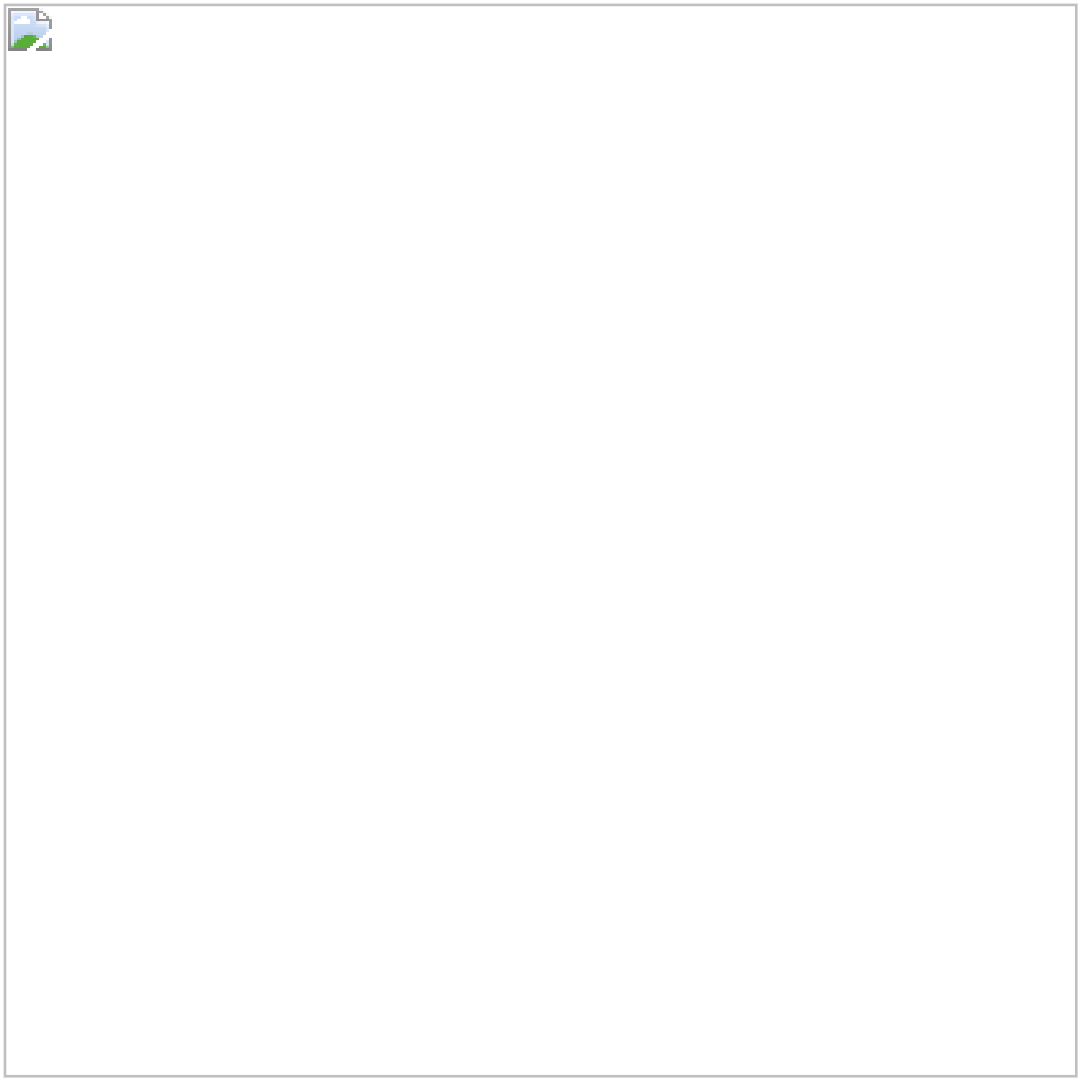

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RESEARCH ARTICLE

Timing of migration and prebasic molt in tidal marsh sparrows with different breeding strategies: Comparisons among sexes and species

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ABSTRACT

Breeding strategies can shape the timing of other events and processes, including arrival on the breeding grounds, prebasic molt, and departure for fall migration. We studied these relationships in sympatric Saltmarsh Sparrows (*Ammodramus caudacutus*) and Seaside Sparrows (*A. maritimus*), 2 closely related species with notably different breeding strategies. On average, females of both species arrived on the breeding grounds later, initiated molt later, and departed from the breeding grounds later than did conspecific males. Furthermore, we found that female Saltmarsh Sparrows—which mate with multiple males and care for nests, eggs, and chicks alone—were last to arrive on the breeding grounds and last to initiate molt, had the shortest molt duration, and were last to depart for the nonbreeding grounds. Both species exhibited protandry, but Seaside Sparrows averaged earlier arrival on the breeding grounds than Saltmarsh Sparrows. Molt and departure timing also differed between the species, with Seaside Sparrows initiating molt and departing before same-sex Saltmarsh Sparrows. These observations support the hypotheses that breeding strategies can influence arrival timing and that reproductive investment can have carryover effects on molt and departure.

Keywords: Ammodramus caudacutus, *A. maritimus*, reproductive investment, migration, molt, Saltmarsh Sparrow, Seaside Sparrow

Chronologie de la migration et de la mue annuelle chez des bruants habitant les marais côtiers et utilisant différentes stratégies de reproduction: comparaisons entre les sexes et les espèces

RÉSUMÉ

Les stratégies de reproduction peuvent modeler la chronologie d'autres événements et processus, dont l'arrivée dans l'aire de reproduction, la mue annuelle et le départ pour la migration automnale. Nous avons étudié ces relations chez *Ammodramus caudacutus* et *A. maritimus*, deux espèces sympatriques étroitement apparentées utilisant des stratégies de reproduction différentes. En moyenne, les femelles des deux espèces sont arrivées dans l'aire de reproduction plus tard, ont amorcé la mue plus tard et ont quitté l'aire de reproduction plus tard que leur congénères mâles. De plus, nous avons trouvé que les femelles d'*A. caudacutus*—lesquelles s'accouplent avec plusieurs mâles et s'occupent seules des nids, des œufs et des jeunes—étaient les dernières à arriver dans l'aire de reproduction, les dernières à amorcer la mue, avaient les durées de mue les plus courtes et étaient les dernières à quitter les aires de reproduction. Les deux espèces présentaient de la protandrie mais *A. maritimus* arrivait en moyenne plus tôt dans l'aire de reproduction qu'*A. caudacutus*. La chronologie de la mue et du départ différait également entre les espèces, *A. maritimus* amorçant la mue et quittant le site avant les individus du même sexe d'*A. caudacutus*. Ces observations supportent les hypothèses que les stratégies de reproduction peuvent influencer la chronologie d'arrivée et que l'investissement reproducteur peut avoir un impact sur la mue et le départ.

