Interactions between sexual and natural selection on the evolution of a plumage badge

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Abstract The evolutionary stability of signals varies due to interactions between sexual and natural selection. A tidal-marsh sparrow, *Melospiza georgiana nigrescens*, possesses darker pigmentation than an inland-marsh sparrow, *M. g. georgiana*. Studies of feather-degrading bacteria and convergent evolution among salt-marsh vertebrates suggest this dark coloration is due to environmental selection. Sexually dichromatic swamp sparrow crowns, however, may be additionally under sexual selection. We investigated ties between two plumage patches (rusty cap and black forehead) and two behaviors (male-male aggression and parental care) in the coastal and inland subspecies to test the effect of sexual versus natural selection on badge evolution. Across both subspecies the extent of rusty feathers in the cap patch was correlated positively with parental care and negatively with aggression, and the extent of black feathers in the forehead patch was correlated positively with aggression. Males with larger forehead patches produced more offspring along the coast, while males with larger cap patches did so inland. The date of the first nesting attempt for both subspecies correlated with cap patch extent, suggesting a similar role for female choice. Natural selection likely accounts for darker coastal females. Coastal male head color, however, is darker due to increased selection for larger forehead patches via intrasexual competition, yet it remains largely rusty due to female choice for larger cap patches. Increased sexual dichromatism among coastal plain swamp sparrows thus

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provides a clear example of the interplay between sexual and natural selection in sub-species divergence.

Introduction

Sexual dimorphism can result from inter-sexual niche partitioning, intra-sexual competition, or female choice (Andersson 1994). The evolution of sexually dimorphic signals is also influenced by levels of predation, foraging strategies, and the background sensory environment; all of which affect the balance between natural and sexual selection (Endler 1978, 1989, 1992; Andersson 1994). Thus the fitness conferred by both a given signal and the phenotype it symbolizes can vary by environment (Qvarnström 2001; Hale 2008; Missowelt et al. 2008), and this variation could cause sexually selected signals to diverge across populations due to varying local natural selection regimes (Dunn et al. 2008).

The precise nature of sexual signals, however, can be influenced by causes beyond the immediate environment, with shared signal form within genera or families. Therefore, the influence of phylogenetic history must be controlled to understand the role of natural selection in the evolution of sexually selected traits. In Emberizid sparrows (family Emberizidae), seasonally acquired sexual dichromatism is rare. Among the related genera *Melospiza*, *Junco, Passerella,* and *Zonotrichia*, it is found only in the swamp sparrow, *Melospiza georgiana* Latham (Greenberg 1988). In this species, therefore, phylogenetic inertia presumably contributes little to dichromatism, making it a suitable system for studying the interaction of natural and sexual selection in the evolution of plumage signals.

Dichromatic plumage of the swamp sparrow

The socially monogamous swamp sparrow possesses a seasonally molted, sexually dichromatic head plumage, which includes distinct forehead and cap patches colored by both eumelanins (dark brown to black or gray pigmentation) and phaeomelanins (light brown/buff to rust pigmentation). Cap patches range in color from dark brown or black with a gray median stripe in some females to completely rusty in many breeding males. Both sexes possess a forehead patch that varies from brown to black (Greenberg 1988). These patches vary greatly among individuals of both sexes in both their size and color, and variation is dependent upon the amount of melanin and the proportion of each melanin type produced (Jawor and Breitwisch 2003; McGraw et al. 2005). Among males, variation in both the cap and forehead patches (hereafter "crown") is correlated with both territorial acquisition ability and the production of young outside of the social pair bond (Olsen 2007; Olsen et al. 2008a). This suggests that crown patch sizes may be subject to sexual selection by two pathways: (1) intrasexual competition for habitat among males and (2) mate selection by females.

Plumage differences by environment

The plumage of the tidal-salt-marsh endemic, coastal plain swamp sparrow (*M. g. nigrescens* Bond and Stewart) is generally less rusty (less phaeomelanic) overall than the two freshwater-breeding subspecies (*M. g. georgiana* Latham and *M. g. ericrypta*

