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Effects of Life History Strategies on Annual Events and Processes in the Lives of Tidal Marsh Sparrows

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Effects of Life History Strategies on Annual Events and Processes in the
Lives of Tidal Marsh Sparrows

Alyssa Caitlin Borowske, PhD

University of Connecticut, 2015

For long-lived organisms, every annual cycle contains a series of events and processes that represent an individuals' life history. The breeding season can have a particularly strong influence on the rest of the annual cycle because individuals' reproductive investments may influence behavioral decisions, physical condition, and physiological state in ways that lead to differences in decisions and condition among individuals. I investigated ways in which events and processes within the annual cycle of migratory birds differ between the sexes of individual species, and between two closely-related species with different breeding systems. Specifically, I used comparisons of male and female Saltmarsh Sparrows (*Ammodramus caudacutus*), which are highly promiscuous, non-territorial, and have female-only care, and Seaside Sparrows (*A. maritimus*), which are socially monogamous, territorial, and have bi-parental care, to investigate how differential life histories influence: 1) the timing of migration and molt events; 2) feather quality and condition throughout the year; 3) within-season body condition and survival during the breeding and non-breeding periods; and 4) migration patterns. The most significant conclusions were as follows: 1) early male arrival to the breeding grounds may occur for different reasons in different species; 2) reproductive investment can delay pre-basic molt and migratory departure and reduce molt rate; 3) most feather damage occurs in the breeding season and can be influenced by a bird's reproductive status and investment; 4) reproductive investment can lead to poor body condition that carries over into the winter, and fat stores may

be a response to unpredictable circumstances such as those experienced by incubating females and wintering individuals, but condition differences do not necessarily translate into survival differences; 5) early male arrival may not correspond with sex-based latitudinal segregation on the wintering grounds, and 6) extensive banding efforts imply low connectivity between breeding and wintering sites in Saltmarsh Sparrows. Together, these results suggest that breeding strategies influence the performance of individuals throughout the annual cycle, and, while parental care can be costly, indirect forms of reproductive investment are costly too.

Effects of Life History Strategies on Annual Events and Processes in the
Lives of Tidal Marsh Sparrows

Alyssa Caitlin Borowske

B.A., Cornell College, 2007

A Dissertation

Submitted in Partial Fulfillment of the

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APPROVAL PAGE

Doctor of Philosophy Dissertation

Effects of Life History Strategies on Annual Events and Processes in the Lives of Tidal Marsh Sparrows

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DEDICATED TO

My maternal grandfather, Bob Eikum (12-29-1920 to 10-25-1989)

I know that he would be as proud of me as I am proud to be following in his footsteps and working to protect, understand, and appreciate the incredible planet we live on.

My undergraduate advisor, Bob Black (4-31-1949 to 1-13-2012)

Thanks to Bob, I held my first bird (a cooper's hawk), began turning into a biologist, and realized that studying birds was what I wanted to do academically and as a career.

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INTRODUCTION

For organisms with life-spans greater than a year, every annual cycle consists of a series of stages, each of which is made up of particular events and processes that represent an individual's life history (McNamara and Houston 2008; Wingfield 2008; Newton 2011). These stages are often discrete and energetically demanding, such as the pre-alternate molt, spring migration, reproduction, pre-basic molt, and fall migration that make up the annual cycles of many birds (Sherry and Holmes 1995; Newton 2011). Each stage is associated with particular behaviors and physiological processes, and individuals' body condition, probability of survival, and behavior may vary both by stage and based on things that happen in other stages. Many external factors can also influence birds, including interactions with conspecifics (e.g. Catry et al. 2004; Ward and Schlossberg 2004; Krams et al. 2013), resource distribution and availability (e.g. Barg et al. 2006; Brown and Sherry 2006; Danner 2012), predation risk (e.g. Ydenberg et al. 2003; Cresswell et al. 2010), weather (e.g. Brown and Brown 1998; Butler 2000), and habitat quality (e.g. MacFaden and Capen 2002; Studds and Marra 2005; Perlut et al. 2008). Many of these factors also vary somewhat predictably throughout the annual cycle, or vary annually in the degree to which they impact birds' condition, reproduction and survival (Sherry and Holmes 1995; Newton 1998).

Despite a historical "breeding system bias" in bird research, there is no simple "here or there" answer to the long-term debate over whether the breeding or non-breeding period is more important for limiting populations, (Alerstam and Hogstedt 1982; Cox 1985; Sherry and Holmes 1995; Faaborg et al. 2010). Instead, a bird's annual cycle is a complicated process that may be influenced by seasonal characteristics and cross-seasonal interactions (Donovan et al.

2002; Faaborg et al. 2010; Harrison et al. 2011). Knowing when, where, and how populations are limited is important for understanding a species' ecology and evolution, and for making informed conservation decisions. For example, a population could do well on the breeding grounds, with high levels of reproduction and survival, but if mortality was high during the non-breeding season due to a lack of appropriate habitat on the wintering grounds, the population could still decrease. Similarly, even if high-quality winter habitat was abundant, it would not prevent population declines if survival was lower during the breeding season or if reproduction was insufficient to compensate for adult mortality, no matter when it occurred.

Life History Strategies: An organism's life history characteristics reflect the specific way in which it lives, from how often and with which individuals it mates, to how many years it is likely to survive and reproduce. Each strategy is the product of natural selection operating on individual traits within physiological and environmental pressures and constraints. Three life history components that are defining elements of many avian breeding systems are territoriality, mate fidelity, and parental care (Crook 1965; Lott 1991). There is much interspecific variation in the degree to which these three components are employed—if at all—by birds (Verner 1977; Griffith et al. 2002; Cockburn 2006). Variation within each component can also exist among conspecifics, because what is best for one individual may not be best for another, leading to differences in males vs. females or in older vs. younger individuals (Trivers 1972; Lott 1991). Each life history strategy's specific combination of behaviors and physiological processes is associated with both fitness benefits and costs. The costs may be related to energetic expenditures (e.g. Visser and Lessells 2001; Neto and Gosler 2010), to behaviors with high risk

levels (e.g. Post and Götmark 2006; Minderman et al. 2006), or to a combination the two (Newton 1998; Liker and Székely 2005; Sibly et al. 2012). As each strategy is the result of an adaptive trade-off between benefits and costs, the relative benefits and costs between different strategies might vary significantly (Queller 1997; Sibly et al. 2012).

Reproductive Effort: One source of variation in costs among different life history strategies arises from differences in reproductive effort. Investment in reproduction varies by strategy and may include expenses ranging from maintaining territory boundaries, to egg-laying and incubating, to provisioning chicks. While parental care increases offspring survival, reproductive effort theory asserts that there is a trade-off between expenditure on current reproduction and investment in later reproduction (Williams 1966; Trivers 1972; Clutton-Brock 1991). This trade-off occurs because maximizing care may prevent the parent from reproducing again in the current cycle, reduce fertility in future cycles, or even reduce the parent's chance of surviving to reproduce again (Trivers 1972; Wesolowski 1994; Owens and Bennett 1997). Thus, to optimize fitness, each individual should invest as little as possible in current offspring without compromising the offspring's survival. If chicks can survive with the care of just one parent, care should be maintained by whichever parent has the most to gain (or the least to lose) from the investment (Wesolowski 1994; Burley and Johnson 2002; Houston and McNamara 2002). In most species, if one parent deserts, it is the male, because the female has a greater gametic investment and the male cannot guarantee his paternity (Wesolowski 1994; Burley and Johnson 2002).

Carry-over Effects: Cross-seasonal interactions, or carry-over effects, occur when non-lethal events and processes in one season influence a bird's performance in a subsequent season (Norris et al. 2004; Norris and Marra 2007; Harrison et al. 2011). Negative carry-over effects typically originate from circumstances that leave a bird in poor body condition or make it less competitive (Harrison et al. 2011), but can manifest in a variety of ways, such as poor feather quality (e.g. Nilsson and Svensson 1996), inadequate plumage ornamentation (e.g. Saino et al. 2004), late breeding-ground arrival (e.g. Reudink et al. 2009), or late breeding completion date (e.g. Mitchell et al. 2012). The energetic basis of carry-over effects may be due to reproductive investment during the breeding season (e.g. Dawson et al. 2000; Merilä and Hemborg 2000) or to environmental quality related to local habitat characteristics (e.g. Norris et al. 2004; Gunnarsson et al. 2005) or wide-spread trends in weather and food availability (e.g. Saino et al. 2007; Studds and Marra 2007).

Study System: Saltmarsh (*Ammodramus caudacutus*) and Seaside (*A. maritimus*) Sparrows are uniquely suited for a study on the influences of life history strategies and reproductive investment on other key events and processes in the annual cycle. Despite overlapping habitat requirements and ranges, the two species have dramatically different reproductive strategies. Specifically, Saltmarsh and Seaside Sparrows differ in their degrees of territoriality, monogamy, and bi-parental care, with Seaside Sparrows following strategies typical of most songbirds, and Saltmarsh Sparrows exhibiting a reproductive system unlike that of most birds. While Seaside Sparrows have been documented defending territories that range from large, all-purpose spaces, to smaller nesting territories, there is no evidence that Saltmarsh Sparrows engage in

territorial behavior around nest sites, mating locations, or feeding locations (Woolfenden 1956; Post 1974; Post and Greenlaw 1982). Seaside Sparrows are socially monogamous, with fairly low rates of extra-pair-fertilizations (Post and Greenlaw 2009; Hill and Post 2005). By contrast, Saltmarsh Sparrows do not maintain pair bonds, and their rate of female multiple mating is one of the highest documented in any bird species (Cornwallis et al. 2010; Hill et al. 2010). Finally, both male and female Seaside Sparrows participate in nest building and parental care, although only females incubate the eggs, and only males engage in extensive territorial defense (Woolfenden 1956; Post 1974; Post and Greenlaw 1982). In Saltmarsh Sparrows, all parental care, from nest building to incubation of eggs and feeding of chicks, is done exclusively by females, while males engage in competitive and, at times, agonistic mating (Woolfenden 1956; Post and Greenlaw 1982; Greenlaw and Post 2012). These differences result in distinct degrees and types of reproductive investment exhibited by males and females of the two species. Moreover, these differing degrees of reproductive investment may be associated with different costs, risks, and behavioral decisions during the breeding season and throughout the year.

Despite having such different breeding systems, Saltmarsh and Seaside Sparrows are closely related and are both tidal marsh specialists. Seaside Sparrow is sister to Saltmarsh and Nelson's Sparrows (*A. nelsoni*), which diverged from each other more recently (Klicka et al. 2014). Saltmarsh Sparrows breed from Maine to Virginia, and winter from Virginia to Florida, almost exclusively on the Atlantic Coast (Greenlaw and Rising 1994; Greenlaw and Woolfenden 2007). During the breeding season, Saltmarsh and Seaside Sparrows co-occur as far north as southern New England, and Seaside Sparrows also breed along the southern Atlantic and Gulf coasts (Post and Greenlaw 2009). The two species co-occur during the non-breeding season

throughout the entire Saltmarsh Sparrow winter range (Greenlaw and Rising 1994; Post and Greenlaw 2009). Both species are of high conservation concern (Butcher et al. 2006-2007), due to their reliance on tidal marshes, which are manipulated and threatened by invasive species (e.g. Benoit and Askins 1999; Warren et al. 2001), drainage and ditching (e.g. Clarke et al. 1984; Grant and Kirby-Smith 1998; Pepper and Shriver 2010), coastal development (e.g. Zhang and Leatherman 2011; Brittain and Craft 2012), contamination by toxins such as mercury (e.g. Weis et al. 2011; Winder and Emslie 2012), and, particularly, the potential for extreme habitat loss—of high marsh in particular—due to sea level rise from climate change (e.g. Rahmstorf 2007; Craft et al. 2009; Yin et al. 2009; Menon et al. 2010). Saltmarsh Sparrows, in particular, have a high risk of extinction (BirdLife 2013) due to their more restricted range and greater chance of nest failure due to flooding (Bayard and Elphick 2011; R. Kern and K. Ruskin unpublished data).

Research Objectives: The aim of my study was to investigate ways in which events and processes within the annual cycle of migratory birds differ between the sexes of individual species, and between two closely-related species with different breeding systems. Through intensive mist-netting that spanned both temporally, across the breeding and non-breeding periods, and spatially, throughout the non-breeding range, my study looked into the interactions of life history strategies and the annual cycle of tidal marsh sparrows. My underlying hypothesis was that an individual's reproductive investment influences its behavioral decisions, physical condition, and physiological state in ways that lead to differences in decisions and condition among individuals. Although many of these differences originate during the breeding season, they may carry-over to influence individuals throughout the annual

cycle. These differences may also lead to varying abilities among individuals to cope with environmental challenges. By following these species throughout the year, my study provided valuable full-life-cycle information about two species of conservation concern. In particular, I used comparisons of male and female Saltmarsh and Seaside Sparrows to investigate how differential life histories influence key components in the birds' annual cycles: 1) the timing of migration and molt events; 2) feather quality and condition throughout the year; 3) within-season body condition and survival and during the breeding and non-breeding periods; and 4) migration patterns.

My project was designed to build on the Elphick Lab's extensive work with Saltmarsh and Seaside Sparrows in Connecticut (e.g. Gjerdrum et al. 2005; Humphreys et al. 2007; Hill et al. 2010; Bayard and Elphick 2011; Meiman et al. 2012), as well as current collaborative work on tidal marsh birds through the Saltmarsh Habitat and Avian Research Program, and extend to new sites within the species' non-breeding ranges. Using three focal marshes in Connecticut, I began mist-netting each year in late April to capture birds soon after they returned to the breeding grounds. I continued systematic mist-netting to band and recapture individuals throughout the breeding period and then into the fall to infer departure times. My non-breeding period work took place at two focal marshes in South Carolina, and at various sites along a latitudinal gradient that covered the Saltmarsh Sparrows' non-breeding range. I identified all captured birds to species, and to age and sex, when possible. When the sex of an individual could not be determined visually, I collected a feather sample for genetic sex determination. I banded each bird, and took measurements for wing chord, tarsus length, culmen length, head length, fat score, muscle score, and body mass. I took systematic

photographs of each bird's wing and tail for assessment of feather condition and wear. I released all birds as promptly as possible close to the capture locations. Because the sparrows exhibit high degrees of within and between-season site fidelity on both the breeding and non-breeding grounds (DiQuinzio et al. 2001; Winder et al. 2012), I was able to capture and recapture many of the same individuals throughout each season, and even some of the same individuals on both the breeding and non-breeding grounds. The aims of my dissertation chapters were as follows:

1) *To determine the degree to which breeding strategies influence the timing of events that take place before or after the breeding season.* I used changes in within-species sex ratios and daily capture rates of each species and sex to infer relative arrival and departure timing. I also quantified molt initiation and duration from molt data collected in the field to determine the influence of reproductive activities on molt timing and rate.

2) *To relate birds' activities, particularly during the breeding season, to the condition of their feathers and to the presence of fault bars, one indicator of poor feather quality.* I quantified flight feather damage, including abrasion and breaks across entire feathers, throughout the breeding and winter seasons. I also compared the presence of fault bars for adult and juvenile Saltmarsh and Seaside Sparrows during the breeding season and of male and female Saltmarsh and Seaside Sparrows during the winter to infer the degree to which stress from nest flooding or reproductive investment leads to fault bar formation.

3) *To assess the influence of reproductive investment on body condition and within-season survival.* I evaluated the relative effects of sex, species, and season on three indicators of body condition: size-scaled mass, fat stores, and pectoral muscle condition. I also evaluated whether the probability of apparent within-season survival differed for male and female Saltmarsh and Seaside Sparrows during each of the breeding and winter seasons, and whether survival was influenced by body condition and/or body size.

4) *To evaluate connectivity patterns between breeding and non-breeding populations.* Through catching sparrows throughout most of the Saltmarsh Sparrow winter range, I looked for patterns in body size and sex ratio along a latitudinal gradient. I also qualitatively described apparent patterns of migratory connectivity based on long-distance recapture records that exist thanks to an extensive network of researchers who are currently banding tidal marsh sparrows on the breeding and/or wintering grounds.

Statement Concerning Use of Animal Subjects: All work for this project was conducted in accordance with approved Institutional Animal Care and Use Committee (IACUC) protocols (# A08-024 and A11-013) from the University of Connecticut. Banding for this project was done under Federal Bird Banding Permit number 22664.

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CHAPTER 1: REPRODUCTIVE STRATEGIES INFLUENCE TIMING OF MIGRATIONS AND PRE-BASIC MOLT IN TIDAL MARSH SPARROWS

ABSTRACT

Behavior during the breeding season can shape the timing of other events and processes, including arrival to the breeding grounds, pre-basic molt, and departure for fall migration. I studied these relationships in male and female Saltmarsh and Seaside Sparrows, two closely-related species with notably different reproductive systems. On average, females of both species arrived to the breeding grounds later, initiated molt later, and departed the breeding grounds later than did conspecific males. These observations support the hypotheses that reproductive strategies can influence arrival timing and that breeding investment can carry-over to impact molt and departure. Furthermore, I found that female Saltmarsh Sparrows, which mate with multiple males and care for nests, eggs and chicks alone, were last to arrive to the breeding grounds, last to initiate molt, with the shortest molt duration, and last to depart for the non-breeding grounds. Both species exhibited protandry, but because Seaside Sparrows of both sexes averaged earlier arrival to the breeding grounds than Saltmarsh Sparrows of either sex, early male arrival appears to be driven mainly by mating opportunities in Saltmarsh Sparrows and mainly by territoriality in Seaside Sparrows. Molt and departure timing also differed between the two species, with Seaside Sparrows initiating molt and departing before same-sex Saltmarsh Sparrows. This difference suggests that relative degrees of reproductive investment may be important for driving sex-based differences within species, but that other factors are also influential regarding differences between species.

INTRODUCTION

To cope with predictably variable seasonal environments, animal lives are structured into series of annual stages, each comprising particular events and processes. This sequence of stages can enhance individuals' fitness by partitioning reproduction from other energetically-demanding processes (Wingfield 2008; Newton 2011). Temperate migratory birds' annual stages typically include: pre-alternate molt, migration to the breeding grounds, reproduction, pre-basic molt, migration to the non-breeding-grounds, and overwintering (Sherry and Holmes 1996; Wingfield 2008; Newton 2011). For these species, migration and breeding are fundamentally driven by seasonal changes in the environment. Spring migration takes place as soon as conditions are amenable, and can be influenced by proximate causes such as temperature, food availability, and photoperiod (Lehikoinen et al. 2004; Helm et al. 2009; Studds and Marra 2011; Chambers et al. 2014). The breeding season corresponds with peak food availability, and begins early to maximize the potential for re-nesting (Goutis 1992; Dunn et al. 2011; Wesolowski and Rowiński 2014). Fall migration begins in time to avoid inclement weather, both on the breeding grounds and en route (Newton 2006), and storm events or changes in wind direction can trigger migratory departures (Åkesson and Hedenström 2000; Mitchell et al. 2012a).

The timing of annual cycle stages can also be influenced by the stages that come before and after (Wingfield 2008; Newton 2011). First, if stages cannot overlap, there could be a "domino effect" of successive delayed stages. For example, a bird that is late to arrive to the breeding grounds could then be late to initiate breeding (e.g. Yohannes et al. 2010). Second, an optimal strategy in one stage may require particular timing in another stage. For example, if early arrival to the breeding grounds increases reproductive success, individuals may migrate

more quickly in the spring, with shorter stop-over durations, than during fall migration (e.g. Lemke et al. 2013). Third, an individual's physiological condition at the end of one stage can carry-over to influence its performance in subsequent stages. For example, a bird wintering in poor-quality habitat may be unable to maintain good condition during the winter, causing it to arrive at the breeding grounds later and have reduced reproductive success compared to other individuals (e.g. Norris et al. 2004b).

Although most migrants go through the same annual stages, there is much variation between, and within, species in the exact timing of the stages, and many of these differences may be driven by specific reproductive strategies (McNamara et al. 1998; Barta et al. 2008; Verhulst and Nilsson 2008; Newton 2011). Three components of breeding systems that vary greatly among, and within, species are territoriality, mate fidelity, and parental care (Crook 1965; Verner 1977; Lott 1991; Griffith et al. 2002; Cockburn 2006). Investigating differences in timing among individuals with different reproductive strategies may give insights into the role of reproductive systems in structuring individuals' annual cycles.

In many bird species, males return to the breeding grounds before females (Mills 2005; Saino et al. 2010; Morbey et al. 2012), possibly due to competition (Kokko 1999). The "rank advantage hypothesis" posits that males compete for territories, while females compete for males with high quality territories (Morbey and Ydenberg 2001; Kokko et al. 2006). This hypothesis predicts protandry because selective pressure is greater on males, which are unlikely to mate without a territory, than on females, which are unlikely to be excluded from reproduction (Morbey and Ydenberg 2001; Kokko et al. 2006). The "mate opportunity hypothesis" similarly predicts protandry, based on the idea that males, more than females,

benefit by maximizing the number of potential mates they encounter (Morbey and Ydenberg 2001; Kokko et al. 2006). The pressure for protandry may be especially powerful in species with strong sexual selection, high sperm competition, frequent polygamy, and a male-biased sex ratio (Rubolini et al. 2004; Morbey et al. 2012), due to the heightened degree of competition among males. A third explanation for protandry is the “susceptibility hypothesis,” which suggests that larger individuals return to the breeding grounds earlier because they can better withstand cool temperatures, leading to protandry when males are larger than females (Weatherhead and Clark 1994; Saino et al. 2010).

Differences in reproductive investment may lead to differences in physiological states during and at the end of the breeding season. Important aspects of physiological state could include energy reserves, protein and nutrient stores, or feather quality (McNamara and Houston 1996; Norris et al. 2004a; Norris and Marra 2007; Barta et al. 2008; Harrison et al. 2011). Caring for offspring may reduce fertility in future seasons, or reduce the chance of survival (Williams 1966; Trivers 1972; Owens and Bennett 1994; Wesolowski 1994). This trade-off can manifest in reductions in body condition, as parents caring for chicks may fast and lose weight (Hörak et al. 1999; Kern et al. 2005). These state-based effects may carry-over from the breeding season into later stages of the annual cycle (McNamara and Houston 1996, 2008). Females, in particular, may end the breeding season more stressed and in poorer condition than males (Hörak et al. 1998; Jakubas et al. 2008). Even if both sexes participate in some aspects of parental care, egg laying and, in many species, incubation, are costs endured only by females, and those costs can be associated with reduced survival (Visser and Lessells 2001; Post and Götmark 2006). Although females of many species invest more than do males in post-

mating parental care, males may invest largely in other activities, such as defending territories and competing for mates (Queller 1997).

Because molt is energetically-demanding, most temperate migratory species do not begin pre-basic molt until breeding is finished (Dolnik and Gavrilov 1979; Svensson and Nilsson 1997; Vega Rivera et al. 1998; Bridge 2011). Overlapping molt and breeding can lead to reduced body condition of adults and their offspring (Hemborg and Lundberg 1998). Birds that expend less energy during the breeding season or end reproductive activities earlier may initiate molt sooner than birds with greater reproductive investment (Morton and Welton 1973; Hemborg 1999; Mitchell et al. 2012b). Molt rate may also be influenced by reproductive activities, although alternative hypotheses exist as to the direction of this relationship. Molt rate might correlate negatively with investment, if birds in better condition are able to molt more quickly (Gienapp and Merilä 2010; Saino et al. 2013). Alternatively, there may be a cost to increasing molt rate, if feathers grown quickly are poor quality (Dawson et al. 2000). The molt-constraint hypothesis posits that individuals with greater reproductive investment initiate molt late and then molt quickly to compensate for the loss in timing, but that this trade-off leads to the growth of feathers that are prone to damage and have poor insulating capacity (Nilsson and Svensson 1996; Dawson et al. 2000; Dawson 2004; Vágási et al. 2012).

The timing of departure from the breeding grounds can be influenced by reproduction, as a bird will not migrate until breeding and, in most cases, molt is complete (Vega Rivera et al. 1998; Newton 2011). Early nesters may be ready to migrate before late nesters, as indicated by correlations between nest initiation or completion and migratory departure (Ellegren 1990; Mitchell et al. 2012a). Breeding investment may influence when a bird reaches migration-ready

condition and departs for the non-breeding grounds. Birds do not accumulate fat while molting (Bonier et al. 2007; Minias et al. 2010), and do not migrate without sufficient fat stores (Payne 1972; Morton and Pereyra 1994; Newton 2011; Stutchbury et al. 2011). Birds with lower reproductive investment are predicted to reach migratory condition and depart sooner (Catry et al. 2013).

I looked at how varying degrees of territoriality, mate fidelity, and parental care influence the timing of when individual Saltmarsh (*Ammodramus caudacutus*) and Seaside (*A. maritimus*) Sparrows return to the breeding grounds, undergo pre-basic molt, and depart for the non-breeding grounds. While the two species are closely-related tidal marsh specialists with short-distance migrations along the eastern seaboard of the USA, they differ dramatically in their degrees of territoriality, monogamy, and bi-parental care. Saltmarsh Sparrows do not engage in territorial behavior (Woolfenden 1956; Shriver et al. 2010), do not maintain pair bonds (Greenlaw and Post 2012), have a higher rate of female multiple-mating than nearly any bird species (Cornwallis et al. 2010; Hill et al. 2010), and exhibit female-only parental care (Woolfenden 1956; Post and Greenlaw 1982). In contrast, Seaside Sparrows are territorial (Woolfenden 1956; Marshall and Reinert 1990; Hill and Post 2005) socially monogamous, with fairly low rates of extra-pair fertilizations (Post and Greenlaw 2009; Hill and Post 2005), and exhibit bi-parental care (Woolfenden 1956; Post and Greenlaw 1982).

Given the breeding system differences, I predicted differences in the timing, between both species and sexes, of annual cycle stages that occur immediately before and after breeding (Table 1). With their breeding investment limited to seeking mates and copulations, I predicted that male Saltmarsh Sparrows end reproduction first and in the best condition. I

predicted that female Saltmarsh Sparrows, as the sole care-givers to their eggs and chicks, invest most and end reproduction in the poorest condition. I also predicted that male and female Seaside Sparrows, with their bi-parental care, would be intermediate between the Saltmarsh Sparrow sexes. Despite their territorial defense and parental care roles, I predicted that male Seaside Sparrows have lower investment and end the breeding season in better condition than female Seaside Sparrows because only the females lay eggs and incubate, although both sexes feed the young (Post and Greenlaw 1982; Lockwood et al. 1997).

Both the rank opportunity and mate opportunity hypotheses predict protandry in breeding-grounds arrival in Seaside Sparrows. Since Saltmarsh Sparrows are non-territorial and lack pair bonds, only the mate opportunity hypothesis predicts protandry. As neither species is strongly sexually dimorphic, the susceptibility hypothesis does not apply. Because Seaside Sparrows are larger than Saltmarsh Sparrows (Greenlaw and Rising 1994; Post and Greenlaw 2009), however, the susceptibility hypothesis would predict that Seaside Sparrows arrive earlier than Saltmarsh. I also predicted that, at the end of the breeding season, male Saltmarsh Sparrows would molt earliest, followed by male and female Seaside Sparrows, and, finally, female Saltmarsh Sparrows. If better-condition individuals are able to molt more quickly, I predicted the same order for molt rate, with the fastest and slowest rates in male and female Saltmarsh Sparrows, respectively. Alternatively, if accelerated molt rate is a response, with negative consequences, to late molt initiation, I expect the reverse pattern, with male Saltmarsh Sparrows molting most slowly, female Saltmarsh Sparrows molting most quickly, and male and female Seaside Sparrows molting at intermediate rates. Finally, I predicted different

breeding-ground departure times, with male Saltmarsh Sparrows departing first, followed by male and female Seaside Sparrows, and then female Saltmarsh Sparrows.

METHODS

Study Sites: I mist-netted Saltmarsh and Seaside Sparrows from April to October during 2011-2013, which encompassed the period between spring arrival on the breeding grounds through to fall migration. Study sites were located within three tidal marshes in Connecticut, USA: the East River Marsh (Madison, 41°16'19.49"N, 72°39'9.97"W), Hammonasset State Park (Madison, 41°15'39.63"N, 72°32'57.96"W), and Barn Island Wildlife Management Area (Stonington, 41°20'15.10"N, 71°52'7.05"W). For my molt analyses, I also used data collected between August 6 and October 21 2002, July 16 and August 28 2003, and July 26 to August 12 2004, at two additional marshes: Stewart B. McKinney National Wildlife Refuge (Westbrook, 41°16'56.19"N, 72°28'47.72"W), and the Charles Wheeler Marsh Wildlife Management Area (Milford, 41°11'12.57"N, 73° 6'12.25"W). All five sites are dominated by salt-tolerant vegetation, especially *Spartina patens*, *S. alterniflora*, *Juncus gerardii*, and *Distichlis spicata*. The sites are geographically distinct from one another and are located along a 75 km section of the Long Island Sound coast.

Mist-netting: During the pre- and post-breeding stages, I netted opportunistically by moving pairs of two-panel, 12-m, 38-mm mesh mist-nets around the marsh. During the breeding season, I followed a systematic mist-netting procedure in which I opened three sets of six nets for three hours, beginning shortly after dawn. During the systematic sampling period, I visited

four or five subplots within each study site in a rotating schedule, for a total of three visits per subplot.

I banded all new captures, aged each bird using plumage or skull ossification, and sexed each adult based on the presence of a brood patch or an enlarged cloaca. If a bird was not in breeding condition, and therefore could not be sexed visually, I collected a feather sample by gently pulling two rectrices or breast feathers and/or collecting any feathers that were dropped during handling and used these feathers to sex birds via genetic markers.

Molt Scoring: I evaluated molt data from 263 Saltmarsh Sparrows (140 males, 123 females) and 37 Seaside Sparrows (17 males, 20 females) caught on the breeding grounds in Connecticut. I scored each flight feather on a scale of 0 to 5 using methods modified from Ginn and Melville (1983) (Appendix A). I scored each of the primaries, secondaries, tertials, and rectrices as follows: 0 (old, no molt), 1 (missing or small pin), 2 (feather sheath broken to one-quarter grown), 3 (one-quarter to three-quarters grown), 4 (three-quarters to almost fully grown), 5 (new, fully grown). Birds with a complete set of new flight feathers had a molt score of 240. I scored body molt by individually scoring primary coverts, secondary coverts, and the alula, with the same method as for remiges, and by estimating the proportion of molting feathers in five regions on the bird: head, back, underparts (throat, breast and belly), underwing coverts, and lesser and median coverts. Categories were 0 (all, or nearly all, old feathers, less than 10% of feathers in molt), 1 (10 - 30% of feathers in molt), 2 (31 - 50%), 3 (51 - 70%), 4 (71 - 90%), 5 (91% new to all new feathers). Birds with all new body feathers had the maximum body molt score of 130.

I also evaluated Saltmarsh Sparrow molt data with a mass-scaled scoring system, using feathers plucked from a dead male Saltmarsh Sparrow (donated to the University of Connecticut vertebrate collection: UCM 2128). I weighed each flight feather individually, and weighed body feathers in the groups that were used in the molt scoring. I weighed primary and secondary coverts by tract. With this information, I re-calculated the molt scores for each feather, or group of feathers, proportional to its contribution to the total feather mass, (after Dawson and Newton 2004). As the results of the Saltmarsh Sparrow molt analyses using the weighted and un-weighted scores did not differ (Appendix B), I report results comparing molt in Saltmarsh and Seaside Sparrows using the un-weighted scores. I lacked a specimen with which to conduct a comparable analysis with Seaside Sparrow feathers, but similarities in size and structure between the two species suggest no reason why species should differ.

I also examined 25 Saltmarsh Sparrow (13 male and 12 female) and 116 Seaside Sparrow (66 male and 50 female) museum specimens to expand my sample sizes. All specimens were adult birds collected between July 1 and November 1 and were housed in the collections of the Museum of Comparative Zoology, Harvard University, the University of Connecticut Biological Collections, or the American Museum of Natural History. I established sex from specimen labels. I used forceps to lift feathers of the right wing and tail to quantify flight feather molt. I only examined one wing in order to minimize handling of the specimens. I used the same procedure to score flight feather molt on the museum specimens as described for live birds. Given the smaller number of feathers examined, museum specimens with all new flight feathers (right wing and tail) had a maximum score of 150. I did not score museum specimens for body molt.

Genetic Sexing: I extracted DNA from 2 rectrices or 2-6 breast feathers (Segelbacher 2002), using NucleoSpin Tissue DNA extraction kits (Macherey-Nagel, Duren, Germany). I amplified the DNA according to Griffiths et al. (1998). This process involves a single PCR with gender primers P2 and P8, which were designed to amplify sections of two avian sex genes, CHD-W, which is only present in females, and CHD-Z, which is present in males and females (Griffiths et al. 1998). I confirmed the method's accuracy with six males and six females from my study sites that had been visually sexed in the field by the presence of a brood patch (female) or enlarged cloaca (male). Following amplification, I resolved the samples on 1.5% agarose gels and determined the sex identifications based on the presence of one (male) or two (female) bands.

Statistical Analyses: To compare arrival and departure patterns among the four sex-species combinations of male and female Saltmarsh and Seaside Sparrows, I counted the number of birds of each class that I captured each day and assessed capture patterns throughout the banding period. I ran a set of four generalized additive models using the R package mgcv (Wood 2006) in R 3.1.1 (R Core Team 2014). In these models, I used the number of each class of bird captured each day as the dependent term. All models assumed a negative binomial distribution and included year and the amount of netting effort per day (net/hours). The models differed by the number of smoothed curves that were fit: 1) a single smoother for all captures; 2) a separate smoother for each species; 3) a separate smoother for each sex; 4) a separate smoother for each sex/species class. Because sex, species, and class were factors, models 2, 3, and 4 also included the respective factor as a term outside of the smoothed function, to allow

both the intercept and the shape of the smoothed curve to vary by category (Wood 2006). I compared the four models using AIC_c scores using the function AICctab from the R package bbmle (Bolker 2014).

I also quantified changes in the daily sex ratio of each species throughout the banding periods in 2011-2013 to infer whether conspecific males and females arrive and depart the breeding grounds synchronously. Because it is unlikely that I caught the very first birds to arrive back to the breeding grounds, I set day 0 as April 24, four days before the earliest capture I had during the three-year period. I ran two generalized additive models to infer arrival and departure patterns of male:female Saltmarsh Sparrows and male:female Seaside Sparrows. With sex ratio as the dependent variable, both models assumed a binomial distribution and featured a smoother for day, an effect of year, and used cross-validation with a cubic-regression spline to select the optimal degree of smoothing.

