spread that could be a signal acted on by sexual selection. The variation was also not significantly correlated with age or age class. This indicates that there is a large amount of individual variation within each class that could be dependent on condition and used as a signal for sexual selection.

Finding distinctive carotenoid spectra from the superciliaries of the white-throated sparrow was hypothesized due to their color and confirmed with our results. This confirms the presence of a molecule in this species that is heavily involved in sexual selection in other bird species, due to limited access (Brawner et. al 2000; McGraw & Hill 2000; Hill 2002, 2006). This suggests that the color of the superciliaries are a sexually selected indicator of quality as they are in many other species (Møller et al. 2000; Lozano 1994). Sexual selection may also be occurring in the melanistic patches. Melanin can be produced from the amino acid tyrosine (McGraw 2006) which is not limited by the diet but has shown to be used in the

immune system as an antioxidant and may be the target of sexual selection (McGraw 2003; Roulin et al. 2000, 2001).

It is important to note that correlations between brightness in patches are only present in males of both morphs. This may indicate that males are investing heavily in their plumage to display their quality to females and that a high quality male is able to produce a darker LCS with lighter MCS, superciliaries, and throat (). This also indicates that if there is a signal given by plumage, it is likely from multiple patches and not simply a single one. Females would not have a correlation between patches if they were not heavily investing in plumage and thus quality and plumage were not related. Female plumage may also not be adaptive, as genes are carried in the females that are only adaptive in the males.

The repeatabilities of most of the patches indicated that the machine and technique were reliable in achieving accurate measurements from the samples. The low repeatability of the measurements of the back, and some of the reason the other regions are not higher, may be due to variability within each feather patch. The back feathers are brown and black and create a mix of colors on the bird (Figure 2), which was recreated when the feathers were taped down. This would mean that slight changes in the placement of the probe could cause a large change in the measured score, reducing the repeatability. This also probably happened, but to a lesser degree, in other patches where there were feathers that were half white and half black (MCS), patchy black/brown (LCS), and differing amounts of yellow and darkly pigmented areas (Scil).

We can use repeatability to indicate variability within a feather patch, or how variable a patch is within an individual with scores closer to 1 being less variable. The males of each morph have relatively constant variability across their patches, while females exhibit more

variation (Table 2.7). The amount of variation within a patch may act as a signal of gender. Females could be subject to aggression from their mates if they were indistinguishable from an intruding male, therefore there may be redundant signals differentiating the females of each morph from their male counterparts, such as differences in brightness of patches but also in differences in the variability in brightness within each patch. WF are the most different in variability with patches from the WM, and this would be expected because WM are the largest threat to a males paternity in his nest due to their promiscuous strategy and he should respond more aggressively. This would result in selection on WF to distinguish themselves from WM as best they can to reduce aggression. Differences in brightness may not be able to be achieved due to sharing genes on the rearranged 2nd chromosome, but other genes may be present in white females that mottle the plumage or disrupt its deposition so that there is a great deal of variation in brightness within a patch. Variation within patches could signal to others that it is not a WM but a WF and reduce the risk of aggression from their mate or neighbors.

Both tan and white females may be patchier in certain areas to aid in crypsis. High investment in plumage may cause patches in males to be less variable, creating a clearer signal than in females. Higher levels of stress in females (e.g. from preparation to breed and lay eggs) may also inhibit the equal distribution of pigment in feathers as well during their molt (Hill 2002, 2006). The effects of preparation for breeding may also be apparent in the belly patches of females where less variability was observed than in the belly patches of males. This may be due to females investing energy in these feathers so they are high quality for insulating the brood patch, eggs, and chicks, whereas the males do not need to do this.

The variation within a patch of feathers for these birds is interesting and needs further work to discriminate its function.

With the two different reproductive strategies, signals may be needed by the white males that are not needed for tan males, and vice versa. Multiple correlated plumage patches could indicate that they are used in different ways, such as one patch being a signal to females of quality where another is a signal to other males, such as a badge of status, and signals may be redundant as well (Johnstone 1995; Candolin 2003; Chaine & Lyon 2008; Budden & Dickinson 2009; Martin & Lopez 2009). To determine the function of the signal from each plumage patch, mate choice and social dominance studies will be needed along with manipulation of the plumage characteristics of these birds.

This species is not the only species with genetically based color morphs. Ruffs have independent, satellite, and female mimic males, all with different plumage (Lank et al. 1995; Jukema & Piersma 2006). Other species such as the arctic skua, the lesser snow goose, and the bananaquit have genetic color polymorphisms and may exhibit mating patterns in relation to their morph (Wunderle 1981 a,b; O'Donald 1983; Cooke et al. 1976,1995; Phillips & Furness 1998). These morphs appear to be controlled by mutations to the melanocortin-1 receptor (MC1R) gene that controls the amount of melanin in the feathers (reviewed in Mundy 2005). This suggests that the MC1R gene or ones that control it may be located on the 2nd chromosome of the white-throated sparrow. This may cause more melanin to be produced in the tan birds, darkening their white and yellow feathers compared to their white counterparts. This hypothesis is supported by my observation of dark pigment, likely melanin, in the superciliaries of many tan birds, and no dark pigment was present in most white birds (personal observation). The melanin masks the carotenoids of the tan males.

This study is a first step in understanding the plumage of this unique species, how selection has affected it, and how it helps to maintain the polymorphism in the population. Here I have demonstrated some basic relationships among the plumage characteristics in this unique species, such as what pigments are used and that different plumage characteristics are indicative of each morph/sex class. This suggests that birds can use plumage to distinguish among individuals of different morph and sex classes and respond appropriately. I have also shown that there is enough variation within each class that the variation could be acted upon by sexual selection if it is a signal.



Figure 2.1. Photographs of the morphs of the White-throated Sparrow

Photographs of the White-throated sparrow morphs showing a white male (a) with a white median crown stripe, black lateral crown stripe, and bright yellow superciliaries and a tan male (b) showing a tan median crown stripe, brownish black lateral crown stripe, and dull mustard superciliaries.

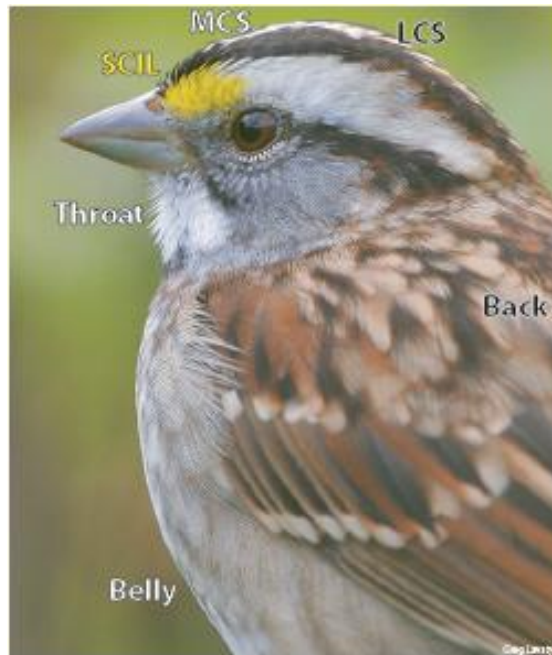


Figure 2.2 Patch sampling locations

Patches where feathers were taken from the white-throated sparrow. The Median Crown Stripe (MCS), Lateral Crown Stripe (LCS), Superciliaries (SCIL), Throat, Belly and Back. Photo credit of Greg Lavaty.

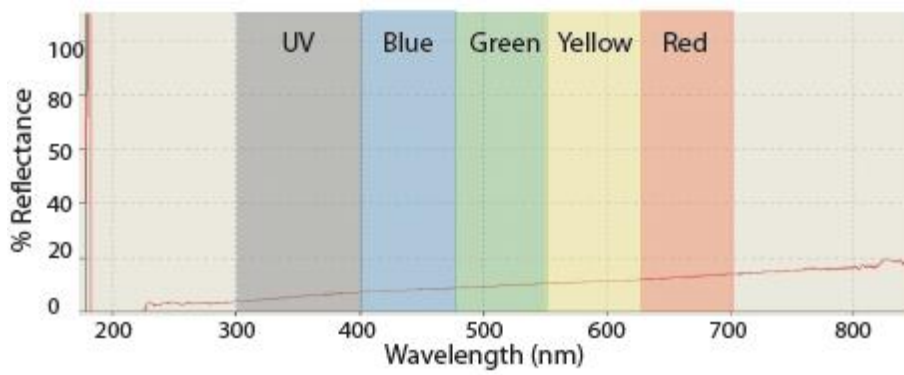


Figure 2.3 White male lateral crown stripe reflectance spectrum

The reflectance spectrum from the black lateral crown stripe (LCS) of a white male. It rises slowly over all wavelengths, characteristic of a melanin pigmented feather.

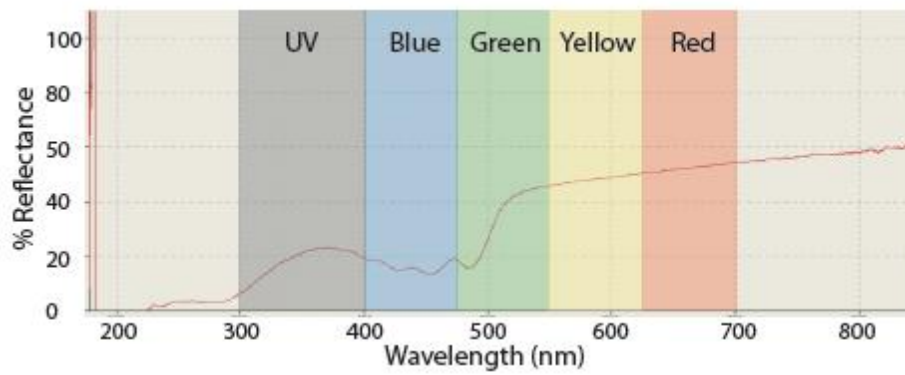


Figure 2.4 White male superciliary reflectance spectrum

Reflectance spectrum from the superciliaries of a white male. It shows reflectance in the UV range and the characteristic carotenoid absorbance between 430-500nm.