Mots-clés: Ammodramus caudacutus, *A. maritimus*, investissement reproducteur, migration, mue

INTRODUCTION

To cope with predictably seasonal environments, animal lives are structured into series of annual stages of events and processes, the timing of which can influence fitness (Wingfield 2008, Newton 2011). Although most migrant birds go through the same stages, differing breeding strategies can lead to different timing (McNamara et al. 1998, Verhulst and Nilsson 2008, Newton 2011). An optimal strategy in one stage may require particular timing in another stage; if stages cannot overlap, there may be a domino effect if one stage is delayed. An individual's physiological state can also "carry over" and influence its performance in subsequent stages (Harrison et al. 2011).

TABLE 1. Predicted timing of arrival on the breeding grounds, prebasic molt initiation and duration, and departure from the breeding grounds in male and female Saltmarsh Sparrows (SALS) and Seaside Sparrows (SESP).

	SALS ♂ vs. ♀	SESP ♂ vs. ♀	Female SALS vs. SESP	Male SALS vs. SESP
Arrival timing: rank advantage hypothesis	No difference	♂ Earlier	N/A	N/A
Arrival timing: mate opportunity hypothesis	♂ Earlier	♂ Earlier	N/A	N/A
Arrival timing: susceptibility hypothesis	No difference	No difference	N/A	N/A
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

In many bird species, males return to the breeding grounds before females (Mills 2005, Saino et al. 2010, Morbey et al. 2012). Such protandry is frequently attributed to competition, either for territories—the "rank advantage hypothesis"; or for mates—the "mate opportunity hypothesis" (Morbey and Ydenberg 2001). Under both hypotheses, protandry is predicted if the benefit of early arrival—a high-quality territory or extended mating opportunities, respectively—is greater for males than for females (Morbey and Ydenberg 2001, Kokko et al. 2006). A third explanation for protandry, the "susceptibility hypothesis," suggests that larger individuals can better withstand cool temperatures, leading to protandry when males are larger than females (Weatherhead and Clark 1994, Saino et al. 2010).

The timing of departure from the breeding grounds can be influenced by reproduction, given that birds do not migrate until breeding—and, in many species, molt—is complete (Vega Rivera et al. 1998, Newton 2011). Thus, individuals with late nest-completion dates may depart later than individuals that finished nesting earlier (Ellegren 1990, Mitchell et al. 2012a). High reproductive investment may also delay departure timing by increasing the amount of time a bird needs to reach migration-ready condition (Newton 2011, Catry et al. 2013). Additionally, birds do not accumulate fat while molting (Bonier et al. 2007, Minias et al. 2010) and cannot migrate without sufficient fat stores (Payne 1972, Morton and Pereyra 1994, Stutchbury et al. 2011).

Most temperate-zone migratory species do not overlap reproduction with prebasic molt (Svensson and Nilsson 1997, Vega Rivera et al. 1998, Bridge 2011). In such species, individuals that expend less energy during the breeding season or end reproduction earlier may initiate molt sooner than those with greater reproductive investment (Morton and Welton 1973, Hemborg 1999, Mitchell et al. 2012b). Molt duration may be correlated negatively with reproductive investment if birds in better condition are able to molt more quickly (Gienapp and Merilä 2010, Saino et al. 2013). However, there may be a cost to shortened molt duration, and the "molt constraint hypothesis" posits that individuals with high reproductive investment initiate molt late and then molt quickly to compensate for the loss in timing, leading to a trade-off in feather quality (Nilsson and Svensson 1996, Dawson et al. 2000, Dawson 2004, Vágási et al. 2012).

We studied how breeding strategies influence the timing of breeding-ground arrival, prebasic molt, and departure for the nonbreeding grounds in male and female Saltmarsh Sparrows (*Ammodramus caudacutus*) and Seaside Sparrows (*A. maritimus*). While the 2 species are closely related tidal-marsh specialists with short-distance migrations to the southeastern United States (Greenlaw and Rising 1994, Post and Greenlaw 2009), they differ dramatically in their breeding strategies. Saltmarsh Sparrows do not form territories (Woolfenden 1956, Shriver et al. 2010) or pair bonds (Greenlaw and Post 2012), have a higher rate of female multiple mating than most other bird species (Hill et al. 2010), and exhibit female-only parental care (Woolfenden 1956, Post and Greenlaw 1982). By contrast, Seaside Sparrows are territorial (Woolfenden 1956, Marshall and Reinert 1990, Hill and Post 2005) and exhibit both social monogamy, with low rates of extrapair fertilizations (Hill and Post 2005, Post and Greenlaw 2009), and biparental care (Woolfenden 1956, Post and Greenlaw 1982).

Given these breeding dissimilarities, we predicted differences between both species and sexes in the timing of the annual cycle (Table 1). Both the rank advantage and the mate opportunity hypotheses predict protandry in breeding-ground arrival in Seaside Sparrows. Since Saltmarsh Sparrows are nonterritorial and lack pair bonds, only the mate opportunity hypothesis predicts protandry. Neither species is strongly sexually dimorphic, so the susceptibility hypothesis does not predict protandry in either species. 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 Sparrows.

We also predicted, based on reproductive investment, that male Saltmarsh Sparrows would molt earliest,

followed by male and female Seaside Sparrows and, finally, female Saltmarsh Sparrows. If individuals with low reproductive investment can molt more quickly, we predicted the same order for molt rate, with the fastest and slowest rates in male and female Saltmarsh Sparrows, respectively. Alternatively, if accelerated molt is a response to late molt initiation and the need to migrate by a given date, we expected the reverse pattern. Finally, we predicted different breeding-ground departure times, with male Saltmarsh Sparrows departing first, and female Saltmarsh Sparrows last.

METHODS

Study Sites

We mist netted Saltmarsh and Seaside sparrows from April to October during 2011–2013, which encompassed the period from spring arrival on the breeding grounds through fall migration. Study sites were located within 3 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 our molt analyses, we also used data collected between August 6 and October 21, 2002; July 16 and August 28, 2003; and July 26 and August 12, 2004, at these sites and 2 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 sites are dominated by salt-tolerant vegetation, especially *Spartina patens*, *S. alterniflora*, *Juncus gerardii*, and *Distichlis spicata*. The sites are geographically distinct and located along a 75 km section of the Long Island Sound coast.