I compared average molt initiation date and duration for adult male and female Saltmarsh and Seaside Sparrows using the R package moult (Erni et al. 2013). This package is based on the Underhill-Zucchini maximum-likelihood approach for predicting the initiation and duration of avian molt (Underhill 1985; Underhill and Zucchini 1988). I specified data type 5, which is designed for populations in which individuals depart for migration soon after completing molt (Underhill et al. 1990; Erni et al. 2013). I assessed the proportion of flight feather molt completed using data from the field and museum scored birds (using data from only the right wing for the field scored birds, so the total scores would be comparable) and assessed the proportion of body molt completed using only the field scored birds. I ran models to test the effect of species, sex, and a sex*species interaction on molt initiation and duration

by grouping birds in three ways: 1) by species 2) by sex, and 3) as belonging to one of four classes: male Saltmarsh, female Saltmarsh, male Seaside, and female Seaside. In addition to running a null model in which neither start date nor duration varied by group, I ran the following sets of models for each of my grouping versions: a) duration varied by group; b) start date varied by group, c) start date and duration varied by group. I compared the AIC_c scores of the 10 models. To compare start date and duration for the four sex/species classes, I used the estimates generated by the top model, and present the results as date or days \pm SE.

RESULTS

Arrival and Departure: I found distinct occupancy patterns on the breeding grounds for male and female Saltmarsh and Seaside Sparrows. Specifically, in my analysis of daily captures throughout the banding period, the best-supported model included separate smoothers for each sex/species class (Table 2). In this model, the smooth terms for each class were highly significant (Table 3), the effect of year was not significant ($z = 0.3$, $p > 0.7$), and the deviance explained was 53%. The fitted curves from the top model (Figure 1) indicate that male Seaside Sparrows arrive to the breeding grounds earlier than do male Saltmarsh Sparrows, and that female Seaside Sparrows arrive to the breeding grounds earlier than female Saltmarsh Sparrows. For both sexes, Seaside Sparrows also depart the breeding grounds before Saltmarsh Sparrows (Figure 1).

I also found evidence for protandry in both arrival to and departure from the breeding grounds in Saltmarsh and Seaside Sparrows. In looking at changes in sex ratios throughout the banding period, I found that my captures of both species were strongly male-biased at the

beginning of the banding period, then decreased to become female-biased by the end of the period. Specifically, in both species, the models included linear decreases in M:F ($\chi^2 = 91.1$ and $p < 0.001$ for Saltmarsh; $\chi^2 = 5.7$ and $p < 0.05$ for Seaside Sparrows). The effects of year were not significant ($p > 0.3$ in both species), and the deviance explained was 12% for Saltmarsh Sparrows and 5% for Seaside Sparrows. In both species, the fitted curves from the models show a decline in the probability that a captured bird was male from around 0.7 in late April, to less than 0.3 by mid October (Figures 2A and B).

Molt: Flight feather molt initiation and duration differed by both sex and species. Body feather molt initiation also differed by sex and species, but there was no evidence that body feather molt duration differed (Table 4). In both species, males initiated flight feather and body molt before females. This difference in timing of flight feather molt was slightly greater in Seaside (mean initiation was July 30 ± 3 days for males and August 10 ± 2 days for females) than in Saltmarsh Sparrows (mean initiation was August 8 ± 2 days for males and August 15 ± 1 day for females) (Figure 3A). For body molt, the difference in molt initiation between the sexes was about 10 days in both species: mean body molt was initiated on July 30 ± 4 days and August 10 ± 3 days for male and female Seaside Sparrows, and August 15 ± 2 days and August 24 ± 1 day for male and female Saltmarsh Sparrows (Figure 3B). In both species, flight feather molt lasted longer in males than in females. This difference was greater in Seaside (mean duration for males versus females was 67 ± 6 days and 47 ± 7 days, respectively) than in Saltmarsh Sparrows (mean duration for males versus females was 54 ± 3 days and 48 ± 2 days) (Figure 3A).

Estimating body molt duration separately for each sex and species did not improve model fit (Table 4). The estimate for body molt duration of all individuals combined was 37 ± 2 days.

DISCUSSION

I took advantage of a unique study system of two closely-related species with strikingly different reproductive strategies to test predictions related to the timing of events, apart from reproduction, that take place on the breeding grounds. My study highlights the role that breeding systems play in structuring annual cycles. Specifically, my results support the hypotheses that mating strategies influence arrival timing to the breeding grounds, and that reproductive investment influences the timing of post-breeding molt and migration departure, potentially leading to negative carry-over effects between seasons.

Both the within- and between-species comparisons of molt and departure timing suggest that females may pay a cost for their uniparental care in the form of late molt and breeding ground departure compared to conspecific males. A correlation between molt initiation and reproductive investment has been observed in several other systems, with females initiating molt after males (Morton and Morton 1990; Svensson and Nilsson 1997; Newton and Rothery 2005; Flinks et al. 2008), and females that had been abandoned initiating molt later than females raising chicks with help from mates (Hemborg 1999). My result that female Saltmarsh Sparrows have delayed molt and departure compared to both conspecific males and Seaside Sparrows contrasts with an earlier study. Post and Greenlaw (1982) found no evidence for higher reproductive costs sustained by female Saltmarsh Sparrows than by males or Seaside Sparrows, despite documenting that female Saltmarsh Sparrows delivered food to

chicks at twice the rate and flew four times as far as did female Seaside Sparrows. Specifically, Post and Greenlaw (1982) found no differences in seasonal weight changes or estimated annual survival in female Saltmarsh Sparrows versus male Saltmarsh Sparrows or in male and female Seaside Sparrows. I also found (Chapter 3) that male and female Saltmarsh and Seaside Sparrows do not differ in probability of apparent survival during either breeding or winter. However, I found (Chapter 3) that females of both species had reduced body condition, as indicated by a scaled mass index (Peig and Green 2009), compared to conspecific males in both seasons, and that female Saltmarsh Sparrows had poorer body condition than female Seaside Sparrows. Together, my results suggest that body condition at the end of breeding may influence molt initiation, duration, and departure, all of which are potential non-lethal costs of reproduction that could contribute to the lower condition I observed in wintering females.

Female Saltmarsh Sparrows' delayed molt could occur if their breeding activities are completed at a later date than that of male Saltmarsh Sparrows and Seaside Sparrows. In other systems, females with later clutches initiate molt after females with earlier nest completion dates (Stutchbury et al. 2011; Mitchell et al. 2012b). Late departure timing in female Saltmarsh Sparrows could, then, be caused by their later molt initiation. Although the Saltmarsh Sparrow breeding system is unusual in birds, the Aquatic Warbler (*Acrocephalus paludicola*) also has no territoriality (Schaefer et al. 2000), high degrees of multiple mating in both sexes, and female-only care (Schulze-Hagen et al. 1999). As in Saltmarsh Sparrows, male Aquatic Warblers depart the breeding grounds before females (Wojczulanis-Jakubas et al. 2013), but both sexes molt on the wintering grounds in West Africa (Tegetmeyer et al. 2012) and the timing of their molts have not been quantified.

Delayed molt can be costly. In both Saltmarsh and Seaside Sparrows, the later molt initiation by females was coupled with shorter flight feather molt durations than in conspecific males. This pattern supports the molt constraint hypothesis, which asserts that accelerated molt rate is a cost of delayed molt initiation (Nilsson and Svensson 1996). High feather growth rates can lead to the production of poor-quality feathers, with shorter lengths, thinner rachis, more fault bars, less resistance to wear, and poorer insulating capacities, compared to feathers that were grown more slowly (Nilsson and Svensson 1996; Dawson et al. 2000). This reduction in feather quality at accelerated molt rates may be especially strong in poor-condition individuals (Vágási et al. 2012). There is not, however, universal support for the molt constraint hypothesis, feathers grow faster in male than in female Siberian Jays (*Perisoreus infaustus*) (Gienapp and Merilä 2010), and in birds that were experimentally given abundant food compared to birds that were given limited food during molt (Jenkins et al. 2001; Pap et al. 2008). Elsewhere, I found that feather condition varied by sex and species during the breeding season, but that all individuals had low degrees of feather damage during the winter (Chapter 2). I did not evaluate feather microstructure, but if any differences existed between sexes or species, they apparently were not severe enough to lead to differential feather damage during the winter.

Since molt is energetically demanding, molting birds typically do not accumulate the fat stores that are necessary for migration (Newton 2006). Birds that remain on the breeding grounds late into the season may have a harder time gaining reserves, as food resources become more limited as autumn progresses (McNamara et al. 1998; Newton 2006). Migration also becomes increasingly risky as departure is delayed: both migratory flight and stopovers are

more costly in cold than warm weather (Wikelski et al. 2003), storms become more potentially dangerous due to ice and snow (Newton 2007), and stopover sites become increasingly food-depleted (Newton 2006). Although this is not an issue for Saltmarsh or Seaside Sparrows, for species that are territorial during the winter, individuals that depart the breeding grounds late may be forced to occupy poor-quality habitat during the winter, which can continue to impact their performance and condition even during the following breeding season (Norris et al. 2004b; Studds and Marra 2005).

Seaside Sparrows initiated flight feather and body molt before female Saltmarsh Sparrows. But, contrary to my prediction, male Saltmarsh Sparrows' molt initiation was no earlier than that of female Seaside Sparrows. Although male Saltmarsh Sparrows do not invest highly in their offspring, the energetic expenditures associated with seeking multiple mating opportunities (Woolfenden 1956; Post and Greenlaw 1982) and, to a lesser extent, high sperm production (Tuttle and Pruett-Jones 2004) may still impose important costs.

In my assessment of breeding ground arrival, I set out to compare two hypotheses for protandry, the mate opportunity hypothesis and the rank opportunity hypothesis (Morbey and Ydenberg 2001). I found evidence for protandry in both species, but Seaside Sparrows arrived to the breeding grounds earlier than did Saltmarsh Sparrows. This between-species comparison suggests that the rank-opportunity hypothesis may be the primary force behind protandry in Seaside Sparrows. If, instead, extended mating opportunities were driving male arrival timing in both species, I would expect male Saltmarsh Sparrows to arrive earlier than male Seaside Sparrows, as the selective pressure is predicted to increase with higher degrees of promiscuity and sperm competition (Coppack et al. 2006; Kokko et al. 2006). It is unlikely that differences in

body size and temperature sensitivity, as suggested by the susceptibility hypothesis, drive arrival time in these species because neither body size nor the scaled mass index (Peig and Green 2009) proxy for body condition were associated with tidal marsh sparrow survival during the winter or breeding season (Chapter 3). Additionally, during the winter, I found that Seaside Sparrows have a lower probability of apparent survival than Saltmarsh Sparrows (Chapter 3).

In addition to reproductive strategies and investment, other system-specific processes likely contribute to the timing differences between, and within, the two species. For example the number of male Saltmarsh Sparrows that I captured early in the season could have been heightened by males staying longer at stopover sights. Also, virtually all Saltmarsh Sparrow nests that are initiated in early May fail due to flooding at the first spring tide (Shriver 2002; Elphick unpublished data). This phenomenon may influence when female Saltmarsh Sparrows arrive, as early nesting wastes energy. In contrast, Seaside Sparrows have higher average nest placement (Marshall and Reinert 1990; Humphreys et al. 2007), leading to nests that are less prone to flooding; many early nests do produce offspring (Gjerdrum et al. 2005). These differences in early nest success could drive earlier arrival of female Seaside than Saltmarsh Sparrows. The two species winter in the same area, so differential wintering grounds is also unlikely to be an explanation for the patterns in arrival time.

Post-breeding, Seaside Sparrows initiated molt earlier and with more feather tracts at once, and departed the breeding grounds before Saltmarsh Sparrows. Molting a greater number of feathers simultaneously can be a way of reducing overall molt duration (Dawson 2004), and can explain molt duration differences among species. In a comparison of 43 species from 26 families, 60% of the variation in molt duration was explained by the number of

primaries growing simultaneously, whereas only 4.4% of the variation was explained by differences in growth rate (Rohwer and Rohwer 2013). In my system, these different molt strategies may have altered the timing of migration, as the overlapping feather molts of Seaside Sparrows may allow them to complete molt faster, potentially accounting for their earlier departure from breeding sites compared to the situation of Saltmarsh Sparrows. Incidentally, I also observed that juvenile Saltmarsh Sparrows undergo a full body molt before departing the breeding grounds, whereas juvenile Seaside Sparrows do not begin molt until after departure (Borowske unpublished data), which provides further evidence for the differences between the two species in molt and departure strategies.

My results underscore the importance of taking an integrated approach to thinking about the timing of annual cycle stages. Doing so may show costs that carry over from one season to another (reviewed by Harrison et al. 2011), or may reveal surprising degrees of flexibility in recovering from a setback during one annual cycle stage (Lourenço et al. 2011; Senner et al. 2014).

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Table 1: Predictions regarding the timing of arrival to the breeding grounds, pre-basic molt initiation and duration, and departure from the breeding grounds in male and female Saltmarsh (SALS) and Seaside (SESP) Sparrows.

	Saltmarsh	Seaside	Female	Male
	♂ vs. ♀	♂ vs. ♀	SALS vs. SESP	SALS vs. SESP
Arrival timing: rank- advantage hypothesis	no difference	♂ earlier	no difference	SESP earlier
Arrival timing: mate- opportunity hypothesis	♂ earlier	♂ earlier	no difference	SALS earlier
Arrival timing: susceptibility hypothesis	n/a	n/a	SESP earlier	SESP earlier
Molt initiation	♂ earlier	♂ earlier	SESP earlier	SALS earlier
Molt rate: lower investment → faster rate	♂ faster	♂ faster	SESP faster	SALS faster
Molt rate: lower investment → slower rate	♀ faster	♀ faster	SALS faster	SESP faster
Departure timing	♂ earlier	♂ earlier	SESP earlier	SALS earlier

Table 2: Comparisons of generalized additive models describing daily captures of male and female Saltmarsh and Seaside Sparrows on their Connecticut, USA, breeding grounds. All models fit a smoother for day, assumed a negative binomial distribution, and included year and netting effort as additive effects. The models differed by the number of smoothers fit: one smoother for all birds; one smoother for each sex; one smoother for each species, or one smoother for each sex and species (four total).

Models	ΔAIC_c	df	<i>w</i>
Smoothers by sex and species	0	27	1
Smoothers by species	190.3	16	<0.001
Smoothers by sex	424.6	16	<0.001
One smoother for all birds	549.6	10	<0.001

Table 3: Approximate significance of smoothed terms in the best-supported generalized additive model for daily captures of male and female Saltmarsh and Seaside Sparrows on their Connecticut, USA, breeding grounds. This model fit a separate smoother for each sex of each species.

Smoothed term	edf	Ref.df	Chi sq.	p
Female Saltmarsh	4.80	5.88	23.08	<0.001
Male Saltmarsh	6.79	7.90	136.44	<0.001
Female Seaside	2.96	3.71	15.78	0.003
Male Seaside	3.45	4.31	51.28	<0.001

Table 4: Comparisons of models of pre-basic flight feather and body molt initiation and duration for Saltmarsh and Seaside Sparrows on their Connecticut, USA. breeding grounds.

Flight feather and body molt were analyzed separately.

Models—flight feather molt	ΔAIC_c	df	w
Initiation and duration vary by sex and species	0	9	0.920
Initiation varies by sex and species	5.1	6	0.071
Initiation and duration vary by sex	9.8	5	0.007
Initiation varies by sex	12.8	4	0.002
Initiation varies by species	35.1	4	<0.001
Initiation and duration vary by species	35.9	5	<0.001
Duration varies by sex	38.1	4	<0.001
Duration varies by sex and species	39.4	6	<0.001
Neither initiation nor duration vary	42.8	3	<0.001
Duration varies by species	43.9	4	<0.001
Models—body molt			
Initiation varies by sex and species	0	6	0.540
Initiation and duration vary by sex and species	0.3	9	0.460
Initiation varies by species	19.0	4	<0.001
Initiation and duration vary by species	21.1	5	<0.001
Initiation and duration vary by sex	32.4	5	<0.001
Initiation varies by sex	33.5	4	<0.001
Duration varies by species	41.6	4	<0.001
Duration varies by sex and species	43.0	6	<0.001
Duration varies by sex	48.9	4	<0.001
Neither initiation nor duration vary	49.4	3	<0.001

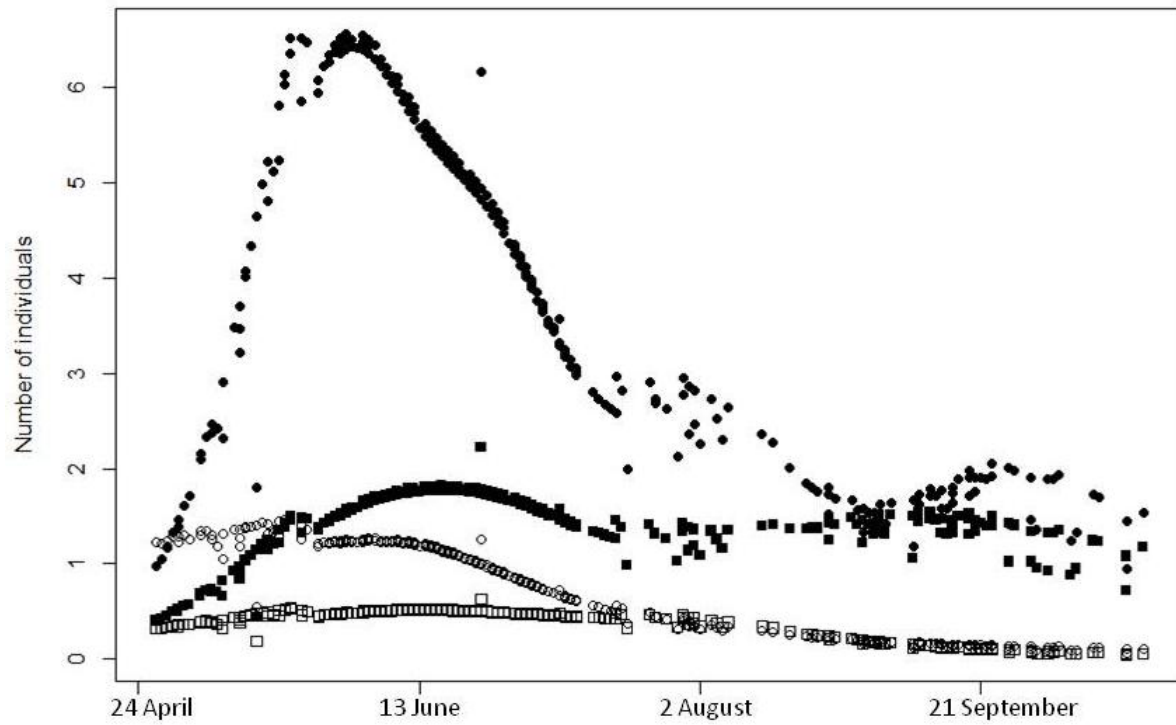


Figure 1: Fitted curves for the top generalized additive model depicting capture patterns of male and female Saltmarsh and Seaside Sparrows on their Connecticut, USA, breeding grounds, with separate smoothers for each category of bird: male Saltmarsh (closed circle), female Saltmarsh (closed square), male Seaside (open circle), and female Seaside (open square) Sparrows. The y axis depicts number of birds caught on a given day.

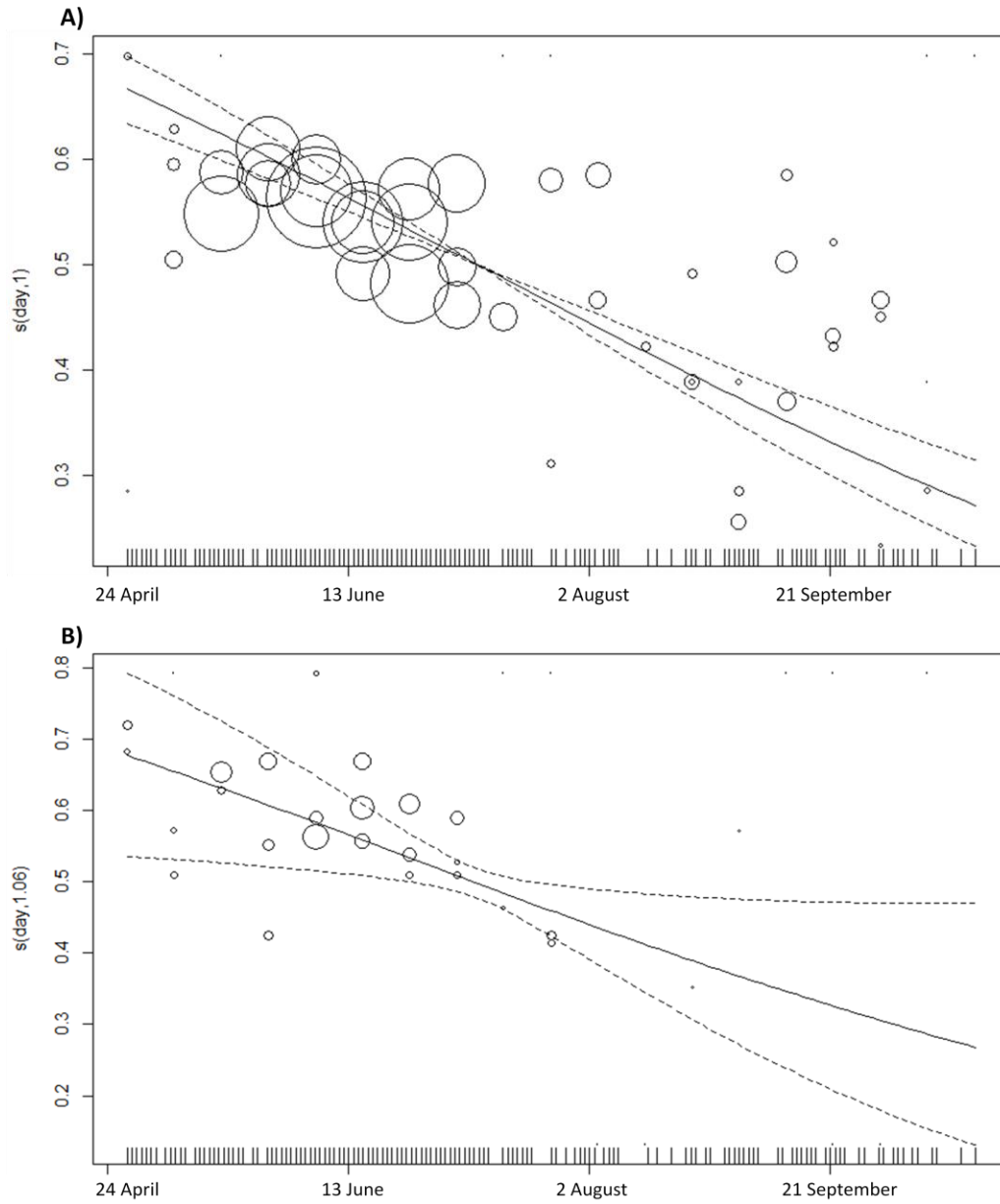


Figure 2: Plots of the smoothers from generalized additive models showing changes in the probabilities that a captured bird is male for A) Saltmarsh Sparrows and B) Seaside Sparrows throughout the banding period. The dotted lines represent 95% confidence intervals. The circles represent the raw data, with their size scaled to the number of birds caught during 10 day periods, calculated separately for each year.

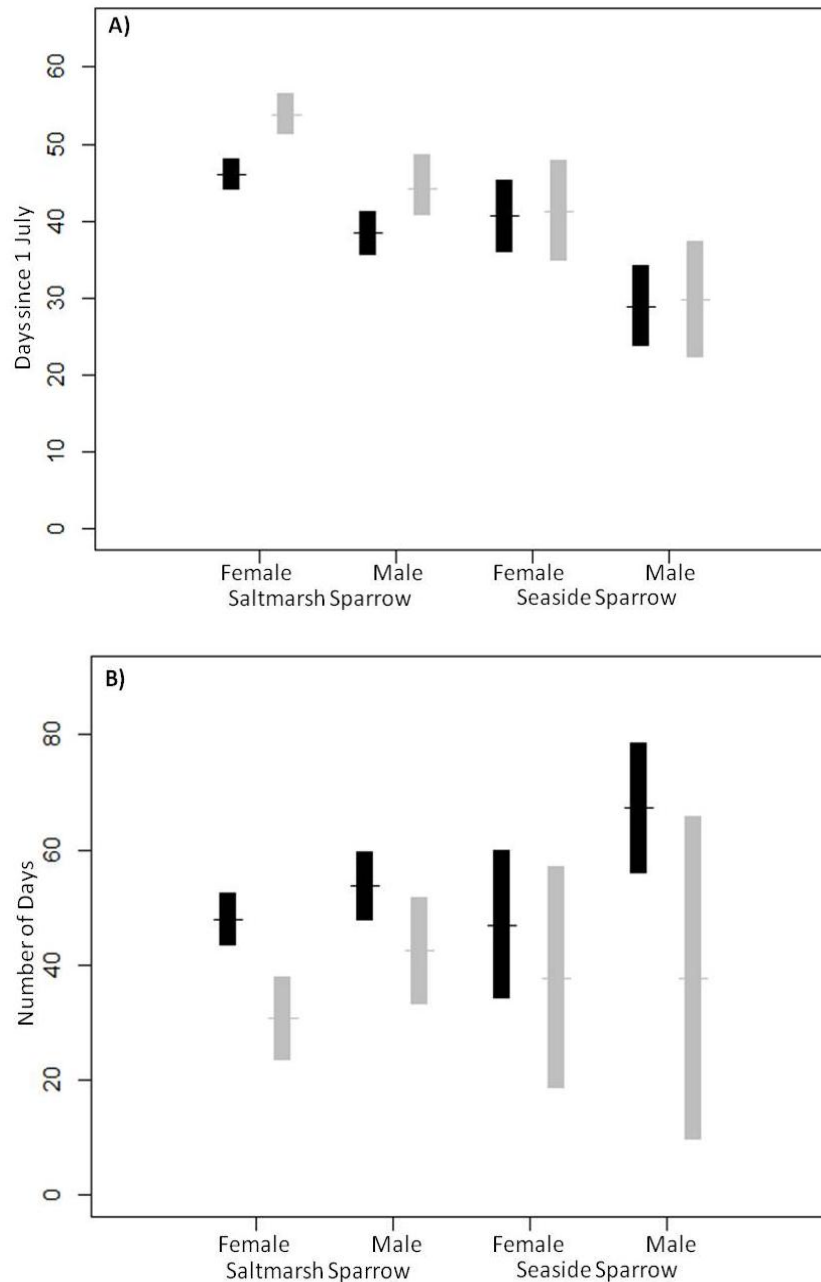


Figure 3: Model estimates of A) molt initiation and B) duration for male and female Saltmarsh and Seaside Sparrows. The bars represent model estimates with 95% confidence intervals about the means. The black bars depict flight feathers and the gray bars depict body feathers.

CHAPTER 2: FEATHER DAMAGE AND FAULT BARS THROUGHOUT

THE ANNUAL CYCLE OF TIDAL MARSH SPARROWS

ABSTRACT

I quantified feather quality and condition of male and female Saltmarsh (*Ammodramus caudacutus*) and Seaside (*A. maritimus*) Sparrows throughout the annual cycle to test predictions regarding the influence of breeding-related activities on feather damage and the effect of breeding- and tidal flooding-related stress on the formation of fault bars. Less feather damage occurred during the winter than during the breeding season, with no difference in remige or rectrix damage between the sexes or species during winter. Within the breeding season, damage patterns differed among sexes and species, in terms of when damage occurred and what type of damage predominated. Together, these patterns indicate that feather damage may be a cost of reproductive activities for both males and females, with different types and degrees of damage associated with different activities, potentially including copulations, territorial disputes, and nest-tending. There was no difference in the number or severity of fault bars between juveniles of the two species but, compared to breeding adults, juveniles had more severe and more bars. During the winter, there was mixed evidence that the number or severity of fault bars differed among sexes or species, with female Saltmarsh Sparrows having more fault bars than conspecific males, but with Seaside Sparrows of both sexes having more severe fault bars than Saltmarsh Sparrows.

INTRODUCTION

Reproduction is highly demanding; individuals caring for offspring may fast and lose weight (Hörak et al. 1999; Kern et al. 2005), become physiologically stressed (Hörak et al. 1998; Jakubas et al. 2008), and have reduced chances of survival (Owens and Bennett 1994) compared to individuals providing little or no care. Because reproductive investment can be so costly, theory predicts that individuals invest only as much as necessary to produce viable offspring (Williams 1966; Trivers 1972; Wesolowski 1994). The balance of reproductive costs and benefits can play out in countless ways; there are vast differences among birds in degrees of parental care, ranging from none, in the case of brood parasites and megapodes, to male- or female-only care, to bi-parental care, to cooperative breeding (Cockburn 2006). In addition to parental care, there can also be distinct inter- and intra-specific differences in territoriality and monogamy (Verner 1977; Griffith et al. 2002; Cockburn 2006). As degrees of reproductive investment are so variable, with sexes and ages often investing their time and energy differently during the breeding season, the costs incurred during and after the breeding season may also vary widely.

Reproductive investment may influence birds' feathers both indirectly and directly. First, if an individual finishes reproduction in poor condition, that physiological state may carry-over and influence the quality of feathers produced during the next molt (Dawson 2004). Individuals with high reproductive investment, such as those exhibiting uniparental care, or successful versus unsuccessful breeders, may initiate molt later (Morton and Welton 1973; Hemborg 1999; Mitchell et al. 2012) or molt at a faster rate (Vágási et al. 2012) than other individuals. Feathers grown quickly may be lighter and structurally weaker than feathers grown more slowly

(Dawson et al. 2000; Vágási et al. 2012). Thus, poor feather quality can be a non-lethal cost of reproduction (Nilsson and Svensson 1996). Additionally, stress from reproduction may lead to feathers that contain fault bars, bands of structural deformities with reduced barbule density and strength (King and Murphy 1984; Bortolotti et al. 2002). Fault bars can also be caused by acute stress events during feather growth (Machmer et al. 1992; Jovani and Diaz-Real 2012).

Second, while all feathers wear throughout the year, some activities might cause more feather damage than others, leading to differential wear in summer versus winter or for individuals with different activity budgets (Merilä and Hemborg 2000; Vágási et al. 2011; Flinks and Salewski 2012). Specifically, feather wear can be a direct cost of reproduction if activities that take place during breeding, such as incubating and chick provisioning, cause physical damage to a bird's feathers, leaving the feathers heavily abraded, or broken (Merilä and Hemborg 2000; Flinks and Salewski 2012).

Feather condition is the cumulative result of a feather's initial quality and everything a bird has gone through since the feather was grown. Because fault bars are structural weak points, barbs along the bar may break, altering the vane shape and reducing its area (Sarasola and Jovani 2006). If the fault bar is severe enough, the rachis may also break, truncating the feather (Møller et al. 2009; Jovani et al. 2010). Poor-quality feathers are more susceptible to abrasion than higher quality feathers, due to differences in rachis diameter, barbule density, and feather strength (Dawson 2000).

Because even heavily worn or broken feathers are not replaced until the next molt, feather condition and body condition may feed-back on each other. Poor-condition birds are more likely to grow poor-quality feathers (Vágási et al. 2012), which are more prone to damage

and, once damaged, might reduce flying and thermoregulation efficiency, thus keeping the bird in poor condition (Blanco and de la Puente 2002; Bortolotti et al. 2002). Specifically, smooth, intact feathers enable a bird to function most efficiently in flight, as feather wear reduces lift and drag (Bridge 2009) and decreases energy gain per wing beat (Williams and Swaddle 2003). Wing gaps could occur due to broken feathers, similar to those experienced during molt, and decrease flight efficiency (Chai 1997) and maneuverability, leading to greater risk of predation (Slagsvold and Dale 1996; Swaddle et al. 1996). Low barbule density and other structural deformities also decrease a feather's functionality for thermoregulation (Nilsson and Svensson 1996) and water repellence (Kennedy 1970; Rijke and Jesser 2011).

The aim of this paper was to quantify fault bars and feather wear throughout the annual cycle to better understand how feather quality and condition are influenced by situations that birds experience, particularly during the breeding season. To assess the effects of reproductive investment, I compared flight feather wear and fault bars in adult male and female Saltmarsh (*Ammodramus caudacutus*) and Seaside (*A. maritimus*) sparrows, two species that are closely-related (Klicka et al. 2014), with overlapping breeding and wintering ranges and habitats (Greenlaw and Rising 1994; Post et al. 1994), but which have dramatically different breeding systems. Saltmarsh Sparrows are non-territorial, have extensive male and female multiple-mating, with no pair bonds, and exhibit female-only care of eggs and chicks (Woolfenden 1956; Hill et al. 2010; Shriver et al. 2010; Greenlaw and Post 2012). In contrast, Seaside Sparrows are territorial, socially monogamous, with relatively low rates of extra-pair copulations, and exhibit bi-parental care (Woolfenden 1956; Post and Greenlaw 1982; Marshall and Reinert 1990; Hill and Post 2005). Due to these differences in breeding strategies, male and female Saltmarsh

Sparrows differ greatly in their direct reproductive investment and the activities they engage in during the breeding season: in addition to their gamete contributions, female Saltmarsh Sparrows build nests, incubate eggs, and provision and care for chicks and fledglings, whereas males seek and compete for copulations (Woolfenden 1956; Post and Greenlaw 1982; Greenlaw and Post 2012). In Seaside Sparrows, male and female breeding investments and activities are more similar, although males engage in more territorial defense, and females build nests and incubate eggs alone (Woolfenden 1956; Lockwood et al. 1997).

I tested the following hypotheses and predictions. First, that feather damage increases over time, as feathers become abraded by colliding with airborne particles during flight (Burt 1986) and by hitting against vegetation (Willoughby 1991). Second, because the breeding season involves activities that do not occur during the rest of the year, such as territory defense, nest construction, incubation, and chick provisioning, I expected all adults, regardless of reproductive activities, to have more opportunities for feather abrasion (Flinks and Salewski 2012), and thus greater feather wear, during the breeding than non-breeding season. Third, because females of both species build nests and incubate eggs (Greenlaw and Rising 1994; Post et al. 1994; Lockwood et al. 1997) and molt more quickly than conspecific males (Chapter 3), which has been shown to lead to poorer feather quality in other species (Dawson et al. 2000), I predicted that females of both species will have greater breeding-season feather wear than conspecific males (Flegg and Cox 1975; Francis and Wood 1989; Merilä and Hemborg 2000; Flinks and Salewski 2012). Additionally, because reproductive activities can reduce body condition and increase physiological stress (Hörak et al. 1998; Hörak et al. 1999; Kern et al. 2005; Jakubas et al. 2008), I predicted that females will have more severe and more fault bars

than males. Fourth, as female Saltmarsh Sparrows do all parental care activities alone, including provisioning chicks at the same rate as a pair of Seaside Sparrows (Post and Greenlaw 1982, 2006), I expected female Saltmarsh Sparrows to have greater wear and more severe fault bars than female Seaside Sparrows. Finally, since male Saltmarsh Sparrows do not participate in parental care at all, while male Seaside Sparrows do (Greenlaw and Rising 1994; Post et al. 1994), I expected male Saltmarsh Sparrows will have less breeding season feather wear and fewer fault bars than male Seaside Sparrows.