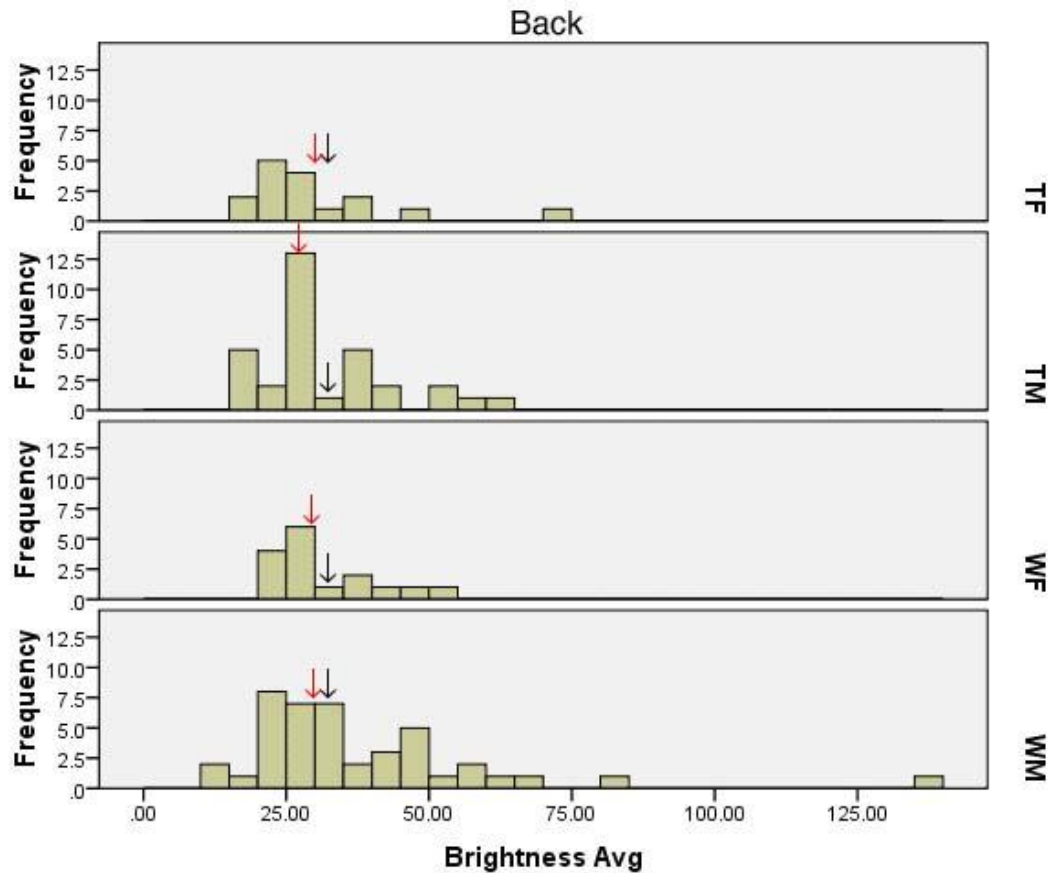


Figure 2.5 Brightness scores frequency distributions for the back

Frequency distributions of the average brightness scores for each morph/sex class for the back feathers. Bars represent a range of 5 on the brightness average score. No great differences in frequencies are observable on these graphs. Where, TF = tan females,

TM = tan males, WF = white females and WM = white males. Black arrows point to the mean and red arrows point to the median. The distributions of the brightness scores are relatively similar between each morph/sex class for this patch.

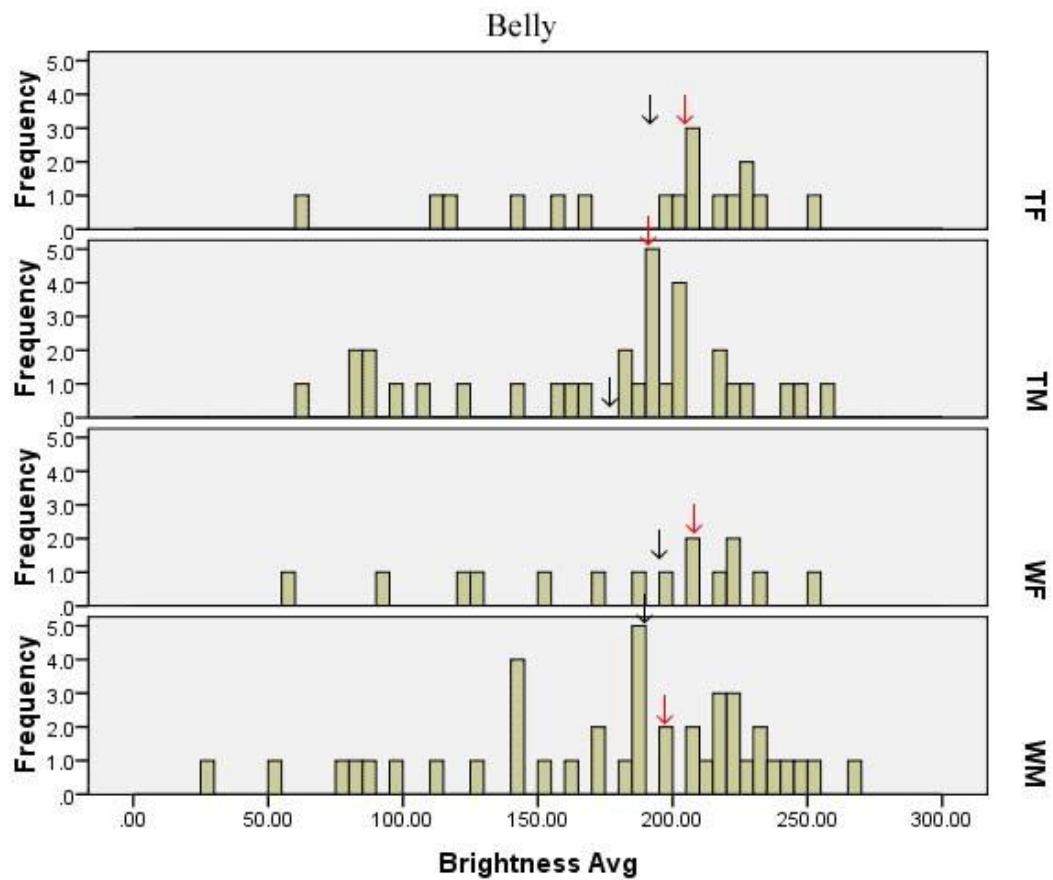


Figure 2.6 Brightness scores frequency distributions for the belly

Frequency distributions of the average brightness scores for each morph/sex class for the belly feathers. Bars represent a range of 5 on the brightness average score. Most distributions are similar, but white males are slightly darker on average. Where, TF = tan females, TM = tan males, WF = white females and WM = white males. Black arrows point to the mean and red arrows point to the median. The distributions of the brightness scores are relatively similar between each morph/sex class for this patch.

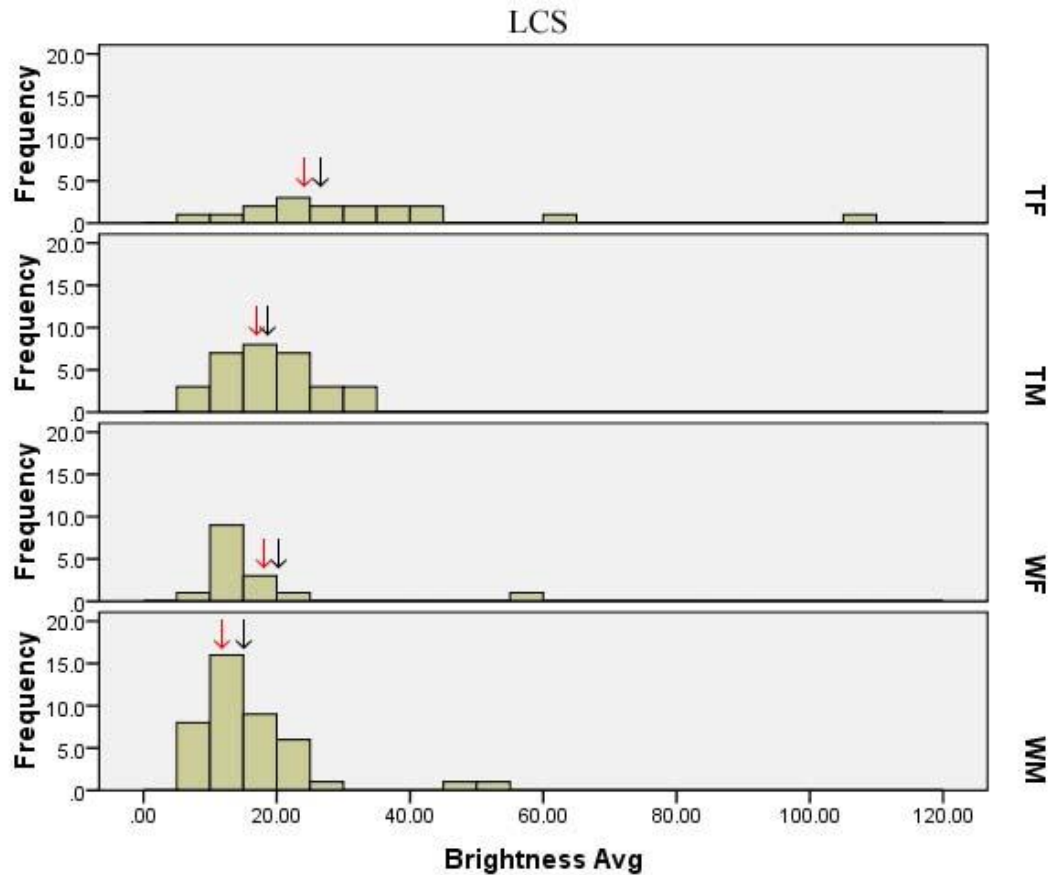


Figure 2.7 Brightness scores frequency distributions for the lateral crown stripe

Frequency distributions of the average brightness scores for each morph/sex class for the LCS feathers. Bars represent a range of 5 on the brightness average score. TF are the brightest individuals here, also with the most variance, as the others were consistently very dark brown-black. Where, TF = tan females, TM = tan males, WF = white females and WM = white males. Black arrows point to the mean and red arrows point to the median. The distributions of the brightness scores are relatively similar between each morph/sex class for this patch, except for the tan females being brighter on average and having a higher variance around the mean.