Mist Netting

During the prebreeding and postbreeding stages, we netted opportunistically by moving pairs of 2-panel, 12-m, 38-mm-mesh mist nets around the marsh. During the breeding season, we followed a systematic procedure in which we opened 3 sets of 6 nets for 3 hr sessions, beginning shortly after dawn. Each of our study sites was subdivided into 4 or 5 subplots, which were visited on a rotating schedule, for a total of 3 visits per subplot each summer. In addition to passive capture, at regular intervals during each netting session, field technicians would form a line and walk slowly across the subplot being sampled, thereby flushing birds toward the line of nets (Correll et al. 2016). Because subplots were small (15–24 ha), nets bisected much of the area being sampled and we were able to traverse the entire area, thus limiting any risk that sampling would be biased toward a given sex or species. Mark–recapture analysis also showed no evidence that capture probability differed by sex or species during the breeding season (Borowske 2015).

We banded all new captures, aged birds using plumage or skull pneumatization, 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 could not be sexed visually, we collected 2 rectrices or breast feathers and used them to sex the bird via genetic markers.

Molt Scoring

We evaluated molt data from 263 Saltmarsh Sparrows (140 males, 123 females) and 37 Seaside Sparrows (17 males, 20 females) captured on the breeding grounds in Connecticut, including premolt and postmolt individuals, as well as those actively molting. We scored each flight feather on a scale of 0–5 using methods modified from Ginn and Melville (1983) (Appendix A). We scored each primary, secondary, tertial, and rectrix 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), or 5 (new, fully grown). Birds with a complete set of new flight feathers had a molt score of 240. We 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 5 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; $<$10% of feathers in molt), 1 (10–30% of feathers in molt), 2 (31–50%), 3 (51–70%), 4 (71–90%), and 5 (91% new to all new feathers). Birds with all new body feathers had the maximum body molt score of 130.

We also evaluated Saltmarsh Sparrow molt data with a mass-scaled scoring system, using feathers plucked from a dead male Saltmarsh Sparrow (University of Connecticut vertebrate collection: UCM 2128). We weighed each flight feather individually and weighed body feathers in the groups used for molt scoring. We weighed primary and secondary coverts by tract. With this information, we recalculated the molt scores for each feather, or group of feathers, proportional to its contribution to the total feather mass (after Dawson and Newton 2004). Results of the analyses using the weighted and unweighted scores did not differ (Appendix B), and we report all results using unweighted scores. We lacked a specimen with which to conduct a similar comparison for the Seaside Sparrow, but similarities in size and structure suggest no reason why the species should differ.

We also examined 25 Saltmarsh Sparrow (13 male, 12 female) and 116 Seaside Sparrow (66 male, 50 female) museum specimens to expand our sample sizes. All specimens were adults 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. We established sex from specimen labels. We used forceps to lift feathers of the right wing and tail to quantify flight feather molt. We used the same procedure to score flight feather molt on the museum specimens as described for live birds, but examined only one wing to minimize specimen handling. Given the smaller number of feathers examined, museum specimens with all new flight feathers (right wing and tail) had a maximum score of 150. We did not score museum specimens for body molt.

Genetic Sexing

We extracted DNA from rectrices or breast feathers (Segelbacher 2002), using NucleoSpin Tissue DNA extraction kits (Macherey-Nagel, Duren, Germany). We amplified the DNA using a single polymerase chain reaction with sex-linked primers P2 and P8, which were designed to amplify sections of 2 avian sex genes: CHD-W, which is present only in females; and CHD-Z, which is present in males and females (Griffiths et al. 1998). We confirmed the method's accuracy with 6 males and 6 females from our study sites that had been sexed by the presence of a brood patch (female) or enlarged cloaca (male). Following amplification, we resolved the samples on 1.5% agarose gels and determined the sex by the presence of 1 (male) or 2 (female) bands.

Statistical Analyses

To compare arrival and departure patterns among the 4 sex–species classes, we conducted separate analyses on the number of birds of each class that we captured per day in the arrival period (end of April through June 1) and the departure period (August 1 through end of October). For the arrival analysis, we used only the first capture of each individual in a given year. For the departure analysis, we used only the last capture of each individual. For each analysis, we ran a set of 4 generalized additive models using the R package mgcv (Wood 2006) in R 3.1.1 (R Development Core Team 2014), in which we 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 to describe the capture of birds by date in the arrival or departure periods: (1) a single smoother for all captures; (2) a separate smoother for each species; (3) a separate smoother for each sex; or (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). We compared the 4 models in each analysis using Akaike's Infomation Criterion corrected for small sample sizes (AIC_c) with the function "AICctab" from the R package bbmle (Bolker 2014).

We 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 arrived on and departed from the breeding grounds synchronously. Because it is unlikely that we captured the very first birds to arrive on the breeding grounds, we set day zero as April 24, which is 4 days before the earliest capture we had during the 3 yr period. We ran 2 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, featured a smoother for day and an effect of year, and used cross-validation with a cubic-regression spline to select the optimal degree of smoothing.

We compared the estimated date on which individuals initiated molt and the time it took for them to complete molt for adult male and female Saltmarsh and Seaside sparrows using the R package "moult" (Erni et al. 2013), which is based on the Underhill-Zucchini maximum-likelihood approach for predicting the initiation and duration of avian molt (Underhill 1985, Underhill and Zucchini 1988). This method estimates the date on which an average bird initiates molt and its standard deviation, and the mean molt duration, by maximizing the combined likelihood of the probabilities from all individuals i of having a molt score y_i at time t_i (Underhill and Zucchini 1988, Erni et al. 2013). We 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). We assessed the proportion of flight feather molt completed by using data from the field- and museum-scored birds (using data from only the right wing for the field-scored birds, so that the total scores would be comparable) and assessed the proportion of body molt completed using only the field-scored birds. We ran models to test the effects of species, sex, and a sex*species interaction on molt initiation and duration by grouping birds in 3 ways: (1) by species, (2) by sex, and (3) as belonging to one of the 4 sex–species classes. For each of these 3 groupings, we ran the following models: (a) null, in which neither start date nor duration varied by group; (b) duration varied by group; (c) start date varied by group; (d) start date and duration varied by group. For both flight and body feathers, we compared AIC_c scores of the 10 models. To compare average start date and duration for the 4 sex–species classes, we used the estimates generated by the top model, and we present the results as date or days ± SE.

TABLE 2. Comparisons of generalized additive models describing daily captures of male and female Saltmarsh and Seaside sparrows on their breeding grounds in Connecticut, USA, during the arrival and departure periods, 2011–2013. For each analysis, 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 (4 total).