All adults of both species undergo a complete molt at the end of the breeding season (Pyle 1997), non-breeding habitats for the sexes and species are similar, and often the same, and the winter time budgets for both sexes and species include dispersing into the marshes at low tide, then congregating at dry marsh islands or edges during extreme high tides (A. Borowske personal observation). Consequently, I predicted no differences between sexes or species in flight feather wear during the overwintering period. Alternatively, reproductive investment could carry-over and lead to differential molt timing, rate, and subsequent feather quality (Nilsson and Svensson 1996; Dawson et al. 2000). To test the molt constraint hypothesis, that reproductive investment influences feather quality in the pre-basic molt, I predicted female Saltmarsh Sparrows to have the most feather wear during the winter, followed by female and male Seaside Sparrows and, finally, male Saltmarsh Sparrows. Because heavily worn feathers can decrease flight efficiency (Williams and Swaddle 2003; Bridge 2009), thermoregulation (Wolf and Walsberg 2000), and water repellence (Rijke and Jesser 2011), I further predicted that birds with extensive flight feather wear would also have poorer body condition than birds with less worn feathers.

Finally, I predicted differences in fault bar occurrence and severity in juvenile Saltmarsh and Seaside Sparrows. Although the two species can occur in the same marshes and often build nests meters away from each other (C. S. Elphick unpublished data), they typically construct nests in somewhat different vegetation. On average, Seaside Sparrows nest in areas with more *Spartina alterniflora*, whereas Saltmarsh Sparrows are more likely to nest in areas dominated by *S. patens* (Gjerdrum et al. 2005, 2008a). The nest height off of the ground also differs significantly between species, due, at least in part, to differences in vegetation, as *S. alterniflora* blades are much taller and wider than those of *S. patens*. The bottom of Seaside Sparrow nests in *S. alterniflora* range from an average (mean \pm standard deviation) of 19 ± 4.5 SD to 22 ± 5.5 cm off the ground (Marshall and Reinert 1990), and the bottom of Saltmarsh Sparrow nests sit an average (mean \pm 95% confidence interval) of 12 ± 4 cm off the ground (Humphreys et al. 2007). Due to these differences in nest placement, Saltmarsh Sparrow nests are more likely than Seaside Sparrow nests to flood while chicks are in the nest (Gjerdrum et al. 2005). Because nest flooding forces chicks to either sit in water or temporarily climb out of the nest until the tide drops (Gjerdrum et al. 2008b; Bayard and Elphick 2011), I predicted more severe and more fault bars in juveniles than adults, of both species, and more severe and more fault bars in juvenile Saltmarsh than juvenile Seaside Sparrows.

METHODS

Mist-netting: I captured adult and juvenile Saltmarsh and Seaside Sparrows in mist-nets on the breeding grounds in Connecticut (CT) and, with help of a collaborator, in New Jersey in 2012 and 2013, and on the non-breeding grounds in Florida (FL), Georgia (GA), North Carolina (NC),

and South Carolina (SC) during winters 2012-2013 and 2013-2014. The breeding sites were located within the East River Marsh (Madison, CT, 41°16'19.49"N, 72°39'9.97"W), Hammonasset State Park (Madison, CT, 41°15'39.63"N, 72°32'57.96"W), Barn Island Wildlife Management Area (Stonington, CT, 41°20'15.10"N, 71°52'7.05"W), Manahawkin Wildlife Management Area, (Manahawkin, NJ, 39°42'0.13"N, 74°12'50.21"W), Mullica Wilderness Area (Batsto, NJ, 39°32'15.15"N, 74°26'22.57"W), and Edwin B. Forsythe National Wildlife Refuge (Galloway, NJ, 39°30'20.30"N, 74°25'38.14"W). The non-breeding sites were located within Fort Macon State Park (Atlantic Beach, NC, 34°41'53.60"N, 76°41'5.81"W), Huntington Beach State Park (Murrell's Inlet, SC, 33°31'15.98"N, 79° 3'3.79"W) and the North Inlet-Winyah Bay National Estuarine Research Reserve (Georgetown, SC, 33°20'19.32"N, 79°11'16.66"W), public land along the causeway to Jekyll Island (Brunswick, GA, 31° 6'26.71"N, 81°29'15.78"W), Big and Little Talbot Island State Parks (near Jacksonville, FL, 30°27'45.06"N, 81°25'42.47"W), Timucuan Ecological and Historical Preserve (30°27'18.58"N, 81°27'9.60"W), and Faver-Dykes State Park (near St. Augustine, FL, 29°42'10.64"N, 81°14'44.33"W).

On the breeding grounds, netting took place between April and October. Each bird was identified to species and age (by plumage or skull ossification), and visually sexed by the presence of a brood patch (female) or enlarged cloaca (male). On the non-breeding grounds, netting took place between December and March. For birds that could not be sexed visually on the breeding grounds, and all birds on the non-breeding grounds, I collected a feather sample for genetic sexing by pulling up to two rectrices or breast feathers and/or collecting feathers that dropped during handling. I banded each bird, took standard measurements, including tarsus length, and weighed each bird using a Pesola scale, to the nearest 0.1 g. I took three

photographs of each bird: one of the spread primaries of the right wing, one of the spread secondaries and tertials of the right wing, and one of the spread rectrices. I took all photos against a whiteboard as a standard backdrop, and under an umbrella to standardize shade.

Body Condition: I used structural measurements to calculate a scaled mass index (SMI) for each individual as a body condition proxy, following the method of Peig and Green (2009) (Chapter 3, Appendix C). I assessed the correlation between each structural measurement and mass and the fit with standardized major axis (SMA) regression using the R package *smatr* (Warton et al. 2012). I selected tarsus length as the structural measurement for SMI calculations because it correlated most strongly and consistently with mass, and had the best SMA regression fit. I used mass and tarsus data from winter male and female Saltmarsh and Seaside Sparrows combined to calculate a scaling coefficient for individual SMI calculations. I selected winter birds as opposed to breeding birds because breeding females carry egg mass during laying, which would increase mass variation in a manner unrelated to condition. Also, my captures on the breeding grounds ranged from May to October, and relationships between mass and body size fluctuate during this time more than during my winter sampling period due to post-migratory fat depletion and pre-migratory fuel loading (Barboutis et al. 2013; Kobylkov et al. 2014). I combined sexes and species because, during the winter, the SMA slopes between mass and tarsus for these four categories of birds were not significantly different (likelihood ratio statistic = 0.6701; df = 1, p = 0.413).

Genetic Sexing: I extracted DNA from 2 rectrices or 2-6 breast feathers (Segelbacher 2002), using NucleoSpin Tissue DNA extraction kits (Macherey-Nagel, Duren, Germany). I amplified the

DNA according to Griffiths et al. (1998). This process involves a single PCR with gender primers P2 and P8, which were designed to amplify sections of two avian sex genes, CHD-W, which is only present in females, and CHD-Z, which is present in males and females (Griffiths et al. 1998). I confirmed the method's accuracy with six males and six females from my study sites that had been visually sexed in the field by the presence of a brood patch (female) or enlarged cloaca (male). Following amplification, I resolved the samples on 1.5% agarose gels and determined the sex identifications based on the presence of one (male) or two (female) bands.

Feather Scoring: Using the photographs I took in the field, I had each primary, secondary, tertial, and rectrix scored for wear, breaks, and the number and severity of fault bars. All scoring was done by the same person (C. Roberts). I evaluated feather wear and fault bar data from 904 Saltmarsh Sparrows (474 adult males, 182 adult females, and 248 juveniles) and 236 Seaside Sparrows (118 adult males, 70 adult females, and 48 hatch-years) during the breeding season and 119 Saltmarsh Sparrows (117 males and 82 females) and 185 Seaside Sparrows (99 males and 86 females) during the winter. For each feather, I noted if it was missing or broken completely across the rachis. If the feather was present and unbroken, I scored it for feather wear on a 0-5 scale: 0 = vane edges smooth with all barbs and barbules intact; 1 = some shallow notches in the vane due to broken barbs; 2 = some deep notches in the vane with a few barbs broken at the rachis; 3 = vane edges ragged, with many broken barbs; 4 = large sections of vane missing, with many barbs broken at the rachis; 5 = vane missing and frayed along most of the rachis (Appendix C). On each unbroken feather, I counted the number of fault bars. If at least one fault bar was present, I looked at the most prominent bar on the feather and scored its

severity: 1 = fault bar is in only one vane and is not associated with broken barbs; 2 = fault bar crosses the rachis, but no barbs are broken; 3 = fault bar is associated with a break in barbs along at least part of the bar (Appendix C). For birds that were molting ($n = 17$), I treated new or partially-grown feathers as missing, so as to not bias the scores. For each bird, I calculated the following: total number of missing feathers, total number of broken feathers, mean feather wear score across unbroken feathers, total number of fault bars on unbroken feathers, and cumulative fault bar severity score across unbroken feathers. For the number of broken feathers and mean wear, I calculated values for the remiges and rectrices separately.

Statistical Analyses: I used ordinal day as a proxy for feather age during each season. For the breeding season, I set day 0 to 1 May. For the analyses of feather wear and breaks, I only used birds that were caught before 1 September, to include the entire breeding season, but to also avoid individuals with large numbers of new or molting feathers. For the wintering season, I set day 0 to 1 Oct to represent an approximate molt-completion date (A. Borowske unpublished data; Chapter 3). Because I had data from two breeding and two winter seasons, I used year as a categorical variable to test for differences between the four field seasons. In all analyses, I used data from only the first encounter of each individual.

To describe trends in feather damage over time, and to compare trends for male and female Saltmarsh and Seaside Sparrows during the breeding and winter seasons, I used generalized additive models with cubic regression splines via the gam function in the package mgcv (Wood 2006) in R 3.1.1 (R Core Team 2014). I ran four separate analyses for mean feather wear and cumulative number of broken feathers in remiges and rectrices. The base models for

mean feather wear included year, state, and a smoother for day (as a proxy for feather age). To analyze patterns in the number of broken feathers, I used zero-inflated Poisson models, due to the large number of birds with only intact feathers. The base models for the number of broken feathers included a smoother for day, the number of missing feathers, year, and state. For each set of analyses, I compared the base model to seven others, each of which had a different categorical factor specified with the “by” argument to indicate the number of smoothers and the categories by which the smoothing took place. The categorical factors were also included in the models outside the smoothed terms to enable both the intercept and the shape of the smoother to vary according to the categories (Wood 2006). Alternative models specified: 1) separate smoothers by season, to test the prediction of greater damage during breeding than winter; 2) separate smoothers by sex, to test the prediction that females have greater damage than males; 3) separate smoothers by species, to test the prediction that damage differs between the species; 4) separate smoothers by sex and species, to test the prediction that each sex of each species has a unique degree of damage; 5) separate smoothers by sex and season, to test the prediction that the sexes have different degrees of damage during breeding and winter; 6) separate smoothers by sex, season, and species, to test the prediction that each sex of each species has unique degrees of damage during both seasons; 7) separate smoothers for each sex and species during the breeding season, but one smoother for all winter birds combined, to test the prediction that winter birds have equal damage, but breeding birds’ damage varies by sex and species. I did not have a priori hypotheses relating SMI specifically to season, sex, or species, but I predicted that birds with greater degrees of feather damage would have lower SMI values. Therefore, for each of these eight models, I also fit a version that

included SMI as a factor. I compared the 16 models in each set via AIC_c scores using the `AICcTab` function in the R package `bbmle` (Bolker 2014).

To assess patterns in fault bar number and severity, I fit zero-inflated Poisson generalized linear mixed models in the `glmmADMB` package (Skaug et al. 2006) in R. To test the predictions that juveniles have more severe and more fault bars than adults during the breeding season, and that juvenile Saltmarsh Sparrows have more severe and more fault bars than juvenile Seaside Sparrows, I ran a set of analyses on individuals from the breeding season only. The models for cumulative fault bar number included the number of feathers that were not scored because they were missing or broken. Similarly, models for cumulative fault bar severity included the number of feathers that contained fault bars. Every model included random effects of year and state. I used AIC_c scores to compare the base models to four other models: 1) the inclusion of species; 2) the inclusion of age; 3) the inclusion of age and species; 4) the inclusion of age, species, and an age*species interaction. To test the prediction that reproductive investment influences fault bars, I ran a second set of analyses on only winter birds. These birds were all genetically sexed, but could not be aged reliably. The structure of this analysis was the same as for the breeding season birds, except that the factor age was replaced by sex.

RESULTS

As predicted, flight feather damage generally increased over time (Figures 1 and 2). Also as predicted, wear was greater during breeding than winter for remiges and rectrices of both species and sexes (Figure 1 A and D). The top models for both remige and rectrix wear fit

separate smoothers for each sex of each species during the breeding season, and a smoother for all winter birds combined (Table 1). The top models for broken remiges and rectrices fit separate smoothers for each sex and species, regardless of season (Table 2). However, some candidate models in the analyses of broken remiges and rectrices failed to converge. In all feather damage analyses, model performance was improved by the inclusion of SMI (Tables 1 and 2). However, the partial effects of SMI were consistently close to zero (Tables 3 and 4).

Contrary to prediction, breeding females did not have consistently more feather damage than breeding males in either species. In fact, the only variable for which breeding females had notably more feather damage than males was broken rectrices in female Saltmarsh Sparrows: although the number of breaks was lower than that for male Saltmarsh Sparrows early in the summer, it increased to higher values later in the season (Figure 2C). In the middle of the breeding season, breeding male Saltmarsh Sparrows had greater remige wear and more broken remiges than female Saltmarsh Sparrows, although the rate of female remige wear increased more dramatically by the end of the summer (Figures 1B and 2A). In Seaside Sparrows, the patterns and degrees of remige and rectrix damage were similar in males and females (Figures 1C and F, 2B and D).

Female Saltmarsh Sparrows showed more breeding season feather damage than female Seaside Sparrows. Early in the season, greater wear and more breaks were visible in Seaside Sparrows, but over time both the rate and final degree of wear (Figure 3A) and the greatest number of breaks (Figures 4A and C) were in Saltmarsh Sparrows. In contrast, there was little support for my hypothesis that breeding male Saltmarsh Sparrows would have less feather

damage than breeding male Seaside Sparrows (Figures 3B and D), although they did have more broken remiges by the later half of the summer (Figure 4B).

As predicted, juveniles of both species had more fault bars than adults of either species (Table 5, Figure 5). There was, however, no evidence that the number of fault bars differed between juvenile Saltmarsh and Seaside Sparrows. In contrast, the top model for fault bar severity included both age and species (Table 5), and suggested that Seaside Sparrows have more severe fault bars than Saltmarsh Sparrows (Table 6). Juveniles of the two species had nearly identical rates of fault bar occurrence, with 66% (164/248) of juvenile Saltmarsh and 67% (32/48) of juvenile Seaside Sparrows having at least one fault bar. During the breeding season, the fault bar occurrence rate for adults was 44% (80/182) for female Saltmarsh Sparrows, 37% (175/474) for male Saltmarsh Sparrows, 43% (30/70) for female Seaside Sparrows, and 40% (47/118) for male Seaside Sparrows.

I found mixed evidence that fault bar number and severity in birds caught on the wintering grounds is related to reproductive investment. The top model for fault bar number included sex, species, and the sex*species interaction (Tables 5 and 6). In Saltmarsh Sparrows, the fault bar occurrence rate was higher for females (66%; 54/82) than for males (54%; 47/86), with similar occurrence rates for female (63%; 74/117) and male (64%; 63/99) Seaside Sparrows. Contrary to prediction, the top model for fault bar severity only included species, and there was no evidence for differences between sexes (Tables 5 and 6, Figure 6).

DISCUSSION

Both the seasonal differences in feather damage and the effects of sex and species within the breeding season support the hypothesis that birds' activities, particularly activities that occur only in the breeding season, influence the condition of their feathers. Moreover, my data suggest that costs are incurred by both males and females, and that there are no carry-over effects from the breeding season leading to differential feather damage during the winter. As the activities that birds engage in vary predictably throughout the annual cycle (Wingfield 2008; Newton 2011), it is unsurprising that season emerged as an important factor influencing feather condition.

Within the breeding season, feather damage may be a direct consequence of reproductive investment. The exact causes of feather damage are not straightforward, however, but when damage occurred and the nature of the damage can give insights into possible sources. Contrary to prediction, males generally had more remige damage than females. This difference was more pronounced in Saltmarsh Sparrows, but only until later in the season, when damage increased in females. These patterns suggest that males may abrade and break their wing feathers early in the season, when there is strong competition for territories and/or mates, while females accumulate remige wear over the course of the breeding season, with an increased rate of deterioration toward the end of the summer. Feather damage also may be associated with an individual's number of nesting attempts, (Merilä and Hemborg 2000), and can be an indicator of poor-quality individuals (Fitzpatrick and Price 1997; Rohwer et al. 2011).

Greater feather damage in female Saltmarsh Sparrows than in conspecific males and female Seaside Sparrows supports the hypothesis that they pay a particularly high cost of reproductive investment. Over the breeding season, female Saltmarsh Sparrows had greater rates of remige damage and more broken remiges and rectrices than male Saltmarsh or, especially, female Seaside Sparrows. For instance, my dataset included 11 individuals with 5 or more broken rectrices; all were breeding females, and all but one were Saltmarsh Sparrows. Male Saltmarsh Sparrows also had higher levels of remige and rectrix wear, and more broken remiges than male Seaside Sparrows. One explanation for these patterns is that differences in copulatory roles may lead to differential feather damage among the sexes and species. Saltmarsh Sparrow mating has been described as scramble competition polygamy, and can include aggression and potentially forced copulations (Greenlaw and Post 2012). As similarly aggressive interactions and copulations are not typical in Seaside Sparrows, these behavioral differences between the species could cause the high level of tail damage that I observed in female Saltmarsh Sparrows. For males, frequent, agonistic copulations and within-sex aggression could contribute to high levels of remige damage from quite early in the summer.

I found low levels of wear and breaks in the winter compared to the summer, suggesting, that most feather damage takes place during the breeding season (see also Francis and Wood 1989; Vágási et al. 2011; Flinks and Salewski 2012). In addition to the influence of season-specific activities, feather age could contribute to seasonal differences in feather damage. During the winter, flight feathers of all Saltmarsh and Seaside Sparrows are approximately the same age, but the number of flight feathers that individual Saltmarsh and Seaside Sparrows renew during their pre-alternate molts vary widely: some individuals retain all

flight feathers, and others molt one-to-all remiges and/or rectrices (Pyle 1997). While I was not able to age feathers precisely during the breeding season, there is evidence that feathers wear at a faster rate once the tips are abraded than they do initially (Flinks and Salewski 2012). If, however, the pre-alternate molt in these species is a preventative adaptation against feather wear, as has been suggested in species that do not undergo distinct plumage changes (Willoughby 1991; Jenni and Winkler 1994), the feathers replaced during the pre-alternate molt may be the ones most prone to damage.

For all individuals, the types of feather damage that I observed may reduce fitness. For instance, Merilä and Hemborg (2000) found that Collared Flycatchers (*Ficedula albicollis*) with heavily worn feathers were less likely to survive until the next breeding season. Although extreme tail damage (i.e. all rectrices broken) is rare, even in female Saltmarsh Sparrows, this degree of damage could have significant consequences. Tails are important for balancing and stabilizing birds in flight (Tucker 1992; Sachs 2007). They also increase agility by acting as a rudder and generating lift during turns (Thomas 1997), and increase flight efficiency at low speeds (Thomas 1996). Feather damage, including wear, can reduce take-off speed and decrease maneuverability (Slagsvold and Dale 1996; Swaddle et al. 1996). Feather damage from lice has also been associated with reduced body condition and survival, although it is difficult to determine whether the poor feather condition contributes to poor body condition and reduced chance of survival or whether individuals that are already in poor condition are more susceptible to parasites (Pap et al. 2005). Feather damage could also decrease thermoregulatory efficiency.

During the breeding season, juveniles had more numerous and more severe fault bars than adults. This pattern has been observed in a range of species, including Hooded Crows (*Corvus corone cornix*) (Slagsvold 1982), Black-billed Magpies (*Pica pica*) (Blanco and de la Puente 2002), White Storks (*Ciconia ciconia*) (Jovani and Blas 2004), and House Sparrows (*Passer domesticus*) (Leloutre et al. 2014). The intense period of growth during chick development (Ricklefs 2008), coupled with the extensive post-fledging molts found in many species, leads to the prediction that all juveniles are more prone to fault bars than conspecific adults (Leloutre et al. 2014). However, an analysis of fault bar occurrence in more than 50 species found no evidence for a general pattern of increasing fault bar occurrence in juveniles compared to adults (Møller et al. 2009). This lack of a ubiquitous pattern suggests that species- or scenario-specific explanations of age-based patterns of fault bar occurrence must exist. Despite a consensus that fault bars are the result of stress during feather growth, the exact causes are unknown. Experiments suggest that food deprivation does not correlate with fault bar occurrence (King and Murphy 1984; Negro et al. 1994; Witter and Lee 1995), while human handling during feather growth can (King and Murphy 1984; Machmer et al. 1992; Negro et al. 1994); but this does not explain the occurrence of fault bars in birds that were never handled during molt. My results suggest that some sort of stress experienced only by juveniles leads to the formation of fault bars in these species. Tidal flooding is a likely source of stress for young tidal marsh sparrows that could cause fault bars in both species.

I found that female Saltmarsh Sparrows had more fault bars than conspecific males; other studies have also found that females have more fault bars than males (Slagsvold 1982; Bortolotti et al. 2002) and have suggested links between fault bar prevalence and poor body

condition, reduced likelihood of breeding, and reduced probability of survival in both sexes (Bortolotti et al. 2002). Nonetheless, the mechanism linking long-term energetic stress, such as that experienced during breeding, with the formation of fault bars is unknown. Combined evidence from an experiment on chronic stress versus recurrent acute stress, and a study on both fault bars and growth bands suggests that fault bars are due to acute rather than chronic stress (Strochlic and Romero 2008; Jovani and Diaz-Real 2012). There is also evidence, however, for a link between fault bar prevalence and bacterial infection, suggesting that birds in poor physiological condition may be more susceptible to the external stressors behind fault bars (Jovani et al. 2014). If stress from reproduction contributes to the formation of fault bars, it is likely to be by reducing an individual's condition so that it is more susceptible to other, acute, stressors than it otherwise may have been.

It is clear that a bird's activities during the breeding season can have a significant impact on its feathers, and my results suggest that both reproductive investment and a bird's age can play a role. Feather damage can result both from long-term cumulative effects of abrasion, and from isolated events. The precise activities that a bird engages in, and when and where those activities take place, influence the degree to which its feathers are exposed to highly abrasive surfaces and/or to damage-inducing events. These factors, coupled with the base strength of the feathers, as determined by color, quality, bacterial load, and age, combine to determine how damaged—or how well-maintained—an individual's feathers are at any particular point in the annual cycle.

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Table 1: AIC_c score comparisons for two sets of generalized additive models: A) wear per remige and B) wear per rectrix. The base models fit a smoother for day, and included effects of year and state. Alternative models differed in the number of smoothers to test for differences between species, sexes, and seasons, and in whether or not they included scaled mass index (SMI). The model descriptions indicate the categories by which smoothers were fit. Where smoother names are abbreviated, SALS refers to Saltmarsh Sparrow, SESP to Seaside Sparrow, F refers to female, M to male, B to breeding season, and W to winter.

A) Wear per remige	ΔAIC_c	df	w
All winter birds, SALSFB, SALSMB, SESPFB, SESPMB; SMI	0	34.7	0.998
SALSFB, SALSMB, SESPFB, SESPMB, SALSFW, SALSMW, SESPFW, SESPMW; SMI	12.9	37.9	0.002
Female Breeding, Male Breeding, Female Winter, Male Winter; SMI	80.3	31.1	<0.001
SALSF, SALSM, SESP, SESP; SMI	105.0	34.4	<0.001
Breeding, Winter; SMI	124.2	20.3	<0.001
SALS, SESP; SMI	127.3	24.1	<0.001
All winter birds, SALSFB, SALSMB, SESPFB, SESPMB	155.0	33.9	<0.001
SALSFB, SALSMB, SESPFB, SESPMB, SALSFW, SALSMW, SESPFW, SESPMW	169.7	37.1	<0.001
Female, Male; SMI	191.5	23.4	<0.001
Base model + SMI	203.1	17.8	<0.001
Female Breeding, Male Breeding, Female Winter, Male Winter	229.1	30.3	<0.001
SALSF, SALSM, SESP, SESP	241.8	31.8	<0.001
SALS, SESP	263.8	22.9	<0.001
Breeding, Winter	272.7	19.1	<0.001
Female, Male	323.0	22.4	<0.001
Base model	336.2	14.8	<0.001
B) Wear per rectrix			
SALSFB, SALSMB, SESPFB, SESPMB, SALSFW, SALSMW, SESPFW, SESPMW; SMI	0	37.8	0.71
All winter birds, SALSFB, SALSMB, SESPFB, SESPMB; SMI	1.8	29.3	0.29
SALSFB, SALSMB, SESPFB, SESPMB, SALSFW, SALSMW, SESPFW, SESPMW	49.6	33.7	<0.001
All winter birds, SALSFB, SALSMB, SESPFB, SESPMB	56.8	28.2	<0.001
SALSF, SALSM, SESP, SESP; SMI	78.2	30.9	<0.001
SALS, SESP; SMI	95.8	20.0	<0.001
Female Breeding, Male Breeding, Female Winter, Male Winter; + SMI	110.4	24.1	<0.001
SALSF, SALSM, SESP, SESP	131.5	30.3	<0.001

Breeding, Winter; SMI	146.3	14.7	<0.001
SALS, SESP	152.0	19.2	<0.001
Female Breeding, Male Breeding, Female Winter, Male Winter	173.8	22.9	<0.001
Female, Male; SMI	181.6	19.4	<0.001
Base model + SMI	189.1	14.3	<0.001
Breeding, Winter	211.6	13.7	<0.001
Female, Male	244.5	18.6	<0.001
Base model	252.0	13.4	<0.001

Table 2: AIC_c score comparisons for two sets of zero-inflated Poisson generalized additive models: total number of broken remiges and total number of broken rectrices. In each analysis, the base model fit a smoother for day, and included effects of year and state. Alternative models differed in the number of smoothers to test for differences between species, sexes, and seasons, and in whether or not they included scaled mass index (SMI). Models that failed to converge are not shown. The model descriptions indicate the categories by which smoothers were fit. Where smoother names are abbreviated, SALS refers to Saltmarsh Sparrow, SESP to Seaside Sparrow, F refers to female, M to male, B to breeding season, and W to winter

A) Number of broken remiges	ΔAIC_c	df	w
SALSF, SALSM, SESPF, SESPM; SMI	0	23.2	1
SALS, SESP; SMI	13.9	17.2	<0.001
Base model + SMI	43.0	10.0	<0.001
Female, Male; SMI	93.2	12.0	<0.001
SALSF, SALSM, SESPF, SESPM	123.9	19.4	<0.001
SALSFB, SALSMB, SESPF, SESPM, SALSFW, SALSMW, SESPF, SESPMW	135.7	27.0	<0.001
SALS, SESP	150.3	12.3	<0.001
Female Breeding, Male Breeding, Female Winter, Male Winter	169.3	19.2	<0.001
Base model	202.8	11.8	<0.001
Female, Male	218.0	13.5	<0.001
B) Number of broken rectrices			
SALSF, SALSM, SESPF, SESPM; SMI	0	22.9	0.851
All winter birds, SALSFB, SALSMB, SESPF, SESPM; SMI	4.1	24.4	0.110
Female, Male; SMI	6.2	21.9	0.039
Female Breeding, Male Breeding, Female Winter, Male Winter	25.1	23.2	<0.001
SALSF, SALSM, SESPF, SESPM	25.6	21.5	<0.001
All winter birds, SALSFB, SALSMB, SESPF, SESPM	27.6	23.4	<0.001
Female, Male	30.1	20.8	<0.001
Base model + SMI	61.0	12.7	<0.001
SALS, SESP; SMI	61.7	16.6	<0.001
Breeding, Winter	86.3	12.0	<0.001
Base model	90.5	12.6	<0.001
Breeding, Winter; SMI	90.7	12.9	<0.001
SALS, SESP	91.4	15.3	<0.001

Table 3: Results from the best-supported generalized additive models for mean remige and mean rectrix wear. Each model fit separate smoothers for all winter birds, female Saltmarsh Sparrows in the breeding season (SALSFB), male Saltmarsh Sparrows in the breeding season (SALSMB), female Seaside Sparrows in the breeding season (SESPFB) and male Seaside Sparrows in the breeding season (SESPMB) and included effects of scaled mass index (SMI). All candidate models also included effects of year and state. Edf stands for effective degrees of freedom and is a measure of the degree of ‘wiggleness’ of the fit.

Wear per remige	estimate	Standard error	T	Pr(> t)	edf	F	p-value
All winter birds; SALSFB, SALSMB, SESPFB, SESPMB, SMI; 48.1% deviance explained							
All winter birds (intercept)	0.47	0.095	4.93	<0.001	4.78	3.35	0.005
SALSFB	0.20	0.097	2.01	0.045	5.62	11.15	<0.001
SALSMB	0.25	0.089	2.77	0.006	3.08	95.06	<0.001
SESPFB	0.34	0.110	3.11	0.002	5.40	3.36	0.002
SESPMB	0.27	0.099	2.75	0.006	3.84	4.10	0.002
SMI	-0.0002	0.001	-0.21	0.836			
Wear per rectrix	estimate	Standard error	T	Pr(> t)	edf	F	p-value
All winter birds; SALSFB, SALSMB, SESPFB, SESPMB, SMI; 51.3% deviance explained							
All winter birds (intercept)	1.07	0.116	9.23	<0.001	2.44	5.26	0.001
SALSFB	0.35	0.096	3.68	<0.001	1.00	82.89	<0.001
SALSMB	0.46	0.108	4.29	<0.001	4.39	90.19	<0.001
SESPFB	0.87	0.119	7.29	<0.001	2.78	16.96	<0.001
SESPMB	0.66	0.512	1.29	0.197	6.68	6.18	<0.001
SMI	-0.007	0.030	-2.28	0.023			

Table 4: Results from the best-supported zero-inflated Poisson generalized additive models for the total numbers of broken remiges and rectrices. Each model fit separate smoothers for female Saltmarsh Sparrows (SALSF), male Saltmarsh Sparrows (SALSM), female Seaside (SESPF) and male Seaside Sparrows (SESPM), regardless of season, and included effects of scaled mass index (SMI). All candidate models also included effects of year and state. Edf stands for effective degrees of freedom and is a measure of the degree of ‘wiggleness’ of the fit.

Top model							
Broken remiges	estimate	Standard error	z	Pr(> z)	edf	Chi sq.	p-value
SALSF, SALSM, SESPF, ESPM, SMI; 45.2% deviance explained							
SALSF (intercept)	-9.48e-01	4.98e-01	-1.91	0.056	1.08	20.95	<0.001
SALSM	2.02e-01	3.45e-01	0.61	0.545	5.63	52.20	<0.001
SESPF	1.09e+00	3.68e-01	4.07	<0.001	1.46	0.47	0.746
SESPM	1.24e+00	2.58e-01	4.80	<0.001	1.01	3.77	0.054
SMI	1.48e-02	1.12e-02	1.32	0.187			
Broken rectrices	estimate	Standard error	z	Pr(> z)	edf	Chi sq.	p-value
SALSF, SALSM, SESPF, ESPM, SMI; 45.3% deviance explained							
SALSF (intercept)	2.56	0.77	3.31	<0.001	3.13	39.55	<0.001
SALSM	-2.77	0.55	-5.01	<0.001	2.31	2.19	0.523
SESPF	0.52	0.32	1.59	0.111	1.00	10.46	0.001
SESPM	-0.66	0.45	-1.45	0.146	1.00	21.86	<0.001
SMI	-0.03	0.02	-1.30	0.193			

Table 5: AIC_c score comparisons for four sets of zero-inflated Poisson generalized linear mixed models for A) fault bar number during the breeding season; B) fault bar severity during the breeding season; C) fault bar number during the winter; D) fault bar severity during the winter. The breeding season analyses assessed effects of age, species, and their additive and interactive effects. The winter analyses assessed effects of sex, species, and their additive and interactive effects. All candidate models included effects of year and state.

A) Number of fault bars—breeding season	ΔAIC_c	df	w
Age	0	6	0.53
Age + species	1.0	7	0.33
Age + species + age*species	2.5	8	0.15
Species	56.5	6	<0.001
Base model	56.7	5	<0.001
B) Cumulative Severity of fault bars—breeding season	ΔAIC_c	df	w
Age + species	0	7	0.482
Age + species + age*species	1.3	8	0.250
Age	2.5	6	0.137
Species	3.2	6	0.097
Base model	5.3	5	0.033
C) Number of fault bars—winter	ΔAIC_c	df	w
Sex + species + sex*species	0	8	0.85
Species	3.6	6	0.14
Sex	14.5	6	<0.001
Base model	14.5	5	<0.001
Sex + species (did not converge)	-	-	-
D) Cumulative severity of fault bars—winter	ΔAIC_c	df	w
Species	0	6	0.539
Sex + species	1.3	7	0.279
Sex + species + sex*species	2.6	8	0.147
Base model	6.3	5	0.024
Sex	7.8	6	0.011

Table 6: Results from the best-supported zero-inflated Poisson generalized linear mixed models for fault bar number and severity during the breeding and winter seasons. The top model for fault bar number in the breeding season included the effects of age. The top model for breeding season fault bar severity included effects of age and species. The top model for winter fault bar number included sex and species. The top model for winter fault bar severity included effects of species. Each model also included effects of year and state.