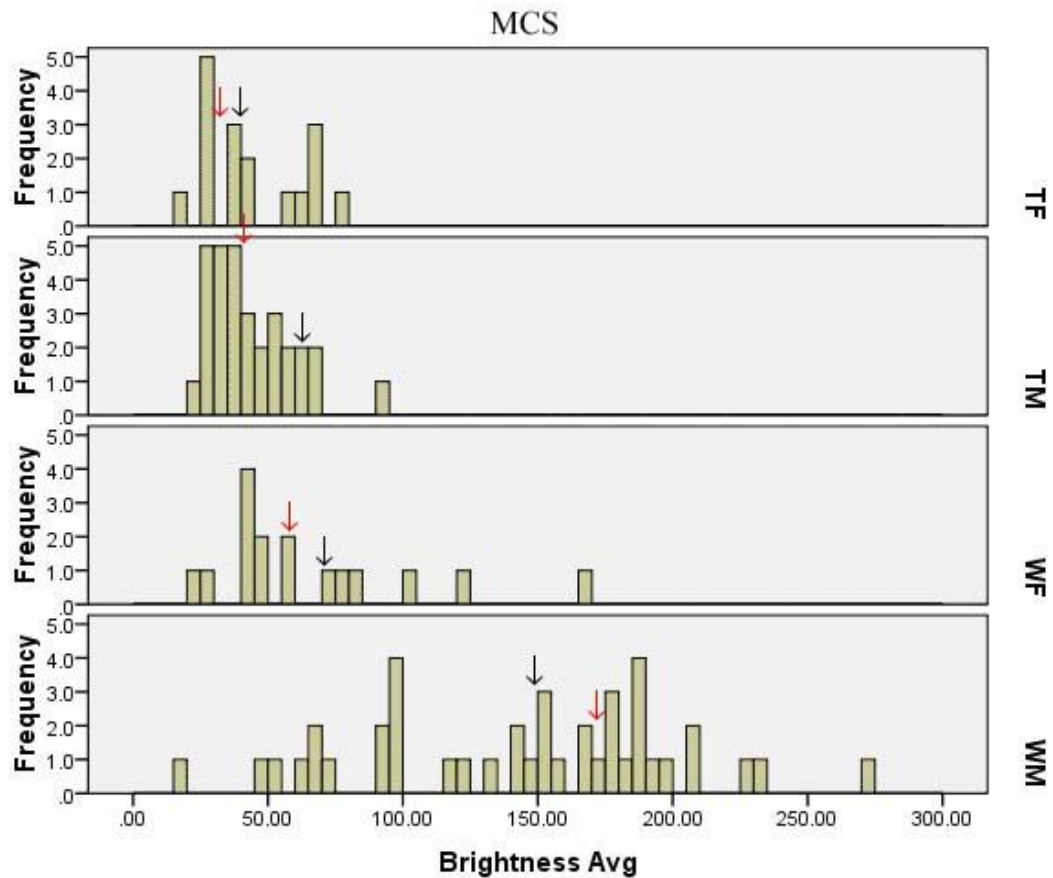


Figure 2.8 Brightness scores frequency distributions for the median crown stripe

Frequency distributions of the average brightness scores for each morph/sex class for the MCS feathers. Bars represent a range of 5 on the brightness average score. White males are the brightest individuals here, with the greatest variance in brightness as well. High variance means there is more raw material for selection to act on. White females are also brighter than either of the tans. Where, TF = tan females, TM = tan males, WF = white females and WM = white males. Black arrows point to the mean and red arrows point to the median. This graph shows that white males are much brighter and more variable than the other morph/sex classes. White females are also brighter and more variable than either the tan males or tan females.

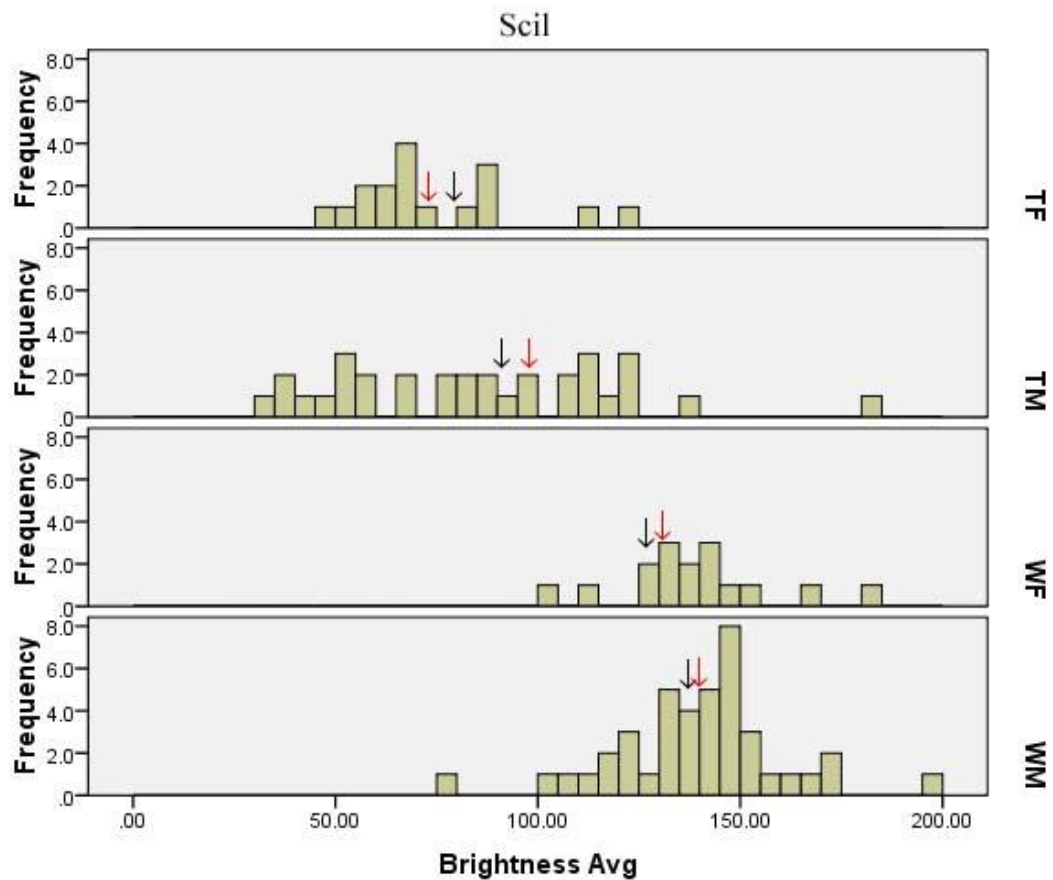


Figure 2.9 Brightness scores frequency distributions for the superciliaries

Frequency distributions of the average brightness scores for each morph/sex class for the superciliaries. Bars represent a range of 5 on the brightness average score. Both sexes of the white morph were brighter than the sexes of the tan morph. Where, TF = tan females, TM = tan males, WF = white females and WM = white males. Black arrows point to the mean and red arrows point to the median. This graph shows that both the white males and white females are brighter than either the tan males or tan females. Tan males however show the highest degree of variation around the mean for this patch.

