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Variations in Plumage Wear in Three Closely Related Tidal Marsh Sparrow Species

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VARIATIONS IN PLUMAGE WEAR IN THREE CLOSELY RELATED TIDAL MARSH SPARROW SPECIES

by

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ABSTRACT

Tidal marsh sparrow species like Saltmarsh Sparrows (*Ammospiza caudacuta*), Nelson's Sparrows (*Ammospiza nelsoni*) and Seaside Sparrows (*Ammospiza maritima*) are particularly vulnerable to the environmental stressors related to climate change and human activity like sea-level rise, warming temperatures, and increased coastal development, as they nest in the grasses of tidal marsh ecosystems where the principal mode of nest mortality is flooding. With increased sea-level rise, these species may not be equipped to adapt to changing tidal cycles, and thus have reduced fitness and population sizes. Saltmarsh Sparrows are experiencing sharp declines in population, so it is more vital than ever to investigate patterns in breeding behaviors, plumage wear, and latitudinal differences to develop feasible conservation strategies. My study investigates the differences in plumage wear and severity across conspecifics in Saltmarsh, Nelson's, and Seaside Sparrows and identifies significant relationships between the date of capture, latitude, and severity of feather wear observed. I observed a decrease in plumage wear and broken feather percentage with latitude but an increase in these metrics in relation to date. Conversely, fault bars and severity displayed an increase with latitude but a decrease with date. Lastly, my findings demonstrate high amounts of feather wear in Seaside Sparrows compared to Saltmarsh and Nelson's Sparrows.

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This thesis could not have been accomplished without the support, guidance, and kindness of the many amazing people in my corner. Above all, I'd like to thank my advisor, Kate Ruskin. Her guidance, not only throughout this process but also throughout my entire undergraduate career, has been nothing short of invaluable. I could not ask for a better mentor and can't think of a more influential professor to all four years of my University of Maine experience than her. She fielded *many* Program R questions and helped me work through the arduous coding process with the utmost patience. I had never used this program before, at least not to this extent, and I simply could not have done it without her help. I would also like to thank the members of my committee: Danielle Levesque, Erin Grey, Alice Hotopp, and Sharon Tisher for their kindness, flexibility, and patience throughout the process of scheduling and participating in this project with me.

Next, my friends and family played key roles in keeping me sane during this hectic and stressful time. Though they may have been unfamiliar with statistical analyses or the intricate details of tidal marsh sparrow ecology, they proof-read emails and drafts, and listened to me talk through the process, which gave me a useful second pair of eyes and a sounding board for any snares or doubts I had along the way.

Lastly, I would like to thank Meaghan Conway and other researchers and field technicians with the Saltmarsh Habitat & Avian Research Program (SHARP) for collecting and curating the dataset I utilized for my thesis. Without their hard work, this project could not have been accomplished.

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INTRODUCTION

The Tidal Marsh Ecosystem

Compared to other ecosystems, tidal marshes are host to few species of terrestrial vertebrates, many of which are endemic to this habitat (Greenberg et al. 2006). One study places 25 terrestrial vertebrate species that are either endemic to tidal marshes or have subspecies that are restricted to marshes, including Saltmarsh, Seaside, and Nelson's Sparrows that are the focus of this study. Of these 25 species endemic to tidal marshes, most are found in North America, and 15 are established on the Atlantic and Gulf coasts (Greenberg et al. 2006). This not only has implications for species-area relationships, wherein this area has the greatest extent of tidal marsh conditions in the world so more endemic species will be found here, but it also speaks to the necessity of conservation in these regions.

There are numerous factors affecting the tidal marsh landscape including, but not limited to, sea-level rise, coastal development, and invasive species (Greenberg et al. 2006). Sea-level rise is of particular interest to these tidal marsh sparrow species as they have specialized nesting cycles that allow them to breed successfully in the marsh, which is flooded twice daily (low marsh) or once per month (high marsh). In New England in particular, Saltmarsh Sparrow populations have developed a nesting cycle that takes place between monthly high tides in this region (Shriver 2002). Near-term projections of sea-level rise anticipate an increase in global mean sea-level rise ranging from 0.3m to 2.5m (Sweet et al. 2022), which will decrease the window between flooding events in the high marsh. There are already observed declines in Saltmarsh Sparrow populations within their range (Correll et al. 2017), and they are recognized as conservation priorities on the

IUCN Red List as well as Audubon's Priority Birds List as of 2020 and 2021 (BirdLife International 2020, Michel et al. 2021).

Target Species

Saltmarsh Sparrows

One of the species I investigate in this project is the Saltmarsh Sparrow (*Ammospiza caudacuta*), a recent taxonomic split from Nelson's Sparrows (*Ammospiza nelsoni*) (Greenlaw, et al 2020). Together, Saltmarsh and Nelson's were known as one species, the Sharp-tailed Sparrow, so named because they exhibited high degrees of feather wear on their retrices, resulting in bare rachis. This feather wear was hypothesized to result from these taxa spending much of their time running among grasses of the tidal marsh, resulting in abraded feathers. This species is unique among the order of Passeriformes in that it is an obligate tidal-marsh specialist species, restricted to a narrow range of tidal marsh habitats along the east coast of the United States (Greenlaw, et al 2020). These individuals are active in dense stands of high marsh vegetation including species like Saltmeadow Cordgrass (*Spartina paten*) and Saltmeadow Rush (*Juncus gerardii*), which is often used for foraging and protective behaviors (Greenlaw, et al 2020). The northern-most area of the Saltmarsh Sparrow's breeding range has been identified as South Thomaston Maine and extends south into the Delmarva Peninsula and lower Chesapeake Bay in eastern Maryland and northeastern Virginia respectively (Montagna 1942, Trollinger et al. 2001, Hodgman et al. 2002, Rottenborn et al. 2007).

In terms of breeding behaviors, males and females participate in promiscuous mating in which individuals mate with multiple partners throughout the breeding season

(Greenlaw et al. 2012). These behaviors typically include males pulling feathers from a female during the mounting process as well as female resistance (Greenlaw et al. 2012). This physically demanding mating strategy has been observed to have seasonal carryover effects on the females of this species, wherein female Saltmarsh Sparrows often experience shorter molt duration of flight feathers, later molt initiation, and later fall departures by some females (Borowske et al. 2016). Extreme feather wear in female Saltmarsh Sparrows associated with this mating system is also well-documented and acts as a basis for the hypotheses associated with this project (Borowske 2016). After mating, females are exclusively responsible for parental care acts including brooding, the feeding of young, and nest protection, which also plays a role in overall body condition (Post et al. 1982).