Breeding season FB number	estimate	Standard error	Z	Pr(> z)
Adult (intercept)	0.12	0.30	0.39	0.69
Juvenile	0.54	0.07	7.56	<0.001
Breeding season FB severity				
Adult (intercept)	-0.23	0.12	-1.97	0.049
Juvenile	0.12	0.05	2.29	0.022
SESP	0.15	0.07	2.16	0.031
Winter FB number				
Female (intercept)	1.28	0.18	7.01	<0.001
Male	-0.03	0.12	-0.26	0.797
SESP	-0.16	0.14	-1.08	0.281
Male*SESP	-0.43	0.20	-2.14	0.032
Winter FB severity				
SALS (intercept)	-0.10	0.11	-0.91	0.363
SESP	0.22	0.08	2.90	0.004

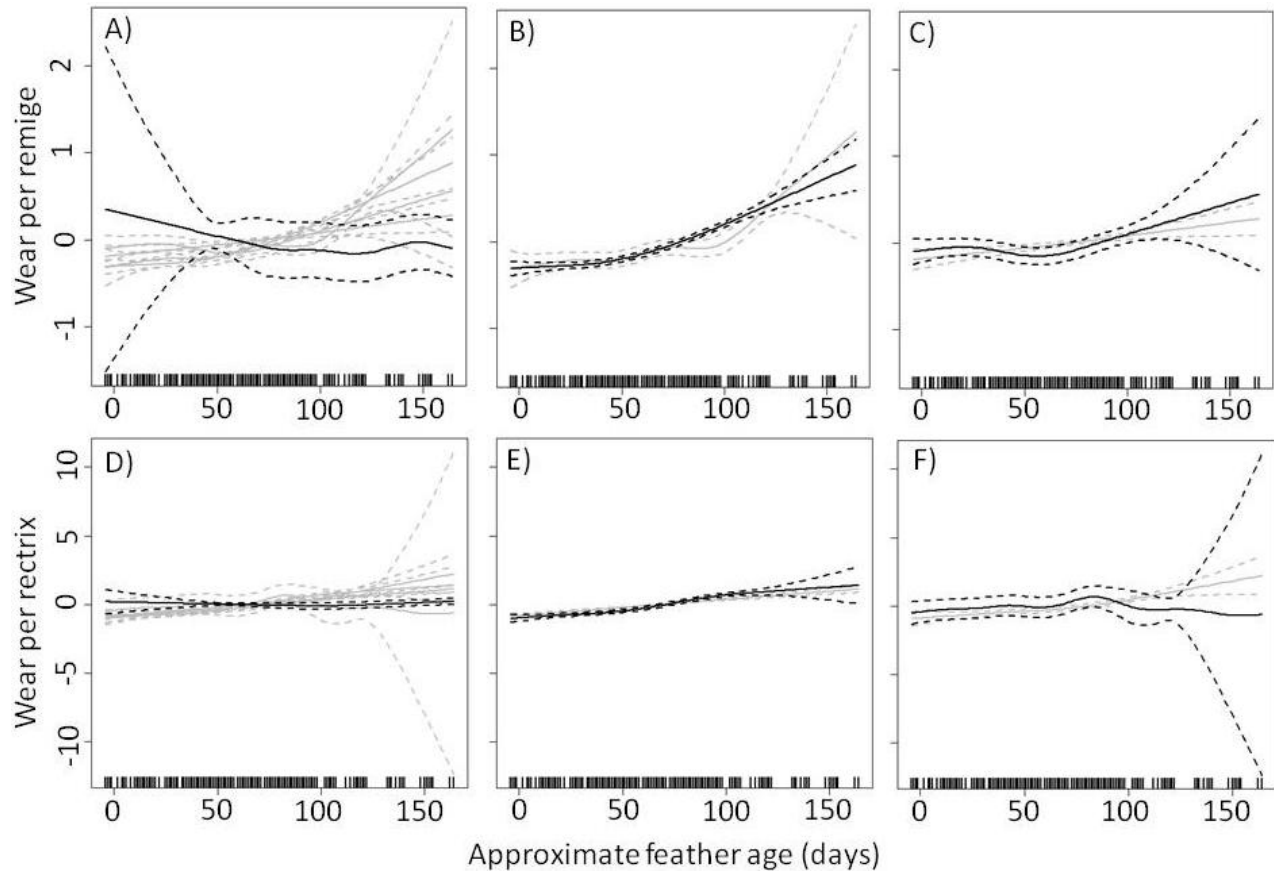


Figure 1: Estimates of feather damage for remiges (A-C) and rectrices (D-F) from a GAM with approximate feather age (in days) as the smoothed term. In each analysis, the best supported model included five separate smoothers: 1) all winter birds, 2) breeding female Saltmarsh, 3) breeding male Saltmarsh, 4) breeding female Seaside, and 5) breeding male Seaside Sparrows. A and D depict the smoothers for winter birds (black) over the separate smoothers for the four classes of breeding birds (gray). B and E depict the smoothed curves for female (gray) and male (black) Saltmarsh Sparrows. C and F depict the smoothed curves for female (gray) and male (black) Seaside Sparrows. The component curves are plotted without intercepts, so they are centered at 0.

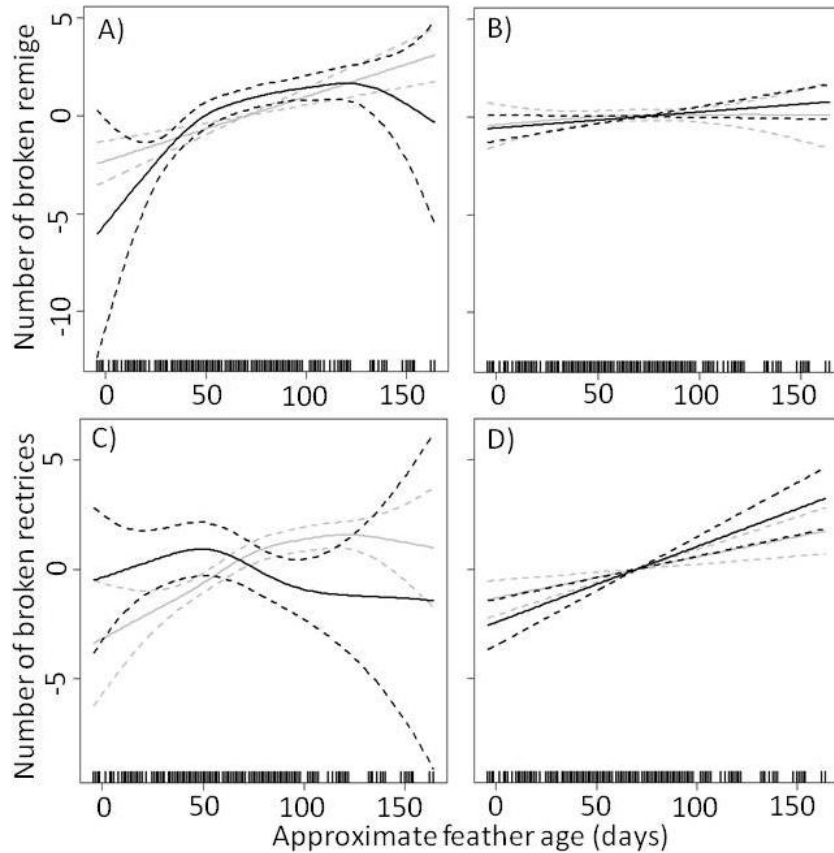


Figure 2: Estimates of the number of broken remiges (A and B) and rectrices (C and D) from a GAM with approximate feather age (in days) as the smooth term. In each analysis, the best supported model included four separate smoothers: 1) female Saltmarsh, 2) male Saltmarsh, 3) Seaside, and 4) male Seaside Sparrows. A and C depict the smooth curves for female (gray) and male (black) Saltmarsh Sparrows. B and D depict the smooth curves for female (gray) and male (black) Seaside Sparrows. The component curves are plotted without intercepts, so they are centered at 0.

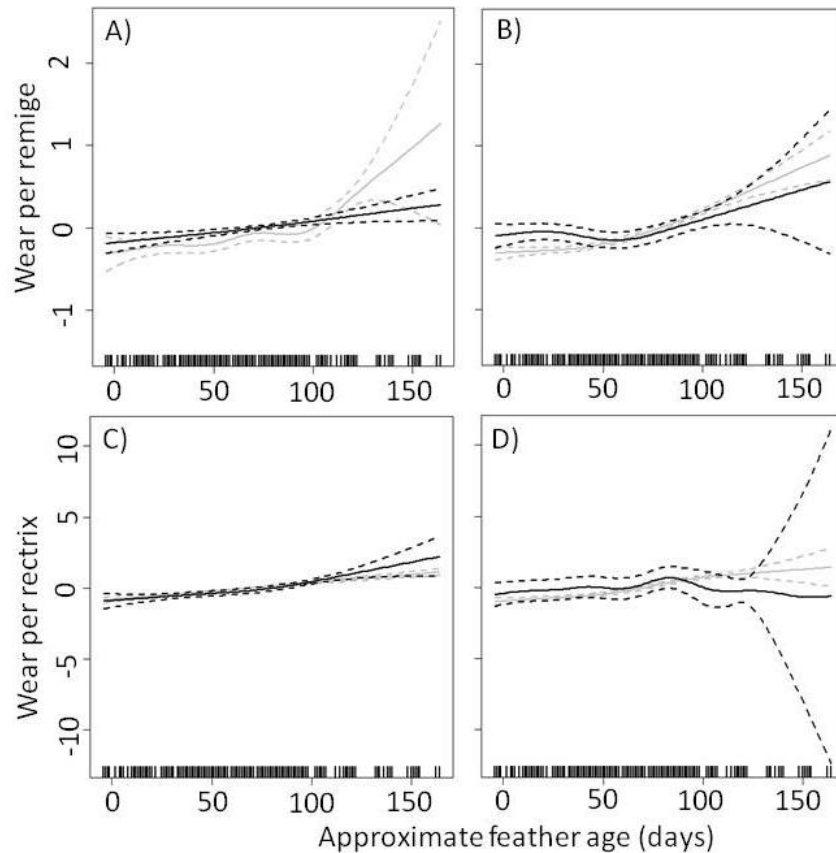


Figure 3: Estimates of feather damage for remiges (A and B) and rectrices (C and D) from a GAM with approximate feather age (in days) as the smooth term. These curves are repeats from Figure 1. Here, A and C depict the smooth curves for female Saltmarsh (gray) and female Seaside (black) Sparrows. B and D depict the smooth curves for male Saltmarsh (gray) and male Seaside (black) Sparrows. The component curves are plotted without intercepts, so they are centered at 0.

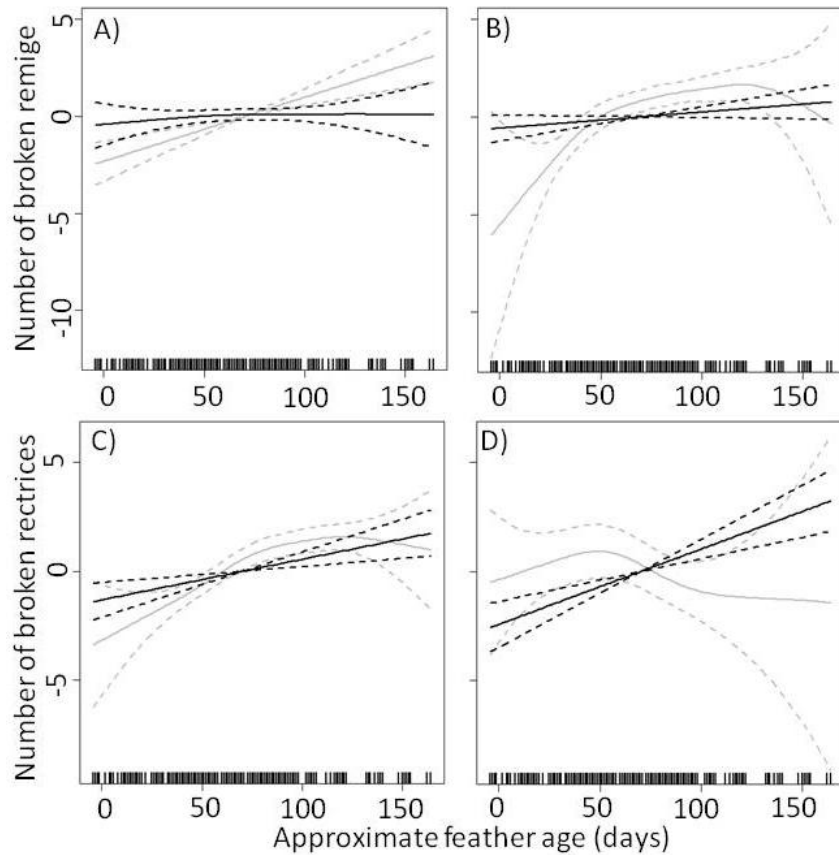


Figure 4: Estimates of the number of broken remiges (A and B) and rectrices (C and D) from a GAM with approximate feather age (in days) as the smooth term. These curves are repeats from Figure 2. Here, A and C depict the smooth curves for female Saltmarsh (gray) and female Seaside (black) Sparrows. B and D depict the smooth curves for male Saltmarsh (gray) and male Seaside (black) Sparrows. The component curves are plotted without intercepts, so they are centered at 0.

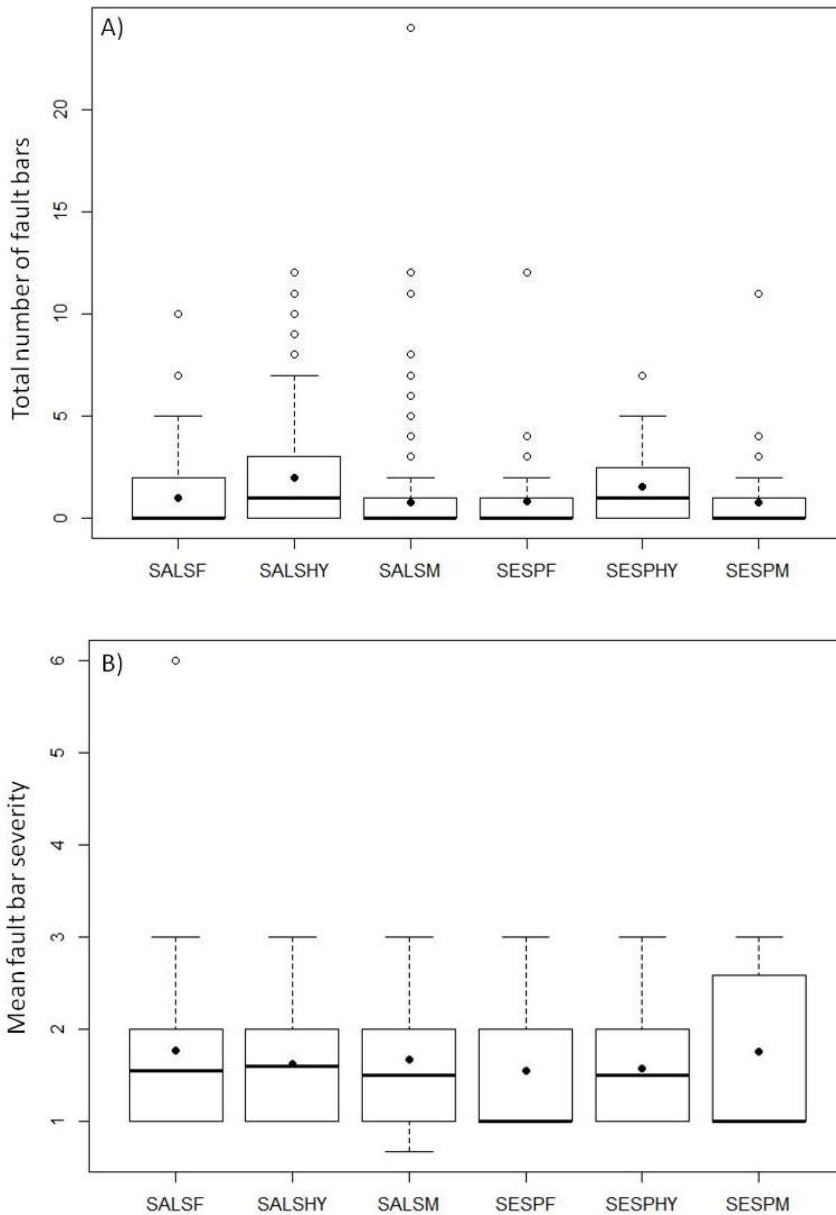


Figure 5: Boxplots depicting A) total number of fault bars and B) average severity of fault bars (on birds with at least one bar) for female Saltmarsh (SALSF), juvenile Saltmarsh (SALSHY), male Saltmarsh (SALSMM), female Seaside (SESPF), juvenile Seaside (SESPHY), and male Seaside (SESPM) Sparrows during the breeding season. The black lines represent median values and the black dots represent mean values.

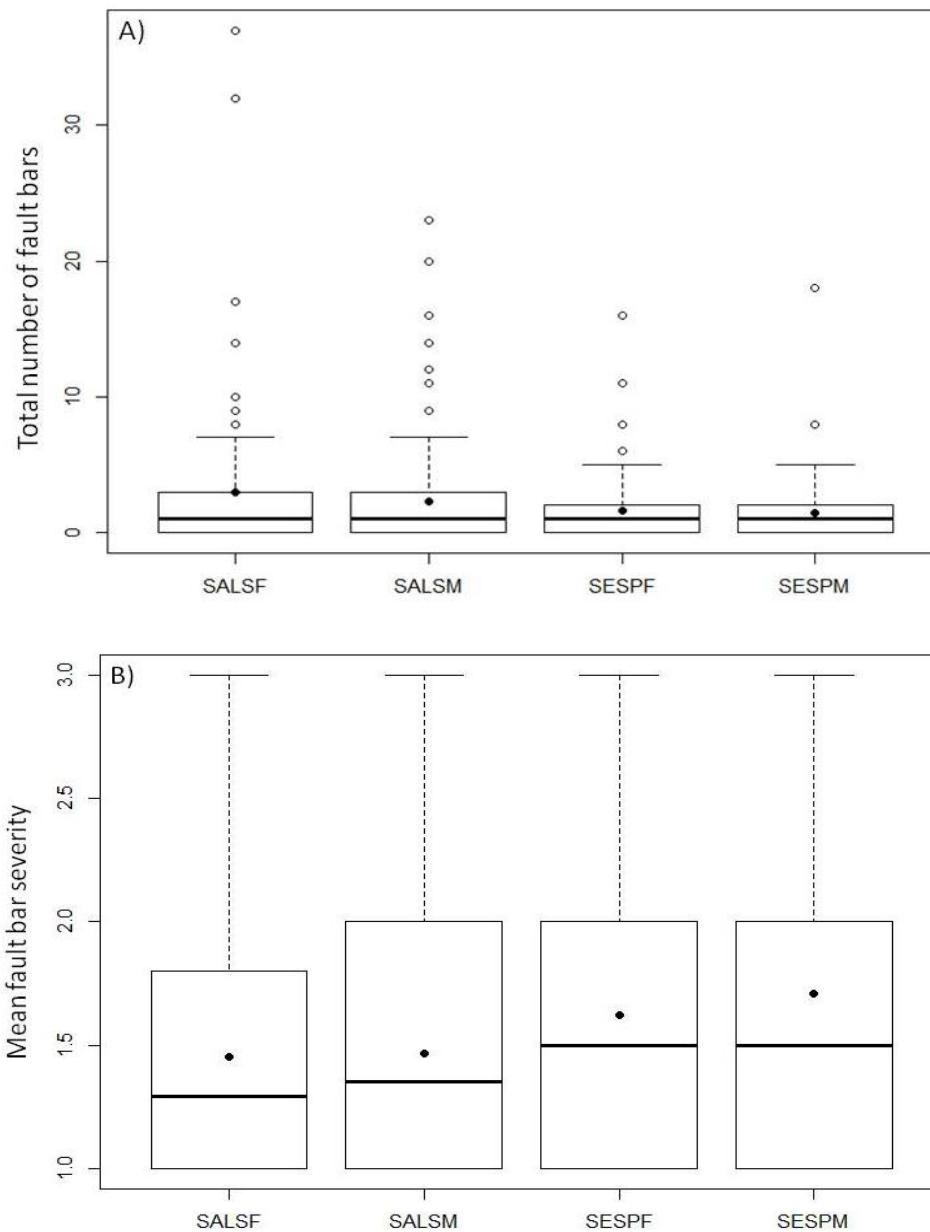


Figure 6: Boxplots depicting A) total number of fault bars and B) average severity of fault bars (on birds with at least one bar) for female Saltmarsh (SALSF), male Saltmarsh (SALSM), female Seaside (SESPf), and male Seaside (SESPM) Sparrows during the winter. All of the birds were unknown-age. The black lines represent median values and the black dots represent mean values.

CHAPTER 3: BODY CONDITION AND SURVIVAL THROUGHOUT THE ANNUAL CYCLE OF TIDAL MARSH SPARROWS

ABSTRACT

An individual's body condition and probability of survival can change throughout the year, based on the combined effects of many factors, including activities related to reproduction and parental care. As degrees and types of reproductive investment vary among individuals based on sex and species, an individual's body condition and probability of survival may vary accordingly. I tested predictions derived from reproductive effort theory in two closely related species with very different reproductive systems. Male and female Saltmarsh Sparrows (*Ammodramus caudacutus*) represent extremes in parental care: males perform none and females do everything from building nests to caring for fledglings. Male and female Seaside Sparrows (*A. maritimus*), with bi-parental care, represent similar, intermediate, levels of reproductive investment. Through extensive mist-netting during both the breeding and non-breeding periods, I found no effect of sex or species on the probability of apparent survival in the breeding season. On the wintering grounds, I found that Seaside Sparrows had lower apparent survival than Saltmarsh Sparrows, but again no effect of sex. Females, however, had poorer body condition than conspecific males during both seasons, suggesting non-lethal carry-over effects of reproduction. Fat scores varied by sex during the breeding season, with females carrying slightly more fat, but not during the winter, with all sexes and species carrying more fat than during the breeding season. During the breeding season, the tarsus length was the best predictor of apparent survival, with lower survival associated with the largest tarsus lengths.

Comparisons of within-season apparent survival to published estimates of annual survival suggests that migration mortality is high, even in these short-distance migratory species.

INTRODUCTION

Fitness is a product of survival and reproduction, both of which may be correlated with body condition. A migrant bird's body condition may influence its ability to reproduce by affecting whether and when it returns to the breeding grounds (e.g. Gordo and Sanz 2008; Matyjasiak 2013), the quality of territory and mates it can acquire (e.g. Fitzpatrick and Price 1997; Marks et al. 2010), and the number of young it can successfully rear (e.g. Cooper et al. 2011; Rohwer et al. 2011). Reproductive investment may go on to influence an individual's subsequent body condition and probability of survival. According to reproductive effort theory (Williams 1966; Trivers 1972), there is a trade-off between current and future reproduction, and this trade-off may manifest in reduced condition and survival of individuals with high degrees of reproductive investment compared to individuals with lower investment. Reproductive investment may encompass acquiring and defending a territory, finding and guarding mates, copulating, nest-building, incubating, brooding, and caring for offspring. Reproductive investment can also involve physiological processes, such as the production of sperm and eggs. The particular types of investment that an individual exhibits depend, largely, on its reproductive strategy. Breeding strategies are often species-specific, and can vary greatly among birds, particularly in degrees of territoriality, monogamy, and parental care (Crook 1965; Verner 1977; Griffith et al. 2002; Cockburn 2006). Strategies can also vary within species, such as those that are facultatively polygamous (e.g. Trnka and Prokop 2010). In many breeding systems, there are distinct

differences in the types and degrees of reproductive investment exhibited by males and females (Queller 1997; Cockburn 2006).

An individual's probability of survival can vary throughout the annual cycle based on its behavior, body condition, and other factors, including diseases, habitat, and predator abundance (Newton 1998). In many bird species, mortality is greater in females than in males (Liker and Székely 2005), and this bias may correlate with sex-based differences in reproductive investment, particularly parental care (Owens and Bennett 1994). Conspicuous appearance and behavior increase predation risk (Huhta et al. 2003; Post and Götmark 2006b). Predation risk may be especially high during foraging, due to prolonged conspicuousness and trade-offs between vigilance and consumption (Newton 1998; Post and Götmark 2006a), and at stop-over sites during migration (Ydenberg et al. 2003). Migration itself also poses many risks, and mass in-flight die-offs can occur due to extreme weather events, such as rain or snowstorms, tornados, or heavy fog (Butler 2000; reviewed by Newton 2006). Before or after migration, too, extreme weather events cause spikes of mortality, particularly for small birds (e.g. Brown and Brown 1998; reviewed by Newton 2006), and differences in temperature and the likelihood for inclement weather can be associated with variation in survival rates among wintering locations (Williams et al. 2005; Thatcher et al. 2006; Lok et al. 2011). Heterogeneous or unpredictable food availability, coupled with cold temperatures, can also lead to variation in winter survival (Danner et al. 2013).

Causes and consequences of variation in body condition also vary throughout the annual cycle, for many of the same reasons as survival (Newton 1998; Harrison et al. 2011; Labocha and Hayes 2012). Body condition is a broad term that does not have a single precise

meaning. Condition can encompass any traits that can influence an individual's performance, such as the degree of feather abrasion (e.g. Merilä and Hemborg 2000), the susceptibility of individuals to parasites or diseases (e.g. Santiago-Alaon et al. 2013), or changes in blood chemistry (e.g. Hórak et al. 1998). Commonly, however, condition refers to a measure of energy reserves, with the assumption that an individual's reserves correlate with its performance and risk of mortality (Cresswell 2009; Labocha and Hayes 2012). Protein from muscle can be used as an energy reservoir (Jenni and Jenni-Eiermann 1998; Cottam et al. 2002), but muscle size can also change adaptively to accommodate wing gaps caused by molting or broken feathers (Hedenström 2003) or increases in fat (Driedzic et al. 1993). Fat is the primary fuel-source for birds, and fat stores can fluctuate rapidly, even within the course of a day (Cresswell 2009). Mass-based condition indices, such as size-corrected residuals (Green 2001) or the scaled mass index (Peig and Green 2009), are commonly used as measures of condition, and encompass mass from fat and muscle, as well as structural elements such as bones and feathers that are less changeable. High mass per size is typically considered "good" condition (Peig and Green 2009), but there are circumstances in which lower mass is more beneficial (Cresswell 2009). Reproductive investment can lead to reduced body condition due to increased energetic expenses (Newton 1998; McNamara and Houston 2008). If reproductive investment has a negative effect on body condition during the breeding season, the effect may carry-over to influence individuals' condition or survival during subsequent stages in the annual cycle (Newton 2004; Harrison et al. 2011). Environmental factors such as climate and the distribution of resources can also influence body condition (Newton 2004; Brown and Sherry 2006; Danner

2012). In cold weather, larger individuals may be able to better maintain body heat and hold greater fat stores (Pravosudov and Grubb 1997).

The aim of this study was to test predictions derived from reproductive investment theory in adult male and female Saltmarsh (*Ammodramus caudacutus*) and Seaside (*A. maritimus*) Sparrows. Saltmarsh and Seaside Sparrows are closely-related tidal marsh specialists that co-occur on the breeding grounds from New England to Virginia, USA, and on the wintering grounds from Virginia to Florida, USA (Greenlaw and Rising 1994; Post and Greenlaw 2009). Despite similarities in habitat use, the two species have notably different breeding systems. Saltmarsh Sparrows are non-territorial, individuals do not develop pair bonds, both males and females engage in extensive multiple-mating, and only females provide care for eggs and chicks (Woolfenden 1956; Hill et al. 2010; Shriver et al. 2010; Greenlaw and Post 2012). In contrast, Seaside Sparrows are territorial, socially monogamous, with relatively low rates of extra-pair copulations, and exhibit bi-parental care (Woolfenden 1956; Post and Greenlaw 1982; Marshall and Reinert 1990; Hill and Post 2005). These differences in breeding strategies correspond to intra- and inter-species differences in reproductive investment, particularly regarding parental care (Chapter 1). Male Saltmarsh Sparrows exhibit no parental care; their only direct form of reproductive investment is the production of sperm (Greenlaw and Rising 1994). As the sole care-givers, female Saltmarsh Sparrows build nests, incubate eggs, and provision and care for chicks and fledglings (Woolfenden 1956; Post and Greenlaw 1982; Greenlaw and Post 2012). Male and female Seaside Sparrows have similar levels of parental care, although females build nests and incubate eggs alone, while males defend territories (Woolfenden 1956; Lockwood et al. 1997). According to reproductive investment theory (Williams 1966; Trivers 1972), these

differences in parental care could lead to differences in adult survival and body condition during the breeding season and, potentially, during molt, migration, and winter.

I quantified apparent weekly survival rates and within-season body condition of male and female Saltmarsh and Seaside Sparrows in the breeding and wintering seasons to test the following hypotheses and associated predictions: H1) Body condition and the probability of survival are directly reduced by breeding effort, with the predictions that a) during the breeding season, body condition is poorest and within season survival is lowest for female Saltmarsh, then female Seaside, male Seaside, and, lastly, male Saltmarsh Sparrows; b) the probability of survival is greater for birds with good body condition during both seasons; H2) Breeding effort can carry-over to reduce body condition and the probability of survival at other times of the year, with the prediction that during the winter, body condition is poorest and within-season survival is lowest for female Saltmarsh, then female Seaside, male Seaside, and, lastly, male Saltmarsh Sparrows. H3) Body condition and survival are influenced by temperature, with the predictions that a) larger individuals have a higher probability of survival; and b) the probability of survival is lower in the winter than during the breeding season.

METHODS

Study Sites: I mist-netted Saltmarsh and Seaside Sparrows within five tidal marshes in Connecticut, USA between May and August during the 2010-2013 breeding seasons, and within tidal marshes in North and South Carolina, Georgia, and Florida, USA between November and March during the 2011-2012, 2012-2013, and 2013-2014 winters. The Connecticut sites comprised plots located within the East River Marsh (Madison, 41°16'19.49"N, 72°39'9.97"W),

Hammonasset State Park (Madison, 41°15'39.63"N, 72°32'57.96"W), Pattagansett Marsh (East Lyme, 41°19'4.97"N, 72°12'45.56"W), Waterford Beach Park (Waterford, 41°18'19.13"N, 72°6'21.28"W), and Barn Island Wildlife Management Area (Stonington, 41°20'15.10"N, 71°52'7.05"W). These plots were selected as the primary Connecticut demographic study units for a north-eastern region-wide project on tidal marsh birds, the Saltmarsh Habitat and Avian Research Program (www.tidalmarshbirds.org). The primary wintering sites were located in South Carolina, within Huntington Beach State Park (Murrell's Inlet, 33°31'15.98"N, 79°3'3.79"W) and the North Inlet-Winyah Bay National Estuarine Research Reserve (Georgetown, 33°20'19.32"N, 79°11'16.66"W). Within each state, the sites were geographically distinct from one another and span a 68 km section of the Long Island Sound coast, and a 25 km section of the South Carolina coast. Also on the wintering grounds, I conducted supplemental mist-netting within the following additional sites: Fort Macon State Park (Atlantic Beach, North Carolina, 34°41'53.60"N, 76°41'5.81"W), the Anne Tilghman Boyce Coastal Reserve (Cherry Grove Beach, South Carolina, 33°50'57.34"N, 78°35'17.67"W), Cape Romain National Wildlife Refuge (Awendaw, South Carolina, 32°59'29.96"N, 79°37'19.07"W), public land along the causeway to Jekyll Island (Brunswick, Georgia, 31°6'26.71"N, 81°29'15.78"W), Big and Little Talbot Island State Parks (near Jacksonville, Florida, 30°27'45.06"N, 81°25'42.47"W), Timucuan Ecological and Historical Preserve (30°27'18.58"N, 81°27'9.60"W), and Faver-Dykes State Park (near St. Augustine, Florida, 29°42'10.64"N, 81°14'44.33"W).

Mist-netting: I conducted all mist-netting with two-panel, 12-m, 38-mm mist-nets. I did not conduct netting on days with rain, excessive wind, or temperatures below 4.5° C, and I released

all birds close to their capture location. I conducted three types of mist-netting in plots within my focal marshes on the breeding grounds: 1) Constant-effort systematic netting during the breeding season. Beginning shortly after dawn, I put up three sets of six nets. I kept the nets open for three hours, during which time I walked toward the nets every 15-20 minutes, flushing birds into the nets. 2) Targeted netting of females on nests. I placed a pair of nets in a V-shape, with the nest located at the apex. I captured females either when they returned to the nest or when I flushed them off of the nest after they had evaded the net during return. 3) Opportunistic netting before and after the systematic period. I set pairs of nets across mosquito control ditches, walked along the ditches, and flushed birds into the nets. I moved nets from ditch to ditch, as necessary, depending on the number of birds present and caught. During the systematic netting, I divided each plot into four or five subplots and visited them on a rotating schedule to ensure full and regular coverage of the entire plot area. I visited each subplot three times during the course of the breeding season. Targeted and opportunistic netting took place within the same total area, but often included more than one subplot on a single day.

On the wintering grounds, the netting locations were high points in the marshes at which sparrows congregate during the spring tides that occur in the days close to new and full moons. I only netted during high tide on the days with sufficient tidal amplitude to flood the marsh, giving us two bouts of netting per month, each lasting about one week. I began banding sessions 1.5-2 hours before peak tide, or at dawn, if peak tide occurred before daybreak. I ended banding sessions when the tide had fallen to the point that I was no longer catching birds. Due to the unique configuration of each high tide roost, the number and locations of nets varied by site, but I typically used one to three nets at a time. I left the nets open during the

banding period if there were not many sparrows, but I closed them during processing if there was a risk of catching more birds at one time than I could safely extract and process. I had two high tide netting locations at each of my primary South Carolina marshes. The sites at Huntington Beach were separated by 0.3 km and the sites at North Inlet were separated by 0.4 km. At high tide, the banding locations at each site were separated by open water that the birds are not seen to cross. Tidal marsh sparrows exhibit high fidelity to particular roost sites (Winder et al. 2012).

Field Data Collection: I identified each bird to species and, during the breeding season, to sex by the presence of a brood patch (female) or enlarged cloaca (male). For birds that could not be sexed visually on the breeding grounds, and all birds on the wintering grounds, I collected a feather sample for genetic sexing by gently pulling up to two rectrices or breast feathers and/or collecting feathers that dropped during handling. I banded each bird with a standard USGS aluminum band, took measurements for tarsus, unflattened wing chord, culmen, nares to bill tip, and head length, and weighed each bird to the nearest 0.1 g using a Pesola scale. I visually assessed each bird for fat accumulation in the furcular hollow and on the abdomen by gently blowing aside feathers to reveal skin and subcutaneous fat deposits, which I differentiated from skin based on shape and yellow coloration. I scored furcular and abdominal fat separately, using two 7-point scales: 0) no visible fat; 1) fat fills < 25% of the furcular hollow, light fat under ribcage, none on abdomen; 2) fat fills 26-50% of the furcular hollow, heavy fat under ribcage, none on abdomen; 3) fat fills 51-75% of the furcular hollow, fat under ribcage and partially covering abdomen; 4) fat fills 76-99% of the furcular hollow, fat under ribcage and completely

covering abdomen; 5) fat flush with furcular hollow, fat on abdomen flush with ribcage; 6) fat convex (exceeding furcular hollow), fat convex (exceeding the ribcage) (Danner 2012; Appendix D). I tactilely assessed pectoral muscle condition relative to the keel by lightly rubbing one finger across the breast bone. I scored muscle condition on a 7-point scale: 0) no pectoral muscle; 1) muscle concave and not covering all of ribs, keel very prominent and sharp to the touch; 2) muscle concave and covering all of ribs and keel sharp to the touch; 3) muscle concave, half way up keel, but keel sharp to touch; 4) muscle concave, almost flush with keel, can feel keel; 5) muscle flush with keel and cannot feel keel; 6) muscle convex and bulging past keel (Danner 2012; Appendix D).