	ΔAIC_c	df	w_i
Models for arrival			
Smoothers by sex and species	0	15	1
Smoothers by sex	54.7	7	<0.001
Smoothers by species	58.3	10	<0.001
One smoother for all birds	103.1	5	<0.001
Models for departure			
Smoothers by sex and species	0	15	0.79
Smoothers by species	2.6	10	0.21
Smoothers by sex	145.7	6	<0.001
One smoother for all birds	146.9	7	<0.001

RESULTS

Arrival and Departure

We found distinct occupancy patterns on the breeding grounds for male and female Saltmarsh and Seaside sparrows in both the arrival and departure periods. The best-supported model of daily captures in both periods included separate smoothers for each sex–species class (Tables 2 and 3), with 53% and 49% of deviance explained for the top arrival and departure models, respectively. Comparison of alternative models suggests that species differences had a greater effect on departure timing than did sex differences, but that both were very influential during spring (Table 2). No differences among year were detected in either model (arrival: $z = 0.08$, $P > 0.9$; departure: $z = -0.72$, $P > 0.4$).

TABLE 3. Approximate significance of smoothed terms in the best-supported generalized additive models for daily captures of male and female Saltmarsh and Seaside sparrows on their breeding grounds in Connecticut, USA, during the arrival and departure periods, 2011–2013. Both of the top models fit a separate smoother for each sex of each species (Table 2).

Smoothed term	edf	Ref.df	χ^2	P
Arrival analysis				
Female Saltmarsh	1.86	2.32	18.05	<0.001
Male Saltmarsh	2.06	2.57	33.31	<0.001
Female Seaside	1.27	1.49	5.75	0.033
Male Seaside	1.10	1.18	0.66	0.475
Departure analysis				
Female Saltmarsh	1.00	1.00	2.50	0.114
Male Saltmarsh	2.79	3.45	14.55	0.004
Female Seaside	1.19	1.36	6.27	0.022
Male Seaside	1.96	2.49	1.75	0.526

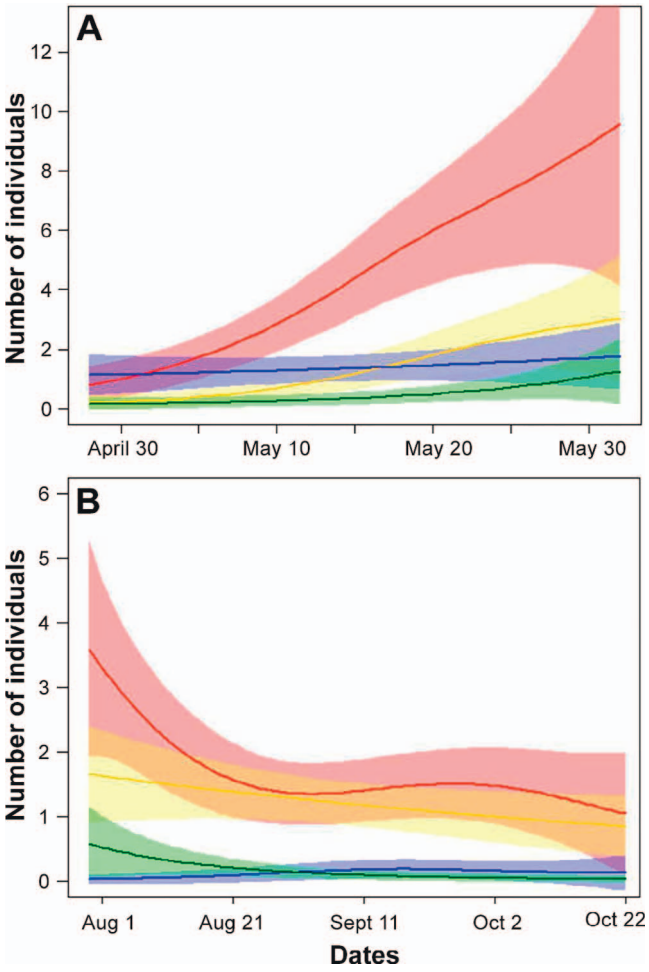

FIGURE 1. Fitted curves for the top generalized additive models depicting capture patterns of male and female Saltmarsh and Seaside sparrows on their breeding grounds in Connecticut, USA, during (**A**) the arrival period and (**B**) the departure period, 2011–2013. There are separate smoothers and 95% confidence intervals for male Saltmarsh (red), female Saltmarsh (yellow), male Seaside (blue), and female Seaside (green) sparrows. In A, the *y*-axis depicts the number of birds captured for the first time in a given year, captured on a given day. In B, the *y*-axis depicts the number of birds captured on a given day that were not captured on a subsequent day in a given year.

In both species, we found that male numbers increased earlier and faster in the spring than those for females, which suggests earlier male arrival (Figure 1A); and that male numbers declined earlier in the fall, which suggests earlier male departure (Figure 1B). When matched by sex, and accounting for the fact that Saltmarsh Sparrows are more abundant at our study sites than Seaside Sparrows, the fitted smoothers, particularly for males, also suggest that Seaside Sparrows arrive on the breeding grounds earlier than Saltmarsh Sparrows (Figure 1A) and that they depart sooner (Figure 1B).

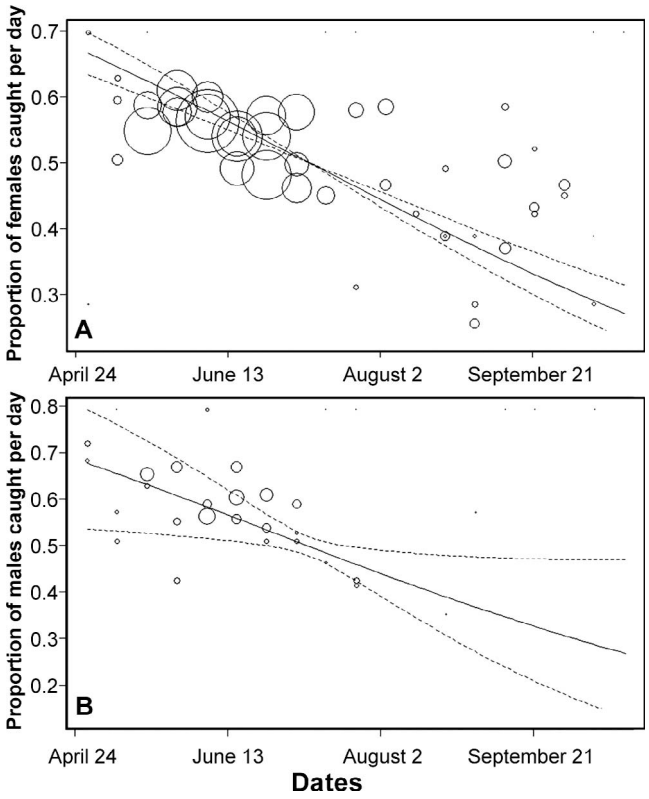

FIGURE 2. Plots of the smoothers from generalized additive models, showing changes throughout the banding period in the probabilities that an individual was male, for (**A**) Saltmarsh and (**B**) Seaside sparrows captured on the breeding grounds in Connecticut, USA, 2011–2013. Dotted lines represent 95% confidence intervals. Circles represent the raw data, with their size scaled to the number of birds captured during 10-day periods, calculated separately for each year.