Nelson's Sparrows

As previously stated, Nelson's Sparrows (*Ammospiza nelsoni*) are closely related to Saltmarsh Sparrows, and thus, their breeding ranges often overlap in coastal New England, specifically in southern Maine where some interbreeding occurs (Hodgman et al. 2002). This species is restricted in its breeding grounds, mainly occurring in wet meadows and salt marshes along the Atlantic Coast of North America (Shriver et al. 2020). With this species, we see three distinct breeding populations ranging from (1) east-central British Columbia and down into both North and South Dakota; (2) from James and Hudson bays to Manitoba, Canada; (3) south through southern Maine and into Massachusetts (Greenlaw et al. 1994).

When comparing the breeding strategies of this species to the closely related Saltmarsh Sparrow, far less is known about their habits and behaviors, though it is believed that copulations are similar in that males may force copulations and these mate interactions often lack pair bonds (Shriver et al. 2005). One of the main populations relevant to this project is the subspecies *subvirgata*, which arrives at Maine breeding grounds in late May, similar to that of Saltmarsh Sparrows. Another similarity between these two species are their parental care strategies. In this species, just as in Saltmarsh Sparrows, females are responsible for choosing the nest site, building the nest and collecting the materials necessary, and finally incubating and caring for young (Shriver et al. 2020). These similar breeding and care strategies, as well as the remaining uncertainty about their life history, make distinctions between the two difficult. However, an important difference to note is renesting time. Females in Nelson's Sparrow populations typically renest approximately 10 days after nest failure, which is less quickly than Saltmarsh Sparrows (Shriver et al. 2007).

<u>Seaside Sparrows</u>

Seaside Sparrows (*Ammospiza maritima*) are habitat specialists of salt and brackish marshes and their breeding ranges span along the Atlantic coast from southern Maine and into northeastern Florida. However, it is considered a rare breeder in Maine and New Hampshire and an uncommon one in Massachusetts (Post et al. 2020, Foss 1994, Petersen et al. 2003). This species nests above the mean high tide mark in supratidal and intertidal marsh zones and their breeding populations typically require nest sites these marsh zones and areas with openings in the vegetation to promote a productive breeding season (Post 1974).

In contrast with the species described previously, Seaside Sparrows form socially monogamous mate pairs that exhibit bi-parental care of young (Greenlaw et al. 1985). Typically, both sexes participate in feeding young, with similar delivery rates of food sources among conspecifics, however, females are often responsible for brooding behaviors (Post et al. 2020). Mate-guarding is also performed by males and is typically associated with territorial defense as well, however, males do not protect females that leave the territory (Post et al. 2020). Females have also been documented to be aggressive during the breeding season, and it appears that this aggression is nest-centered, but definitive conclusions regarding its role in monogamous behaviors is unclear (Greenlaw et al. 1985).

Body Condition

Body condition is a general measure of energy reserves in an individual. As such, body condition has been found to be related to an individual's performance (e.g., reproductive success, mortality) (Cresswell 2009). Therefore, condition has been proposed as a tool for assessing environmental conditions and monitoring population dynamics (Frauendorf et al. 2021). For example, breeding females may have lower body mass relative to standard species sizes when compared to conspecifics during the breeding season has been cited to be indicative of the stress related to reproduction (Borowske et al. 2018, Neto et al. 2010). This reproductive related stress can then lead to poor quality feathers and a reduced ability to fly or perform other life functions and have carryover effects for subsequent seasons (Vágási et al. 2012, Harrison et al. 2010).

Environmental factors informing energy stores include time of day, weather, and habitat quality. In both Seaside and Saltmarsh Sparrow species, regardless of sex, individuals had higher amounts of visible fat in winter than in the breeding season which researchers have attributed to responses to decreased temperatures and a potential reduction in viable food sources (Borowske et al. 2018). On a longer timescale, the impacts that climate change may have on body condition and resulting changes in fitness are also being addressed. For example, the body conditions of two species (*Malurus elegans* and *Sericornis frontalis*) were examined to explore the relationship between increases in temperature (attributed to climate change) and body condition in both summer and winter (Gardner et al. 2018). This study found discrete relationships between temperature fluctuations and changes in body condition and emphasize the value in adopting thermoregulatory frameworks for the exploration of the impacts of climate change on body condition, survival, and sensitivity to environmental changes (Gardner et al. 2018). Condition, such as feather wear, is a promising tool for assessing wildlife populations. Because it is quick and relatively non-invasive to collect, it is especially valuable as a monitoring tool for species of conservation concern such as Saltmarsh, Nelson's, and Seaside Sparrows that have exhibited population decline. However, for body condition to be useful as a monitoring too, we must understand baseline variation that can stem from factors that are intrinsic (e.g., sex) as well as extrinsic but not of interest for conservation management (e.g., date).

Hypotheses

In this project, I aim to characterize the patterns in plumage wear across three different, but closely related, species of tidal marsh sparrows: the Saltmarsh Sparrow (*Ammospiza caudacuta*), Nelson's Sparrow (*Ammospiza nelsoni*), and Seaside Sparrow (*Ammospiza maritima*). I test whether plumage wear is predicted by species, sex, time in breeding season, and latitude for each species. In all species, I expect that individuals captured later in the breeding season will exhibit greater feather wear than those examined earlier in the season due to a longer amount of time since their last molt, and more time spent utilizing the landscape. Based on the life history strategies of each of these species, I expect that female Saltmarsh Sparrows would incur more feather wear than their sister species, while Seaside Sparrows would experience the least amount of feather wear based on their bi-parental care strategy. I expect that Seaside Sparrows will exhibit the least amount of variation between sexes based on this strategy as well, while differential plumage wear will be greatest in Saltmarsh Sparrows. I expect differential plumage wear by sex will be intermediate in Nelson's Sparrows. Lastly, I anticipate that with increased latitude, I will see an increase in feather wear based on the expected wear in Saltmarsh Sparrows.