Scaled Mass Index: I used the structural measurements to calculate a scaled mass index (SMI) for each individual as a body condition proxy, following the method of Peig and Green (2009) (Appendix E). I assessed the correlation between each structural measurement and mass and the fit with standardized major axis (SMA) regression using the R package *smatr* (Warton et al. 2012). I selected tarsus as the structural measurement for SMI calculations because it correlated most strongly and consistently with mass, and produced the SMA regression with the best fit. For individuals that were captured multiple times, I used the first tarsus measurement that was taken (usually, but not always, on the first time a bird was captured). I used mass and tarsus data from winter male and female Saltmarsh and Seaside Sparrows combined to calculate the scaling coefficient for individual SMI calculations. I selected winter birds as opposed to breeding birds because breeding females carry egg mass during laying, which would increase variation in mass in a manner unrelated to condition. As SMA slopes

between $\ln(\text{mass})$ and $\ln(\text{tarsus})$ were not significantly different between sexes and species (likelihood ratio statistic = 0.67, 1 df, $p = 0.413$), I used the slope from an SMA regression including all wintering birds.

Genetic Sexing: I used NucleoSpin Tissue DNA extraction kits (Macherey-Nagel, Duren, Germany) to extract DNA from feathers collected in the field. I amplified the DNA according to Griffiths et al. (1998), using gender primers P2 and P8 in a single PCR. This process amplifies sections of two avian sex chromosome genes, CHD-W, which is only found in females, and CHD-Z, which is found in both sexes. Following amplification, I resolved the samples on 1.5% agarose gels and determined the sex identifications based on the presence of one (male) or two (female) bands. This banding pattern is due to a length polymorphism in the two gene variants. I validated the methods by confirming accurate sexing for six males and six females from my Connecticut study sites that had previously been sexed in the field by the presence of a brood patch (female) or enlarged cloaca (male).

Body Condition: We compared SMI, fat, and muscle between sexes, species, and seasons, with linear mixed effects models using the lmer function in the lme4 package (Bates et al. 2014) in R. I ran three separate analyses, each using a different condition metric as the dependent variable: SMI, total fat score (furcular fat score + abdominal fat score), and muscle score. I conducted each analysis using all birds captured on the wintering grounds, and all birds captured on the breeding grounds between 15 May and 15 August, including individuals captured during systematic, targeted, and opportunistic netting. I calculated the number of

days since the start of the typical breeding period (15 May) and typical wintering period (15 November) and used this factor “day” as an explanatory variable in my models. I selected these dates based on personal observations on the breeding grounds and information from collaborators who band during migration periods on the non-breeding grounds (personal communication, F. Smith and A. Given; Winder et al. 2012).

I conducted the analysis for each condition metric with a two-stage framework: first to determine the effect of any interactions, second to determine the main effects. At each stage, I used ΔAIC_c scores from the AICctab function in the bbmle package in R (Bolker 2014) to compare candidate models; if two or more nested models were within 2 AIC_c points of each other, I selected the model with the fewest terms (Arnold 2010). In the first stage, I began with a global fixed-effects model containing sex, species, season, day, and the interactions of sex*species, sex*season, and sex*species*season and fit subsets of this model. I used the best-supported model from this stage to determine which, if any, interactions should be considered during the second stage of model comparisons. In the second stage, I compared a base model that contained only random effects of site, year, and individual, to models that varied in their inclusion of sex, species, and season. If the first stage of model comparison suggested that an interaction term should be included, I ran two models that contained the factors present in the interaction term: one with the interaction term and one without. I used restricted maximum likelihood to determine whether the random effect was significant, and maximum likelihood to perform model selection on the fixed effects. Because I predicted that condition might decrease with time, particularly during the breeding season, I also ran a set of models in which day was added as an additional factor.

Apparent Survival: I conducted separate analyses of apparent weekly survival for captures on the breeding and wintering grounds using Cormack-Jolly-Seber capture-mark-recapture models. On the breeding grounds, I only used birds captured during the systematic netting at three primary marshes; I did not include individuals captured at Pattagansett or Waterford marshes due to low sample sizes. On the wintering grounds, I used all individuals captured at my primary banding locations in North Inlet and Huntington Beach State Park. I created and compared models through program MARK (White and Burnham 1999) using the RMark package (Laake and Rextad 2008) in R 3.1.1 (R Core Team 2014). For each season, I created a daily capture history for each individual. The capture histories comprised a series in which I used “1” if I captured an individual on a particular day, “0” if I was at that bird’s capture location but did not capture it; and “.” if I was not at that bird’s capture location that day. The total number of potential capture days spanned from the earliest banding date to the latest banding date in each season, for 53 and 107 potential capture days during the breeding and winter seasons, respectively. I converted the daily capture histories into weekly capture histories in R prior to model-building.

Because I was only interested in capture probability in so far as it increased the precision of my survival probability (Φ) estimates, I modeled capture probability (p) alone first (Danner et al. 2013). In each season, I compared models based on the null and global specifications of Φ with the following 12 specifications of p : 1) null; 2) species effect only; 3) sex effect only; 4) species and sex effects; 5) species*sex interaction; 6) site effect only; 7) week effect only; 8) species and week effects; 9) sex and week effects; 10) species and sex and week effects; 11) species*sex interaction and week effects; 12) site and week effects. I compared

these 12 models using Akaike's Information Criterion corrected for small sample sizes, (AIC_c; Burnham and Anderson 2002), and selected the specification of p from the model with the lowest AIC_c score. If multiple nested models had scores within 2 AIC_c units, I selected the model with the fewest parameters (Arnold 2010).

To test the hypothesis that survival is influenced by sex, species, and body size, I fit a global model for Φ that contained species, sex, SMI, tarsus, week, and interactions between species and sex and species and tarsus. I fit several subset models of the global model, including a null model. I evaluated the 23 candidate models for each season using Δ AIC_c scores and Akaike weights. I used model averaging across the entire set of candidate models to generate estimates for Φ and p for each season. Using these estimates, I calculated seasonal survival for twelve weeks to represent the breeding season (i.e. mid-May to mid-August) and a comparable period during the winter (early December to early March). I also calculated two annualized survival estimates for each species by assuming weekly survival during migration (28 weeks) was equal to weekly survival during the winter (12 weeks) and alternately assuming it was the same as during the breeding season (12 weeks).

RESULTS

The top model for SMI, which carried 99.7% of the weight, contained effects of sex, species, season, day, and the sex*species*season interaction (Table 1A). The top-performing model for fat score, which carried nearly 100% of the weight, included effects of sex, species, season, day, and the sex*season interaction. Specifically, my results indicate that, during both seasons, females had lower average SMI than conspecific males (Table 2A and Figure 1A). All categories

of individuals had lower SMI values during the winter than during the breeding season (Figure 1A). Seaside Sparrows had higher SMI values than Saltmarsh Sparrows in both seasons (Table 2A and Figure 1A). Females had slightly higher fat scores than conspecific males during the breeding season, but, although all individuals had higher fat scores in the winter than in the breeding season, the winter fat scores were similar for both sexes and species (Table 2B and Figure 1B). For SMI and fat scores, models that included effects of day performed better than comparable models that did not include day (Table 1). My top four models for muscle scores all included species and day in combination with other variables, but the more complex models did not result in better fit (Table 1C), providing little evidence that muscle scores vary with sex or season. Collectively, these top four models received almost all the model weight (Table 1). Seaside sparrows had slightly higher average muscle scores than Saltmarsh Sparrows (Table 2C and Figure 1C).

For the survival analyses, I captured 470 male and 147 female Saltmarsh Sparrows and 104 male and 40 female Seaside Sparrows during systematic netting sessions on the breeding grounds. On the wintering grounds, I captured 162 male and 105 female Saltmarsh Sparrows and 75 male and 91 female Seaside Sparrows at my primary South Carolina sites. In my three years of winter banding, I captured 242 individuals at the two North Inlet banding locations, and caught only three individuals at both sites within the same year, and four at both sites, but in different years. At Huntington Beach, I caught 96 individuals total, and captured only one individual at both sites, but in different years.

In the first stage of model comparisons, the top four models for the breeding season each included week in the specification of capture probability (p), and the specification that

contained only week had the lowest AIC_c score and carried 38% of the model weight (Table 3A). For the winter, the top-performing model, which carried 97% of the model weight, included only site in the specification of p (Table 3B). Model-averaged estimates of p (23 models) were lower during the breeding season, 0.036 ± 0.007 se (95% confidence interval 0.024-0.053), than during the winter, 0.240 ± 0.027 se (95% confidence interval 0.191-0.297).

For Φ , in the breeding season, tarsus appeared in five of the top six models (Table 4A). Together, these five models carried 76% of the model weight, and none of the more complex models had an AIC_c score that improved notably upon the model with tarsus alone (Table 4A). The model-averaged estimates for breeding season survival of all individuals as a function of tarsus showed extremely high apparent survival for small individuals, with decreasing probabilities of survival for individuals with tarsus lengths longer than 22 mm (Figure 2). The model-averaged estimate of apparent weekly survival for all individuals during the breeding season was 0.9997 ± 0.0084 se (95% confidence interval 0-1).

In winter, species appeared in the top six models (Table 4B). These six models carried 71% of the model weight, and none of the more complex models had an AIC_c score that improved notably upon the model with species alone, although three of the top four models also contained tarsus (Table 3B). As in the breeding season, there was no evidence for an effect of week (table 3B). Model-averaged apparent survival during the winter was slightly lower for Seaside than for Saltmarsh Sparrows: 0.9919 ± 0.0127 (95% confidence interval 0.8449-0.9996) for Seaside and 0.9986 ± 0.0024 (95% confidence interval 0.9606-0.9999) for Saltmarsh.

Overall, mean apparent survival was highest during the breeding season and lowest for wintering Seaside Sparrows, with a notable overlap in the confidence intervals between

wintering Saltmarsh and Seaside Sparrows (Figure 3), and, by far, the greatest uncertainty in the breeding season estimate. My weekly apparent survival rates correspond with 99.6% survival during twelve weeks of the breeding season, for both species, and 98.3% and 90.7% survival for Saltmarsh and Seaside Sparrows, respectively, during 12 weeks of winter. If I assume weekly survival is the same during migration as during the breeding season, the estimate of annual Saltmarsh Sparrows survival is 97.1%; if I assume weekly survival is the same during migration as during winter, the estimate of annual survival is 94.2%. For Seaside Sparrows, if I assume weekly survival is the same during migration as during the breeding season, the estimate of annual survival is 89.6%; if I assume weekly survival is the same during migration as during winter, the estimate of annual survival is 72.0%.

DISCUSSION

My results suggest that female salt marsh-obligate sparrows may pay a reproductive cost in body condition relative to conspecific males, and that this cost may carry over into the non-breeding season, but that body condition does not correspond with reduced survival in either season. These results support the first link in reproductive effort theory (Williams 1966; Trivers 1972), that parental investment can lead to a reduction in body condition, but does not support the second link, between reduced body condition and lowered probability of survival.

During the breeding season, female Saltmarsh and Seaside Sparrows had lower SMI values than conspecific males, and female Saltmarsh Sparrows had lower SMI values than female Seaside Sparrows. The SMI score is based on body mass relative to a standard size (Peig and Green 2009); breeding females had lower SMI values than conspecific males despite

carrying higher levels of visible fat, and despite potentially carrying eggs at the time of measurement. As fat and egg mass would both contribute to bringing the females' total masses closer to those of males, the actual difference in non-fat mass between the sexes is greater than that depicted by my comparison of SMI values. This pattern was observed in Savi's Warbler (*Locustella luscinioides*), and was suggested to be evidence for greater reproductive stress in females than males (Neto and Gosler 2010). Individuals with poor body condition at the end of the breeding season may have delayed molt, as I found with female tidal marsh sparrows compared to conspecific males (Chapter 2), and may grow poor-quality feathers with reduced thermoregulatory capability and increased risk of abrasion (Dawson et al. 2000; Vágási et al. 2012). Poor-condition individuals may also have delayed departure timing (Newton 2011), with increased mortality risk due to inclement weather and food depletion (Newton 2006), increased risk of mortality during migration (Newton 2007), and poor condition or survival during the winter (Harrison et al. 2011). These factors can then carry-over again and influence individuals' performance during the subsequent breeding season (Ward and Schlossberg 2004; Norris and Marra 2007; Dale and Leonard 2011).

Sex differences in fat levels could reflect differential trade-offs between carrying fat, which helps guard against inconsistent food availability (Macleod et al. 2008; Cresswell 2009), and maintaining low body weight, which aids in take-off-speed and agility (Metcalf and Ure 1995; Krams 2002). Females' higher fat levels during the breeding season could be a response to maintaining the energy required for incubation (Bolduc and Guillemette 2003; Cresswell 2009), coupled with potentially unpredictable food intake due to reduced opportunities for foraging. Additionally, if females do not spend as much time flying while they are incubating

eggs or brooding chicks (Post and Götmark 2006b), they may be able to afford carrying extra fat. Males' low fat levels could be a response to the need for efficient flight and predator evasion (Cresswell 2009). Between species, male Saltmarsh Sparrows, which search for females over relatively large home ranges (Shriver et al. 2010), may spend more time in flight than male Seaside Sparrows, which engage in territorial defense and chick provisioning, but which maintain smaller home ranges (Post 1974). This pattern of home range size and time spent flying matches my observed patterns of fat stores: male Saltmarsh Sparrows had the lowest levels of fat during the breeding season.

The combination of agility, influenced by fat accumulation, and parental roles may have a large influence on predation risk. A study on Pied Flycatchers (*Ficedula hypoleuca*) found that males were killed by avian predators at a higher rate than females during nesting but, when the analysis accounted for the observation that incubating females spent 77% of the day on the nest, females were nearly 5 times more vulnerable to predation than males during the times they were off the nest (Post and Götmark 2006b). If larger individuals are less agile or are more easily noticed by predators, differential risk of predation could also explain the pattern I observed during the breeding season, with the largest tarsi corresponding with lower apparent survival. Larger individuals may also be more aggressive and take more risks (Funghi et al. 2014), which could also decrease probability of survival.

Despite the difference in SMI values for male and female Saltmarsh and Seaside Sparrows during the breeding season, my model comparisons gave weak evidence that apparent weekly survival differs for male or female Saltmarsh or Seaside Sparrows or for individuals with different SMI values during the breeding season. The extremely large

confidence interval around my breeding season estimate probably stemmed from the low capture probability I observed during the breeding season. However, my results agree with those of Post and Greenlaw (1982), who calculated annual survival based on cumulative return rates, and both DiQuinzio et al. (2001) and Field et al. (in prep), who found no difference in annual survival rates between male and female Saltmarsh Sparrows or between male and female Seaside Sparrows. The mechanisms behind mortality could still differ for males and females, with males vulnerable due to territorial or mate-seeking activities, and females vulnerable due to reduced body condition and high fat loads. The disparate mechanisms could lead to similar overall survival rates between sexes and species. In a meta-analysis of mortality rates in 194 bird species, Liker and Székely (2005) found that most bird species had higher female than male mortality rates. Among species with higher mortality rates in males, there was a strong correlation between the degree of male-bias in mortality and the extent of competition among males, as indicated by both polygyny frequency, and testis size (Liker and Székely 2005). Among species with higher female mortality, there was no relationship between the extent of female-biased mortality and the extent of female-biased parental care (Liker and Székely 2005).

Scaled mass index was lower for males and females of both species in winter than during the breeding season, but the differences between sexes and species were still detectable, with females having lower SMI values than conspecific males and female Saltmarsh Sparrows having lower SMI than female Seaside Sparrows. This pattern suggests that the negative effects of reproduction on body condition is not completely overcome by females, even months after breeding is over, giving support for the carry-over hypothesis (Harrison et al.

2011). As in the breeding season, however, I did not observe a significant sex difference in apparent weekly survival during the winter. Additionally, Seaside Sparrows had the lower probability of survival, rather than Saltmarsh Sparrow as originally predicted. This result, coupled with the fact that neither body size nor SMI were significantly associated with winter survival, suggests that the temperatures experienced by wintering tidal marsh sparrows in central South Carolina, where the average coldest monthly temperature in December through March 2010-2015 was -3.5° (<http://weather-warehouse.com>), is not cold enough to reduce survival. I did, however, find that all individuals had higher levels of visible fat in the winter than in the breeding season, which could be a response to the colder and less predictable temperatures (Rogers and Reed 2003), and, potentially, to less predictable food sources (Brown and Sherry 2006; Danner et al. 2013).

My annualized apparent survival estimates for Saltmarsh Sparrows were over 90% whether I carried the breeding or the winter estimate over through migration. For Seaside Sparrows, the annualized survival estimates were 72% or 90%, depending on the assumption I made about migration survival. All of these estimates are notably higher than those of Post and Greenlaw (1982), which ranged from 41.38% to 63.63% for annual survival, DiQuinzio et al. (2001), who calculated Saltmarsh Sparrow apparent annual survival between 27% and 66%. Both of these studies, however, estimated survival from return rates and did not account for recapture probability, so their values most likely under-estimate true survival. Yet, Field et al. (in prep), estimated apparent annual survival at 44% for female and 49% for male Saltmarsh Sparrows, and 52% for female and 57% for male Seaside Sparrows, which is within the range of the earlier estimates, and does not match my result of lower Seaside Survival. The only previous

study that estimated survival of tidal marsh sparrows captured on the wintering grounds found apparent annual survival rates of 52% and 48% for Saltmarsh and Seaside Sparrows, respectively (Winder et al. 2012). These estimates are similar to the estimates made on the breeding grounds, although they match my observed difference between the two species. Because my annualized estimates do not include separate estimates of migration mortalities, it seems likely that the higher annual estimates of these other studies arise from significant mortality during migration. This mortality appears to exist even though Saltmarsh and Seaside Sparrows are short-distance migrants that are able to migrate along a more or less continuous stretch of suitable habitat. High survival during stationary periods and lower survival during migration was inferred for Black-throated Blue Warblers (*Dendroica caerulescens*) by Sillett and Holmes (2002), who calculated both annual and monthly survival estimates on the breeding grounds in New Hampshire and the wintering grounds in Jamaica. Their analysis indicated survival rates of 99% and 93% during the breeding and wintering periods, respectively, and calculated migration survival of 67% during each spring and fall migration (Sillett and Holmes 2002). Saltmarsh and Seaside Sparrows' short-distance coastal migrations mean that they do not face long stretches of open water with no food or shelter, but their continual proximity to terrestrial habitats could lead to consistently high exposure to predators.

While reproductive effort theory (Williams 1966; Trivers 1972) asserts that parental care is an important component of reproductive investment, and empirical studies have found evidence supporting this hypothesis (Owens and Bennett 1994), it is clearly not the only factor contributing to individuals' body condition and risk of mortality at any point in the annual cycle. Activities that are typically male-only and do not directly contribute to parental care, such as

territorial defense and mate-seeking behaviors, may be highly costly in terms of energetic expenses and predation risk. High levels of risk and vulnerability, even if they are produced through different mechanisms, can lead to similar overall probabilities of survival for individuals with even dramatically different reproductive roles. The potential for non-lethal carry-over effects linking individual performance in separate seasons, and events that take place during parts of the annual cycle that are difficult to monitor, such as migration, should also not be ignored when thinking about the events and processes that cumulatively determine population dynamics.

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Table 1: Comparisons of linear mixed models for A) scaled mass index (SMI), B) combined furcular hollow and abdominal fat score, and C) muscle score. The analyses included all birds captured during both the breeding seasons 2011, 2012, 2013, and wintering seasons 2011-2012, 2012-2013, and 2013-2014; the effect of “season” refers to which season an individual was captured in. Day was calculated separately for each season to represent approximate time since arrival to either the breeding or wintering location. I determined which (if any) interactions should be considered in a previous stage of model-comparisons.

Model	df	ΔAIC_c	w
A) SMI			
Sex + species + season + day + sex*species*season	13	0	0.99
Sex + species + season + day	9	11.7	0.003
Sex + species + day	8	16.2	<0.001
Sex + species + season + sex*species*season	12	98.1	<0.001
Sex + species + season	8	108.8	<0.001
Sex + species	7	115.4	<0.001
Species + season + day	8	340.1	<0.001
Species + day	7	348.1	<0.001
Species + season	7	447.1	<0.001
Species	6	457.4	<0.001
Sex + season + day	8	1792.7	<0.001
Sex+ day	7	1795.6	<0.001
Sex + season	7	1862.7	<0.001
sex	6	1864.3	<0.001
Season + day	7	1868.9	<0.001
Season	6	1942.3	<0.001
Base model	5	1943.0	<0.001
B) Fat score			
Sex + species + season + sex*season + day	10	0	1
Sex + species + season + sex*season	9	39.8	<0.001
Sex + species + season + day	9	76.6	<0.001
Sex + species + day	8	80.0	<0.001
Sex + species + season	8	110.0	<0.001
Sex + species	7	112.6	<0.001
Sex + season + day	8	114.3	<0.001

Sex + day	7	118.5	<0.001
Sex + season	7	142.8	<0.001
Sex	6	146.3	<0.001
Species + season + day	8	157.9	<0.001
Species+ day	7	161.5	<0.001
Species + season	7	182.0	<0.001
Species	6	184.9	<0.001
Season + day	7	198.3	<0.001
Season	6	218.0	<0.001
Base model	5	222.0	<0.001
C) Muscle score			
Species + season + day	8	0	0.36
Species + day	7	0.3	0.32
Sex + species + season + day	9	2.5	0.17
Sex + species+ day	8	1.7	0.15
Species	6	20.9	<0.001
Species + season	7	21.9	<0.001
Sex + species	7	22.8	<0.001
Sex + species + season	8	23.8	<0.001
Season + day	7	69.9	<0.001
Sex + season + day	8	70.8	<0.001
Sex + day	7	72.8	<0.001
Season	6	86.3	<0.001
Base model	5	86.9	<0.001
Sex + season	7	87.9	<0.001
Sex	6	88.5	<0.001

Table 2: Effects from the best-supported models for A) scaled mass index (SMI), B) total fat score, and C) muscle score of Saltmarsh and Seaside Sparrows throughout the annual cycle. Each of the models also included random effects of site, year, and individual. The terms separated by colons represent additive components of the interaction effects.

	Estimate	Standard error
A) SMI (Sex + species + season + day + sex*species*season)		
(Intercept)	17.441	0.367
Male	2.342	0.179
Seaside	7.8262	0.334
Winter	-1.236	0.500
Day	-0.013	0.001
Male:seaside	-0.034	0.400
Male:winter	-0.657	0.313
Seaside:winter	0.013	0.430
Male:seaside:winter	1.309	0.537
B) Fat (Sex + species + season + sex*season + day)		
Female (Intercept)	1.516	0.442
Male	-0.945	0.071
Seaside	0.383	0.059
Winter	1.020	0.590
Day	-0.007	0.001
Male:winter	0.961	0.106
C) Muscle (Species + day)		
Saltmarsh (Intercept)	3.557	0.107
Seaside	0.317	0.036
Day	-0.003	0.001

Table 3: Comparisons of Cormack-Jolly-Seber capture-mark-recapture models for capture probability of Saltmarsh and Seaside Sparrows during A) breeding seasons 2011, 2012, 2013 and B) winters 2011-2012, 2012-2013, and 2013-2014. All were fit with the global specification of Φ , which includes effects of species, sex, the species*sex interaction, SMI, tarsus, the species*tarsus interaction, and week. I used the best-performing specification of p for each season in my second stage of model comparisons, determining which factors influence Φ .

p	df	ΔAIC_c	w
A) Breeding			
Week	20	0	0.38
Week + sex	21	1.12	0.22
Week + species	21	2.01	0.14
Week + site	22	2.54	0.11
Species + sex	22	3.13	0.08
Week + species*sex + species + sex	23	3.88	0.05
Sex	15	7.62	0.008
Null	14	7.88	0.007
Species	15	8.90	0.004
Species + sex	16	9.61	0.003
Site	16	9.81	0.003
Species*sex + species + sex	17	10.01	0.003
B) Winter			
Site	26	0	0.97
Null	23	6.99	0.03
Sex	24	11.53	0.003
Species + sex	25	13.36	0.001
Species	24	13.45	0.001
Species*sex + species + sex	26	17.64	<0.001
Sex + week	39	22.76	<0.001
Species + week	39	23.32	<0.001
Site + week	41	23.91	<0.001
Week	38	24.67	<0.001
Species + sex + week	40	25.11	<0.001
Species*sex + species + sex + week	41	25.62	<0.001

Table 4: Comparisons of Cormack-Jolly-Seber capture-mark-recapture models for apparent weekly survival of Saltmarsh and Seaside Sparrows during A) breeding seasons 2011, 2012, 2013 and B) winters 2011-2012, 2012-2013, and 2013-2014. The specification for p in each season was selected in a previous stage of model comparisons, using only the null and global specifications for Φ .

Φ	p	Df	ΔAIC_c	w
A) Breeding				
Species*sex + tarsus + species + sex	week	12	0	0.32
Species + sex + tarsus	week	11	0.84	0.21
Tarsus	week	9	1.52	0.15
Species + SMI	week	10	2.04	0.12
Sex + tarsus	week	10	3.56	0.05
Species *tarsus	week	10	4.29	0.04
SMI	week	9	5.15	0.02
Species + sex + SMI	week	11	5.44	0.02
Null	week	8	5.76	0.02
Species*sex + SMI + species + sex	week	12	6.20	0.01
Sex + SMI	week	10	6.31	0.01
Sex	week	9	7.70	0.01
Species	week	9	7.71	0.01
Species + sex + SMI + tarsus + week	week	18	8.22	0.003
Species + sex	week	10	9.54	0.002
Species*sex + species*tarsus + SMI + tarsus + week + species + sex	week	20	10.49	0.001
Species*sex + species + sex	week	11	11.03	0.001
Species + tarsus	week	14	11.49	0.001
Species + week	week	15	11.91	0.001
Week	week	15	13.40	< 0.001
Sex + week	week	16	13.71	< 0.001
Species + sex + week	week	17	20.42	< 0.001
B) Winter				
Species + tarsus	site	7	0	0.28
Species + sex + tarsus	site	8	2.05	0.10
Species	site	6	2.06	0.10
Species*sex + tarsus + species + sex	site	9	2.21	0.09
Species + SMI	site	7	2.46	0.08
Species + sex	site	7	3.18	0.06

Null	site	5	3.18	0.06
SMI	site	6	3.53	0.05
Species + sex + SMI	site	8	4.16	0.04
Tarsus	site	6	4.17	0.04
Sex + SMI	site	7	4.37	0.03
Sex	site	6	5.03	0.02
Species*sex + species + sex	site	8	5.10	0.02
Sex + tarsus	site	7	5.27	0.02
Species*sex + SMI + species + sex	site	9	6.21	0.01
Species + week	site	21	19.85	<0.001
Species*sex + species*tarsus + SMI + tarsus + week + species + sex	site	26	21.38	<0.001
Species + sex + week	site	22	21.65	<0.001
Species*sex + week + species + sex	site	23	23.59	<0.001
Species + sex + SMI + tarsus + week	site	24	23.81	<0.001
Week	site	20	27.01	<0.001
Sex + week		21	27.02	<0.001
Species*tarsus	site	8	1358.15	<0.001

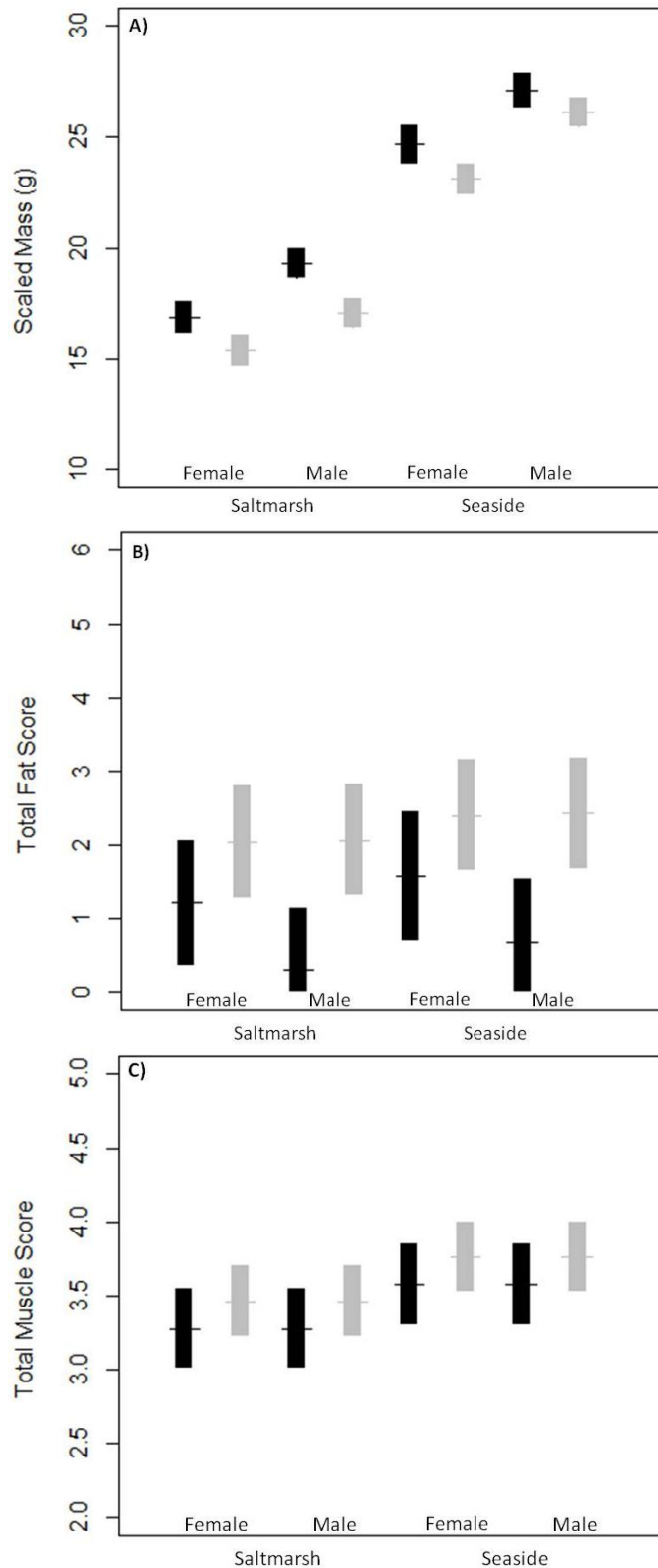


Figure 1: Predicted values and 95% confidence intervals from the top models for A) Scaled Mass Index; B) total fat scores; and C) muscle score for female Saltmarsh (SALSF; N = 325 for breeding and 195 for winter), male Saltmarsh (SALSM; N = 942 for breeding and 267 for winter), female Seaside (SESPF; N = 86 for breeding and 175 for winter) and male Seaside (SESPM; N = 174 for breeding and 195 for winter) sparrows during the breeding (black) and winter (gray) seasons.

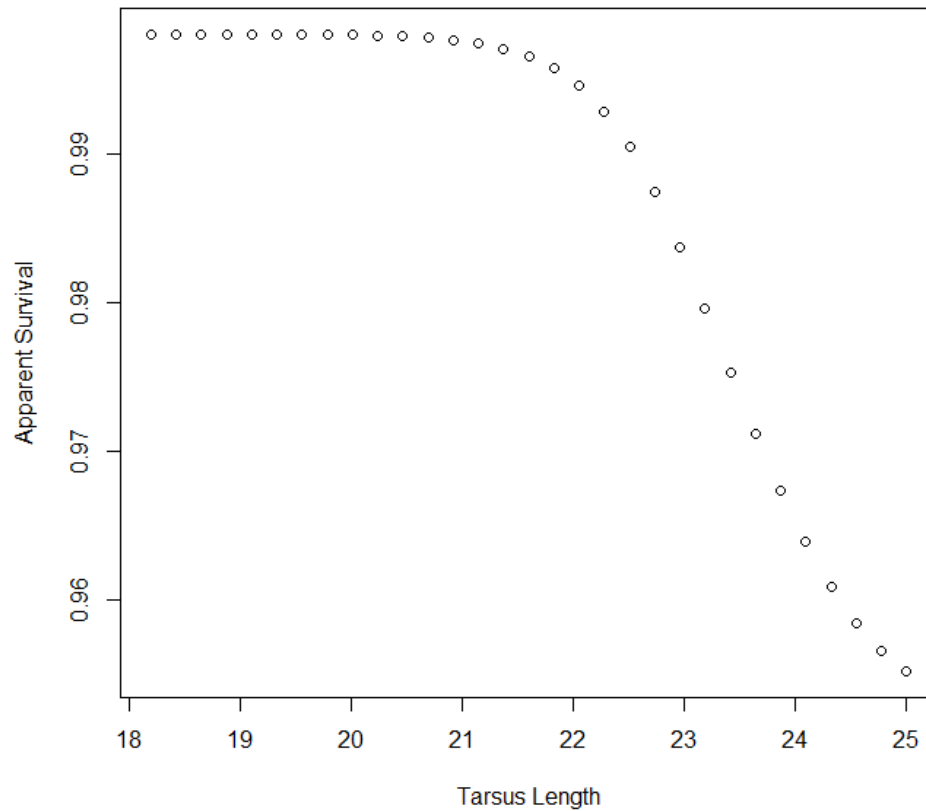


Figure 2: Model-averaged estimates of apparent weekly survival by tarsus size for Saltmarsh and Seaside Sparrows, averaged across all individuals, pooled by sex and species, during the breeding season. The 95% confidence interval spans from 0-1.

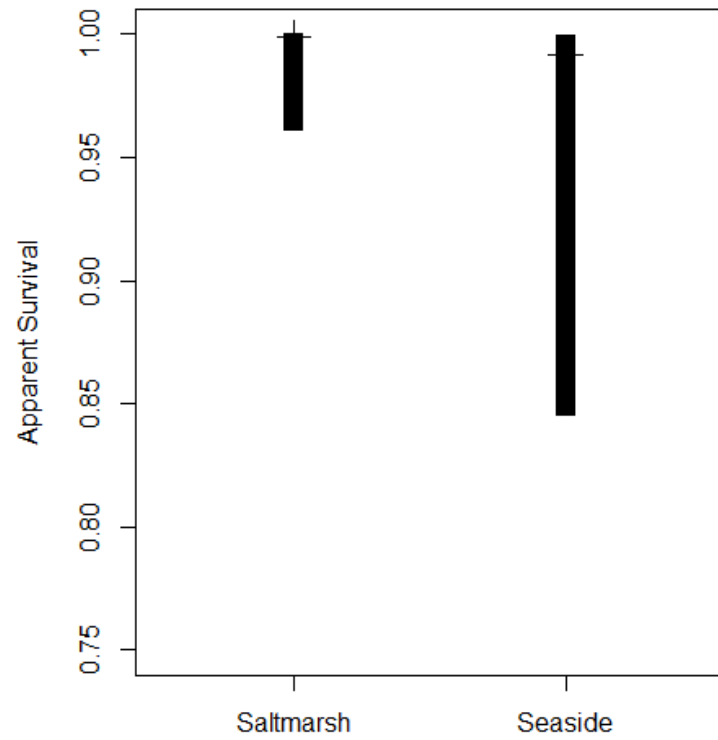


Figure 3: Model-averaged estimates of apparent weekly survival for Saltmarsh and Seaside Sparrows during the winter. The bars represent 95% confidence intervals around the mean (indicated by the plus sign).