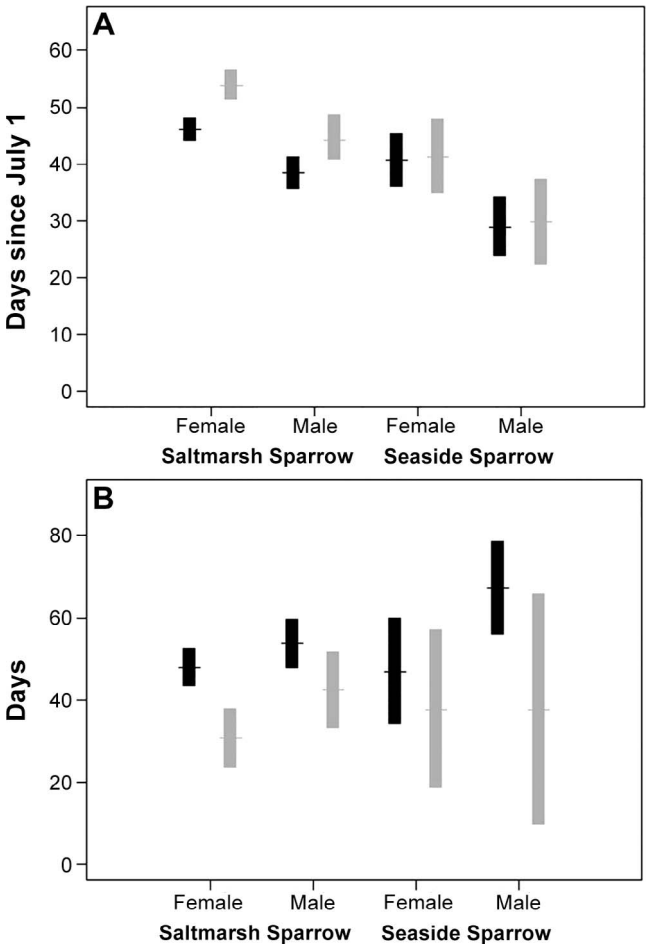

FIGURE 3. Model estimates of (**A**) molt initiation and (**B**) duration for male and female Saltmarsh and Seaside sparrows captured on the breeding grounds in Connecticut, USA, 2011–2013. Bars represent model estimates with 95% confidence intervals about the means; black bars depict flight feathers, and gray bars depict body feathers.

Sex ratios of both species also shifted from being male-biased to female-biased between late April and mid-October, providing further evidence for protandry in arrival on and departure from the breeding grounds (Saltmarsh Sparrow: $\chi^2 = 91.1$, $P < 0.001$; Seaside Sparrow: $\chi^2 = 5.7$, $P = 0.020$; Figure 2). Year had no effect on sex ratio ($P > 0.3$ in either species), and the deviance explained was 12% for Saltmarsh Sparrows and 5% for Seaside Sparrows.

Molt

Initiation and duration of flight feather molt differed by both sex and species (Figure 3 and Table 4). Initiation of body feather molt also differed by sex and species, but there was no evidence that the duration of body feather molt differed (Figure 3 and Table 4). In both species, males initiated flight feather and body molts before females. This difference in mean initiation of flight feather molt was greater in Seaside Sparrows (males: July 30 ± 3 days; females: August 10 ± 2 days) than in Saltmarsh Sparrows (males: August 8 ± 2 days; females: August 15 ± 1 day) (Figure 3A). The difference between sexes in body molt initiation 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 on 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 Sparrows (mean duration for males: 67 ± 6 days; females: 47 ± 7 days) than in Saltmarsh Sparrows (males: 54 ± 3 days; females: 48 ± 2 days) (Figure 3B). Estimating body molt duration separately for each sex and species did not improve model fit (Table 4), and this molt took 37 ± 2 days, on average, for all individuals combined.

TABLE 4. Comparisons of models of initiation and duration of prebasic flight feather and body molts in Saltmarsh and Seaside sparrows on their breeding grounds in Connecticut, USA, 2011–2013. Flight feather and body molt were analyzed separately. The R package "moult" quantifies molt initiation and duration using date and molt score data. The models were identical except for the variable by which the data were grouped during the analysis.

Molt initiation grouping term	Molt duration grouping term	ΔAIC_c	df	w_i
Flight feather molt				
Sex and species	Sex and species	0	9	0.920
Sex and species	None	5.1	6	0.071
Sex	Sex	9.8	5	0.007
Sex	None	12.8	4	0.002
Species	None	35.1	4	<0.001
Species	Species	35.9	5	<0.001
None	Sex	38.1	4	<0.001
None	Sex and species	39.4	6	<0.001
None	None	42.8	3	<0.001
None	Species	43.9	4	<0.001
Body molt				
Sex and species	None	0	6	0.540
Sex and species	Sex and species	0.3	9	0.460
Species	None	19.0	4	<0.001
Species	Species	21.1	5	<0.001
Sex	Sex	32.4	5	<0.001
Sex	None	33.5	4	<0.001
None	Species	41.6	4	<0.001
None	Sex and species	43.0	6	<0.001
None	Sex	48.9	4	<0.001
None	None	49.4	3	<0.001

DISCUSSION

We took advantage of a highly unusual study system of 2 closely related species with strikingly different breeding strategies to test predictions related to the timing of migration and molt. Our results support the ideas that breeding strategy influences the timing of arrival on the breeding grounds, and that reproductive investment influences the timing of postbreeding molt and migration departure.