METHODS

Field Collection

Field data collection was completed by University of Maine Ph.D. student Meaghan Conway during the breeding season (May to August) in 2015 and 2016. She collected samples from saltmarshes along the east coast of the United States spanning from Maine to Virginia encompassing the three ranges of Saltmarsh (entire range), Nelson's (southern Atlantic range), and Seaside (northern range) Sparrows. The minimum latitude in these samples was 37.90 with an associated longitude of -75.65. The maximum latitude value was 44.89 and its associated longitude was -67.20. These maximum and minimum values span approximately 1,047.69 kilometers (651 miles). In total, this period of field collection included 134 total locations. This dataset included other tidal marsh species, but those will be omitted for the purposes of this thesis. Field collection followed Saltmarsh Habitat & Avian Research Program (SHARP) protocols for mist-netting and plumage scoring. Briefly, mist-netting involves the selection of sites in areas of approximately 5-20 hectares in size and in areas where sparrow nesting is high. Once sites are established, multi-net arrays (containing six 12-meter nets) are used to capture sparrow species for banding and are generally left in place for approximately 3 hours.

Plumage Scoring

The plumage scoring technique used was developed by Alyssa Borowske, Ph.D (Borowske 2015). Broken tail feathers are denoted by a yes or no designation and other indicators like “X” and “NR” are used to denote missing or not recorded feathers (Borowkse 2015). Wear is valued on a scale from 0 to 5 wherein 0 indicates that the edges of the feather are smooth, and all parts are intact and 5 shows that the vane of the feather is missing and frayed along a majority of the rachis. A total count of fault bars is tallied and if faults are present, they are then ranked from 1 to 3 for their severity. One indicates that a fault bar is present on one vane while 3 acts as an indicator of a fault bar being associated with a break in multiple barbs (Borowkse 2015).

Figure 1. The figure above provides a visual demonstration of feathers broken along the rachis (Borowske 2015).

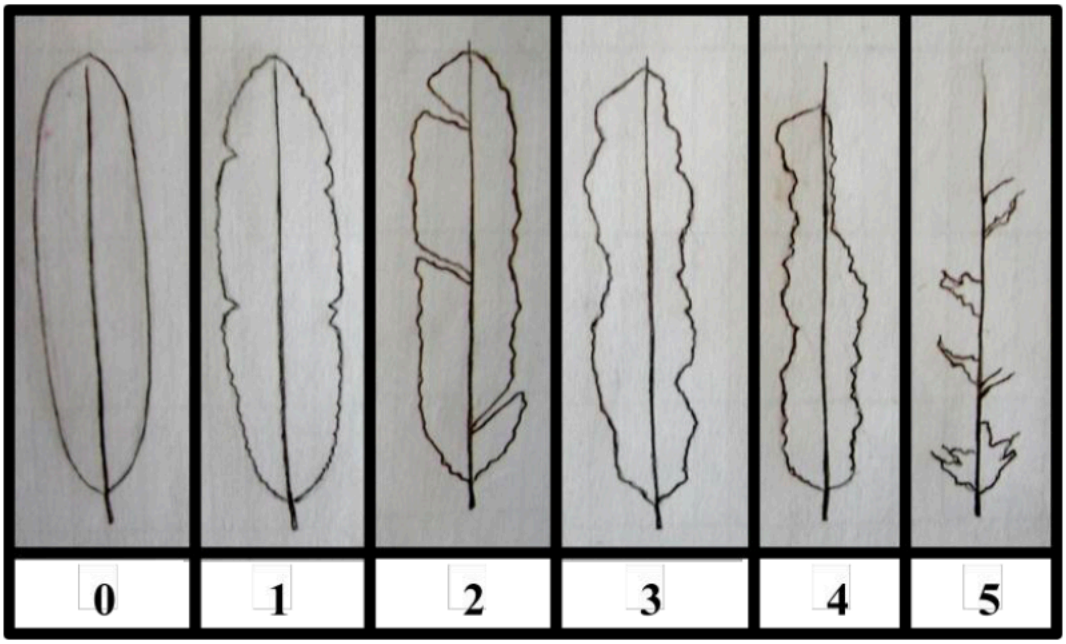

Figure 2. The drawings in the figure above highlight the 6 rankings given to the tail feathers of tidal marsh sparrows when feather wear is investigated (Borowske 2015).

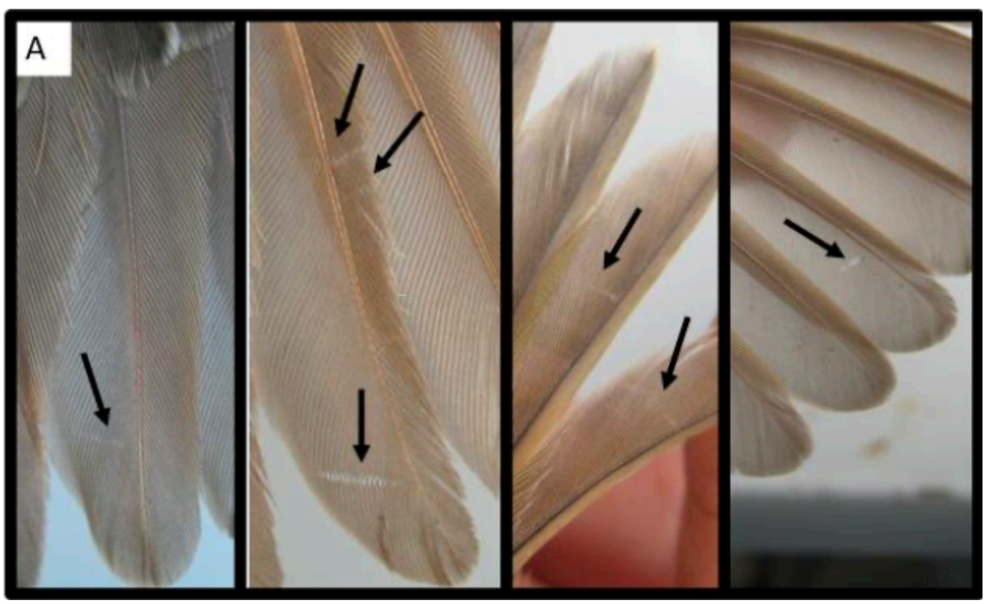

Figure 3. This figure demonstrates fault bars as they present on a tidal marsh sparrow (Borowske 2015).