CHAPTER 4: MIGRATORY CONNECTIVITY IN TIDAL MARSH SPARROWS: INSIGHTS FROM SEX RATIOS, BODY SIZE, AND LONG-DISTANCE RECAPTURES

ABSTRACT

In many migratory species, links between breeding and wintering populations are unknown. Yet, events that take place during migration or winter can influence individuals, and even populations, on the breeding grounds. Consequently, understanding the degree of connectivity between populations on the breeding and wintering grounds is important for understanding the mechanisms behind mortality and for making informed conservation decisions. Weak migratory connectivity can be a result of latitudinal segregation by sex and/or body size on the non-breeding grounds. Through banding along a latitudinal transect from southern North Carolina to northern Florida, I found no evidence for sex- or size-based trends in wintering Saltmarsh (*Ammodramus caudacutus*) or Seaside (*A. maritimus*) Sparrows. Long-distance banding recapture records further imply that Saltmarsh Sparrow populations exhibit only weak connectivity: individuals from similar non-breeding sites were captured at disparate breeding locations and vice versa. I also found no evidence for latitudinal segregation by size in Nelson's Sparrows (*A. nelsoni*). I had insufficient long-distance recapture records for Seaside (one) or Nelson's Sparrows (five) to draw conclusions regarding migratory connectivity in these species.

INTRODUCTION

Estimates of species' vital rates throughout the annual cycle are important for understanding when and where mortality occurs and for making informed decisions about how to allocate conservation money and effort (Holmes 2007; Faaborg et al. 2010). Yet, for most migratory species, defining populations and quantifying population parameters is far from straightforward (Faaborg et al. 2010). Survival rates may differ by season (Robinson et al. 2010), and vary among breeding and/or non-breeding locations due to habitat loss (Zitske et al. 2014), habitat quality (Marra and Holmes 2001), management regimes (Thatcher et al. 2006), and abiotic conditions (Lok et al. 2011). Mortality may also be highest during migration (Sillelt and Holmes 2002; Newton 2006), when populations mix along shared migration routes. Events and processes occurring in one season can also carry-over and continue to influence individuals in subsequent seasons (Holmes 2007; Norris and Marra 2007; Harrison et al. 2011).

Migratory connectivity, or the degree to which individuals from the same breeding populations also make up the same wintering populations, is unknown for most species (Webster et al. 2002; Boulet and Norris 2006; Faaborg et al. 2010). While estimating an average annual survival rate for a population may be sufficient for projecting population dynamics into the future, understanding how survival varies among individuals is important for determining the mechanisms behind mortality rates (Webster et al. 2002). For example, if a species has strong migratory connectivity between breeding and non-breeding populations, large storms or other damaging events on the non-breeding grounds could have a significant impact on a particular breeding population. If, instead, connectivity for the species was weak, the effect of a winter storm on breeding populations would be diffuse.

Strong migratory connectivity, which has been observed in species such as the Snow Bunting (*Plectrophenax nivalis*) (Macdonald et al. 2012), Common Nightingale (*Luscinia megarhynchos*) (Hahn et al. 2013), and Swainson's Thrush (*Catharus ustulatus*) (Cormier et al. 2013), occurs when most individuals in a population begin and end migration in the same regions. Weak connectivity, which has been observed in species as diverse as the Black Oystercatcher (*Haematopus bachmani*) (Johnson et al. 2010), Northern Gannet (*Morus bassanus*) (Fifield et al. 2014), and Brewers (*Artemisiospiza breweri*) and Sagebrush (*A. nevadensis*) Sparrows (Knick et al. 2014), can occur through several mechanisms. In many migratory species, males do not migrate as far as females do, leading to latitudinal segregation by sex on the non-breeding grounds (Cristol et al. 1999; Jenkins and Cristol 2002). One hypothesis as to why this pattern occurs is that a short migration distance facilitates early arrival to the breeding grounds (Cristol et al. 1999). In many species, males return to the breeding grounds earlier than conspecific females to claim territories and/or maximize their mating opportunities (Coppack et al. 2006; Canal et al. 2012; Morbey et al. 2012). Early-arriving individuals might migrate shorter distances than later-arriving individuals in the same breeding population (Ketterson and Nolan 1983).

Weak connectivity could also occur through latitudinal segregation by body size on the wintering grounds (Swanson 1992; Cristol et al. 1999). The farther a bird migrates, the greater amount of energy it spends (Wikelski et al. 2003), and the longer it is exposed to *en route* risks of predation (Ydenberg et al. 2003) and storms (Butler 2000; Newton 2007). Mortality during migration can be significant (Newton 2006), and, in one study, was estimated as 15 times greater than during the breeding or non-breeding periods (Sillett and Holmes 2002). Yet

temperature can influence winter survival and maintenance of body condition (Krams et al. 2013). If an individual's probability of surviving the winter in good condition is sufficiently greater at more distant wintering locations, the benefit could be worth the risks of a long migration. Body size affects susceptibility to cold; larger bodied individuals may be better able to maintain body condition and survive during the periods of cold temperatures found at higher latitudes than smaller individuals can (Ketterson and Nolan 1976; Newton 2006). Unseasonable periods of cold can lead to size-biased spikes of mortality (e.g. Brown and Brown 1998). If larger birds are not penalized by wintering at sites with colder temperatures, they can take advantage of the shorter migration distances, whereas a smaller bird might be better off migrating the longer distance to reach warmer wintering areas (Ketterson and Nolan 1976).

Three closely-related species of sparrows rely on tidal marshes for much—if not all—of their annual cycles, and are species of high conservation concern: Saltmarsh (*Ammodramus caudacutus*), Nelson's (*A. nelsoni*) and Seaside (*A. maritimus*) Sparrows. The aim of this study was to investigate migratory connectivity between breeding and non-breeding populations of these sparrows by assessing the evidence for sex- and size-based latitudinal segregation on the non-breeding grounds. In both Saltmarsh and Seaside Sparrows, males return to the breeding grounds earlier than conspecific females (Chapter 1). This pattern of arrival could be caused by differences in migration distance, reflecting sex-based latitudinal segregation on the non-breeding grounds, with males wintering farther north than females. All three species are short-distance migrants, and the northernmost portion of their wintering ranges (Virginia) is colder, on average, than the southernmost portion (Florida), and has a greater likelihood of snow and ice. These differences in temperatures could lead to size-based segregation, with larger

individuals wintering farther north than smaller individuals. I also compiled long-distance recapture records of tidal marsh sparrows banded on the breeding grounds and recaptured on the wintering grounds, or vice versa. These records are the product of collaboration among a group of researchers with active tidal marsh sparrow mist-netting programs, and represent a series of linkages between breeding and wintering populations. Historically, very few long-distance recaptures have occurred in these species (Greenlaw and Rising 1994; Post and Greenlaw 2009; Shriver et al. 2011).

METHODS

Study System: The Saltmarsh Sparrow is a tidal-marsh endemic, with a global population contained almost entirely on the Atlantic Coast of the USA (Greenlaw and Rising 1994; Greenlaw and Woolfenden 2007). There are two recognized subspecies, the northern *A. c. caudacutus*, which breeds from Maine to New Jersey, and the southern *A. c. diversus*, which breeds from New Jersey to the Delmarva Peninsula (Greenlaw and Rising 1994; F. Smith, unpublished data). Although some *A. c. diversus* are non-migratory, the wintering range of both subspecies is from Virginia to Florida, with the highest concentration of wintering birds in South Carolina and Georgia (Greenlaw and Woolfenden 2007). Nelson's Sparrow has three recognized subspecies with distinct breeding ranges: *A. n. nelsoni* in the northern Great Plains; *A. n. alterus* along the St. James Bay coast, and *A. n. subvirgatus* along the Atlantic coast, from Massachusetts to Nova Scotia (Shriver et al. 2011). The subspecies have overlapping non-breeding ranges along the southern Atlantic and Gulf coasts (Greenlaw and Woolfenden 2007). Saltmarsh and Nelson's Sparrows are sister species (Klicka et al. 2014) and hybridize where

their breeding ranges overlap (Walsh et al. 2011). Seaside Sparrow, which is sister to the Saltmarsh/Nelson's pair (Klicka et al. 2014), is also a tidal marsh specialist, with six recognized extant subspecies that breed along the Atlantic and Gulf of Mexico coasts (with the exception of *A. m. mirabilis*, which is resident of the Everglades, in Florida) (Post and Greenlaw 2009). The northernmost subspecies, *A. m. maritimus*, regularly breeds as far north as Massachusetts and, occasionally, New Hampshire and Maine, and winters from Virginia to northern Florida (Post and Greenlaw 2009). *A. m. macgillivraii* is a non-migratory resident from North Carolina to northern Florida, and the other four subspecies are non-migratory residents of Florida and the Gulf of Mexico coast. Where their ranges overlap, Saltmarsh, Nelson's, and Seaside Sparrows often co-occur in the same marshes. All three species are considered to be of high conservation concern and the Saltmarsh Sparrow is considered vulnerable to extinction (Butcher et al. 2006-2007; BirdLife BirdLife 2013).

Study Sites: I conducted mist-netting along a latitudinal transect comprising tidal marshes in North Carolina (NC), South Carolina (SC), Georgia (GA), and Florida (FL), between 5 December and 13 March during the 2011-2012, 2012-2013, and 2013-2014 winters. From north to south, the banding sites were located within: Fort Macon State Park (Atlantic Beach, NC, 34°41'53.60"N, 76°41'5.81"W), the Anne Tilghman Boyce Coastal Reserve (Cherry Grove Beach, SC, 33°50'57.34"N, 78°35'17.67"W), Huntington Beach State Park (Murrell's Inlet, SC, 33°31'15.98"N, 79° 3'3.79"W), the North Inlet-Winyah Bay National Estuarine Research Reserve (Georgetown, SC, 33°20'19.32"N, 79°11'16.66"W), Cape Romain National Wildlife Refuge (Awendaw, SC, 32°59'29.96"N, 79°37'19.07"W), public land along the causeway to Jekyll Island

(Brunswick, GA, 31° 6'26.71"N, 81°29'15.78"W), Little and Big Talbot Island State Parks (near Jacksonville, FL, 30°27'45.06"N, 81°25'42.47"W), Timucuan Ecological and Historical Preserve (30°27'18.58"N, 81°27'9.60"W), and Faver-Dykes State Park (near St. Augustine, FL, 29°42'10.64"N, 81°14'44.33"W).

These sites encompassed the majority of the Saltmarsh Sparrow and *A. m. maritimus* winter ranges, as well as much of the winter ranges of all three Nelson's subspecies, although *A. n. nelsoni*, in particular, also winters in high numbers along the Gulf coast (Greenlaw and Rising 1994; Post and Greenlaw 2009; Greenlaw and Woolfenden 2007; Shriver et al. 2011). I selected the specific banding locations based on suggestions from collaborators, local birders and sighting records on eBird.org, a website on which birders can submit geo-referenced observations that can then be viewed through the website's mapping tools to visualize temporal and spatial patterns in species' sighting records (Sullivan et al. 2009). I also scouted, unsuccessfully, for appropriate tidal marsh sparrow netting locations in North Carolina, as far north as Currituck National Wildlife Refuge on the Outer Banks, and as far south in Florida as Merritt Island National Wildlife Refuge.

Mist-netting: At low tide, the marshes in my study area are relatively dry and the sparrows are widely dispersed, making them difficult to locate and catch. Consequently, I only netted during spring tides when there was sufficient tidal amplitude to flood the marshes and cause the sparrows to congregate within areas with tall vegetation or high elevation. At these times, which lasted about seven days around each full and new moon, I set nets up at high elevation points, either along the upland edge of the marsh or at high spots within the marsh. Each

banding session began 1.5-2 hours before peak tide, or, if peak tide occurred before daybreak, at dawn. Banding sessions ended when the tide had fallen to the point that I could no longer catch birds. I only conducted netting on days without rain, excessive wind, or temperatures below 4.5° C, and I released every bird close to its capture location. Due to the unique configuration of each high tide roost, the number and locations of nets varied by site, but I typically used one to three 12-m nets at a time. I left the nets open during the banding session if there were not many sparrows, but I closed them during processing if there was a risk of catching more birds at one time than I could safely extract and process. I identified each bird to species, but could not reliably distinguish among subspecies. I banded each bird with a USGS aluminum band, took standard morphological measurements, including tarsus and nares to bill tip, and weighed each bird to the nearest 0.1 g using a Pesola scale. I collected a feather sample from each Saltmarsh and Seaside Sparrow for genetic sexing by gently pulling up to two rectrices or breast feathers and/or collecting feathers that fell out during handling.

Genetic Sexing: I used NucleoSpin Tissue DNA extraction kits (Macherey-Nagel, Duren, Germany) to extract DNA from feathers collected in the field. I amplified the DNA according to Griffiths et al. (1998), using gender primers P2 and P8 in a single PCR. This process amplifies sections of two avian sex chromosome genes, CHD-W, which is only found in females, and CHD-Z, which is found in both sexes. Following amplification, I resolved the samples on 1.5% agarose gels and determined the sex identifications based on the presence of one (male) or two (female) bands. This banding pattern is due to a length polymorphism in the two gene variants. I validated the methods by confirming accurate sexing for six males and six females from our

Connecticut study sites that had previously been sexed in the field by the presence of a brood patch (female) or enlarged cloaca (male).

Long-distance recaptures: In addition to my non-breeding season mist-netting, I compiled records of long distance, between-season movements of tidal marsh sparrows. My network of collaborators includes nearly all individuals who conduct regular mist-netting of tidal marsh sparrows on either the breeding or non-breeding grounds, or who have done so recently. Through this network, I was able to quickly identify the original banding date and location of any tidal marsh sparrow that was recaptured away from its banding location. The majority of the breeding grounds captures were from study sites run by the Saltmarsh Habitat and Avian Research Program (tidalmarshbirds.org), a collaborative effort through which tidal marsh sparrows are systematically mist-netted throughout the breeding season, at sites from southern New Jersey to Maine, following a standardized protocol (see Ruskin et al. in prep for more detail on the systematic mist-netting methods and study sites). I estimated distances between sites using the path tool in Google Earth. I followed along the coast to mimic a migratory route constrained to tidal marshes (as opposed to straight-line distances that included large expanses of open water).

As tidal marsh sparrows have been shown to exhibit high degrees of site-fidelity, both within- and between-seasons (DiQuinzio et al. 2001; Winder et al. 2012; Chapter 3), I assumed that each individual was a member of the breeding population in which it was captured during the breeding season. Similarly, for the non-breeding season, I assumed that each individual spent the winter at the location where it was captured, if that capture occurred between 1

December and 31 March. These are conservative dates that exclude the known migratory periods for these species (Chapter 1; A. Given and F. Smith, personal communication; Winder et al. 2012).

Statistical Analyses: To test for relationships between latitude and the proportion of males out of the total number of birds captured at each location, I ran separate logistic regression models for Saltmarsh and Seaside Sparrows, using base R 3.1.1 (R Core Team 2014). I used AIC scores from the AICcTab function in the bbmle package (Bolker 2014) to compare each model to a null model and to test for an effect of latitude. I lacked sex information for Nelson's Sparrows and did not conduct an equivalent analysis for that species. For each location, I pooled the number of genetically-sexed individuals captured on all winter banding dates, in all years, to create location-specific sex ratios. At nearly all of the locations, I had multiple capture sites (i.e. multiple high tide roosts within the same general vicinity and latitude), from which I pooled all captures. I also pooled captures for the northern Florida sites because the distance between the sites (up to 25 km) was trivial compared to the latitudinal scale of interest, and because the sites were located within a continuous marsh complex.

To test for relationships between latitude and body size for Saltmarsh, Seaside, and Nelson's Sparrows, I estimated separate linear mixed effects regressions of tarsus length against latitude for each species, with sites treated as random effects. I ran the models using the nlme package in R (Pinheiro et al. 2015). I selected tarsus as the body size index because it is a more consistent measurement than wing length, which can change throughout the year due to feather wear (Flinks and Salewski 2012), or culmen length, which varies within tidal

marsh sparrow species based on breeding latitude rather than body size (Greenberg et al. 2011). Tarsus length has been found to be a highly repeatable measurement that does not vary once an individual is fully grown (Danner 2012). All parameter estimates are given \pm standard error.

RESULTS

I genetically sexed 301 Saltmarsh and 280 Seaside Sparrows captured on the wintering grounds. I found no evidence of sex-based latitudinal segregation in either species. In Saltmarsh Sparrows, the sex ratios ranged from 66% males at North Inlet, in central South Carolina, to 20% males at both Jekyll Island, Georgia, to the south, and Fort Macon, North Carolina, to the north (Table 1). The results of the logistic model for Saltmarsh Sparrows showed no relationship between sex ratio and latitude, and the model containing latitude performed worse than the null model (for the model containing latitude: $\Delta AIC_c = 3.2$, $w = 0.17$, $\beta = 0.022 \pm 0.090$, with 26.1% of the residual deviance explained). For Seaside Sparrows, the sex ratios were less variable among sites, ranging from 43% males to 65% males at sites with greater than 10 individuals (Table 1). The logistic regression for Seaside Sparrows also showed no relationship and performed worse than the null model (for the model containing latitude: $\Delta AIC_c = 27.8$, $w = <0.001$, $\beta = -0.011 \pm 0.084$, with 10.3% of the residual deviance explained). Using tarsus length as an indicator of body size, I also found no evidence for size-based latitudinal segregation in Saltmarsh ($N = 300$, $\beta = -0.027 \pm 0.043$, $df = 16$, $t = -0.631$, $p = 0.537$), Seaside ($N = 274$, $\beta = -0.060 \pm 0.045$, $df = 18$, $t = -1.346$, $p = 0.195$), or Nelson's Sparrows ($N = 227$, $\beta = -0.103 \pm 0.051$, $df = 18$, $t = -2.02$, $p = 0.059$).

For Saltmarsh Sparrows, the 17 long-distance recapture records suggest low levels of migratory connectivity between breeding and wintering populations (Figure 1). The majority of the non-breeding capture locations were in South Carolina, within a ~150 km stretch of coast spanning from Kiawah Island north to Murrell's Inlet. Of the nine Saltmarsh Sparrows that were captured within this region, one bred in New Jersey, one in New York, three in Connecticut, one in Rhode Island, two in Massachusetts, and one in New Hampshire; these sites span ~600 km of coast. One of these birds was captured in South Carolina on 7 April 2013, which could be within the migratory period. This bird, however, was in the midst of molt, and Saltmarsh Sparrows are thought to complete pre-alternate molt prior to migration (Pyle 1997; A. Given, personal communication). For the rest of the 17 Saltmarsh Sparrows with long-distance recapture records, one was captured in Maine and Virginia, one in New Hampshire and northern South Carolina; one in New Hampshire and northern Florida (captured in Florida during winters 2012-2013 and 2013-2014), one in Connecticut and southern Georgia, and one in Rhode Island and the Gulf coast of Florida. The remaining three Saltmarsh Sparrows with long-distance recapture records were captured on the non-breeding grounds during migratory periods: one was captured in Maine and North Carolina (24 November, 2006), one in Rhode Island and Virginia (29 September 2009), and one in Connecticut and Virginia (12 September 2012).

I recorded five long-distance recaptures of Nelson's Sparrows (Figure 1). Two were banded in Maine and recaptured in northern Florida, and a third was re-sighted (based on color bands) on the Gulf coast of Florida. During the migratory period, one that was banded in Maine was recaptured in South Carolina (6 November 2014), and one that was banded in New Hampshire was recaptured in Virginia (9 March 2011). Whether these birds were migrating is

unknown; the Virginia capture occurred before the main pulse of spring migrants (F. Smith, personal communication). I only have one long-distance recapture record for Seaside Sparrows (Figure 1). This bird was banded in Connecticut in 2010 and recaptured in South Carolina during winters 2011-2012, 2012-2013, and 2013-2014. It was also recaptured in Connecticut during summers 2012 and 2013.

DISCUSSION

Migratory connectivity is an outcome of individual decisions—how far to migrate and whether to remain faithful to a site—amplified over an entire species (Marra et al. 2006). These decisions may be influenced by the breeding strategies of individuals; for example, if a shorter migration enables individuals to return to the breeding grounds sooner and early arrival is advantageous (Ketterson and Nolan 1983; Cristol et al. 1999). Migration decisions also may reflect the cost:benefit trade-off between a long and potentially risky migration versus wintering in a location that may provide a higher probability of survival and a better chance of maintaining body condition than wintering sites nearer the breeding grounds (Ketterson and Nolan 1983; Cristol et al. 1999). The existence of sex- or size-based latitudinal trends suggests that a species has moderate-to-weak migratory connectivity. The lack of latitudinal trends by sex or size, however, does not automatically imply strong connectivity.

Although male Saltmarsh and Seaside Sparrows return to the breeding grounds before conspecific females (Chapter 1), I found no evidence that males of either species winter farther north than females. Other studies have found that migration distance does not necessarily correspond with arrival timing, as individuals with the longest migrations often depart the non-

breeding grounds earliest (Oppel et al. 2008). Migration distance and duration can be decoupled by flight speed (Nilsson et al. 2013), stopover duration (Smith and McWilliams 2014), and bad weather during migration (Gunnarsson et al. 2006). For Saltmarsh and, to a lesser extent, Seaside Sparrows, mist-net captures during the breeding season tend to be male-biased, especially early in the season (Post and Greenlaw 1982; Gjerdrum et al. 2008a; Chapter 1). Our overall non-breeding sex ratios were 56% males for Saltmarsh Sparrows and 54% for Seaside Sparrows. Saltmarsh Sparrow populations are likely male-biased, as the sex ratio of Saltmarsh Sparrow chicks is skewed, with 59% males (Hill et al. 2013). No similar analysis has been done for Seaside Sparrows. There is no evidence for sex-based differential survival in either species (Post and Greenlaw 1982; DiQuinzio et al. 2001; Chapter 3; C. Field in prep).

Previously, I found that neither body size nor body condition influenced the apparent probability of survival in either Saltmarsh or Seaside Sparrows wintering in central South Carolina (Chapter 3). Correspondingly, I found no evidence for latitudinal segregation on the non-breeding grounds based on body size in Saltmarsh, Seaside, or Nelson's Sparrows. Even if there was a relationship between body size and survival, individuals do not necessarily winter in the location at which they could have the maximum survival potential. A study on Eurasian Spoonbill (*Platalea leucorodia leucorodia*) connectivity and winter survival found that most individuals wintered at a site where survival was lower than at the other sites included in the study (Lok et al. 2011). Anecdotally, each year of my non-breeding banding included days during which the temperature did not rise above 0° C, and winter 2013-2014 included an ice storm that hit my focal South Carolina sites. Despite these inclement conditions, I have no evidence that the cold temperatures or ice storms caused spikes in tidal marsh sparrow

mortality, events that might reveal a connection between body size and/or condition and survival.

Small sample size is a limitation of my dataset. The sample sizes per site ranged from four to 159 genetically-sexed individual Saltmarsh Sparrows, five to 85 genetically-sexed Seaside Sparrows, and 6 to 54 Nelson's Sparrows, none of which were genetically-sexed. For each species, approximately 2/3 of the individuals were banded at two sites in central South Carolina. The small sample sizes at the higher and lower latitudes in the non-breeding range reduce our statistical power for detecting latitudinal trends in sex ratios and body size. Additionally, I could not reliably distinguish between the two Seaside Sparrow subspecies, *A. m. maritimus*, and *A. m. macgillivraii*. *The presence of A. m. macgillivraii could mask a sex-based latitudinal trend in Seaside Sparrows, as the male:female ratio in A. m. macgillivraii should have been constant throughout the annual cycle. The only way to detect a sex bias in migrant Seaside Sparrows (if one existed) would be to capture a sufficient number of A. m. maritimus to noticeably skew the observed sex ratio in one direction or the other.*

The long-distance recapture records suggest that Saltmarsh Sparrows have weak migratory connectivity. The majority of individuals with long-distance recapture records were captured on the non-breeding grounds in central South Carolina, due to the concentration of mist-netting in that area. Two of the Connecticut Saltmarsh Sparrows were banded in the fall (12 September 2012 and 6 October 2011), but they likely bred at their capture locations, because both were undergoing molt, and Saltmarsh Sparrows are thought to complete pre-basic molt at their breeding locations before beginning migration (Chapter 1; Pyle 1997).

Conservation on the wintering grounds is unlikely to appreciably influence breeding populations particularly if breeding and wintering populations of Saltmarsh Sparrows are weakly connected. In species with weak connectivity between breeding and non-breeding populations, conditions in specific non-breeding regions may only be experienced by a portion of a given breeding population. Consequently, population dynamics quantified on the breeding grounds may correlate more strongly with processes occurring on the breeding grounds than with events or processes taking place on the non-breeding grounds (Cresswell 2014). However, Saltmarsh Sparrows have a small range that is restricted to a single habitat. Tidal marshes are at risk from many sources, especially the combination of coastal development and sea level rise (Yin et al. 2009; Zhang and Leatherman 2011; Brittain and Craft 2012). Sea level rise will be particularly detrimental to the species on the breeding grounds, as flooding during high tides is already a primary cause of nest failure (Gjerdrum et al. 2008b; Bayard and Elphick 2011). Predation is more important than flooding as a cause of nest failure towards the southern end of the range (Kern et al. unpublished data; Ruskin et al. unpublished data). However, nest flooding causes a significant portion of failed nests throughout the species' breeding range, with the risk of failure by flooding influenced by nest initiation date and the height of high tide during flooding events (Ruskin et al. unpublished data). The northeast coast of the USA is also predicted to have greater acceleration in sea-level rise than other portions of the Atlantic coast (Yin et al. 2009), which will exacerbate nest flooding for most, if not all, of the Saltmarsh Sparrow range.

Band recaptures identify individual breeding and non-breeding locations much more precisely than most other methods of inferring connectivity, such as stable isotopes (e.g.

Chamberlain et al. 2000; Hobson 2005), trace elements (e.g. Szép et al. 2003; Font et al. 2007), parasites (e.g. von Rönk et al. 2015), or genetic analyses (e.g. Conklin et al. 2011; Irwin et al. 2011). Technological methods, such as geolocators (e.g. Bächler et al. 2010; Stanley et al. 2014) and satellite tracking devices (Oppel et al. 2008; e.g. Combreau et al. 2011) are an exception. These technologies can provide information about migratory routes, destinations, and movements within the non-breeding period, and include temporal as well as spatial information (Robinson et al. 2009; Higuchi 2012). However, each of these technologies also has limitations: geolocators do not give precise locations and require recapturing each individual in order to retrieve the data. Satellite trackers can currently only be carried by relatively large birds, and are only good for the duration of the battery. Automated radiotelemetry arrays can provide precise temporal and spatial information of the path that a tagged bird flies over a receiving tower. These radio tags have been used successfully for generating detailed information regarding migratory departures from breeding grounds and stop-over sites, including timing and initiation direction of flights (e.g. Mitchell et al. 2012; Sjöberg et al. 2015; Woodworth et al. 2015). While they could also be used for assessing migratory connectivity, the primary limiting factor is the number of receiving towers that must exist in the regions of interest. However, once a tower is in place, it can record movements of countless individuals, from multiple species and research projects.

Long-distance between-season recapture records from banding are hard to come by because they require a certain threshold number of birds to be banded and a certain amount of banding effort throughout the annual cycle and range (Thorup et al. 2014). Yet, if sufficient effort is in place during breeding and non-breeding seasons, banding recaptures can give

detailed insights regarding migratory connectivity: exactly where an individual bird was on a particular date. Detailed information about the individuals, including measures of body condition and habitat use, can also be collected. Much of the current knowledge about migratory connectivity has been gained through banding recoveries (e.g. Wernham et al. 2002; Ambrosini et al. 2009; Thorup et al. 2014). In evaluating recapture-based connectivity inferences, it is important to consider sample sizes and also to acknowledge potential differences in the mist-netting effort that has taken place at various sites throughout the breeding and non-breeding ranges. Using multiple methods to assess migratory connectivity can be more productive than relying on single methods (Veen 2013; Rushing et al. 2014), and banding has been informatively combined with stable isotopes and mitochondrial DNA (Boulet et al. 2006; Greenberg et al. 2007). The most appropriate methods for learning about migratory connectivity depend on the species under consideration, including its range, habitat, and life history, as well as the human history of when and where it has been studied (Boulet and Norris 2006).

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Table 1: Sex ratios and sample sizes of Saltmarsh, Seaside, and Nelson’s Sparrows caught on the non-breeding grounds during our mist-netting along a latitudinal transect from southern North Carolina to northern Florida. The sex identifications for Saltmarsh and Seaside Sparrows were determined genetically; the Nelson’s Sparrows were not genetically sexed.

		Saltmarsh Sparrows				Seaside Sparrows				Nelson’s Sparrows
Location	Latitude	♀	♂	Total	♂:♀	♀	♂	Total	♂:♀	Total
Fort Macon, NC	34.696747	4	1	5	0.2	4	5	9	0.56	18
Waities Island, SC	33.849261	2	2	4	0.5	0	5	5	1	19
Huntington Beach, SC	33.521106	34	16	50	0.32	34	26	60	0.43	54
North Inlet, SC	33.3387	54	105	159	0.66	42	43	85	0.51	44
Cape Romain, SC	32.991656	5	8	13	0.62	7	12	19	0.63	6
Jekyll Island, GA	31.058506	4	1	5	0.2	12	22	34	0.64	8
Northern FL	30.455161	23	33	56	0.59	23	31	54	0.57	47
Faver-Dykes, FL	29.702956	6	3	9	0.33	6	8	14	0.57	21

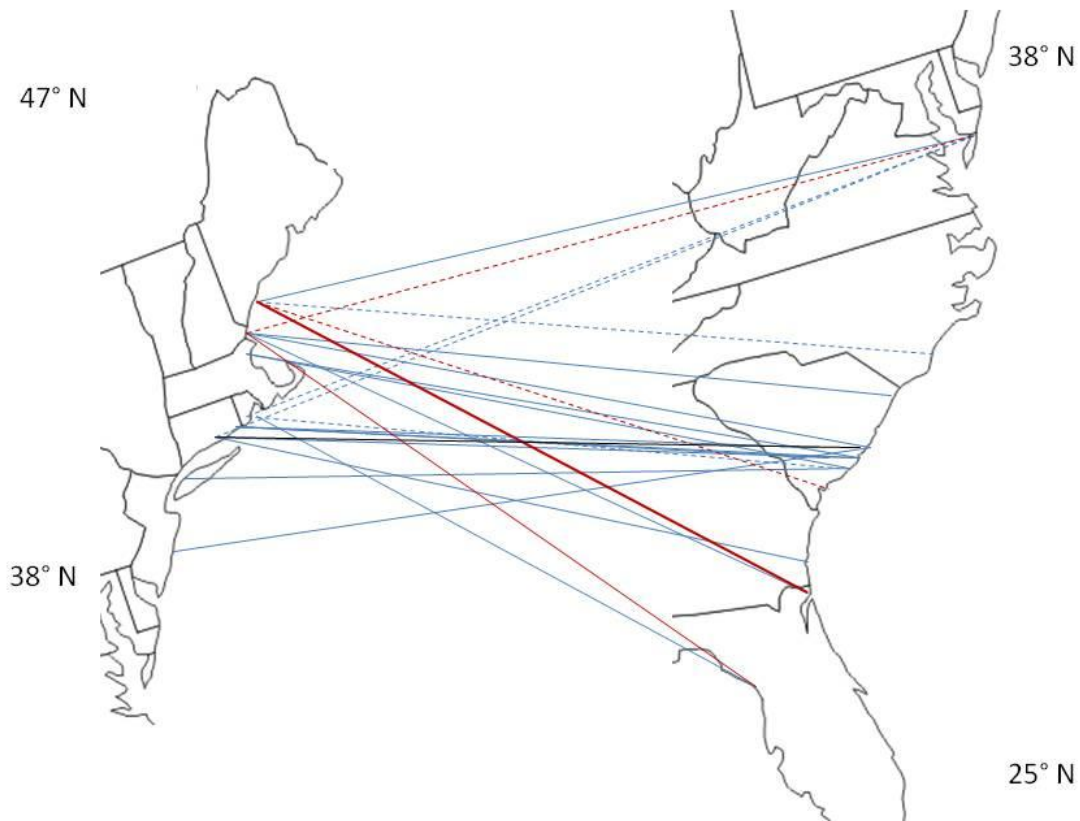


Figure 1: Recapture records of individual Saltmarsh (blue), Nelson's (red) and Seaside (black) Sparrows that were captured both on the breeding grounds, from Maine to New Jersey, and non-breeding grounds, from Virginia to Florida. Individuals that were captured on the non-breeding grounds during migratory periods are depicted with dashed lines. The northern and southern portions of the Atlantic coast are to scale.

CONCLUSIONS

To date, research on tidal marsh sparrows has focused primarily on the breeding grounds, including relationships between habitat features and sparrow occupancy and nesting patterns (e.g. Benoit and Askins 1999; Shriver et al. 2004; Meiman et al. 2012), impacts of management activities (e.g. Brawley et al. 1998; Elphick et al. 2015), and challenges associated with breeding in the tidal marsh environment (e.g. Shriver et al. 2007; Gjerdrum et al. 2008; Bayard and Elphick 2011). Habitat change, however, will be severe throughout the entire annual range (Craft et al. 2009) and events and processes that take place during one season can carry over and influence individuals at other times of the year (Norris and Taylor 2006; Harrison et al. 2011). Consequently, assessing the long-term persistence of these species requires detailed knowledge of the birds' basic biology throughout the entire year (Faaborg et al. 2010). My research objectives addressed fundamental questions about behavioral decisions and body condition/survival consequences of birds with different life history strategies. Studying the ecology of Saltmarsh and Seaside Sparrows, in particular, also has indirect conservation implications and could stimulate research on how individual-based ecological studies can contribute to setting conservation goals.

My underlying hypothesis was that an individual's reproductive investment influences its behavioral decisions, physical condition, and physiological state in ways that lead to differences in decisions and condition among individuals. While reproduction can be viewed as the specific event in which a donation of gametes results in offspring that may survive and reproduce in the future, the influence that reproduction has on an individual's life is much broader. For this reason, I defined reproductive investment as encompassing any behavioral or

physiological processes that occur during the breeding season and contribute to an individual's success in producing offspring. Within this definition, reproductive investment encompasses three broad categories: 1) physiological processes, namely sperm and egg development; 2) overt parental care behaviors such as incubating, brooding, and provisioning chicks; and 3) behaviors other than parental care, including defending territories, acquiring mates, and building nests. There are energetic investments associated with all of these processes and behaviors (Williams 1966; Trivers 1972; Owens and Bennett 1994). There are also risks associated with many of the behaviors, particularly related to predation (Post and Götmark 2006a; Post and Götmark 2006b). Together, the behaviors and physiological processes interact to influence risk levels and vulnerability (Newton 1998). For example, a bird's likelihood of evading predation is related to its flight efficiency which, in turn, is related to its muscle condition and fat stores (Cresswell 2009).