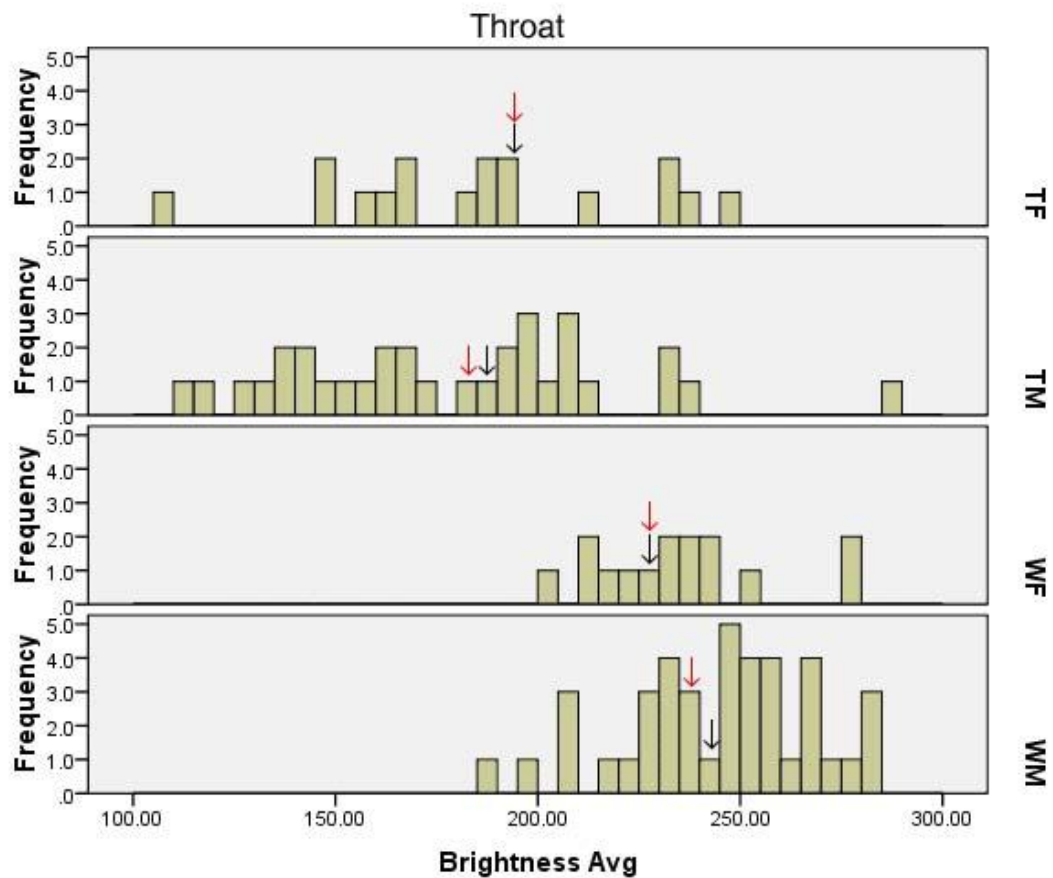


Figure 2.10 Brightness scores frequency distributions for the throat

Frequency distributions of the average brightness scores for each morph/sex class for the throat feathers. Bars represent a range of 5 on the brightness average score. Whites are brighter than tans, but show less variance around the mean. Where, TF = tan females, TM = tan males, WF = white females and WM = white males. Black arrows point to the mean and red arrows point to the median. This graph shows that the white males and white females are brighter in the throat than either the tan males or tan females. The tan males and females appear to have more variation around the mean.

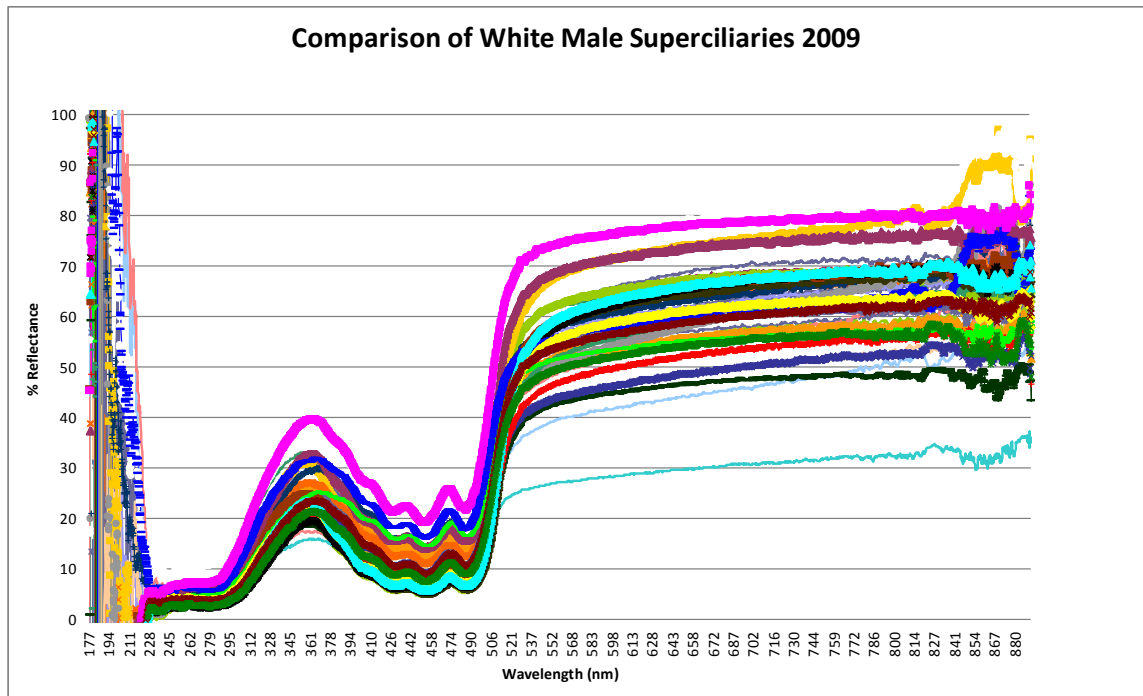


Figure 2.11 Variation in the reflectance spectra of white male superciliaries

Reflectance spectra from all 42 white males sampled for the superciliaries. Each line is a separate male. Variation is shown in how bright the feathers are (the height of the line) but all peak at similar wavelengths in the UV and yellow ranges, giving them similar colors but at different brightnesses. This represents how much variation there is in the reflectance spectra for one class and one patch. This wide variation could mean that this plumage is a signal and related to the quality or health of the bird.

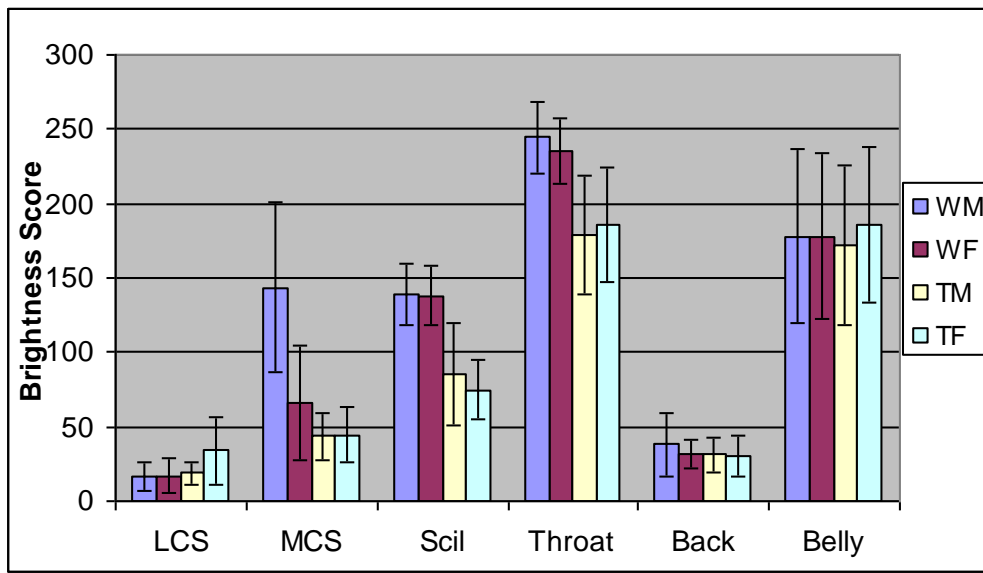


Figure 2.12 Average brightness scores for each patch for each morph/sex class

Average brightness scores of all patches for each morph/class type. Error bars are 1 standard deviation above and below the average. Comparisons between each morph/sex class can be made for each patch. White males are the brightest in the MCS. Both the white males and white females are brighter than either the tan males or tan females in the supercillaries and the throat.

Table 2.1 Repeatabilities

	WM	WF	TM	TF
Back	0.36	0.22	0.47	0.57
Belly	0.78	0.90	0.77	0.86
LCS	0.76	0.29	0.62	0.87
MCS	0.77	0.88	0.68	0.67
Scil	0.76	0.43	0.59	0.66
Throat	0.62	0.72	0.71	0.70

The repeatabilities for each patch for each morph/sex class. Values closer to 1 means more repeatable, and therefore less variable within the patch.

Table 2.2 Equality of Group Means

Tests of Equality of Group Means

Patch		Wilks' Lambda	F	df1	df2	Sig.
Back	Brightness Avg	.955	1.594	3	102	.196
	Saturation Avg	.940	2.165	3	102	.097
	Hue Avg	.960	1.421	3	102	.241
Belly	Brightness Avg	.993	0.225	3	101	.879
	Saturation Avg	.907	3.451	3	101	.019

Patch		Wilks' Lambda	F	df1	df2	Sig.
Hue Avg		.977	0.804	3	101	.494
LCS	Brightness Avg	.790	8.958	3	101	.000
	Saturation Avg	.751	11.184	3	101	.000
	Hue Avg	.992	0.262	3	101	.853
MCS	Brightness Avg	.422	46.074	3	101	.000
	Saturation Avg	.878	4.684	3	101	.004
	Hue Avg	.483	35.983	3	101	.000
Scil	Brightness Avg	.428	45.471	3	102	.000
	Saturation Avg	.960	1.417	3	102	.242
	Hue Avg	.660	17.537	3	102	.000
Throat	Brightness Avg	.508	32.644	3	101	.000
	Saturation Avg	.950	1.771	3	101	.157
	Hue Avg	.683	15.627	3	101	.000

Results from ANOVAs testing for differences among the morph/sex classes for brightness, hue, and saturation in each of the patches. Differences are most apparent for crown feathers.

Table 2.3 Wilks' Lambda

Wilks' Lambda

Patch	Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
Back	1 through 3	.871	14.028	9	.121
	2 through 3	.973	2.784	4	.595
	3	.997	.335	1	.563
Belly	1 through 3	.820	19.902	9	.019
	2 through 3	.989	1.129	4	.890
	3	1.000	.002	1	.963
LCS	1 through 3	.655	42.507	9	.000
	2 through 3	.945	5.681	4	.224
	3	1.000	.038	1	.846
MCS	1 through 3	.315	116.068	9	.000
	2 through 3	.927	7.577	4	.108
	3	.999	.149	1	.700
Scil	1 through 3	.396	93.955	9	.000
	2 through 3	.972	2.860	4	.581
	3	1.000	.015	1	.902

Patch	Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
Throat	1 through 3	.439	82.840	9	.000
	2 through 3	.959	4.164	4	.384
	3	.991	.955	1	.328

Three discriminant functions were calculated for each patch, this table shows the significance levels for the combinations of each function and when using all 3 they are significant for all patches but the back.