Figure 4. The photos above illustrate the fault severity ranking of 3 which is associated with a break in multiple barbs (Borowske 2015).

Fault Bars

Feathers grow due to an accumulation of keratin and when there are keratin deficits, fault bars may form (Jovani et al. 2010). Fault bars are described as translucent sections of feathers generated during feather growth under stressful conditions (Jovani et al. 2010). Such stressors may include the differences in age, wherein younger birds have more fault bars than conspecifics because they may be less equipped to handle environmental factors, diseases caused by parasites or bacterial infections, and habitats that were fragmented or had less vegetation cover were also likely to cause fault bars across numerous taxa (Jovani et al. 2016). Fault bars are also influenced temporally as well, and fault bar occurrence can range on a temporal scale from seconds (perhaps due to handling) to years (often associated with age) (Jovani et al. 2016). The likelihood of fault bars forming can be variable and ultimately exhibit differences within individuals and across species (Jovani et al. 2016).

These faults, which can range in both total number and severity, can have lasting impacts on overall feather quality. Fault bars ultimately weaken the structure of a given feather and may lead to feather breakage, with variable impacts on fitness and survival (Jovani et al. 2010). Plumage often breaks at the sites of these fault bars and are not typically replaced until the following molt, which is the replacement of worn and broken feathers (Jovani et al. 2016, Vágási et al. 2012). Because of this, the impacts of fault bars may last for several years in larger species and can inhibit flight performance in some cases (Jovani et al. 2016).

The molt-constraint hypothesis suggests that breeding and molt are scheduled sequentially to avoid the overlap of costly activities and thus describes the effects of prolonged breeding as producing a delayed molt (Vágási et al. 2012). Consequently, if molt is delayed, functionally inferior feathers may be produced, which in turn, may be exacerbated by seasonal changes and other environmental factors (Vágási et al. 2012). These delayed molts may ultimately lead to reduce flight capacity and fitness, which may inform past, present, and future life history events (Vágási et al. 2012). In House Sparrows (*Passer domesticus*), it has been shown that individuals who experience a shortened molt period developed shorter flight feathers with an increased number of fault bars (Vágási et al. 2012).

In short, fault bars are costly to the feather and body condition of an individual, so developing patterns in both fault bar number and severity across three closely related taxa, as a portion of my study aims to do, may produce more insights regarding the conditions experienced by these target species prior to and during the breeding season. Similarly, with expected sea-level rise due to climate change and the primary mode of nest mortality in all three target species being flooding, increased stress during the breeding season may result in delayed molt, and consequently, the development of poor-quality feathers in the following season (Greenberg et al. 2006, Shriver 2002).

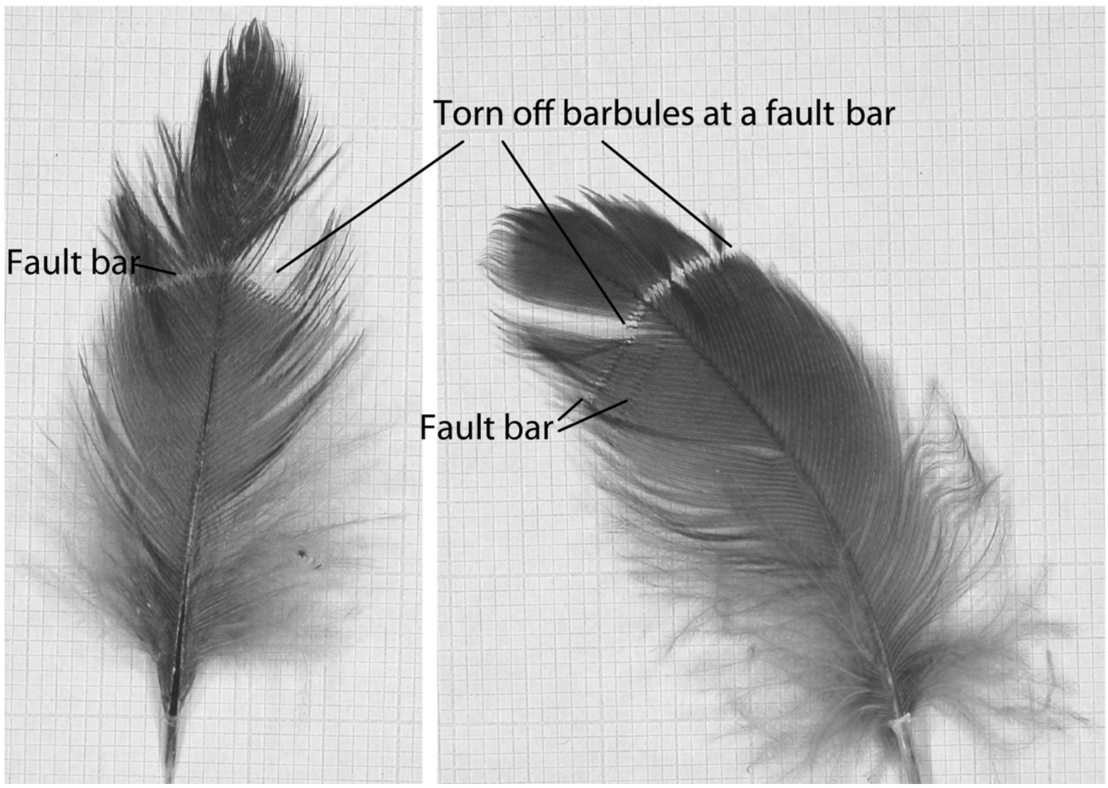

Figure 5. Fault bars are narrow, often transparent, bands perpendicular to the rachis produced under stressful conditions. The photo above is a tail feather of a Jackdaw nestling (Boonekamp et al, 2016).

Data Analysis

Data preparation – In order to prepare the data to be analyzed in R, I cleaned each dataset associated with the variables outlined in this thesis (species, sex, wear, fault bars and severity, and the presence of broken feathers). I removed four other tidal marsh sparrow species from the dataset that were not the focus of this study, and some individuals (less than 1% of total dataset) that were not identified by their sex. In the four categories related to plumage (wear, bars, severity, and broken feathers), there were designations including "NR" (not recorded, typically if a field photo was too blurry to properly assess), "X" (missing), and "-99", all of which were removed in R. Lastly, the capture dates for each individual were converted to Julian day such that May 5, 2015 had the same value in Program R as May 5, 2016, and so on.