Saltmarsh and Seaside Sparrows were an ideal species pair with which to investigate the influence of reproductive investment on other events and processes in the annual cycle. The Saltmarsh Sparrow breeding system, with no territoriality, extensive multiple mating in both sexes, and female only care, is extremely unusual for a passerine (Greenlaw and Rising 1994; Owens and Bennett 1997). Seaside Sparrows follow a more typical passerine breeding system, with territoriality, social monogamy, and bi-parental care (Post and Greenlaw 2009). Because Seaside Sparrows are also very closely related to Saltmarsh Sparrows (Klicka et al. 2014) and have overlapping breeding and non-breeding ranges (Greenlaw and Rising 1994; Post and Greenlaw 2009), they provided a contrast to Saltmarsh Sparrows. I predicted that breeding strategies would structure individual's lives, and that individuals would pay a cost for their

reproductive investment, particularly based on their degree of parental care. Specifically, I predicted that differing priorities at the beginning of the breeding season would lead to females arriving to the breeding grounds later than conspecific males. After the breeding season, I predicted that females would initiate molt later, complete molt faster, molt into poorer-quality feathers with more fault bars and a higher susceptibility to abrasion, have delayed departure from the breeding grounds, and have reduced body condition and a lower probability of survival than conspecific males. I also predicted that females would spend the winter farther south than conspecific males, and that poor condition from the breeding season may carry over and lead to reduced condition in the non-breeding season. Furthermore, I predicted that female Saltmarsh Sparrows would experience greater costs of reproduction than female Seaside Sparrows, and that male Saltmarsh Sparrows would experience lesser costs of reproduction than male Seaside Sparrows.

My data suggested that female Saltmarsh Sparrows return to the breeding grounds later than Seaside Sparrows or conspecific males. During the breeding season, I found that they have lower body condition, carry slightly more fat, and have the most extensive rectrix damage. After breeding, I found that they have delayed molt, a faster molt rate, and depart the breeding grounds later than Seaside or male Saltmarsh Sparrows. My results indicated that the reduced body condition continues into the winter, although I did not find a difference in winter feather condition between the species or sexes. Yet, despite these apparent costs of reproduction that are experienced by female Saltmarsh Sparrows, I found no evidence that female Saltmarsh Sparrows have greater mortality than conspecific males or Seaside Sparrows. I observed similar differences between the sexes in male and female Seaside Sparrows, with females experiencing

only non-lethal costs of reproduction. The contrast between male Saltmarsh and Seaside Sparrows, however, implies that costs of reproduction occur through much more than parental care. Male Saltmarsh Sparrows lie on the opposite end of the parental care spectrum as female Saltmarsh Sparrows, and provide no parental care. Yet, compared to Seaside Sparrows of both sexes, male Saltmarsh Sparrows had neither the best body condition nor the most pristine feathers. Male Saltmarsh Sparrows also neither molted earlier nor departed the breeding grounds before Seaside Sparrows.

Comparing both within and between species provided insights that neither comparison, alone, would have given. Overall, my results support the hypothesis that events and processes that take place during the breeding season are influential in structuring other stages within the annual cycle and are reflected in various aspects of body condition. Yet, my results also indicate that parental care is not the only factor influencing individuals' behavior and condition. Male Saltmarsh Sparrows do not engage in parental care, but their intensive mate-seeking behaviors appear to have costs in terms of feather condition and, compared to Seaside Sparrows, body condition. Additionally, differences between the species, such as Seaside Sparrow's earlier arrival, departure, and molt, and the greater amount of feather wear in Seaside than Saltmarsh Sparrows, may be the result of different proximate and ultimate pressures operating on the two species. These factors may be unrelated to reproductive strategies.

The most significant conclusions of each of my chapters were as follows: 1) protandry may occur for different reasons in different species, reproductive investment can delay timing of pre-basic molt and migratory departure, and reduce molt rate; 2) feather condition can be influenced by a bird's activities, and most feather damage occurs in the breeding season 3)

reproductive investment can lead to poor body condition that carries over into the winter, fat stores may be a response to unpredictable circumstances such as those experienced by incubating females and wintering individuals, and while probability of survival is a combination of vulnerability and risk, the two factors may balance out and lead to no sex-based differences in mortality at any point in the annual cycle; 4) protandry may not always correspond with sex-based latitudinal segregation on the wintering grounds, and extensive banding efforts can lead to inferences regarding migratory connectivity, suggesting low connectivity between breeding and wintering sites in Saltmarsh Sparrows.

If the costs of reproductive investment are not reflected in increased mortality, the next question is whether the patterns and costs are associated with differences in reproductive success. Investigating this question for Saltmarsh and Seaside Sparrows would be best done by following individuals. In the tidal marsh sparrow system, the first step would be to address the following questions on the breeding grounds: do early-arriving male Seaside Sparrows have better territories than late-arriving males? Do early-arriving male Saltmarsh Sparrows have more mates than late-arriving males? How does territory quality and/or mate number influence reproductive success? Is reproductive success of females of either species influenced by arrival time? How do nest initiation and completion dates of individuals influence the timing of molt and migration departure? Do differences in individuals, in terms of territory quality, mate number, number of nesting attempts, and number of chicks fledged correlate with differences in body condition and/or feather damage during the breeding season?

On the non-breeding grounds, following individuals is more difficult, and a lot of basic information regarding the non-breeding ecology of tidal marsh sparrows is currently unknown.

Similarly, very little is known about their migratory habits. Although the assumption that the sparrows migrate along the coast, to stay within tidal marsh habitat, appears to be reasonable, actual migratory routes and use of stopover sites are unknown. The only information that we currently have are the handful of individuals with long-distance recapture records that were caught outside of the breeding grounds during the migratory period. In the spring and fall in Connecticut, we capture Nelson's Sparrows, which we know are migrants because they do not breed in Connecticut. Yet, we cannot determine which Saltmarsh or Seaside Sparrows are also only passing through. The most promising direction for gaining insights about migratory routes and behaviors in these species is through automated telemetry arrays. A network of receiving towers along the entire Atlantic coast could, if enough Saltmarsh and northern Seaside Sparrows were equipped with tags, provide an unusually comprehensive perspective, based on when individuals passed by particular points. If there were enough receiving towers, inferences could also be made regarding stopover durations and over-winter locations. This information could be correlated with weather and with the condition of individuals at the time of banding to provide inferences as to how these factors influence migratory speed, routes and stopover behavior (e.g. Taylor et al. 2011; Mitchell et al. 2012; Sjöberg et al. 2015; Woodworth et al. 2015).

During the non-breeding season, my results suggest no significant effect of body size or condition on survival, but do suggest that Seaside Sparrows have a lower probability of survival than Saltmarsh Sparrows. This result did not match my predictions, which was that larger individuals would have a greater probability of survival, but it did match published differences in annual survival between the two species (Winder et al. 2012). If it is unrelated to body size or

condition, the primary source of mortality may be predation. Investigating predation rates would be difficult, but doing so may be necessary to determine the cause behind the differential mortality. Also, although we know that Saltmarsh and Seaside Sparrows have similar habitat use during spring tides, when the marshes are flooded and birds congregate at high patches, there is anecdotal evidence for subtle roost selection differences. At my two focal South Carolina sites, Huntington Beach State Park and North Inlet, I had several banding locations, some of which were along upland edges, and some of which were at terrestrial “islands” within the marsh. At each of the upland edge sites, I captured more Seaside than Saltmarsh Sparrows; this was not true at any of the mid-marsh locations. Mist-net surveys of which sparrow species occupy different types of high tide roosts, including varying proximities to the upland and varying vegetation communities could provide more information. Sites closer to the upland may have greater risks of predation. Additionally, little is known about how either species uses the marsh at low tide, and differences in space-use could correspond with different risks of predation.

I would also like to reiterate Bridge’s (2011) call for additional research on feathers and molt, and how they influence—and are influenced by—life history strategies and individuals’ fitness. I want to emphasize the importance of studying feathers throughout the full annual cycle and in considering molt within the context of both life history and feather condition. In particular, I want to highlight three areas of study in which future research would be valuable:

- 1) comparative studies of feather wear across the annual cycle to further elucidate relationships between feather damage and habitats, life history strategies, and molt patterns.
- 2) quantification of feather quality, including fault bars, of feathers grown during each molt

period (pre-alternate vs. pre-basic), and for species with partial vs. complete molts, to understand the effects of recent life history events, feather growth patterns, and physiological state on feather quality; 3) specifically within the Saltmarsh and Seaside Sparrow system, documentation of-nest flooding histories of particular juveniles and the occurrence and severity of fault bars on those individuals' feathers to specifically link feather quality to the natural stressor of tidal flooding.

None of these research topics is likely to provide information that is critical to the conservation of tidal marsh sparrows. The reality for these species is that climate change has rapidly joined habitat loss and degradation, invasive species, and pollution as one of the most serious threats to global biodiversity (Wilcove et al. 1998; McCarty 2002; Thomas et al. 2004). Specialist species, with limited conditions under which they can survive, and coastal organisms, with inherent exposure to sea level rise, are among the groups that will be impacted most dramatically (Williams et al. 2008). Saltmarsh and Seaside Sparrows are both—highly specialized to, and dependent upon, their already-limited coastal habitat (Greenlaw and Rising 1994; Post and Greenlaw 2009). Studies on the breeding grounds invariably point to nest flooding—and the increase in flood-induced nest failure with rising sea levels—as the limiting factor to tidal marsh sparrow demography (Gjerdrum et al. 2005; Gjerdrum et al. 2008; Bayard and Elphick 2011; Field et al. unpublished data; Kern et al. unpublished data; Ruskin et al. unpublished data). Consequently, while detailed knowledge of birds' basic biology, including processes taking place during both the breeding and non-breeding periods, will not prevent the species from going extinct, now is the only time to gain information about these species,

including how an unusual breeding system like the Saltmarsh Sparrows' could have evolved and been maintained.

My results join the increasing pool of research that considers species within the context of multiple stages in the annual cycle. The American Redstart (*Setophaga ruticilla*) is arguably the passerine that has been most comprehensively-studied with a full annual cycle perspective. Studies on redstarts have shown sex-based habitat segregation on the non-breeding grounds, with implications for differential winter survival (Marra and Holmes 2001). Studies on the breeding grounds, with non-breeding habitat inferred via patterns in stable isotopes, suggest that poor-quality winter habitat and late arrival to the breeding grounds correspond with reduced reproductive success in both sexes (Norris et al. 2004), including greater confidence in paternity and more extra-pair copulations in males (Reudink et al. 2009). These patterns of migration and reproductive success not only correspond with non-breeding habitat type, but can also vary based on seasonal differences in rainfall on the wintering grounds (Studds and Marra 2007), which influences food availability and can lead to later migratory departures in dry years (Studds and Marra 2011). Black-tailed Godwits (*Limosa limosa islandica*) are a second species that has been the subject of extensive year-round research. Studies on godwits have found that individuals that use high-quality breeding habitat also use high-quality wintering habitat (Gunnarsson et al. 2005a), and that the use of poor-quality sites is increasing on both the breeding and non-breeding grounds, with implications for survival and migratory timing (Gill et al. 2001; Gunnarsson et al. 2005b). Similar work with Bar-tailed Godwits (*Limosa lapponica baueri*) has found greater variation among individuals in the timing of molt and post-breeding migration than in the timing of pre-breeding migration (Conklin et al. 2010). The

timing of arrival to the non-breeding grounds influenced the timing and rate of molt, but did not further carry-over and influence the time of migration back to the breeding grounds (Conklin and Battley 2012). Similar, although less extensive, work has been done in a wide variety of bird species, with the consensus that seasonal interactions and migratory connectivity can be extremely important for understanding the mechanisms behind population dynamics (Newton 1998; Marra et al. 2006; Wingfield 2008; Faaborg et al. 2010; Harrison et al. 2011).

In addition to the extensive empirical work, many theoretical approaches have emerged that create full annual cycle models to incorporate factors influencing population dynamics through the entire year (Hostetler et al. 2015). These theoretical approaches are varied and include: single- or two-season count models (e.g. Link and Sauer 2000, 2007), single-population density-dependent models (e.g. Sutherland 1996; Norris 2005; Sheehy et al. 2010), demographic migratory network models (e.g. Sutherland and Dolman 1994; Taylor and Norris 2010), seasonal matrix models (Mattsson et al. 2012; Flockhart et al. 2015), integrated population models (Besbeas et al. 2002; Brooks et al. 2004; Schaub and Abadi 2011), and individual-based models (e.g. McNamara and Houston 1996; McNamara et al. 1998; McNamara and Houston 2008). Each modeling approach relies on different types of empirical data, some of which are more readily available than others, and each has a unique combination of strengths and limitations (Hostetler et al. 2015). None of the ideas, empirical approaches, or theoretical methods is limited to birds, and our understanding of all organisms—particularly those that are migratory—will benefit from considering the full annual cycle of each focal species. With the combination of empirical studies, aided by technology, and new modeling

techniques, understanding species at the full-annual cycle level, including differences among populations and individuals, is becoming a reality.

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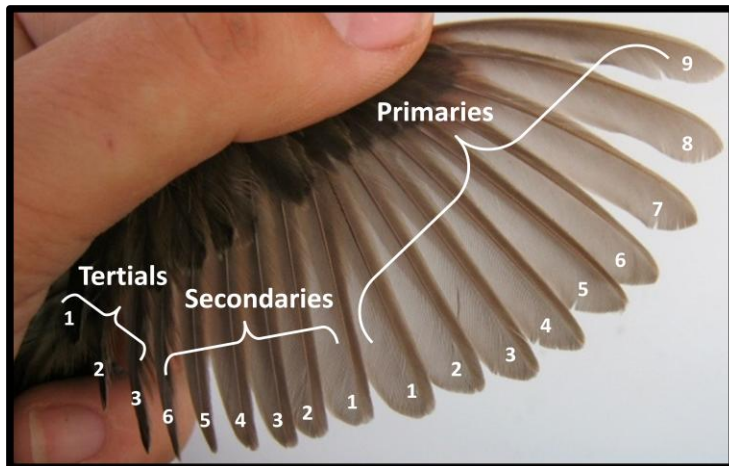
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APPENDIX A: MOLT PROTOCOL

Scoring based on: Ginn, H. B., and D. S. Melville (1983). *Moult in Birds*. British Trust for Ornithology, Thetford, UK.

Before attempting to evaluate a bird's molt status, make sure you are very comfortable with how feathers are named and counted. Saltmarsh and Seaside Sparrows have 9 primaries, 6 secondaries, 3 tertials, and 12 rectrices, as indicated in the pictures below. Note: from the outside of the wing, primaries are counted 9-1, whereas secondaries are counted 1-6, and tertials are counted 3-1. Rectrices are counted 6-1, outside to in, on each side. Birds molt in consistent feather orders, so it is important that you do not mix up the numbering systems.



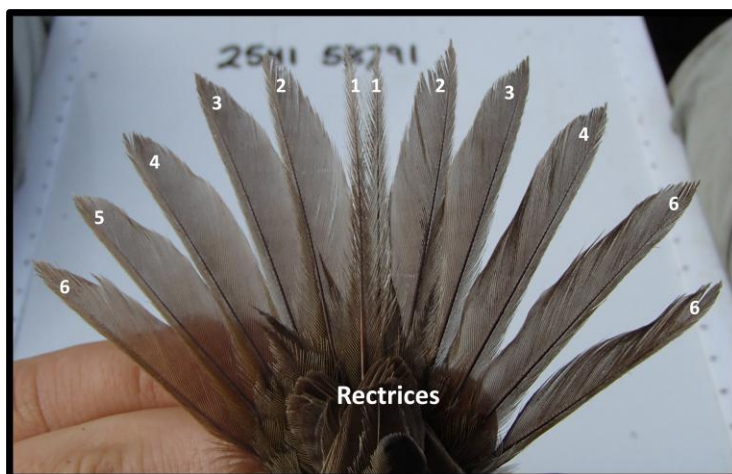


Figure A.1: Identification and numbering of Saltmarsh and Seaside flight feathers.

In the Field: Examine all captured birds for molt. If the bird is not obviously molting, check to be sure that the individual is not simply very early in or nearly done with molt by a) blowing gently on the bird's underparts, upperparts, and head to look for molting feathers; b) counting the flight feathers (primaries, secondaries, tertials and rectrices) to make sure that none are missing/pins.

If you are certain that the bird is not currently molting, designate "N" in the molt card column on the banding datasheet. In the notes section, indicate whether the individual has not yet begun molting, or if it is already finished. Remembering to do this is important, as the best estimates of molt initiation and duration include birds pre- and post-molt as well as birds actively molting (it is possible, however, to conduct analyses on only currently molting birds).

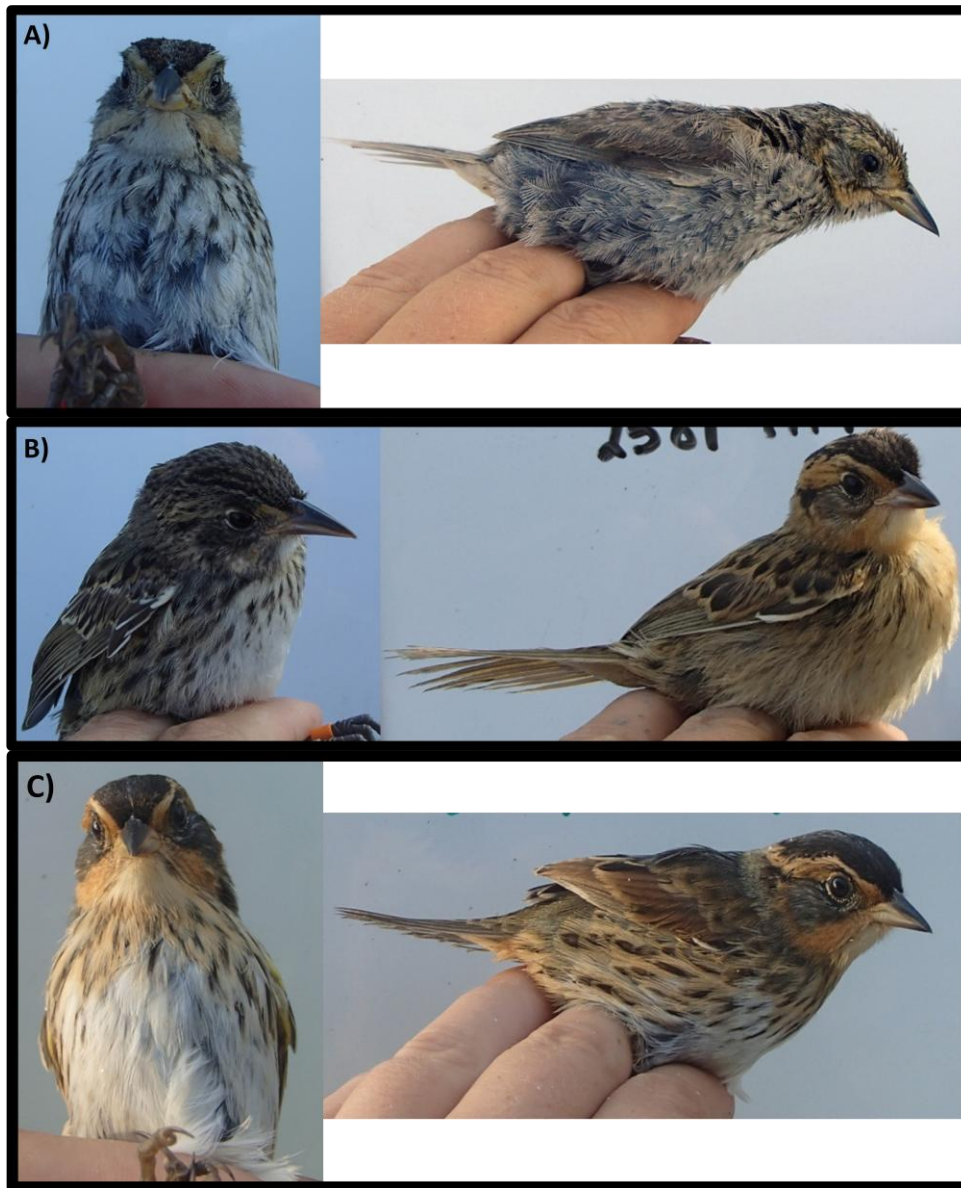


Figure A.2: Examples of sparrows pre- and post-molt. A) adult Saltmarsh Sparrow pre-molt; B) juvenile Seaside Sparrow (left) and Saltmarsh Sparrow (right) that have not yet molted; C) adult or Juvenile Saltmarsh Sparrow that has completed pre-basic molt.

If a bird is currently molting, designate “Y” in the molt card column of the banding datasheet and complete a molt card. Do not forget to complete the top portion of the molt card: species,

sex, age, band number, color band combination (if applicable), date, site, plot/subplot. This section provides the only information connecting the molt scores to the bird you are working with, so make sure it (especially the band number) is complete and accurate!

Scoring for Molt: Hold the bird in bander's grip during the entire molt scoring process. By shifting the bird's position in your hand, you will be able to open both wings and access both the upper and underparts. Never blow on a bird's feathers while it is in photographer's grip. Especially if you are new to molt scoring, this process can take a few minutes, and it is important to hold the bird so that it is secure and calm. If a bird appears stressed, it is more important to release it safely than to complete the molt card! Additionally, when you open a bird's wing, be very careful that you hold the wing by the joint, rather than by the feather; you do not want to injure a bird or damage its feathers!

Score each flight feather individually. If a bird is actively molting, this means that you should count all of the flight feathers before you record any scores so that you can be certain the feather you are scoring is the one you think it is (again, make sure you are very comfortable with the numbering system!). Similarly, make sure that you enter a feather score in the appropriate cell on the datasheet. If a feather has been dropped recently, the pin will not yet be visible, but you will be able to see the spot where the feather was attached—only if you look closely! It is very easy to get your count off due to missing feathers, so it is better to catch this at the beginning than after you have (incorrectly) filled in an entire row on the datasheet.

Score body feathers by region: all tracts of lesser and median coverts; underwing coverts; head (nape of neck to the top of the head + the face); upperparts (back); underparts (flanks and breast). Estimate the percent of feathers within that region that are in molt.

Score the following feathers individually:

Primaries (both wings)

Secondaries (both wings)

Tertials (both wings)

Rectrices

Primary coverts (one wing)

Secondary coverts (one wing)

Alulas (both wings)

Score the following body regions by group (Figure A.3):

Lesser and median coverts (circled in blue below)

Underwing coverts

Head (circled in red below)

Upperparts (circled in yellow below)

Underparts (circled in green below)

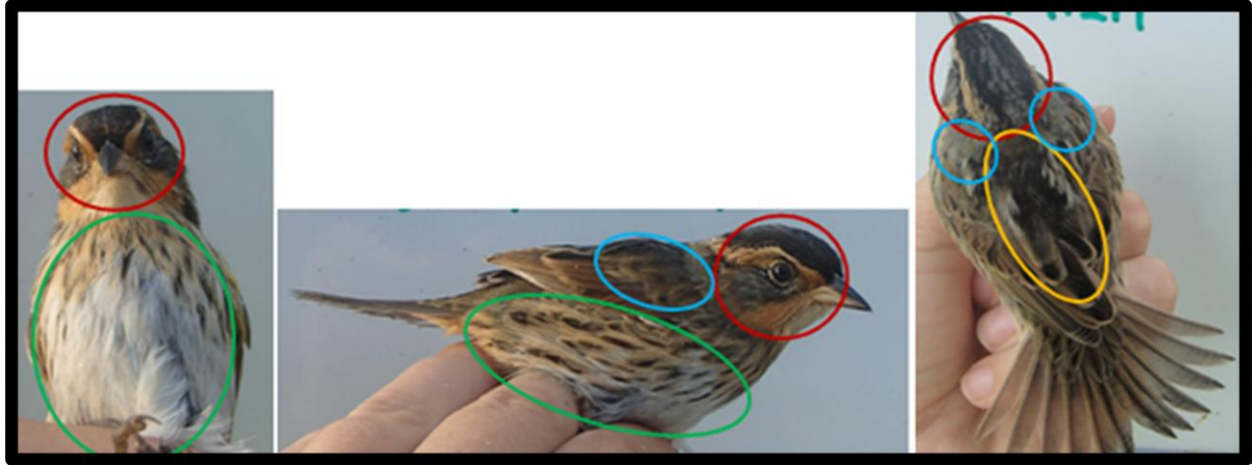


Figure A.3: body regions for molt scoring. Blue indicates “lesser and median coverts,” red indicates “head,” yellow indicates “upperparts,” and green indicates “underparts.”

Score individual feathers on a scale of 0 to 5:

- 0 = old feather
- 1 = missing or pin
- 2 = feather sheath broken to one-quarter grown
- 3 = one-quarter to three-quarters grown
- 4 = three-quarters to almost fully grown
- 5 = new, fully grown, with no sheath

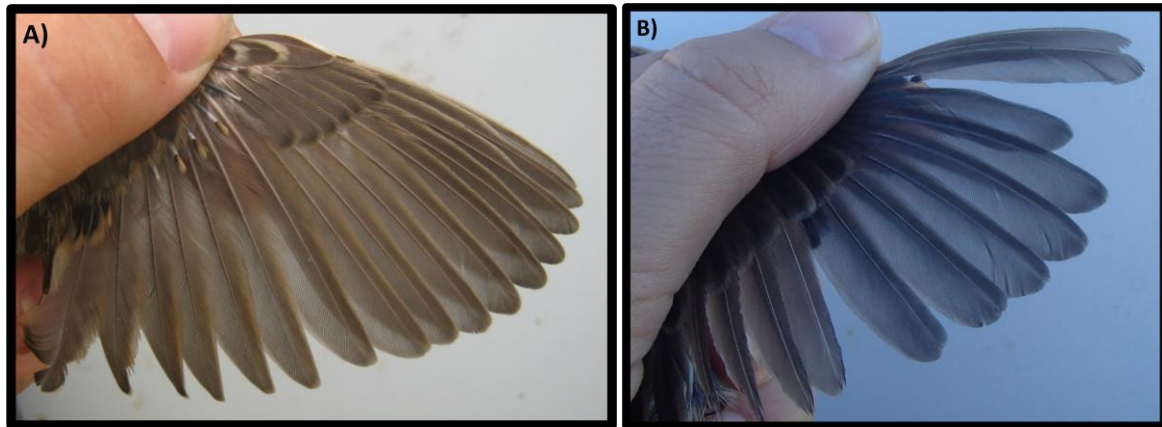
Score body regions on a scale of 0-5

- 0 = all, or nearly all, old feathers; less than 10% of feathers in molt
- 1 = 10 - 30% of feathers in molt
- 2 = 31 – 50% in molt
- 3 = 51 – 70% in molt
- 4 = 71 – 90% in molt
- 5 = 91% new to all new feathers

Molt patterns to keep in mind: Juvenile Saltmarsh Sparrows undergo complete body molts on the breeding grounds. They do not molt primaries, primary coverts, secondaries, or rectrices. These feathers should be scored 0, even if the bird is completely finished with molt (and looks nearly indistinguishable from a newly-molted adult). They do molt secondary coverts and tertials.

Juvenile Seaside Sparrows do not undergo any molt on the breeding grounds—but do not forget to check for molt anyway (atypical things can happen...) and note the status on the banding datasheet!

Adults of both species undergo complete molts on the breeding grounds. Old feathers are a dull brown, often with ragged edges. New feathers are brighter, slightly shiny, and have distinct edges.



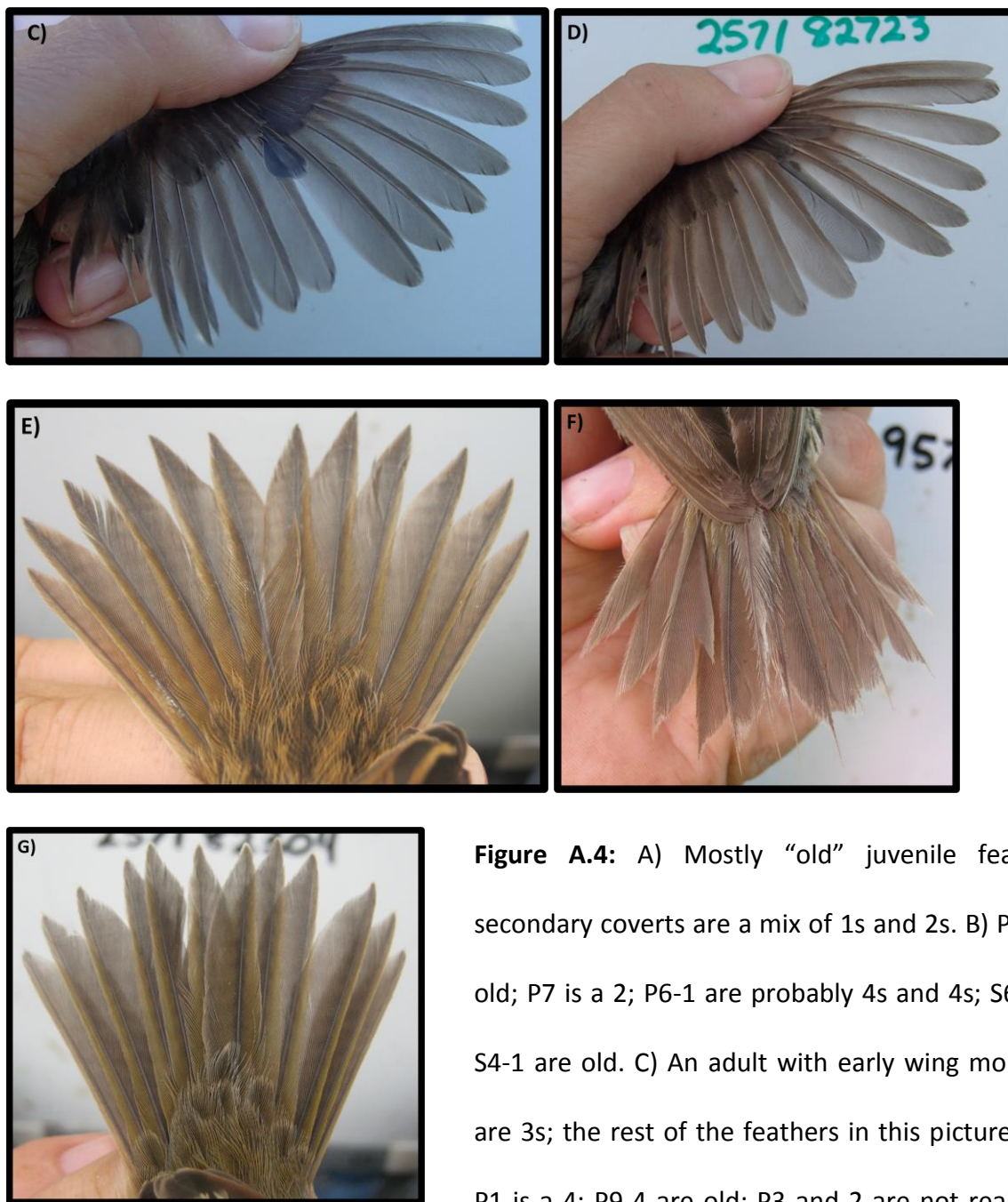


Figure A.4: A) Mostly “old” juvenile feathers. The secondary coverts are a mix of 1s and 2s. B) P9 and 8 are old; P7 is a 2; P6-1 are probably 4s and 4s; S6 and 5 a 2; S4-1 are old. C) An adult with early wing molt: P1 and 2 are 3s; the rest of the feathers in this picture are old. D) P1 is a 4; P9-4 are old; P3 and 2 are not really visible in the picture. E) An adult with old rectrices. F) An adult with new rectrices. G) A juvenile with “old” rectrices.

APPENDIX B: MOLT ANALYSIS WITH AND WITHOUT MASS-CORRECTED SCORES

In molt scoring systems (e.g. Pimm 1976; Underhill 1985; Underhill and Zucchini 1988), each feather is given an analogous score, as though all the feathers were the same size and contributed equally to the energetic demands of the molting process. In actuality, some feathers are significantly larger than others (i.e. tertials compared to primaries) and, for body molt, not all regions of the body contain the same number or size of feathers. To correct for these size-based discrepancies among feathers, I scaled molt scores by feather mass, thus analyzing a “percent feather mass grown” rather than “percent molt score achieved” (Dawson and Newton 2004).

I obtained feather masses from feathers plucked from a dead adult male Saltmarsh Sparrow. I dried the feathers in a fume hood (flight feathers) or in bags with dessicant (body feathers) for one week. I used an electric balance to individually weigh each flight feather, and calculated an average mass for each feather type (e.g. an average of P9 from the left and right wings). For body feathers, I obtained masses for all feathers from a given body region. Flight feather masses ranged from tertial 1, at .0020 g, to primary 9, at .0079 g. For body feathers, I combined the masses from different regions to represent the sections of the bird that were scored during the field molt assessments: individual primary and secondary coverts and alulas; grouped head, upperparts, underparts, lesser and median coverts, and underwing coverts. Overall, this individuals’ feathers weighed 0.9932 g., 0.2582 (26%) of which were flight feathers, and 0.7350 g (74%) of which were body feathers.

I followed the methods in Dawson and Newton (2004) to convert each score in the molt database to % feather mass grown for all Saltmarsh Sparrows for which I had field data (i.e.

excluding museum specimens, as I did not have body molt scores for them). I used the R package *moult* (Erni et al. 2013) to compare molt initiation and duration for male and female Saltmarsh Sparrows.

For both males and females, changing the scoring system did not change the results. Both the patterns and estimates of flight feather and body feather initiation and duration remained nearly the same (Figure B.1).