Table 2.4 Results of classification by plumage

Classification Results

Patch Original Count Type				Predicted Group Membership				
				WM	WF	TM	TF	Total
Back	Original Count	WM	WM	13	17	4	8	42
			WF	2	8	4	2	16
			TM	6	8	7	11	32
			TF	1	4	2	9	16
	%	WM	WM	31.0	40.5	9.5	19.0	100.0
			WF	12.5	50.0	25.0	12.5	100.0
			TM	18.8	25.0	21.9	34.4	100.0
			TF	6.2	25.0	12.5	56.2	100.0
Belly	Original Count	WM	WM	20	6	5	10	41
			WF	5	3	3	4	15
			TM	8	3	10	11	32
			TF	2	2	4	9	17
	%	WM	WM	48.8	14.6	12.2	24.4	100.0
			WF	33.3	20.0	20.0	26.7	100.0
			TM	25.0	9.4	31.2	34.4	100.0
			TF	11.8	11.8	23.5	52.9	100.0

				Predicted Group Membership				
Patch	Type			WM	WF	TM	TF	Total
LCS	Original Count	WM	WM	30	1	7	4	42
			WF	7	2	5	1	15
			TM	4	6	16	5	31
			TF	0	3	5	9	17
	%	WM	WM	71.4	2.4	16.7	9.5	100.0
			WF	46.7	13.3	33.3	6.7	100.0
			TM	12.9	19.4	51.6	16.1	100.0
			TF	.0	17.6	29.4	52.9	100.0
MCS	Original Count	WM	WM	31	7	2	1	41
			WF	2	9	4	1	16
			TM	0	7	15	9	31
			TF	0	4	3	10	17
	%	WM	WM	75.6	17.1	4.9	2.4	100.0
			WF	12.5	56.2	25.0	6.2	100.0
			TM	.0	22.6	48.4	29.0	100.0
			TF	.0	23.5	17.6	58.8	100.0

Patch			Type	Predicted Group Membership				
				WM	WF	TM	TF	Total
Scil	Original Count	WM	18	20	3	0	41	
		WF	7	8	1	0	16	
		TM	1	6	14	11	32	
		TF	0	1	8	8	17	
	%	WM	43.9	48.8	7.3	.0	100.0	
		WF	43.8	50.0	6.2	.0	100.0	
		TM	3.1	18.8	43.8	34.4	100.0	
		TF	.0	5.9	47.1	47.1	100.0	
Throat	Original Count	WM	24	13	1	3	41	
		WF	4	10	1	0	15	
		TM	2	2	20	8	32	
		TF	1	3	6	7	17	
	%	WM	58.5	31.7	2.4	7.3	100.0	
		WF	26.7	66.7	6.7	.0	100.0	
		TM	6.2	6.2	62.5	25.0	100.0	
		TF	5.9	17.6	35.3	41.2	100.0	

a. Back, 34.9% of original grouped cases correctly classified.

b. Belly, 40.0% of original grouped cases correctly classified.

- c. LCS, 54.3% of original grouped cases correctly classified.*
- d. MCS, 61.9% of original grouped cases correctly classified.*
- e. Scil, 45.3% of original grouped cases correctly classified.*
- f. Throat, 58.1% of original grouped cases correctly classified.*

The results from classifying each bird using the 3 discriminant functions. The results are displayed both by count and by percentage that were classified into each category. WM = white male, WF = white female, TM = tan male, TF = tan female. The classifications in bold are the ones correctly classified for that patch. Overall percentages correctly classified are displayed for each patch at the bottom of the table (a-f).

Table 2.5 Summary of the differences between each morph and sex within a morph

	Male	Female
White	Brighter MCS	Duller MCS
Tan	Darker LCS	Lighter LCS

Differences between the sexes of each morph. White males differed from white females in the brightness of the median crown stripe (MCS), with white males being brighter on average. Tan males differed from tan females in the brightness lateral crown stripe (LCS), with the males having darker plumage on average.

Table 2.6 Correlations between patches

Brightness				
	White Males	Tan Males	White Females	Tan Females
▲ LCS	▼ MCS, Scil, Throat	▼ MCS, Scil, Throat	None correlated	None Correlated
	▲ Back	▲ Back and Belly		

Correlations between the patches of each morph/sex class. An increase the brightness of the lateral crown stripe (LCS) correlated with a decrease in the brightness of the median crown stripe (MCS), superciliaries (Scil), and throat in white males, while correlating with an increase in back brightness as well. For tan males, an increase in the brightness of the LCS also correlated with a decrease in brightness of the MCS, Scil, and throat but was correlated with an increase in brightness in the back as well as the belly. No significant correlations were found between patches in the females of either morph.

Table 2.7 Descriptive statistics for plumage patches

Descriptive Statistics

Patch	Type		N	Minimum	Maximum	Mean	Std. Dev.
Back	TF	Brightness Avg	16	18.40	70.96	30.2785	13.40503
	TM	Brightness Avg	32	15.10	60.83	31.4367	11.67265
	WF	Brightness Avg	16	21.17	54.53	31.7412	9.56617
	WM	Brightness Avg	42	13.87	138.05	38.2703	21.52825
Belly	TF	Brightness Avg	17	60.14	254.75	186.0164	51.86293
	TM	Brightness Avg	32	61.16	257.99	172.4344	53.71606
	WF	Brightness Avg	15	58.27	250.38	178.1232	55.61117
	WM	Brightness Avg	41	28.88	266.59	178.0563	58.00599
LCS	TF	Brightness Avg	17	9.69	105.92	33.9316	22.48521
	TM	Brightness Avg	31	7.27	34.38	18.7693	7.21604
	WF	Brightness Avg	15	9.14	58.58	17.0567	11.93960
	WM	Brightness Avg	42	6.61	53.65	16.3566	9.25589
MCS	TF	Brightness Avg	17	19.48	76.33	44.1754	18.46614
	TM	Brightness Avg	31	24.93	92.41	43.4489	15.49553
	WF	Brightness Avg	16	21.71	169.36	65.6965	38.38173
	WM	Brightness Avg	41	17.97	273.53	143.6939	57.55989

Patch	Type		N	Minimum	Maximum	Mean	Std. Dev.
Scil	TF	Brightness Avg	17	49.35	124.36	74.4726	20.04701
	TM	Brightness Avg	32	33.43	182.58	85.3858	34.52657
	WF	Brightness Avg	16	100.31	182.15	138.2470	19.50474
	WM	Brightness Avg	41	76.40	195.02	139.4592	20.67213
Throat	TF	Brightness Avg	17	105.26	249.09	185.6977	38.30049
	TM	Brightness Avg	32	111.04	288.60	178.5939	39.65124
	WF	Brightness Avg	15	204.86	278.48	235.0169	21.70282
	WM	Brightness Avg	41	188.59	282.25	244.3337	23.62356

The count and brightness range, mean, and standard deviation for each patch in each morph/sex class sampled.

Table 2.8 Predicted vs. Actual group membership using PCA

Type			Predicted Group Membership				
			WM	WF	TM	TF	Total
Original Count	WM		33	4	0	3	40
	WF		5	6	2	1	14
	TM		2	7	7	14	30
	TF		0	3	3	10	16
	Ungrouped cases		0	0	0	1	1
%	WM		82.5	10.0	.0	7.5	100.0
	WF		35.7	42.9	14.3	7.1	100.0
	TM		6.7	23.3	23.3	46.7	100.0
	TF		.0	18.8	18.8	62.5	100.0
	Ungrouped cases		.0	.0	.0	100.0	100.0

a. 56.0% of original grouped cases correctly classified.

The results from classifying each bird using the a principle component analysis after using 3 discriminant functions. The results are displayed both by count and by percentage that were classified into each category. The classifications in bold are the ones correctly classified for that patch. Overall percentages correctly classified are displayed for each patch at the bottom of the table.

Appendix A

Equations and wavelengths used by the CLR program for calculating brightness, hue, and Saturation

Blue (400-475nm)	Green(475-550nm)
Yellow (550-625nm)	Red (625-700nm)

Brightness (B)

Area under the reflectance spectrum between desired wavelengths.

Hue

$\text{Arctan}((B_{\text{yellow}} - B_{\text{blue}})/B_{\text{total}})/(B_{\text{red}} - B_{\text{green}})/B_{\text{total}}$

Saturation

$^{300}\Sigma_{400} R_i / \text{Brightness}$

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CHAPTER 3

FITNESS EFFECTS OF PLUMAGE IN THE WHITE-THROATED SPARROW

Introduction

Sexual selection can oppose natural selection and lead to the evolution of costly ornaments in males (Darwin 1871; Fisher 1958). Many studies have examined how these costly ornaments can arise (reviewed in Kirkpatrick & Ryan 1991; Zuk et al. 1992; Owens & Hartley 1998). Ornaments can be used to attract social mates (Møller 1988), or sexual partners (Saino et al. 1997; Safran et al. 2005), or be used in intrasexual competition over mates or territories (Chaine & Lyon 2008) and increase the overall fitness of individuals with the most exaggerated traits (Yezerinac & Weatherhead 1997). Ornaments reflecting male quality have been found in a wide variety of species, from antlers in moose (*Alces alces*) (Solberg & Saether 1993) and roe deer (*Capreolus capreolus*) (Vanpe et al. 2007) to the building of pillars in fiddler crabs (*Uca beebei*) (Backwell et al. 1995).

Some of the most well known sexually selected ornaments occur in the plumage of birds. These plumage ornaments come in a variety of traits such as the size/symmetry of feathers (Møller 1988, 1993, 1994; Pryke & Andersson 2005), melanin pigmented ornaments (O'Donald, 1980; Roulin et al. 2001), carotenoid pigmented ornaments (Hill 1991, 2002; G. Hill et al. 1994, 1999; Wolfenbarger, 1999; McGraw et al. 2001, 2005), and even achromatic (white) ornaments (Sheldon et al. 1997; J. Hill et al. 1999; Sheldon & Ellegren 1999). Organisms may also have

multiple ornaments and these may be used in different contexts (Møller & Pomiankowski 1993; Karubian et al. 2009).