Statistical tests – For three of the metrics of feather wear (wear, and fault bars and severity), I used a linear mixed effects model to tests whether each of these dependent variables was related to the independent variables of sex, species, latitude, date in the breeding season, and an interactive effect between species and sex ("lmer function in the Program R package "lme4" (Bates et al. 2015)). I included an interactive effect between sex and species because I predicted the differential parental behaviors of these species would impact the appearance of plumage wear. In all models, I included band number as a random effect to control for variation among individual birds. For the metric of broken feathers, I used a linear regression to examine the ratio of broken feathers ("yes") to unbroken feathers ("no"), and maintained the above variables (sex, species, latitude, and date) as well as the interactive effect of sex and species. I used p-values derived from type III sum of squares to assess the influence of each variable for predicting feather wear ("Anova" function in the "car" package (Fox et al. 2019)). This function runs an F-test and provides a p-value for each independent variable (Fox et al. 2019).

RESULTS

The dataset examined contained 608 total tidal marsh sparrow individuals. Of these, 93 were Nelson's Sparrows (10 females and 83 males), 273 were Saltmarsh Sparrows (62 females and 211 males), and 242 were Seaside Sparrows (72 females and 170 males). With each individual tail feather accounting for a single observation, this dataset included 7,296 total observations.

Plumage Wear

Random Effects	*Variance*	*Standard Deviation*
Band Number	0.1104	0.3322
Residual	1.1702	1.0817

Table 1. Random effects results from the linear mixed effects model comparing wear to the independent variables. Includes both variance and standard deviation.

The table above examines the results attributed to the random effects of the linear mixed effects model for plumage wear. Residual variance tells us how much variability is found within a given treatment, here this value is 1.1702. Band number variance, on the other hand, accounts for how much of the variance within this model is explained by differences among individuals. Including band number as a random effect was important in controlling for feather wear based on individual variation. This result displays that individual do not vary consistently, which is to be expected, as shown by the variance value approaching zero.

	Estimate	*Std. Error*	*df*	*t-value*	*Pr(>|t|)*
Species: Nelson's	3.558372	0.841635	536.043444	4.228	2.77e-05
Species: Saltmarsh	0.415377	0.169239	503.838944	2.454	0.014450
Species: Seaside	0.685912	0.184423	502.917828	3.719	0.000222
Sex: Male	0.123179	0.155784	486.007648	0.791	0.429504
Latitude	-0.155792	0.020941	545.683801	-7.440	3.94e-13
Date	0.022763	0.001191	552.226593	19.114	< 2e-16
Interaction of SALS*M	-0.191071	0.171593	501.606890	-1.114	0.266019
Interaction of SESP*M	-0.061264	0.170458	498.826935	-0.359	0.719441

Table 2. Fixed effects results from the linear mixed effects model comparing wear to the independent variables.

A one unit increase in the predictor variable latitude is associated with an average change of -0.155792 in the log odds of the response variable of feather wear taking on a value of 1. In other words, feather wear decreases with latitude. A one unit increase in the predictor variable for Nelson's Sparrows is 3.558372, while for Saltmarsh and Seaside Sparrows this value is 0.415377 and 0.685912 respectively. For every one-unit increase, the predictor variable of date is 0.022763.

	Chisq	*Df*	*Pr(>Chisq)*
Intercept	17.8754	1	2.359e-06
Species	15.8825	2	0.0003558
Sex	0.6252	1	0.4291181
Latitude	55.3496	1	1.009e-13
Date	365.3441	1	<2.2e-16
*Species*Sex*	2.2646	2	0.3222967

Table 3. Type III Analysis of Variance (ANOVA) table for the wear linear mixed effects model.

The chi-square value for the variables listed accounts for the variation between sample means as it relates to the variation within the samples. In this case, the higher the chi-square value, the lower the corresponding Pr(>Chisq) value, which works similar to that of a p-value. P-values broadly posed are a measure of the probability that an observed difference may have occurred by chance. Lower p-values act as an inference of statistically significant results. In the table above, almost every variable is associated with a p-value that is less than 0.05, making these results statistically significant given the formula of the relationship between wear and each of these variables. The p-values of <0.05 for species, date, and latitude indicate that these variables are important predictors of feather wear. In contrast, feather wear did not vary by sex or an interactive effect between species and sex.

Fault Bars

	Estimate	*Std. Error*	*df*	*t-value*	*Pr(>|t|)*
Species: Nelson's	-5.142e-01	4.653e-01	3.976e+02	-1.101	0.270
Species: Saltmarsh	6.411e-02	9.464e-02	3.863e+02	0.677	0.499
Species: Seaside	1.652e-01	1.034e-01	3.866e+02	1.598	0.111
Sex: Male	1.054e-02	8.784e-02	3.799e+02	0.120	0.905
Latitude	1.357e-02	1.154e-02	4.002e+02	1.176	0.240
Date	-4.127e-04	6.566e-04	4.039e+02	-0.629	0.530
Interaction of SALS*M	-9.531e-03	9.604e-02	3.852e+02	-0.099	0.921
Interaction of SESP*M	2.264e-02	9.580e-02	3.855e+02	0.236	0.813

Table 4. Fixed effects results from the linear mixed effects model comparing fault bars to the independent variables explained previously.

With respect to Nelson's Sparrows, fault bars decrease by -0.5142 for every one unit increase in the predictor variable. This value is 0.06411 and 0.1652 for Saltmarsh and Seaside Sparrows. Fault bar totals increase with increasing latitude but decrease with increasing date.

	Chisq	*Df*	*Pr(>Chisq)*
Intercept	1.2209	1	0.2692
Species	4.5192	2	0.1044
Sex	0.0144	1	0.9045
Latitude	1.3821	1	0.2397
Date	0.3950	1	0.5297
*Species*Sex*	0.3541	2	0.8377

Table 5. Type III Analysis of Variance (ANOVA) for fault bars linear mixed effects model.

As previously stated, the chi-square value for the variables listed indicates the variation between sample means as it relates to the variation within the samples. In this table, compared to the wear ANOVA result, all variables are associated with a p-value that is larger than 0.05, indicating that all variables explored in the fault bar linear mixed effects model are statistically insignificant.