Although previous work has shown that female Saltmarsh Sparrows can provision their young adequately without the help of males (Post and Greenlaw 1982), our results suggest that they may pay a cost by molting later and departing from the breeding grounds later than they otherwise might. Correlations between molt timing and reproductive investment have been observed in several other systems, with females initiating molt later than males (Morton and Morton 1990, Svensson and Nilsson 1997, Newton and Rothery 2005, Flinks et al. 2008), having early clutch completion (Stutchbury et al. 2011, Mitchell et al. 2012b), or delaying molt after being abandoned by their mates (Hemborg 1999). As predicted by the molt constraint hypothesis (Nilsson and Svensson 1996), later molt initiation was coupled with shorter molt duration in female Saltmarsh and Seaside sparrows, compared to conspecific males. High feather growth rates can lead to the production of low-quality feathers (Nilsson and Svensson 1996, Dawson et al. 2000), and poor-condition individuals may be particularly vulnerable to the trade-off between feather growth rate and quality (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 fed ad libitum compared to birds that were given limited food during molt (Jenkins et al. 2001, Pap et al. 2008). Elsewhere, we found that feather condition varied by sex and species during the breeding season, but that all individuals had little feather damage during the winter (Borowske 2015).

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 fall experience increasingly depleted food resources (McNamara et al. 1998, Newton 2006). Migration also becomes increasingly risky as departure is delayed, with greater potential for ice and snow (Wikelski et al. 2003, Newton 2007). In species that are territorial during winter, individuals that depart the breeding grounds late may be forced to occupy poor-quality habitat, which can affect their performance and condition even during the following breeding season (Norris et al. 2004, Studds and Marra 2005).

Seaside Sparrows initiated flight feather and body molt before female Saltmarsh Sparrows, but, contrary to our prediction, male Saltmarsh Sparrows did not. Although male Saltmarsh Sparrows do not invest much in their offspring, the energetic expenditures associated with seeking multiple matings (Woolfenden 1956, Post and Greenlaw 1982) and, to a lesser extent, high sperm production (Tuttle and Pruett-Jones 2004) may still impose important costs.

We found evidence for protandry in breeding-ground arrival in both Seaside and Saltmarsh sparrows. Since Saltmarsh Sparrows are not territorial, the mate opportunity hypothesis is the most likely explanation for protandry in this species. In Seaside Sparrows, which are territorial, the rank advantage hypothesis may also be a strong force behind protandry. Pressure for protandry is expected to be especially powerful in species with strong sexual selection, high sperm competition, frequent polygamy, and a male-biased sex ratio (Rubolini et al. 2004, Coppack et al. 2006, Kokko et al. 2006, Morbey et al. 2012). Given the differences in the pressures of finding mates, if mating opportunities alone were driving male arrival timing in both species, then we would expect male Saltmarsh Sparrows, with their high levels of multiple mating (Hill et al. 2010) and male-skewed sex ratios (Hill et al. 2013), to

arrive earlier than male Seaside Sparrows, which is not the case.

Earlier arrival of Seaside Sparrows compared to Saltmarsh Sparrows is consistent with the susceptibility hypothesis. Body size is not correlated with within-season survival during the winter, however, and Seaside Sparrows have lower winter survival rates than Saltmarsh Sparrows (Borowske 2015). The between-species differences in arrival time could be related to differences in nest vulnerability. Most Saltmarsh Sparrow nests that are initiated in early May fail during spring tides (Shriver 2002), potentially providing little advantage to earlier arrival by female Saltmarsh Sparrows. By contrast, Seaside Sparrows nest higher in the vegetation, on average (cf. Marshall and Reinert 1990, Gjerdrum et al. 2005); their nests are less prone to flooding; and many early nests do produce offspring (Gjerdrum et al. 2005).

The 2 species both winter in the southeastern United States (Greenlaw and Rising 1994, Post and Greenlaw 2009), and individuals of both species were captured both at our Connecticut study sites and at the same marsh in central South Carolina (Borowske 2015), so a difference in wintering grounds is also unlikely to explain the patterns in arrival time. One concern is that our sample could have included migrating birds that did not breed locally, and that different stopover behavior might have contributed to the patterns we detected. Given that our study sites were at the northern range limit for Seaside Sparrows and relatively near the northern range limit for Saltmarsh Sparrows (Wiest et al. 2016), however, it is likely that most captured individuals were local breeders.

Sex bias in capture rates is a potential concern when evaluating protandry. Elsewhere, and using the same data, we found no evidence of sex-biased capture in either Saltmarsh or Seaside sparrows (Borowske 2015); however, confidence intervals were broad, and an additional analysis with data from the same population suggested that male Saltmarsh Sparrows may have slightly lower capture rates than females (Field 2016). Results of the present study also show a clear decline in sex ratio in both species over the course of the breeding season (Figure 2), which is not consistent with a steady capture bias but is consistent with protandry. Nonetheless, our data suggest male-biased sex ratios, which are common in birds and especially in small and declining populations (Dale 2001, Donald 2007, Morrison et al. 2016). Seaside Sparrows are at the northern end of their range in New England, and populations are small, fragmented, and locally declining (Wiest et al. 2016; C. Elphick et al. personal observation). Saltmarsh Sparrows are also experiencing serious population declines, with a 9% annual decrease across the northeast and a sharper 12% annual decline in New England (Correll et al. 2016). In both species, these demographic factors could contribute to the overall male bias we observed.

Our results show that the timings of events in the annual cycle are interlinked, with the timing of one stage influencing subsequent stages, which underscores why it is important not to consider them in isolation. Examining stages simultaneously may reveal costs that carry over from one to another (reviewed by Harrison et al. 2011) or may reveal surprising degrees of flexibility in recovering from a setback during one stage of the annual cycle (Lourenço et al. 2011, Senner et al. 2014). Better understanding these links will be key to understanding the full life cycle of tidal marsh sparrows.

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Author contributions: A.B. and C.E. conceived the study. A.B., C.E., and C.G. designed the methods, performed the experiments, and wrote the paper. A.B. analyzed the data. A.B. and C.E. contributed substantial materials, resources, or funding.

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APPENDIX A

Saltmarsh Sparrow 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 descrepancies among feathers, we scaled molt scores by feather mass, thus analyzing percent feather mass grown rather than percent molt score achieved (Dawson and Newton 2004).

We obtained feather masses from feathers plucked from a dead adult male Saltmarsh Sparrow. We dried the feathers in a fume hood (flight feathers) or in bags with desiccant (body feathers) for 1 wk. We used an electric balance to individually weigh each flight feather, and we calculated an average mass for each feather type (e.g., an average of P9 from the left and right wings). For body feathers, we obtained masses for all feathers from a given body region. Flight feather masses ranged from 0.002 g (tertial 1) to 0.008 g (primary 9). For body feathers, we 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 individual's feathers weighed 0.993 g, 0.258 (26%) of which was flight feathers (Appendix Table 5) and 0.735 g (74%) of which was body feathers.