There are a variety of costs associated with plumage ornamentation. Larger feathers reduce the flying ability an individual or increase the energetic cost of flying, possibly reducing foraging ability and increasing susceptibility to predators (Evans & Thomas 1992; Pryke & Andersson 2005; Clark & Dudley 2009). Pigments are costly to produce or to obtain (McGraw 2006), so they impose a resource cost to the individual with only high quality individuals able to pay the cost (Andersson 1994). The pigments also have been shown to help strengthen feathers and reduce wear, imposing a cost on those feathers without pigments (Bonser 1995). The presence of bright patches on a bird may also increase its overall brightness and conspicuousness, both to conspecifics and predators (Haskell 1996; Huhta et al. 2003). White plumage patches can have a role in mate choice and male/male competition (J. Hill et al. 1999). It is not clear all of the costs associated with white plumage but they appear to suffer more from abrasion than feathers with melanin in them, causing the bird to suffer costs of worn feathers (Bonser 1995). They also may be seen as a badge of status in some species with brighter patches signaling higher status (Gustafsson et al. 1995).

Plumage attributes have been shown to be under selection via female mate choice as well as intrasexual selection (Berglund et al. 1996; Jones & Hunter 1999; Amundsen 2000; Daunt et al. 2003). With multiple signals, it is possible that different characteristics of a bird signal function in different contexts (Doucet & Montgomerie 2003). These multiple patches may also combine into one signal, such as visual contrast (differences in brightness of patches). Contrast of a bird has been studied, but mostly has focused on the contrast between a bird and its surroundings, not within the plumage itself (Endler & Day 2006). Plumage may signal parental

effort, quality, or many other factors (Balenger et al. 2007). It may also induce the mate of the bird to invest more in a nesting attempt by producing more or more expensive offspring or simply adjust paternity (Kappes et al. 2009).

In most species, males produce the ornaments, and the individuals with the most exaggerated ornaments achieve the highest reproductive success (Hill et al. 1994; Møller 1994; Safran & McGraw 2004) but in other species both males and females produce sexually selected ornaments (Doutrelant et al. 2008; Griggio et al. 2009). In the white-throated sparrow (*Zonotrichia albicollis*) however, there are two different morphs, one more ornamented than the other, that have two different reproductive strategies, and differ greatly in their plumage (Tuttle 1993, 2003). This raises the possibility that sexual selection has acted on the promiscuous white males differently than on the monogamous tan males and they both produce sexually selected ornaments of different types (Tuttle 2003). Females should not have ornaments as natural selection may be stronger than sexual selection for females of this species. The plumage differences between the morphs were quantified previously and could be caused by sexual selection, natural selection or the interaction of both (Rathbun et al. 2010). This study species provides a unique opportunity to examine the effects of natural selection and sexual selection on differing reproductive strategies within the same species so that genetic and environmental factors are controlled for. The two different morphs are not geographically separated and only appear to differ genetically in the 2nd chromosome that directly determines the morph (Lowther 1961; Thorneycroft 1966, 1975; Formica et al. 2004; Tuttle et al. 2006; Romanov et al. 2009; Thomas et al. 2009).

The white-throated sparrow mates disassortatively in relation to the different morphs, with white males pairing with tan females and tan males with white females almost exclusively

(Lowther 1961; Houtman & Falls 1994; Tuttle 2003). These morphs are determined genetically by a large rearrangement of the 2nd chromosome, with whites being heterozygous for the rearrangement and tans being homozygous without the rearranged chromosome (Lowther 1961; Thorneycroft 1966, 1975; Romanov et al. 2009; Thomas et al. 2009).

Promiscuous white males should benefit from advertising their quality, either to females who would then solicit extra-pair copulations (EPCs) or to other males who would then risk intrusion less frequently. I hypothesized that the plumage of the white males would therefore be under sexual selection, with brighter males with higher contrast producing more/better offspring than duller white males. The number of within-pair young (WPY) in a white males nest should also increase with brightness, as the brighter male would be in better condition if he is able to incur the costs of the plumage. A higher quality bird should be able to better defend his female from intrusions or prevent her from mating with the neighbors because she has a high quality mate, depending if EPCs are forced or coerced by females. White males have already been shown to sing more than their tan counterparts, and this selective pressure to be conspicuous for territorial and mating reasons could also have acted on their plumage (Tuttle 1993, 2003).

I also hypothesized that sexual selection would be weaker on the plumage of monogamous tan males because they do not seek out EPCs and provide more parental care to their nestlings (Knapton & Falls 1983; Tuttle 2003). Bright or contrasting plumage would attract attention to the tan male that is not needed once he has a mate, and could result in higher predation. By providing more care to the nestlings than white males, the tan males give predators more chances to follow them to the nest and by having dull plumage they would make this task more difficult for predators. The females of duller tan males would have a lower predation risk

for their nests and should invest more in the nesting attempt because it is more likely to be successful (Haskell 1996).

For females, their plumage should evolve to reduce the risk of predation on their nests. This may be confounded in white females due to the sharing of genes selected for increased brightness in the white males and also due mate choice by tan males that are the preferred mate (Tuttle 1993; Houtman & Falls 1994). Tan females have the lowest survival rate and so should try and decrease their risk of losing all reproductive success through predation because it may be their only chance to reproduce (E.M. Tuttle, unpublished data). The low survival of tan females may be due to their mate giving little parental care, increasing the cost of reproduction on the females (Tuttle 1993, 2003). The tan females are also the lightest as chicks, indicating that they have the least reserve resources to start with and this disadvantage may follow them throughout their lives (E.M. Tuttle unpublished data).

The white-throated sparrow gives a unique opportunity to observe the interaction of sexual and natural selection in one species. By correlating the plumage characteristics of each morph with fitness characteristics, we can determine what a high quality individual of each morph/sex class would look like. Once this is determined, a comparison between the reproductive strategy and plumage in this species can be made with other species and their reproductive strategies. From other species with a high degree of promiscuity we would expect promiscuous males to be brightly colored to signal quality, as it has been shown in Yellow Warblers (*Dendroica petechia*: Yezerinac & Weatherhead 1997). Monogamous males and females would also be expected to be duller to reduce predation risk of the adults or nest (Haskell 1996; Gotmark & Olsson 1997; Miller 1999).

Methods

Study Site

A naturally occurring breeding population of white-throated sparrows was sampled during the summer months (May-August) of 2006-2009 for this study. This population is located in >32 hectares near the Cranberry Lake Biological Station (44°15'N; 74°48'W) in the Adirondack Mountains of New York. This population has been studied extensively by Dr. Elaina Tuttle for over 20 years, so the minimum ages of many of the birds were known when they were sampled. All birds are banded with fish and wildlife bands as well as with unique color bands so that they can be identified visually from a distance.

Feather collection

Feathers were collected from 107 adult white-throated sparrows captured using passive mist netting as well as song playback on their breeding territories. The birds were targeted mainly in the preferred breeding area of the site. Birds with nests already found in the season were also targeted for this study. The feathers were taken from the median crown stripe, lateral crown stripe, superciliaries, throat, back and belly from each bird. At least 3 feathers from each patch were taken but most of the time 5 feathers were collected. Some birds did not have all patches sampled or had fewer than 3 feathers taken from a particular patch. These birds were excluded from the analysis of that patch ($N = 6$). Feathers were stored in the dark in order to prevent pigment degradation in 1.5ml centrifuge tubes. They were then taped down onto blank index cards, recreating a natural reflectance surface.

Feather Analysis

Reflectance spectra data was collected for each patch by using a USB2000+ Miniature Fiber Optic Spectrometer (Ocean Optics, Dunedin, FL). This provided reflectance spectra for each feather patch. Each feather patch was sampled 3 separate times to capture the variance within a feather and to test the reliability of the instrument and repeatability of the process. The probe was removed and replaced on the feather prior to each measurement. Every hour the white reflectance standard on the spectrometer was reset to control for machine changes. Each reflectance spectrum was then analyzed using the CLR program (v1.05) (Montgomerie 2008). This tool scored each feather patch for hue, brightness, and saturation. This gave scores for 3 different measurements for each of the 6 patches on each bird, resulting in 18 measurements of feather color per bird. Brightness (also known as “total reflectance” or “brightness”; Endler 1990) in this study is defined as the amount of total intensity of the light spectrum visible to birds (300 - 700 nm). Hue is the actual color displayed by the feather and saturation is the amount of the color pigment present.

Molecular Analysis

White-throated sparrow nests were located by following breeding pairs and monitoring their behavior. A blood sample (80-200ul) was taken from the brachial vein of all chicks and adults to obtain DNA. Blood was taken from the chicks between 6 and 7 days after hatching, and before they leave the nest. The hematocrit was stored in lysis buffer at 4°C (Longmire et al. 1992) until molecular analysis was conducted. The DNA was extracted from the hematocrit using the DNA IQ® magnetic extraction system (Promega Corp; Madison, WI). Sex of the chicks was determined using the primers, P2 and P8 and published thermal cycle and master mix

(Griffiths et al. 1998), to amplify a conserved region of the CHD gene on the sex chromosomes W and Z. Parentage analysis was conducted on all individuals using five microsatellites; Gf01 and Gf12 (Petren 1998), MME1 (Jeffery et al. 2001), and Dpμ01 and Dpμ03 (Dawson et al. 1997). Morph was determined by a process modified from Michopoulos et al. (2007). All DNA was fluorescently labeled and run on an ABI PRISM 310 Genetic Analyzer® (GMI Inc.; Ramsey, MN) to produce results for parentage, sex, and morph. The morph and sex of chicks was used in association with paternity to determine the relationship between plumage and fitness. Sex of adults was determined at capture by the presence of a brood patch or cloacal protuberance and was confirmed by behavior. Morph of the adults was determined visually at capture by the criteria set forth by Lowther (1961), Piper and Wiley (1989), and Tuttle (1993, 2003). A sample of 10 adult white-throated sparrows were morphed and sexed molecularly and all visual classifications matched with molecular classifications.