Fault Severity

	Estimate	*Std. Error*	*df*	*t-value*	*Pr(>|t|)*
Species: Nelson's	5.389e-01	5.780e-01	2.066e+02	0.932	0.352
Species: Saltmarsh	-1.951e-04	1.099e-01	1.941e+02	-0.002	0.999
Species: Seaside	6.870e-02	1.220e-01	1.958e+02	0.563	0.574
Sex: Male	5.315e-02	1.034e-02	1.907e+02	0.514	0.608
Latitude	6.464e-03	1.385e-02	2.056e+02	0.467	0.641
Date	-3.815e-03	7.597e-04	2.074e+02	-5.022	1.1e-06
Interaction of SALS*M	-8.915e-02	1.121e-01	1.935e+02	-0.796	0.427
Interaction of SESP*M	-5.337e-02	1.123e-01	1.941e+02	-0.0475	0.635

Table 6. Fixed effects results from the linear mixed effects model comparing fault severity to the independent variables explained previously.

Fault severity in Nelson's Sparrows increases by 0.5389 for every one unit increase in the predictor variable while this number is -0.001951 and 0.06870 for Saltmarsh and Seaside Sparrows respectively. Fault severity increases with increasing latitude but decreases with increasing date.

	Chisq	*Df*	*Pr(>Chisq)*
Intercept	0.8693	1	0.3511
Species	1.3069	2	0.5203
Sex	0.2645	1	0.6071
Latitude	0.2179	1	0.6406
Date	25.2183	1	5.119e-07
*Species*Sex*	0.7770	2	0.6781

Table 7. Type III Analysis of Variance (ANOVA) for fault severity linear mixed effects model.

The results of this ANOVA test indicate that there is one significant variable associated with fault severity: date. Here, date displays a p-value that is less than 0.05 at approximately 0.00000005119. A low F-value in this case, as seen with species, sex, latitude, and species*sex interactions, indicates that there is lower variation between sample means relative to the means observed within the samples, leading to higher corresponding p-values.

Percentage of Broken Feathers

	Estimate	*Std. Error*	*z-value*	*Pr(>|z|)*
Species: Nelson's	-2.614554	5.073754	-0.515	0.606526
Species: Saltmarsh	3.624854	1.045898	3.466	0.000566
Species: Seaside	1.417206	1.138558	1.245	0.213714
Sex: M	0.342668	0.975267	0.351	0.725443
Latitude	0.011380	0.125419	0.091	0.927733
Date	0.009884	0.007124	1.388	0.165788
Interactions of SALS*M	-3.090264	1.061984	-2.910	0.003749
Interactions of SESP*M	-0.619490	1.057922	-0.586	0.558383

Table 8. Table of Coefficients based on the results of the linear regression model performed for the percentage of broken feathers.

For this model, the dispersion parameter can be taken to be 1, so for every one unit increase in the predictor variable, we can expect to see an associated change as listed in the coefficient estimate column. A one unit increase in the predictor variable results in a -2.614554 decrease in Nelson's Sparrows, a 3.624854 increase in Saltmarsh Sparrows, and a 1.417206 increase in Seaside Sparrows. Broken feather percentage increases with increasing latitude and increases with increasing date.

	Sum Sq	*Df*	*F-value*	*Pr(>F)*
Species	64.4	2	3.7969	0.02298
Sex	186.0	1	21.9282	3.502e-06
Latitude	0.1	1	0.0082	0.92773
Date	16.3	1	1.9253	0.16579
*Species*Sex*	177.3	2	10.4562	3.438e-05

Table 9. Type III Analysis of Variance (ANOVA) for broken feather percentage linear regression model.

The table above indicates that the percentage of broken feathers has a significant relationship to species, sex, and the interactive effect between them, as demonstrated by the p-values that are less than 0.05.

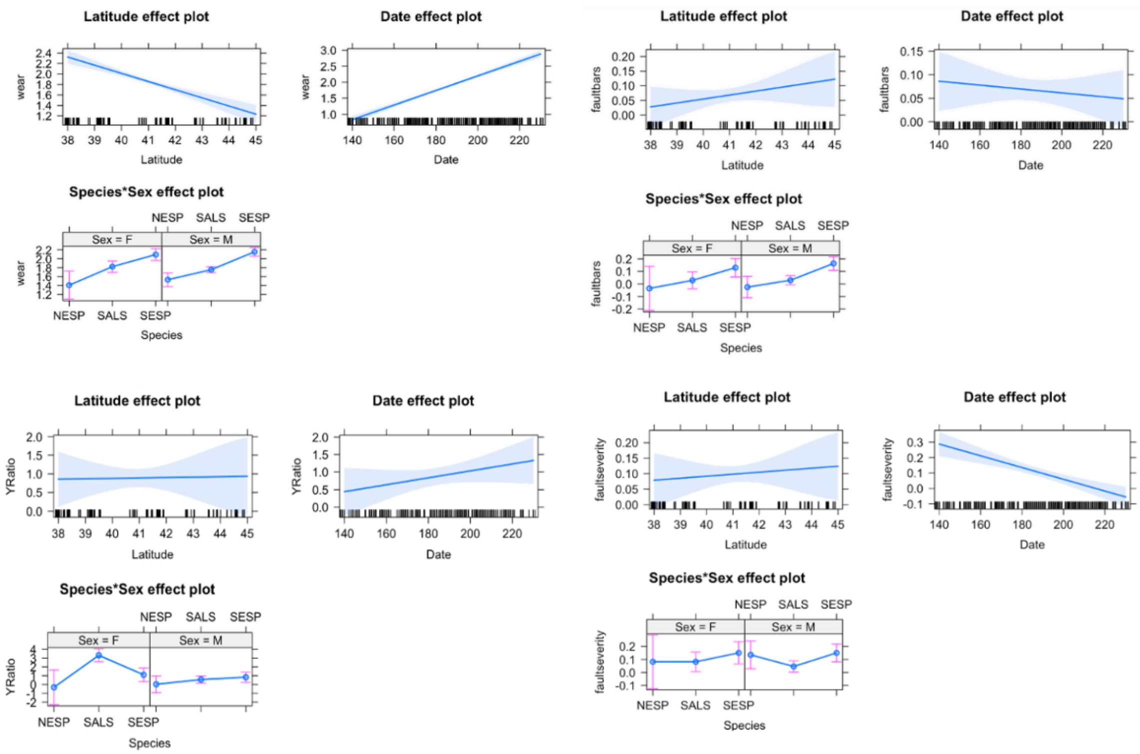

Figure 6. The figure above combines the model results of feather wear (top left), fault bars (top right), percentage of broken feathers (bottom left), and fault severity (bottom right).