APPENDIX TABLE 5. Measured masses of individual flight feathers. Each mass value represents the mean mass of the equivalent feathers on the left and right wings for primaries (P), secondaries (S), and tertials (T), or sides of the tail for rectrices (R). Percent of flight feathers adds up to 0.5 because the full complement of flight feathers includes 2 of each feather type.

Feather	Mean mass	Percent of all feathers	Percent of flight feathers
P 9	0.007925	0.007979420	0.030693261
P 8	0.007315	0.007365231	0.028330751
P 7	0.007215	0.007264544	0.027943455
P 6	0.007080	0.007128617	0.027420604
P 5	0.006555	0.006600012	0.025387297
P 4	0.006260	0.006302986	0.024244771
P 3	0.006135	0.006177128	0.023760651
P 2	0.005845	0.005885137	0.022637490
P 1	0.005535	0.005573008	0.021436871
S 6	0.005255	0.005291085	0.020352440
S 5	0.005325	0.005361566	0.020623548
S 4	0.005090	0.005124952	0.019713400
S 3	0.004730	0.004762480	0.018319132
S 2	0.004440	0.004470489	0.017195972
S 1	0.004185	0.004213738	0.016208366
T 1	0.004090	0.004118085	0.015840434
T 2	0.003400	0.003423347	0.013168087
Tl 3	0.002020	0.002033871	0.007823393
R 6	0.004660	0.004691999	0.018048025
R 5	0.004935	0.004968888	0.019113091
R 4	0.005180	0.005215570	0.020061967
R 3	0.005505	0.005542802	0.021320682
R 2	0.005575	0.005613283	0.021591789
R 1	0.004845	0.004878270	0.018764524

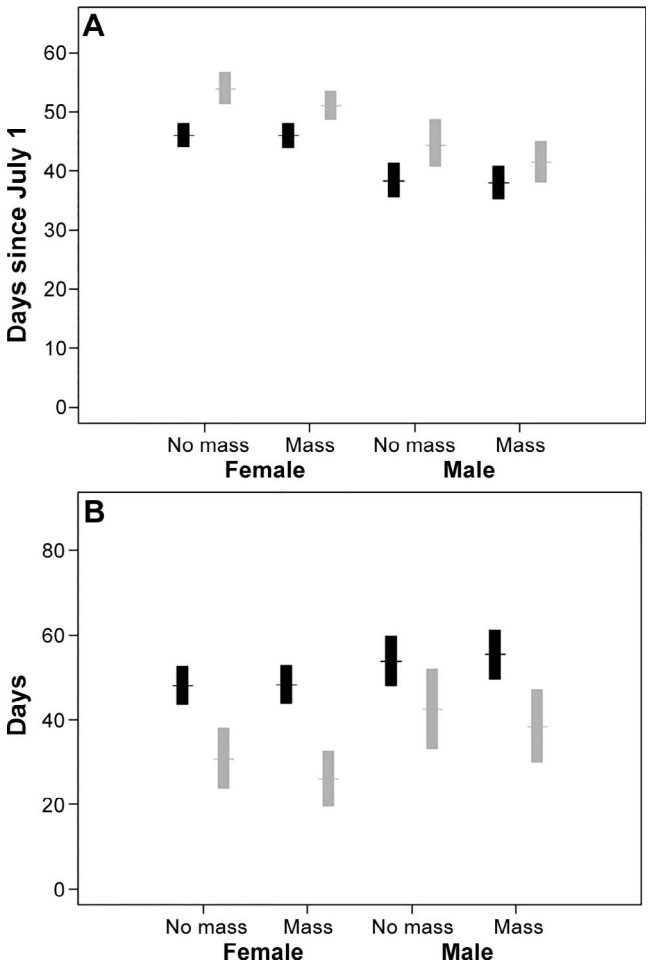
We followed the methods in Dawson and Newton (2004) to convert each score in the molt database to percent feather mass grown for all Saltmarsh Sparrows for which we had field data (i.e. excluding museum specimens, because we did not have body molt scores for them). We used the R package "moult" (Erni 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 (Appendix Figure 4).

APPENDIX B

Molt Protocol

Scoring is based on Ginn and Melville (1983). Before attempting to evaluate a bird's molt status, make sure that you are very comfortable with how feathers are named and counted. Saltmarsh and Seaside sparrows



APPENDIX FIGURE 4. (**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.

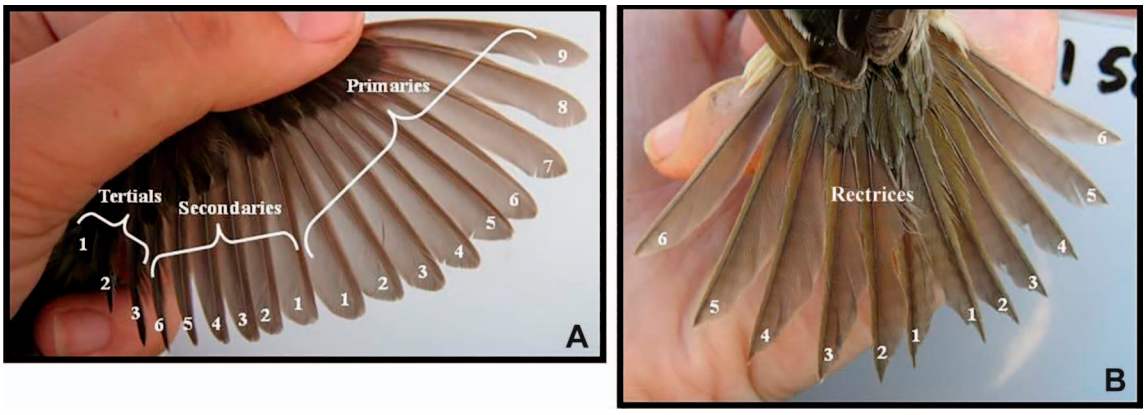
have 9 primaries, 6 secondaries, 3 tertials, and 12 rectrices, as indicated in Appendix Figure 5. Note: From the outside of the wing, primaries are counted from 9 to 1, whereas secondaries are counted from 1 to 6, and tertials are counted from 3 to 1. Rectrices are counted from 6 to 1, outside to in, on each side. Birds molt in consistent feather orders, so it is important that you do not mix up the numbering systems.