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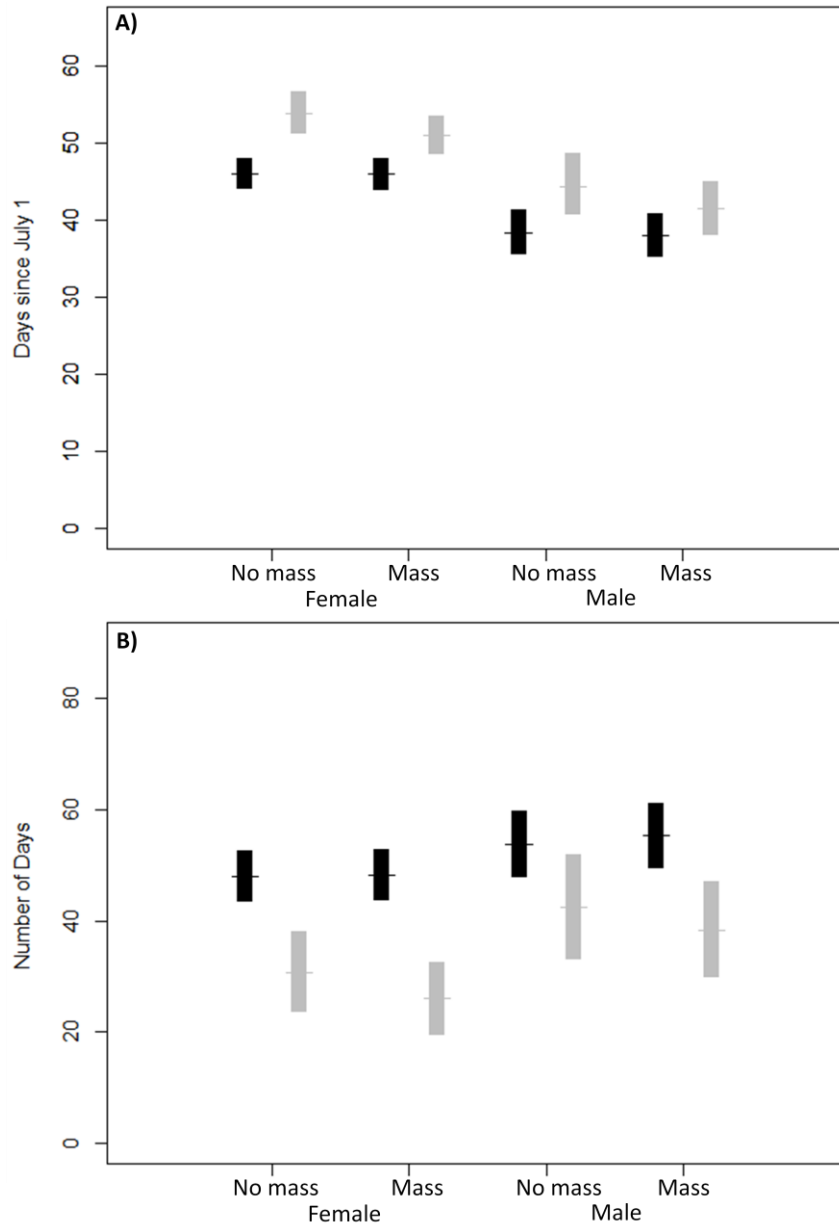


Figure B.1: A) Molt initiation and B) duration estimates for female and male Saltmarsh Sparrows with and without mass-corrected molt scores. The bars represent model estimates with 95% confidence intervals about the means. The black bars depict flight feathers and the gray bars depict body feathers.

APPENDIX C: FEATHER QUALITY AND CONDITION SCORING PROTOCOL

The goal of this protocol is to produce data that allow one to use a bird's feathers as an indicator of its condition. The flight feathers (the 18 primaries, secondaries, and tertials in one wing and the 12 rectrices in the tail) will be individually scored in three categories: 1) whether or not the entire feather is broken (broken feathers will not be scored further); 2) the extent of feather wear; 3) the presence, and severity of fault bars.

Definitions:

Breaks: Complete feather breaks occur when the rachis (the midrib of the feather) breaks, leaving a shortened feather stub. Breaks may be due to fault bars or to other causes, and we will not attempt to assign causation.

Wear: Feather wear occurs over time as the smooth, intact vane edges become increasingly frayed due broken barbs and/or barbules. All feathers wear; some more dramatically than others.

Fault Bars: Fault bars are weak points in feathers that can occur during feather growth. They are visible as translucent lines that run roughly perpendicular to the rachis. Note that fault bars are different from growth bars, which are alternating light and dark bands (especially visible in rectrices). Fault bars are an indication of some sort of stress during feather growth. Most feathers do not contain fault bars.

Feather identification: Flight feathers are named and, for the purposes of this protocol, numbered as shown in Figure C.1:

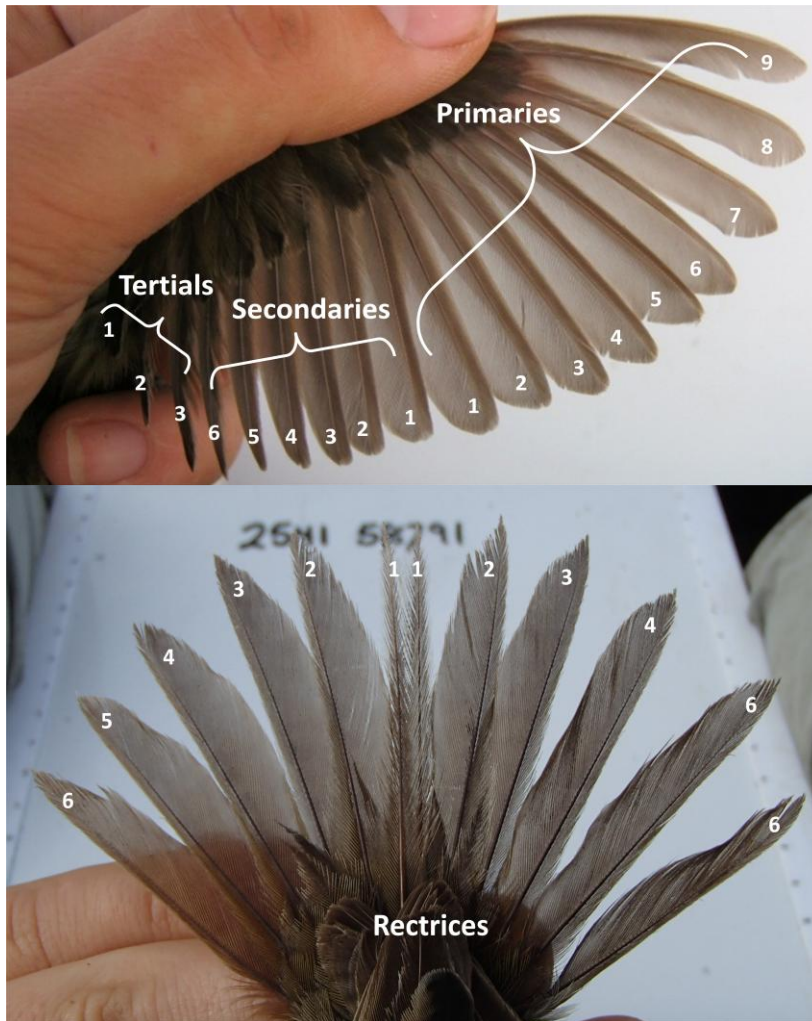


Figure C.1: Naming and numbering of flight feathers.

Feather photos:

For each bird, take a series of three pictures: one of the tail and two of the right wing. Take all three pictures in front of a white-board on which you have written the bird's band number. Be very careful to change the band number before photographing each bird. Make sure that the band number is visible in each picture.

Tail: Take a picture of the rectrices with the feathers spread as far apart as you can (Figure C.2A). Often, if you are holding the bird in photographer's grip (by the legs) and rotate

your hand so that your palm and the bird's back are facing you, the bird will naturally spread its tail feathers. If you hold the bird so that its head is facing you, you can photograph its tail without your hand in the background.

Wing: Hold the bird in bander's grip (its head between your index and middle fingers) and gently open its wing between your thumb and index finger. Take two pictures of the wing. In the first, make sure all of the primaries are visible and in focus (Figure C.2B). In the second, shift your holding position and make sure the tertials and secondaries are visible and in focus (Figure C.2D). It is fine if your fingers are covering the coverts and alula.

Fault bars or breaks: While taking the wing and tail photographs, conduct a quick visual search for fault bars and note their presence or absence (Y/N) on the data sheet. If you see any fault bars or broken feathers, take an additional picture(s) that features that feather (Figure C.2C).

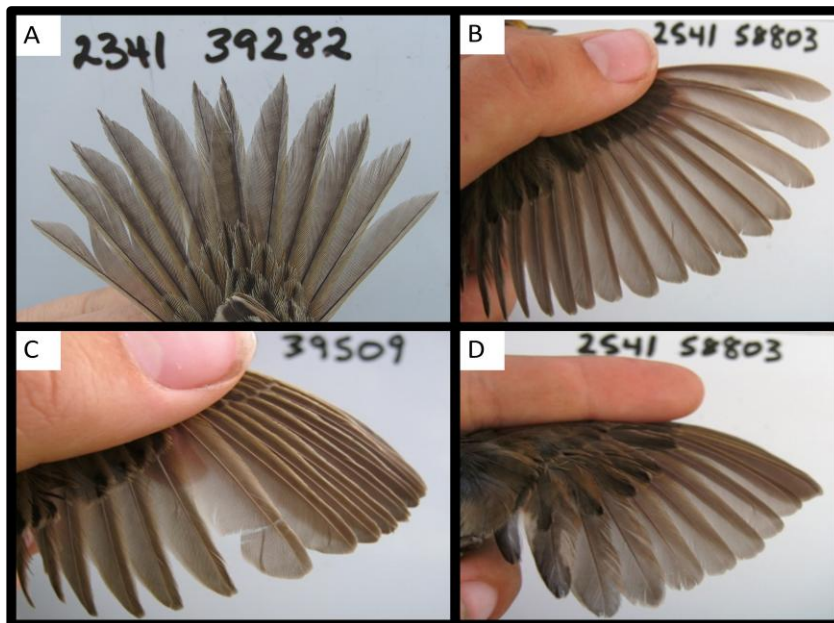


Figure C.2: Example Photos of A) rectrices; B) primaries; C) a fault bar; D) secondaries and tertials.

Organization: After each field day, upload the photos to a computer. Create a folder labeled with the date and the site at which banding took place. Create a sub-folder for each bird, and label each with the bird's band number. Label each photo with the bird's band number, and place all the photos for each bird in the appropriate folder. If two birds were labeled with the same number on the white board, use the datasheet and time stamps on the photos to determine which number actually goes with which bird, and label the photos and folder with the bird's correct band number.

Feather scoring:

Use a minimum of three pictures per bird: one showing the primaries, one showing the secondaries and tertials, and one showing the tail. If additional photos were taken, use whichever give you the clearest view of the target feathers. If there is a discrepancy between the file name and the band number on the white board, assume that the file name is correct.

Create an excel file that contains the following column headers:

Band number

Photo/capture date

Scoring date

Four columns for each of the 30 flight feathers:

Broken?

Wear

Fault bar number

Fault bar severity

For the 30 data columns, also label each with the appropriate feather specification using the letter (“t” for tertial; “s” for secondary, “p” for primary, and “r” for rectrix) and number corresponding to the feather identity (as depicted in Figure S1). It is helpful to color-code the excel sheet by feather.

Determine the identity of each feather:

Refer to Figure S1 to count the feathers and ensure you can locate 9 primaries, 6 secondaries, 3 tertials, and 12 rectrices. If a feather is missing, do your best to determine which feather it is.

Once you have accounted for every feather, assess each of the primaries, secondaries, tertials, and rectrices individually. If a feather is present but you cannot see it well enough to score, mark a “?” on the datasheet.

Fill out the excel sheet as described below, as you answer the following questions regarding each feather:

Is the rachis broken? Yes/No (Figure C.3)

Breaks across the rachis may be associated with a fault bar, but the cause is often impossible to determine.

Y: Feather broken.

N: Feather intact → Continue to assess the feather for wear and fault bars.

How worn is the feather? (Figure C.4 and C.5)

Be careful to ignore feather ruffling that occurred due to handling and could have been smoothed out.

X: Feather missing.

n/a: Feather broken.

0: Vane edges smooth, all barbs and barbules intact.

1: Vane edges not completely smooth; some shallow notches due to broken barbs and barbules; rachis not bare at tip.

2: Vane edges not completely smooth; some deep notches with a few adjacent barbs and barbules broken at rachis, either at the tip or anywhere along the feather.

3: Vane edges ragged; many broken barbs and barbules, rachis might be bare at the tip.

4: Large sections of vane missing, with many barbs broken at the rachis.

5: Vanes missing and frayed along most of the rachis.

How many fault bars does the feather have?

Count the bars. Do not worry if some bars are more intense than others.

X: Feather missing.

n/a: Feather broken (even if you can still see other fault bars on the feather).

0: No bars.

1,2...: One bar, two bars, etc.

What is the greatest intensity of a bar on the feather? (Figure C.6)

If there is more than one bar, only look at the most intense bar.

X: feather is missing.

n/a: feather is broken.

0: No bars.

1: Fault bar is only in one vane, does not cross the rachis, and is not associated with broken barbs.

2: Fault bar crosses the rachis, but no barbs are broken.

3: Fault bar is associated with a break in feather barbs along at least part of the bar.



Figure S3: Examples of feathers with breaks across the rachis.

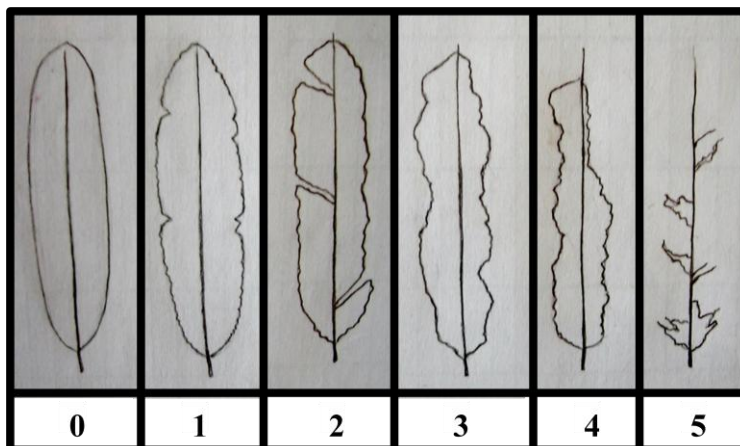


Figure S4: Ranges in feather wear and associated scores.

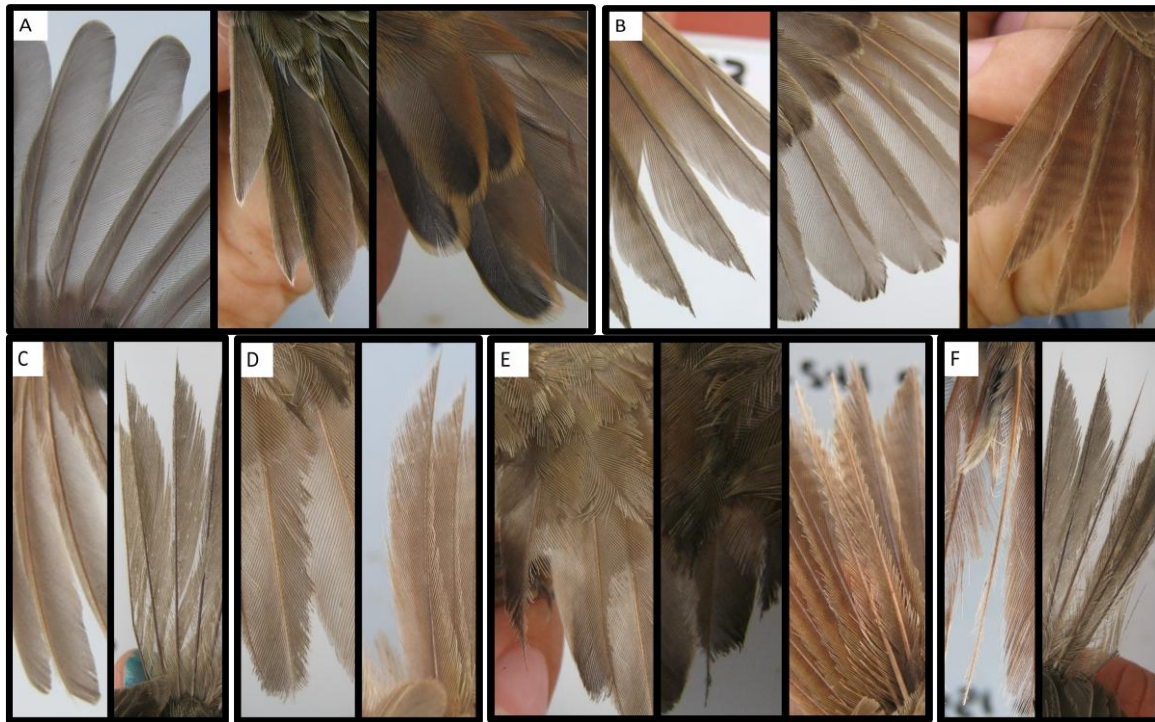


Figure C.5: Examples of feathers representing each of the wear scores. A) score of 0, vane intact, edges smooth; B) score of 1, edges not completely smooth, with some small notches; C) score of 2, edges not completely smooth, with some deep notches; D) score of 3, edges ragged, rachis bare at tip; E) score of 4, large chunks missing out of the vane, with many broken barbs; F) score of 5, most of the rachis is bare due to broken barbs.

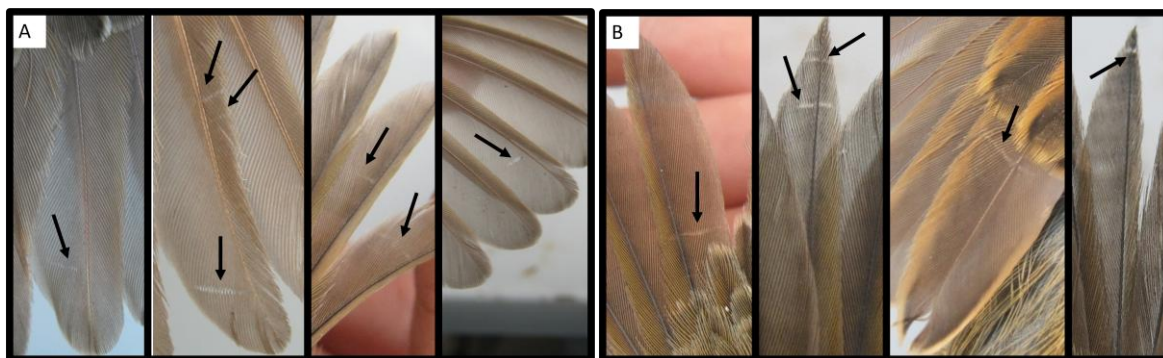




Figure C.6: Examples of feathers with fault bars representing the three scoring categories. A) score of 1, bar does not cross rachis; B) score of 2, bar crosses rachis but no barbs are broken; C) score of 3, some barbs are broken along bar.

APPENDIX D: BODY CONDITION SCORING PROTOCOL

Fat Scoring: Many different fat scoring systems exist, and they are not all easily comparable—even systems with the same number of categories do not necessarily have the same cut-off points between categories. My protocol uses the fat scoring system that Danner (2012) devised for use on Swamp Sparrows (*Melospiza georgiana*). In this system, the fat scores for the furcular hollow and the abdomen are taken separately (most systems use scores that combine information for these two areas).

Hold the bird in bander's grip in one hand and hold its legs in your other hand so that the bird is secure and you have an open view of its throat and breast. From a few inches away, gently blow to part the feathers around the upper and lower breast so you can see the skin. Subcutaneous fat is stored just under the skin. You will be able to recognize it based both on color, which is yellow or orange in contrast to the red/pink areas where the skin covers muscle. Look for fat stores in two places: 1) in the furcular hollow, which is between the throat and the keel; and 2) along the lower abdomen, at the edge of the keel. If there is no fat stored in the furcular hollow, it will appear convex. If there is fat, the surface of the fat will appear flat, unless it exceeds the furcular hollow, in which case it will have a bulging shape. Along the abdomen, fat stores will begin in a line—along the edge of the keel—and, as more fat is deposited, will spread to cover more of the abdomen.

Assign a separate score for furcular hollow and abdominal fat according to the following descriptions:

Furcular hollow fat scores:

- 0 = No visible fat
- 1 = Fat fills <25% of furcular hollow
- 2 = Fat fills 26–50% of furcular hollow
- 3 = Fat fills 51–75% of furcular hollow
- 4 = Fat fills 76–99% of furcular hollow
- 5 = Fat flush with furcular hollow
- 6 = Fat convex (exceeding furcular hollow)

Abdominal fat scores:

- 0 = No visible fat
- 1 = Light fat under ribcage, none on abdomen
- 2 = Heavy fat under ribcage, none abdomen
- 3 = Fat under ribcage and partially covering abdomen
- 4 = Fat under ribcage and completely covering abdomen
- 5 = Fat on abdomen flush with ribcage
- 6 = Fat convex (exceeding the ribcage)

Pectoral muscle scoring: Pectoral muscles should be scored through a combination of tactile and visual inspection. The system is based on examining two related characters, the prominence of the keel and the shape of the muscles. Hold the bird in a standard bander's grip on its back in the palm of your hand so that you are looking at its belly. Gently roll your index finger over the pectoralis muscle on either side of the bird's mid-line, to assess its size relative to the keel. Secondly, you can assess the size of the muscle visually by blowing the feathers apart and looking down the long axis of the bird in a manner similar to that described for fat scores (above).

Pectoral muscle scores:

0 = No pectoral muscle

1 = Muscle concave and not covering all of ribs, keel very prominent (keel sharp to the touch)

2 = Muscle concave and covering all of ribs (keel sharp to the touch)

3 = Muscle concave, half way up keel (keel sharp to the touch)

4 = Muscle concave, almost flush with keel (can feel keel)

5 = Muscle flush with keel (cannot feel keel)

6 = Muscle convex (bulging past keel)

Note that “concave” here refers to the shape of the muscle with respect to the keel – i.e., if you can feel the keel then the muscle is concave. Farther down towards the wings, the muscle will always be concave because the underlying ribcage is concave. In other words, for levels 5 and 6, the muscle should slope in a simple curve from the keel down under the wings. In contrast, for levels 4 and lower, the muscle will have a sinusoidal “S-like” shape following the contour of the underlying skeleton.

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APPENDIX E: SCALED MASS INDEX PROTOCOL

Following the method of Peig and Green (2009), I calculated a scaled mass index (SMI) for each individual. The SMI is a mass-based body condition proxy that accounts for the fact that increases in mass are correlated with increases in body size (Green 2001; Peig and Green 2009, 2010). In the field, I weighed each bird to the nearest 0.1 g using a Pesola scale and collected the following morphological measurements: tarsus length, unflattened wing chord, culmen length, nares to bill tip (nalespi), and head length (back of the head to bill tip). The SMI adjusts mass to a standard body size, using the slope from a standardized major axis (SMA) regression

as a scaling coefficient in the following equation: $\hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$ where L_0 is an average length measurement, L_i and M_i are the length and mass measurements of a particular individual, and b_{SMA} is the slope from an SMA regression (Peig and Green 2009). This method accounts for error in structural length measurements and leaves the standardized mass in the same units as the original mass (Peig and Green 2009).

To be used in an assessment of body condition, a body size measurement should correlate linearly with, yet be independent of mass, be independent of body condition, and reflect overall body size (Green 2001). As numerous body length measurements could fulfill these conditions, Peig and Green (2009) recommend selecting the measurement that correlates most strongly with mass. To select a morphological measurement for use in calculating the SMI scaling coefficient, I assessed the correlation between mass and each structural measurement on a natural log scale. Because mass can change throughout the annual cycle, based on fluctuations in muscle development, fat storage, and, for females, egg growth and laying

(Cresswell 2009), I assessed the mass by length correlations for five groups of Saltmarsh Sparrows representing different periods of the year: 1) all captured on the breeding grounds, 2) all captured during the winter; 3) all captured on the breeding grounds before 1 June (“spring”); 4) all captured on the breeding grounds during the breeding season (1 June through 31 August); 5) all captured on the breeding grounds after 1 September (“fall”).

Tarsus and wing chord had the highest correlations with mass in four of the five groups, including all winter birds and all breeding birds (Table S1 and Figure S1). Because wing chord can vary throughout the entire annual cycle due to feather wear (Flinks and Salewski 2012), I chose to use tarsus as the measurement for calculating the scaling coefficient. Although tarsus was most strongly correlated with mass for fall birds (Table S1), I decided not to use birds captured in the fall because my sample size, particularly for Seaside Sparrows, was lower than during the breeding or winter seasons, and because the fall birds had a wide range of fat scores. I chose to use winter birds rather than breeding birds to avoid including females carrying egg mass.

I used the R package *smatr* (Warton et al. 2012) to run SMA regressions to fit the relationship between $\ln(\text{mass})$ and $\ln(\text{tarsus})$ in winter sparrows. To evaluate sensitivity to my decision to use tarsus as the structural measurement, I also ran SMA regressions with the other structural measurements for male and female Saltmarsh and Seaside Sparrows caught on the wintering grounds. Tarsus had the best SMA regression fit for male Saltmarsh, and male and female Seaside Sparrows, and the second best fit (after wing chord) for female Saltmarsh Sparrows (Table S2). I also conducted pairwise comparisons of the SMA regressions between males and females of each species to evaluate the consistency in slopes between sexes. In nine

of the ten comparisons, via likelihood ratio tests (Warton et al. 2006), there was no difference in the SMA slopes between conspecific males and females (Table S2 and Figure S2A and B). Next, I combined data from both sexes of each species and compared the SMA slopes for $\ln(\text{mass})$ vs. $\ln(\text{tarsus})$ for wintering Saltmarsh and Seaside Sparrows and found no difference (likelihood ratio statistic = 0.67, 1 df, $p = 0.413$), for a combined slope of 2.06 (Figure S2C). I used the SMA slope of $\ln(\text{mass})$ vs. $\ln(\text{tarsus})$ from all wintering birds as the scaling coefficient in all SMI calculations following the formula used by Peig and Green (2009), as indicated above.

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Table E.1: Correlation coefficients depicting correlations between $\ln(\text{mass})$ and the natural log of each structural measurement for the following categories of Saltmarsh Sparrows: captured on the breeding grounds before 1 June (Spring); captured on the breeding grounds after 31 August (Fall), captured on the breeding grounds between 1 June to 31 August (Breeding), captured on the breeding grounds (All breeding grounds); captured on the wintering grounds (Winter).

	Spring	Fall	Breeding	All breeding grounds	Winter
Wing by mass	0.35	0.61	0.48	0.46	0.42
Tarsus by mass	0.29	0.53	0.33	0.34	0.46
Culmen by mass	0.20	0.33	0.11	0.14	0.26
Nalospa by mass	0.26	0.41	0.02	0.15	0.23
Head by mass	0.38	0.44	0.25	0.28	0.50

Table E.2: Slopes and R^2 values from SMA regressions between $\ln(\text{mass})$ and the natural log of each structural measurement for male and female Saltmarsh and Seaside Sparrows. The p values are from likelihood ratio tests of the difference between the slopes for males and females for each structural measurement.

Saltmarsh Sparrow							
	Males		Females				
	Slope	R^2	Slope	R^2	Likelihood ratio statistic	df	p
Wing	2.41	0.097	2.42	0.19	2.635e-05	1	0.99
Tarsus	2.19	0.13	2.55	0.17	2.64	1	0.10
Culmen	1.96	0.03	2.19	0.06	0.93	1	0.33
Nalospi	2.03	0.03	2.33	0.06	2.05	1	0.15
Head	0.06	0.04	0.07	0.03	2.24	1	0.13
Seaside Sparrow							
	Males		Females				
	Slope	R^2	Slope	R^2	Likelihood ratio statistic	df	p
Wing	2.24	0.05	2.10	0.20	0.36	1	0.54
Tarsus	1.98	0.17	2.42	0.22	4.15	1	0.04
Culmen	2.00	0.10	2.13	0.13	0.32	1	0.58
Nalospi	1.64	0.03	1.71	0.06	0.15	1	0.70
Head	3.90	0.14	3.80	0.17	0.07	1	0.79

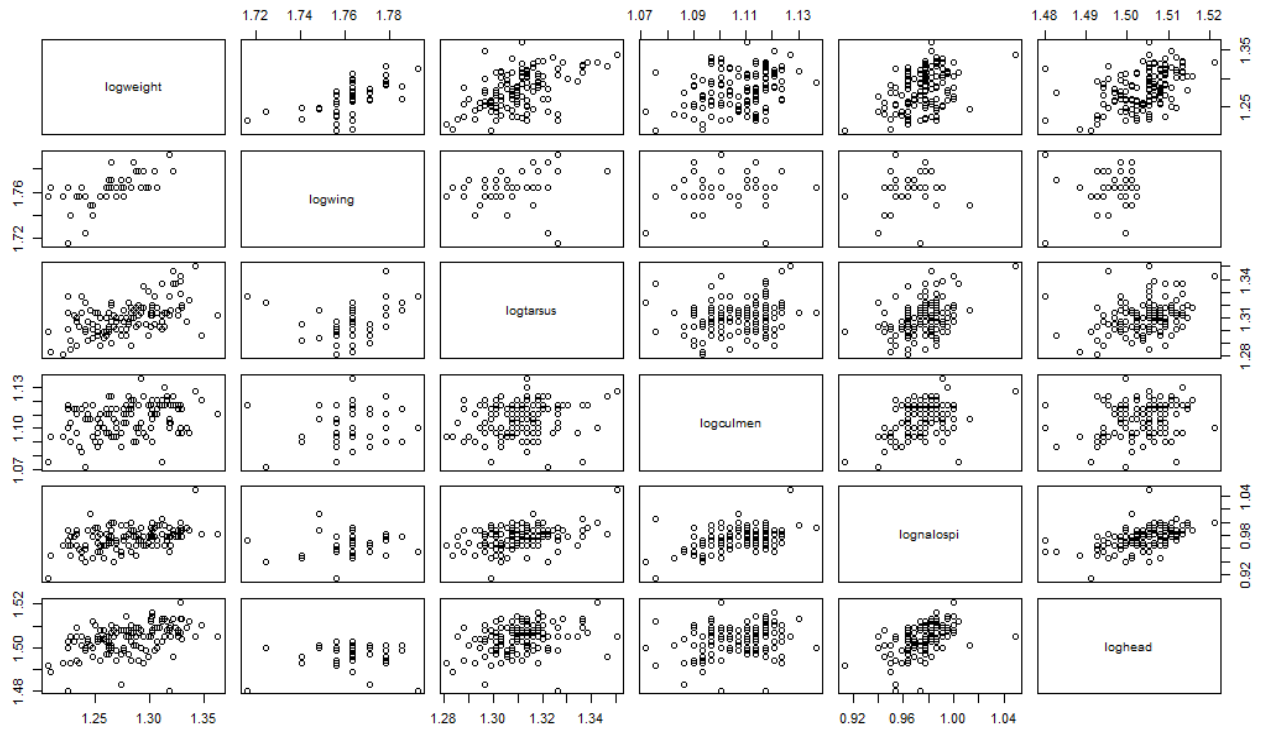


Figure E.1: Pairs plot depicting correlations between $\ln(\text{mass})$ and natural log of each structural measurement. From left, the measurements are wing chord, tarsus, culmen, nalspi, and head length. The data are from all adult Saltmarsh Sparrows caught on the breeding grounds.

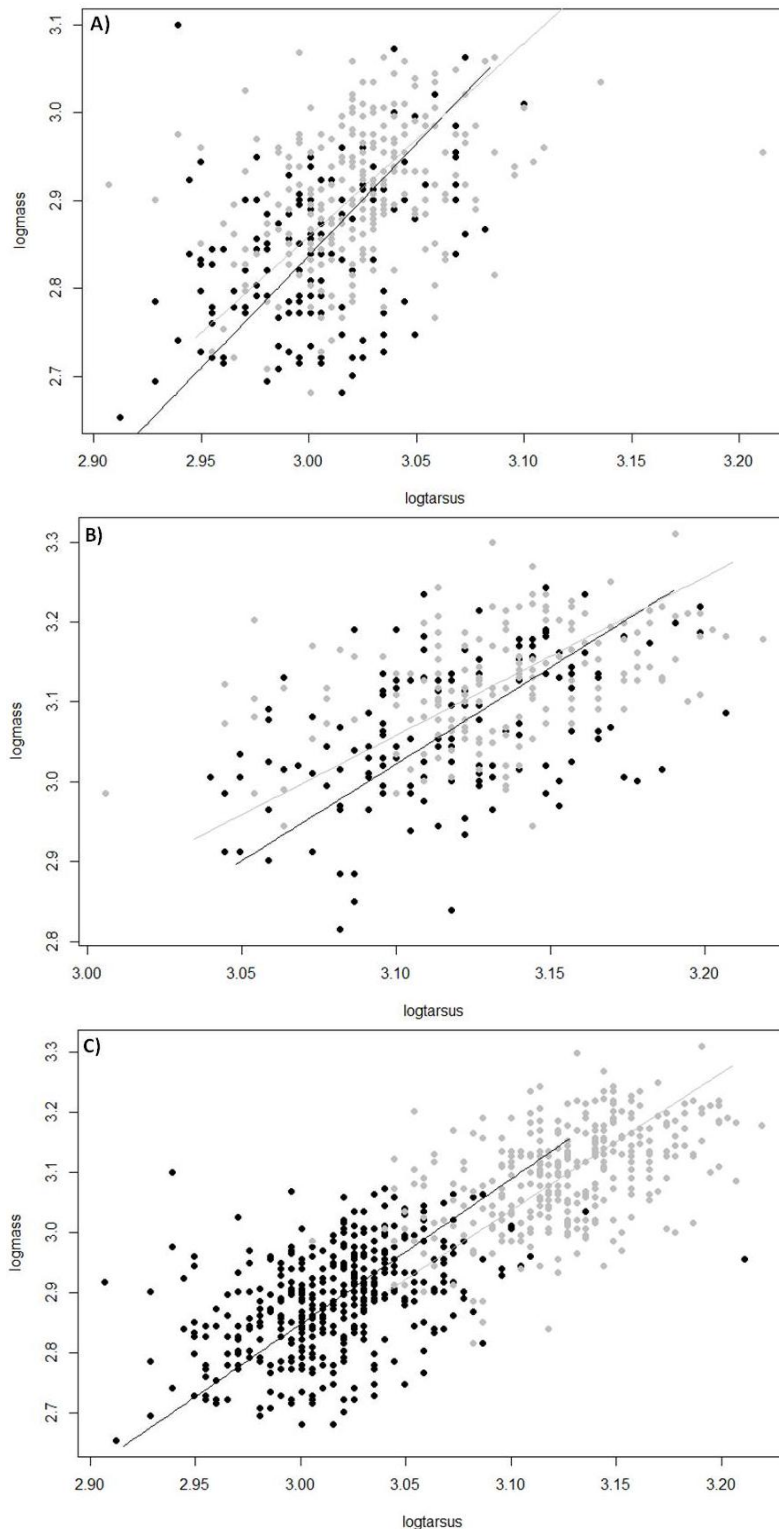


Figure E.2: SMA regressions for $\ln(\text{mass})$ by $\ln(\text{tarsus})$ in A) winter Saltmarsh Sparrows; B) winter Seaside Sparrows; C) all winter birds. In figures A and B, females are in black and males are in gray. In figure C, Saltmarsh Sparrows are in black and Seaside Sparrows are in gray. There was no difference in the slopes for male vs. female Saltmarsh Sparrows (likelihood ratio statistic = 2.64; $df = 1$, $p = 0.104$) or Saltmarsh vs. Seaside Sparrows (likelihood ratio statistic = 0.6701; $df = 1$, $p = 0.413$). There was a significant difference between the slopes for male and female Seaside Sparrows (likelihood ratio statistic = 4.15; $df = 1$, $p = 0.042$).