Figure 6 above demonstrates the relationships between plumage wear, percentage of broken feathers, fault bars, and fault severity and the independent variables of latitude, date, and the species sex interaction.

First, the feather wear latitude effect plot suggests a decrease in feather wear with increasing latitude with a narrow confidence interval. The date effect plot displays that with increasing time in the breeding season, wear increases. Lastly, the species*sex effects plot demonstrates that Nelson's females incurred the least amount of wear when compared to conspecifics while Seaside males incurred the most, only slightly higher than their conspecifics. Saltmarsh Sparrow females saw an increased amount of feather wear in relation to males and demonstrated a similar ranking of wear to that of Seaside females.

Fault bars is examined in the top right portion of this figure. These plots demonstrate the opposite relationship than that of feather wear. With regards to latitude, fault bars were exhibited with more frequency in higher latitudes than feather wear. In terms of date, fault bars decreased with increasing time in the breeding season. The species*sex interaction demonstrates that both sexes of Nelson's Sparrows experienced approximately the same total number of fault bars while Saltmarsh females experienced a slight increase in fault bar number when compared to conspecifics. Seaside Sparrow males experienced more fault bars than females, however, this difference was minimal.

The bottom left portion of this figure examines the relationship between the percentage of broken feathers and the metrics of latitude, date, and the interactive effect of species and sex. This ratio remains relatively consistent with latitude with very slight increases with increasing latitude. The percentage of broken feathers increases with date, similar to the pattern seen in feather wear. This model also highlights that there were higher percentages of broken feathers in Saltmarsh and Seaside females than males. This value displayed little variation in relation to Nelson's Sparrows.

Lastly, fault severity as it relates to the four independent variables described are depicted in the bottom right portion of Figure 6. Here, severity follows the same pattern as seen in fault bars, wherein fault severity increases with latitude and fault severity decreases with regards to date. In terms of species*sex interactions, this model demonstrates a different pattern than that of number of fault bars. In this case, both female and male Nelson's experienced similar fault severity to that of Saltmarsh males, though this ranking was slightly lower. Female Saltmarsh Sparrows displayed higher fault severity than conspecifics, but less than both male and female Seaside Sparrows.

	Latitude	Date
Wear	-	+
Percentage of Broken Feathers	-	+
Fault Bars	+	-
Fault Severity	+	-

Table 10. The table above summarizes the patterns seen in the independent variables of latitude and date compared to the dependent variables of feather wear, percentage of broken feathers, and fault bars and severity.

DISCUSSION

I observed substantial variation in plumage wear associated with all variables tested: latitude, date in the breeding season, sex, species, and an interactive effect between species and sex. Across the four dependent variables I examined, the significant predictors varied, and in fact no two independent variables were predicted by the same set of independent variables. Date in the breeding season and species were commonly identified as important for predicting plumage wear; both date and species predicted plumage wear for three out of the four dependent variables I examined. The patterns supported some of my hypotheses but not others and revealed relationships among these various metrics for plumage wear that were contradictory and not straightforward.

Consistent with my predictions, overall feather wear increased with date, indicating that feather condition degraded over the course of the breeding season. I also observed that feather wear varied by species, but in a pattern that differed from what I expected. In contrast to my predictions, Seaside Sparrows displayed the most amount of feather wear while Nelson's displayed the least. These differences may be explained by their nest locations on the landscape in which Seaside Sparrows nest in the low marsh with more exposure to saltwater and abrasive vegetation in comparison to Saltmarsh and Nelson's Sparrows who nest in the high marsh, with Nelson's nesting the highest on the landscape (Post et al. 2020, Greenlaw et al. 2020, Shriver et al. 2020). High salinity has also been associated with higher rates of feather-degrading bacilli, which may be indicative of these patterns as well (Peele et al. 2009). This frequent exposure to saltwater, and by extension salt-resilient bacterium, as well as more abundant vegetation may reflect the patterns seen in feather wear across species. Similarly, I was surprised that feather wear decreased with latitude though number of nesting attempts and breeding length increases with latitude in Saltmarsh Sparrows (Greenlaw et al. 2020). Instead, my results indicated that stressors to feather condition decrease with latitude, and therefore, they may be instead related to predation rate, which increases with decreasing latitude or vegetation, for example (Ruskin et al. 2017). Percentage of broken rectrices demonstrated similar patterns to overall wear. Specifically, percentage of broken rectrices also significantly differed among species, but differentially by sex. Saltmarsh Sparrow females exhibited the highest rate of feather breakage, significantly higher than that of conspecific males, while Seaside and Nelson's Sparrows exhibited similar levels of breakage regardless of sex. The intraspecific difference I observed between male and female Saltmarsh Sparrows, and similar levels of breakage between male and female Seaside Sparrows, is consistent with my predictions and reproductive investment theory, wherein reproductive investment can influence parental condition and overall survival (Borowkse et al. 2018). Finally, though the pattern was not significant, rate of brokenness also suggested that increased stressors to plumage were found at low latitudes and later in the breeding season, similar to overall wear. It is also important to note that approximately 15% of the total observations in relation to broken feathers were classified as missing. Ultimately, if x's are to be associated with feathers missing due to damage, this estimate of brokenness (the percentage of "yes" classifications) may be conservative.