Statistical Analysis

Overall contrast scores were used as defined in Rathbun et al. (2010). These overall contrast scores were correlated with various measures of reproductive success and fitness, such as within-pair paternity, chance of being cuckolded, as well as the proportion of sons, white offspring, and the proportion of offspring in each morph/sex class. Condition was defined as the birds mass at capture divided by its left tarsus length.

Results

Each different morph/sex class was analyzed separately with various aspects of reproduction and correlated with their plumage characteristics. In tan males (TM), overall

contrast was negatively correlated with the total number of nestlings produced ($F_{1,15}=6.44$, $R^2=0.30$, $p=0.02$), the proportion of white offspring in a nest ($F_{1,15}=4.77$, $R^2=0.24$, $p=0.05$), proportion of white females in a nest ($F_{1,15}=7.09$, $R^2=0.32$, $p=0.02$), and positively correlated with the proportion of tan females in a nest ($F_{1,15}=8.76$, $R^2=0.37$, $p=0.01$). Adult condition (mass/tarsus) was also positively correlated with overall contrast ($F_{1,35}=11.18$, $R^2=0.24$, $p=0.002$).

In white males (WM), the overall contrast was positively correlated with number of nestlings ($F_{1,16}=7.12$, $R^2=0.31$, $p=0.02$). The proportion of males also increased ($F_{1,16}=10.35$, $R^2=0.39$, $p=0.005$) with TM significantly increasing ($F_{1,16}=4.79$, $R^2=0.23$, $p=0.04$) and a trend for WM to increase ($F_{1,16}=3.09$, $R^2=0.16$, $p=0.1$). The increase in males reduced some production of tan females, as the proportion of TF in a nest was negatively correlated with overall contrast ($F_{1,16}=8.90$, $R^2=0.36$, $p=0.009$).

In white females (WF), an increase in overall contrast was correlated with an increase in the proportion of tan females in a nest ($F_{1,7}=11.23$, $R^2=0.62$, $p=0.01$) and a trend for a decrease in the proportion of males produced ($F_{1,7}=4.20$, $R^2=0.38$, $p=0.08$). While the PCA combined all patches together, individual patches were also correlated with fitness. The superciliary brightness in WF was correlated with the total number of nestlings produced in her nest ($F_{1,8}=5.84$, $R^2=0.42$, $p=0.04$). LCS brightness was negatively correlated with total nestlings produced ($F_{1,7}=5.90$, $R^2=0.46$, $p=0.05$).

Tan females (TF) overall contrast was correlated with the number of eggs lost ($F_{1,9}=23.71$, $R^2=0.72$, $p<0.001$). There was a trend for TF LCS brightness to be positively correlated with total nestlings ($F_{1,8}=4.63$, $R^2=0.37$, $p=0.06$). The MCS brightness was negatively correlated with the total number of nestlings ($F_{1,8}=9.35$, $R^2=0.54$, $p=0.02$) and also the proportion

of males in the nest ($F_{1,8}=18.27$, $R^2=0.70$, $p=0.003$). This was partially accounted for by a positive correlation between the MCS brightness and the proportion of TF in a nest ($F_{1,8}=16.53$, $R^2=0.67$, $p=0.004$).

Within pair paternity was analyzed for each type as well, and within pair paternity was only found to be related to plumage in tan birds. Tan females that were brighter overall had fewer within pair young per nest ($F_{1,9}=6.12$, $R^2=0.40$, $p=0.04$) and brighter tan males were less likely to be cuckolded ($X^2=3.84$, $df=1$, $p=0.05$). No relationship was found between plumage attributes or fitness characteristics and age or age class of the birds in this study.

A visual representation of example bright and dull males of each morph and females of each morph are shown in Figures 3.1-3.2. Table 3.1 summarizes the results from this section.

Discussion

In the white-throated sparrow, morph/sex classes appear to experience different selective pressures. This would be expected due to their differing reproductive strategies. In the tan male, and tan birds in particular, high “quality” birds appear to have less contrast in their head plumage (i.e. brighter LCS, duller MCS) possibly decreasing the ability of conspecifics and predators to detect them in the environment as was hypothesized in many other studies (Tuttle 1993; Houtman & Falls 1994). Duller tan males have more nestlings and these nestlings are more likely to be white, especially a white female, and less likely to be a tan female. With fewer nestlings, the parent has to invest fewer resources in the nest to have it succeed with fewer mouths to feed. Tan females are also the cheapest type of offspring to produce, weighing the least (Korpamaki et al. 2000). In the WTSP, males are heavier and thus more costly to produce than females and white offspring are heavier and more costly than tan offspring (E.M. Tuttle unpublished data).

Thus, the mates of the tan males with bright plumage are decreasing production of the costly types (whites) and increasing the proportion of cheapest type (tan females) in correlation with decreasing brightness of the tan males plumage. This may signal that the bright tan males will provide less parental care or that they do not have good genes. The mates response to the plumage of the tan males may simply be a reflection of predation risk, as brighter birds with more contrast will be more visible to nest predators (Haskell 1996; Gotmark & Olsson 1997; Miller 1999). By limiting the brood to the less costly offspring types, the parents would lose less if the nest is depredated. Natural selection and sexual selection could be acting in the same direction to reduce the conspicuousness of the tan birds. Previous studies have also found a correlation between plumage and which offspring are produced in the blue tit (*Parus caeruleus*) (Sheldon et al. 1999).

White males were very different from their tan counterparts. In this morph/sex class, as the overall contrast increased, more nestlings were produced in the males own nest and more of these nestlings were males, with fewer tan females being produced. This indicates that the mates of the white males with brighter plumage are either in better condition and are able to commit more resources to the nestling attempt with more costly (heavier) young (males), or they are swayed by the signal of the male and invest more in a nesting attempt with a high quality male with good genes than invest in a subsequent nesting attempt with a male of unknown quality. Both scenarios would lead to the same result, and comparisons of pairs would be required to distinguish between them. In either case however, the white male displaying the brighter plumage has a reproductive success than a white male displaying duller plumage, either due to gaining a higher quality mate or persuading their mate to invest more resources in the current nesting attempt. This comes in both the form of producing more offspring overall, as well as

producing more males which have a higher reproductive skew than females (due to EPCs). The plumage of the white males may also increase success in extra-pair mating. Brightness of plumage has been shown to correlate with a high degree of extra-pair paternity (Møller & Birkhead 1994)

Included in the overall contrast of a bird is the brightness of the superciliaries. The superciliaries are pigmented with carotenoids, and these pigments cannot be produced by birds and must be acquired through the diet (McGraw 2006). It is interesting that these superciliaries pigmented with a difficult pigment to acquire are correlated with the production of the offspring type that is the most expensive (white males). Superciliary brightness (from carotenoids) could be a signal to females about male quality as it is in many other species (G. Hill et al. 1994, 1999; McGraw et al. 2001).

Female plumage expression is also related to their reproductive effort. For tan females, the LCS brightness was positively the total number of nestlings and the MCS negatively correlated with the total nestlings produced. The overall contrast was not related to these factors because the throat and superciliaries did not correlate with the number of nestlings. A female with more contrast in her crown (brighter MCS, darker LCS) would attract more predators than a dull female, causing selection to favor those individuals with low crown contrast. While contrast has not been studied in relation to predation, bright colors have been shown to attract predators to nests (Haskell 1996). Tan females that are brighter overall have more eggs lost than duller females, indicating a higher predation risk to brighter females nests.

White females seem to be less affected by predation risk, as reflected in their plumage, because there was no trend between predation measures (eggs or chicks lost) and plumage. However, brighter white females had a higher proportion of tan daughters and lowered the

proportion of sons overall. As mentioned before, daughters less costly to produce than sons, and may indicate different allocation of resources, from investing in the current nesting attempt to investing in their own survival or another nesting attempt. Reduced predation may occur because of the help from her tan mate she receives.

Overall contrast increased with condition in tan males, and those that had higher contrast were cuckolded less as well. With a brighter tan male mate, the white females offspring would be more likely to be depredated but would also likely have good genes from their father. For this reason, the female may invest less in the nesting attempt by having less expensive offspring (tan females) but have fewer EPY because they do not have to seek them out to find good genes or because their mate is better able to defend them. With a dull tan male mate, the white female has less predation risk but may have a mate with poor genes or who is unable to defend the female as well. Therefore the female appears to invest more in the expensive offspring (males) but have some young be from a mate other than their social father.

It appears that in white males, higher contrast and overall brightness gives the male higher fitness due to more offspring and males being produced in his nest but whether this due to a higher quality mate or signaling male quality to a female to alter her allocation of resources is unknown. In tan males, it is just the opposite, with duller males with less contrast overall producing more offspring and more white birds; again the mechanism for this is unknown. These plumage attributes may have additional value in male/male competition. White males may advertise their presence with their plumage as well as their song (Tuttle 2003), while tan males are much more inconspicuous. With differing reproductive strategies, white males trying to gain EPCs and tan males staying on their territory to defend their female (Tuttle 2003), this may cause the difference in signaling.