In the Field

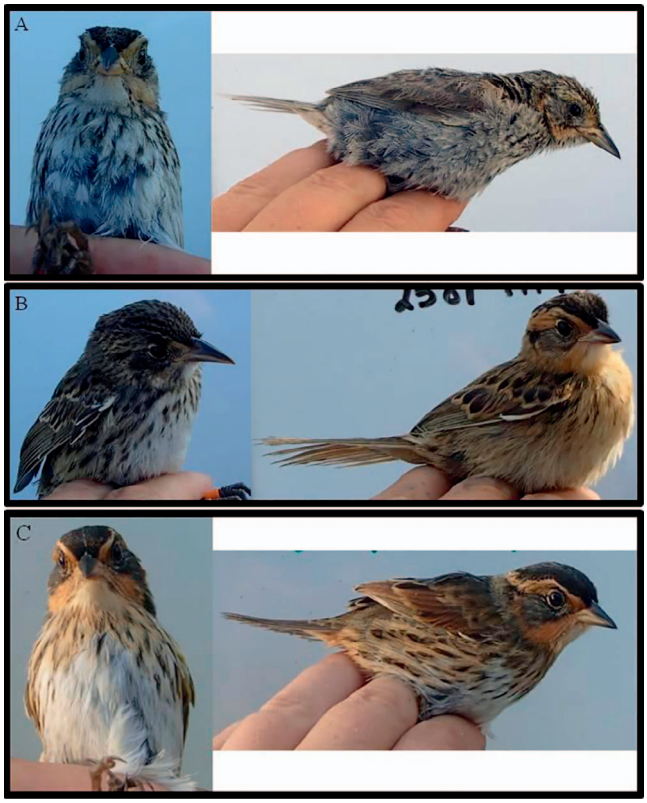
Examine all captured birds for molt (Appendix Figure 6). If the bird is not obviously molting, check to be sure that the individual is not simply very early in, or nearly done with, molt by (1) blowing gently on the bird's underparts, upperparts, and head to look for molting feathers; and (2) counting the flight feathers (primaries, secondaries, tertials, and rectrices) to make sure that none are missing or are pin feathers.

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, because the best estimates of molt initiation and duration include birds premolt and postmolt as well as birds actively molting (it is possible, however, to conduct analyses on only currently molting birds).

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, and 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.



APPENDIX FIGURE 5. Identification and numbering of Saltmarsh and Seaside sparrows' flight feathers.

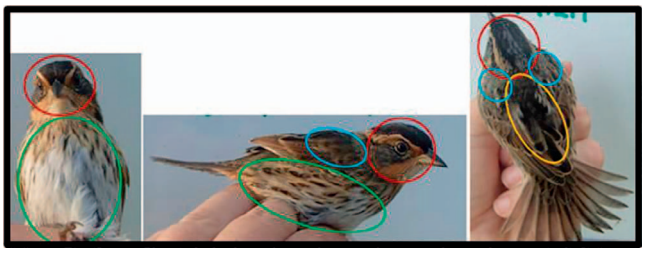


APPENDIX FIGURE 6. Examples of sparrows, premolt and postmolt: (**A**) adult Saltmarsh Sparrow premolt; (**B**) juvenile Seaside Sparrow (left) and Saltmarsh Sparrow (right) that have not yet molted; (**C**) adult or Juvenile Saltmarsh Sparrow that has completed prebasic molt.

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 each wing and access both the upperparts 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 to be 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 by 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.



APPENDIX FIGURE 7. Body regions for molt scoring. Blue indicates "lesser and median coverts," red indicates "head," yellow indicates "upperparts," and green indicates "underparts."

Score body feathers by region: all tracts of lesser and median coverts; underwing coverts; head (nape of neck to the top of the head plus the face); upperparts (back); and 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 (Appendix Figure 7):

Lesser and median coverts (circled in blue)
Underwing coverts
Head (circled in red)
Upperparts (circled in yellow)
Underparts (circled in green)

Score individual feathers on a scale of 0–5:

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:

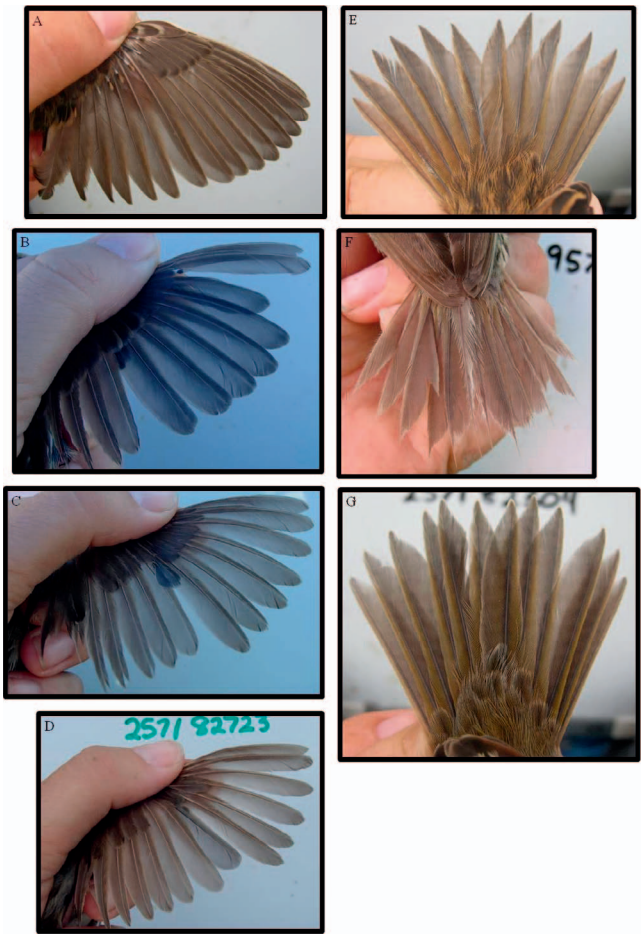
0 = all, or nearly all, old feathers; <10% of feathers in molt
1 = 10–30% of feathers in molt
2 = 31–50% in molt
3 = 51–70% in molt
4 = 71–90% in molt
5 = 91% new to all new feathers

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 (Appendix Figure 8). New feathers are brighter, slightly shiny, and have distinct edges.



APPENDIX FIGURE 8. (**A**) Mostly "old" juvenile feathers. The secondary coverts are a mix of 1's and 2's. (**B**) P9 and P8 are old; P7 is a 2; P6 to P1 are probably 3's and 4's; S6 and S5 a 2; S4 to S1 are old. (**C**) An adult with early wing molt: P1 and P2 are 3's; the rest of the feathers in this picture are old. (**D**) P1 is a 4; P9 to P4 are old; P3 and P2 are not quite visible in the picture. (**E**) An adult with old rectrices. (**F**) An adult with new rectrices. (**G**) A juvenile with "old" rectrices.