Only date predicted fault bar severity and no independent variables explained the variation in number of fault bars, but the trends pointed in the opposite direction of overall feather wear and brokenness. In other words, our metrics of plumage wear (feather wear and broken feathers vs. fault bars and severity) displayed opposite patterns and formed two distinct groups. Feather wear and broken feathers tended to decrease with latitude and increase with date while fault bars and severity tended to increase with latitude and decrease with date. Based on our results, we think these opposite patterns are nonetheless consistent with each other due to molt patterns that are similar across species. The replacement of tail feathers (first prealternate and definitive prealternate molts) in Saltmarsh Sparrows occurs from March to May and from March to April in Nelson's and Seaside Sparrows (Pyle 1997). The next molt period (definitive prebasic molt) occurs from July to October in Saltmarsh Sparrows from July to September in Nelson's and Seaside Sparrows (Greenlaw et al. 2020; Shriver et al. 2020; Pyle et al. 2018). During this period between molts, all three species enter their breeding season, with arrival at breeding grounds and first broods occurring in early to late May (DeRagon 1988, Shriver et al. 2007, Marshall et al. 1990). Given this information, there is a portion of time where feathers are not replaced.

The connection between feather wear and fault bars is not entirely certain, however, here I consider two ideas that may relate these two metrics. First, fault bars, as previously discussed, are generated during feather growth, and are often indicative of environmental stressors like disease and fragmented habitats, which may be more indicative of the stressors faced during the winter season as opposed to the breeding season (Jovani et al. 2010). In contrast, wear is likely a stronger indicator of the stressors to plumage present during the breeding season. For example, Seaside Sparrows nest in the low marsh area, resulting in more frequent interactions with saltwater and dense stands of *Spartina* as they protect and care for young (Post et al. 2020). In other words, wear would be more reflective of the stressors to plumage experienced during the breeding season than those associated with fault bars. Second, fault bars lead to weaker feathers that are more likely to break at the sites of fault bar occurrence and may have carryover effects (Jovani et al. 2010). For example, migratory birds occupying poor-quality winter habitats may arrive to breeding grounds later and in poor body condition (Marra et al. 1998, Gill et al. 2001, Gunnarsson et al. 2005a). This, in turn, may result in expedited molt and contribute to poor quality feathers, reducing overall body condition (Vágási et al. 2012). Therefore, with an increase in fault bars and a prolonged period since the most recent molt, there may be a higher likelihood of broken feathers, which may lower total fault bar counts and severity. In other words, with fault bars increasing the likelihood of broken feathers, less fault bars may occur because feathers are breaking at these locations, resulting in decreased observations of fault bars later in the season. Saltmarsh melanism may also play a role in the contrasting wear and fault bars patterns observed in relation to latitude and date, however, it is inconsistent with the patterns associated with the interactive effect of species and sex. Saltmarsh melanism refers to the tendency of tidal marsh vertebrates to be more gray or black than their upland relatives (Grinnell 1913). It is suggested that the darker the feather, the more melanic keratin is found within it, which results in an increased protection from abrasion within the environment, and therefore reducing the likelihood of plumage wear (Bonser 1995). In contrast, I observed that Seaside Sparrows, who have dark olive-gray dorsal coloration, had the highest plumage wear and broken feather percentages when compared to Saltmarsh and Nelson's Sparrows. Nonetheless, it is clear that these four metrics of plumage wear are displaying different patterns that warrant consideration for their use as a monitoring tool for population assessments. Further, characterizing the relationship among metrics within individuals, and ideally over time, would enable us to understand whether these differing patterns are internally consistent or indicative of varying stressors (e.g., spring molt vs. breeding season, etc.). Feather condition remains a tool that is quick and noninvasive, with much existing data that can be used to parse these remaining questions.

Some of the patterns in latitude observed for plumage wear and broken feathers may also be explained by proximity to edge habitat. The lowest latitude value observed was found to be at 37.899863, which is at the southern edge of the Seaside Sparrow's breeding range and northern edge of their year-round range (Post et al. 2020). In comparison with other species, this location is the southern-most breeding range for Saltmarsh Sparrows, and a migratory location for Nelson's Sparrows (Greenlaw et al. 2020, Shriver et al. 2020). With increasing latitudes, Saltmarsh and Nelson's Sparrows approach the center of their breeding range where the proportion of edge habitat may be lower and resources or mate options are more abundant (Johnson et al. 2001, Marshall et al. 2020). With this increased access to resources and mates, Saltmarsh and Nelson's Sparrows may experience lesser effects of a struggle for existence, and by extension less feather wear and broken feathers, than that of Seaside Sparrows who are existing in edge habitat at this location.

Tidal marshes are sensitive to the impacts of climate changes and other anthropogenic threats including sea-level rise and coastal development. Because of this, species endemic to these locations like Saltmarsh, Nelson's, and Seaside Sparrows are susceptible to such changes as well, and therefore require comprehensive and effective conservation strategies. Saltmarsh Sparrows are estimated to be declining by approximately 9% annually, a sharp 87% decline since 1998, and are potential candidates for the Endangered Species Act in the United States (Hartley et al. 2020, Roberts et al. 2019). Based on low (0.35m) and high (0.75m) estimates for sea-level rise, one study found that Seaside Sparrows would persist under these scenarios, whereas Saltmarsh Sparrows would near extinction within 20 years (Roberts et al. 2019). This further emphasizes the need to characterize the patterns in plumage wear in these species and garner a better understanding of when and how certain plumage patterns occur to inform management strategies on both their winter and breeding grounds. According to the Atlantic Coast Joint Venture, an organization aimed at conserving coastal marsh habitats and the species housed within them, current management solutions to reduce population declines in Saltmarsh Sparrows include protecting key areas that buffer salt marshes to facilitate migration, restoring the health and resiliency of salt marshes to reduce nest flooding (a primary mode of nest mortality in all three species), and lastly, conducting range-wide population surveys and research regarding habitat use to inform conservation actions (Hartley et al. 2020). Conservation in light of climate change and anthropogenic forces is an important step in protecting vulnerable species like the Saltmarsh Sparrow in coming decades.

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Maeve Studholme was born in Boston, Massachusetts on September 13th, 1999. Growing up, she lived in North Easton, Massachusetts where she attended Oliver Ames High School and fostered her love for science with the help of some amazing science teachers. After graduating, she left the familiarity of her hometown behind in favor of attending college at the University of Maine. Here, she studied Ecology and Environmental Sciences (EES) with a concentration in Natural History and Environmental Studies. In her time as an undergraduate student, she volunteered as an ambassador for EES and worked as the program's Social Media Coordinator. When she's not attending classes, meeting with prospective students, or updating Facebook and Instagram pages, Maeve enjoys nature photography, creative writing, and finding new shows and movies to watch with friends.