These signals should be honest if they are correlated with quality. White males experience the costs of producing white (unpigmented) feathers (MCS, throat), producing black (melanin pigmented) feathers, and producing yellow (carotenoid pigmented) feathers. Adding more pigment to create black feathers is costly because melanin molecules are large and metabolically expensive to produce (McGraw 2006). The resources used to produce these molecules could be used in other areas instead, such as invested in reproduction or the immune system. The deposition of melanin into feathers is also dependent on stress, as stress hormones can interrupt the deposition process (Hill 2002, 2006; Roulin et al. 2008). Producing a white feather is also not easy. White feathers are unpigmented, but they are subject to increased wear because they do not have melanin to strengthen the feather (Bonser 1995). This may result in a loss of energy because the worn feathers are less effective in protecting the bird, repelling water, or keeping in heat, costing the bird resources in the long term. Carotenoid pigments are costly because they must be acquired from the diet, and foraging to gain these exposes the bird to extra predation risk and costs energy (Hill 2002, 2006). A high overall contrast with a dark LCS and bright MCS, superciliaries, and throat would also attract the attention of predators. This would expose the bird to higher threat of predation and also may cost it more energy due to the need for increased vigilance and energy expended fleeing from predators that may not have seen it if the bird were duller. Therefore, white males may have the highest “cost of plumage” when the costs of production, maintenance, and plumage effects on predation risk are taken into account. By incurring this cost, white males appear to signal their quality to females and possibly to other males as well.

Tan males also have costs to their plumage. They must produce melanin to pigment their feathers brown, diverting resources from other areas. Some contrast may be beneficial, as no

birds were observed having purely brown plumage all over with no contrast. It may be used for male/male competition, species recognition, or crypsis. The tan males with higher contrast may be advertising their presence by being more conspicuous to prevent territorial intrusions that it would have to spend energy to expel that they cannot afford. This is supported by brighter tan males being less likely to raise another male's offspring in their nest. The tan males with less contrast have more quality offspring in their nest but may lose paternity whereas the brighter tan males have lower quality offspring but they are more likely to father them all. Additionally, it appeared that the superciliaries of tan males had melanin as well as carotenoid pigments. The yellow pigment appeared to be masked by a covering of dark melanin, as the inner portion of the feather was darker than the outer portion. The tan males with brighter superciliaries might therefore not be able to produce the extra melanin to mask the carotenoids so the duller males would be of higher quality. Carotenoids may not in fact be limiting because they are such a small patch of feathers which would require less pigment than a larger patch.

Sexual selection on females may be weak due to limited male mate choice, but natural selection should have a strong effect due to predation on adults as well as the nests they are caring for. White females that are brighter with more overall contrast appear to invest less in their nesting attempt than duller white females. White females share genes on the rearranged 2nd chromosome with white males, possibly causing them to express more genes that have been selected for increased brightness in the white male (Lowther 1961; Thorneycroft 1966, 1975; Thomas et al. 2008). Display traits in females have often been argued to be the result of correlated selection on the ornamentation of males (Amundsen 2000) and the chromosome determining the difference between the white and tan male is present in the female as well (Thorneycroft 1966, 1975), possibly maintaining their brightness in the face of natural selection.

White females in good condition may be able to produce additional melanin to mask these effects and therefore exposing themselves and their nests to less predation. Higher contrast may also be needed by these females to help their males with territorial defense or may be selected for by tan male mate choice (Tuttle 1993; Houtman & Falls 1994).

Tan females appear to be selected solely by predation risk to their nests. Tan females receive the least help from their mates and appear to have the lowest annual survival so a single nesting attempt may be their only chance to reproduce and they would want to achieve at least some reproductive success (Tuttle 2003). By reducing their overall contrast they can invest more in a single nesting attempt than in their own survival and have a lower risk of losing all success due to predation. Constraint of female plumage brightness by nest predation has been shown in other species while males brightness was not constrained (Martin & Badyaev 1996). Tan females with high overall contrast may not only be more visible to predators, but also to intruding males seeking EPCs. This would result in her being the target of more forced copulation attempts and thus have fewer within pair young in her nest. She may also seek out EPCs for genetic diversity to her young (Petrie & Kempenaers 1998; Jennions & Petrie 2000) and would not be subject to a reduction in parental care effort from her mate as Arnqvist and Kirkpatrick (2007) suggested because he already provides little parental care (Tuttle 1993, 2003).

Comparisons of the plumage of mated pairs and mate choice studies would help to determine what selective factors are most responsible for the different plumage, especially in tan males. The condition of the female may also affect their mate choice and pairing in the wild. Determining extra-pair success and overall reproductive success would also help to illuminate the purpose of signaling using plumage in this unique species.

This study is the first to my knowledge that quantitatively examines the overall signal from a bird (overall contrast) in relation to fitness factors. Other studies have focused on contrast and the external environment but have not considered a signal sent by contrast within a birds plumage (Haskell 1996; Miller 1999; Uy & Endler 2004). Different species of bowerbirds create contrast between their plumage and this signal has been shown to be related to fitness (Endler et al. 2005). Contrast within a birds plumage would increase conspicuousness in some environments and should be assessed when examining the signals sent by a bird (Gotmark & Hohlfalt 1995). Crown contrast of varying degrees is the result of sexual selection and natural selection acting independently and trading off reproductive success and survival differently in the different morph/sex classes. The tan birds are selected to have dull plumage with low contrast so that they do not attract predation to a nest, and the same may be the case for the white females as well. The plumage of the white female may be maladaptive because they share genes that could be selected for increased brightness and contrast in the white male by signaling condition and quality to mates and extra-pair partners. In this case, it indicates that the strength of sexual selection on white males is greater than the strength of natural selection, and possibly sexual selection as well, on white females. By studying this system further we can learn a great deal about the interaction between these forces and about evolution in general.

In conclusion, this study showed that the differences in plumage between each morph/sex class are the result of sexual selection and natural selection acting differently on each class. It is interesting how the forces oppose each other at various strengths and create vastly different results. The results of this study have provided strong support for studies that examined plumage and mating system across many species. Higher promiscuity has been correlated with increased ornaments and plumage brightness before (Møller & Birkhead 1994; Badyaev 1997; Cuervo &

Møller 1999; Badyaev & Hill 2003), but this study within a species with differing degrees of promiscuity provides strong evidence that this theory is true.

Table 3.1 Summary of High Quality Birds

WM	TF	TM	WF
High contrast	Low contrast	Low contrast	Low contrast, but bright Scil

What signal do high quality birds give out? This table shows the amount of overall contrast that each morph/sex class displays in a bird with high fitness. Both tan sexes show low contrast in birds with higher fitness, whereas the whites differ between the sexes. White males appear to be selected to display their quality through their plumage while white females may also display this in their superciliaries.

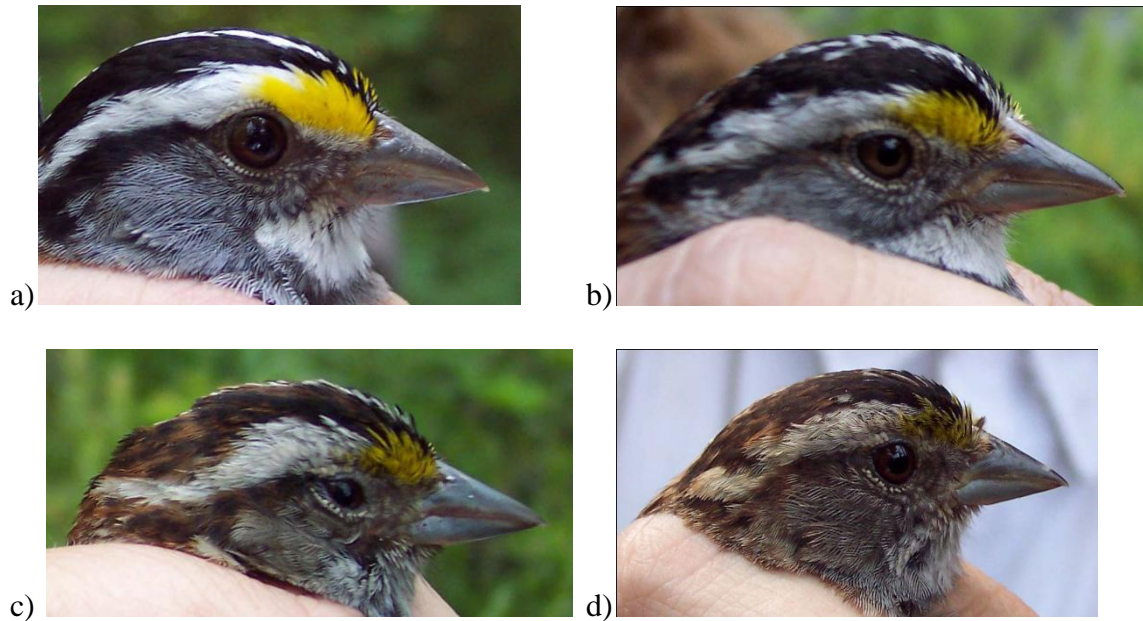


Figure 3.13 Examples of high and low contrast individuals for each of the male morphs.

A high contrast white male (a) and a low contrast white male (b). A high contrast tan male (c) and a low contrast tan male (d). Each morph/sex class showed a great deal of variation in plumage.

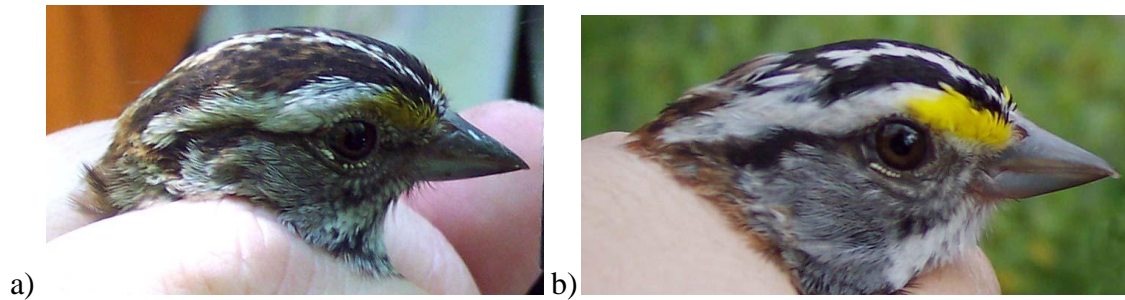


Figure 3.14 A comparison between the females of the different morphs

On the left is a tan female (a) and on the right is a white female(b) with much greater overall contrast and brighter superciliaries.

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