Oberholser), with significantly more black (eumelanic) feathers in the crown, nape, and dorsal body contour feathers. Furthermore, these plumage differences are maintained in nestlings raised in the laboratory (Greenberg and Droege 1990). Similarly high levels of eumelanin characterize the integument of numerous salt marsh vertebrates when compared to closely related taxa in freshwater or upland habitats, including examples from birds, mammals, and reptiles (Grinnell 1913; Greenberg and Droege 1990; Greenberg and Maldonado 2006). Overall this suggests that environmental selection operates similarly on pigmentation across tidal marsh species. This convergent pattern may result from predation pressure against the dark gray to black, anoxic, salt-marsh muds (Von Bloeker 1932; Greenberg and Droege 1990). Recent studies, however, suggested that this convergence results from increases in melanin deposition due to selection caused by keratin-degrading bacteria (Burtt and Ichida 1999, 2004; Goldstein et al. 2004), which cause more damage in the tidal marsh than bacteria in less humid or less saline environments (Peele et al. 2009). Melanin both resists abrasion (Bonser 1995) and possesses antimicrobial properties (Mackintosh 2001), and bacteria collected from swamp sparrows in the same locales as this study show that coastal individuals are three times more likely than those inland to possess feather-degrading bacteria, and concentrations of such bacteria are greater on the coastal birds by over an order of magnitude (Peele et al. 2009). Furthermore, it appears that eumelanin and not phaeomelanin is most important for resisting feather abrasion (Roulin 2007). Thus, it seems clear that natural selection on feather wear has the potential to explain increased eumelanism in the coastal salt marsh.

Implications for sexual selection

Increased crown eumelanization due to natural selection may have implications for intraspecific interactions in this system. Divergence from the more phaeomelanic inland form to the more eumelanic coastal form could affect the male's signal of parental behavior or social dominance. The size of black plumage badges have been shown repeatedly to correlate positively with aggression or social rank (Rohwer 1975; reviewed in Senar 1999) and negatively with energetic investment in offspring (Bókony and Liker 2005), while non-black melanin badges have been shown to correlate positively with parental care (Siefferman and Hill 2003). A tradeoff between aggression and parental behaviors has been noted numerous times (Wingfield et al. 1987; Ketterson et al. 1992; Stoehr and Hill 2000; Duckworth 2006), and this tradeoff may be expressed by a tradeoff between phaeomelanic (parental care) and eumelanic (aggression) pigments in plumage badges. Increased eumelanization among coastal males thus may be a result of sexual selection for more aggressive behaviors, and not simply a result of environmental selection for greater melanin concentration. Additionally, natural selection for more extensive dark plumage may alter the eumelanin-phaeomelanin tradeoff shaped by sexual selection.

Hypotheses and predictions

We hypothesized that the described differences between inland and coastal crowns (Greenberg and Droege 1990) could evolve as a result of change in (1) the natural selection regime, (2) the sexual selection regime, or (3) a combination of changes in both regimes. Furthermore, as there is no evidence to suggest that body plumage is under sexual selection, body color can serve as an indicator of the strength of environmental selection. Thus crown and body coloration together provide unique predictions for each of our three hypotheses (Fig. 1).
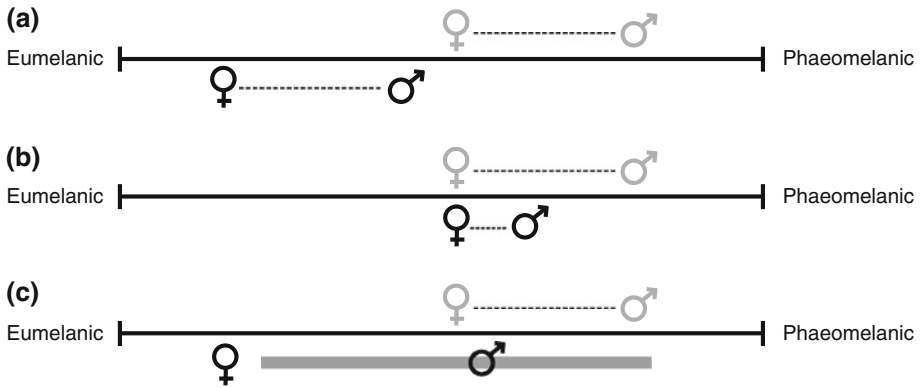
Fig. 1 Predictions of the relative rustiness (phaeomelanins) or blackness (eumelanins) of the crown of male and female swamp sparrows in the coastal subspecies (*Melospiza georgiana nigrescens*) compared to the inland subspecies (*M. g. georgiana*) under plumage divergence scenarios caused by **a** natural selection on crowns of both sexes, **b** sexual selection on the male crown, or **c** natural selection on the female and sexual alone or sexual and natural selection together on the male crown (the *gray bar* indicates the range of possible male values)

First, if the darker crowns of coastal birds are due purely to natural selection in the salt marsh, coastal and inland subspecies should exhibit similar degrees of sexual dichromatism, despite the coastal dichromatism occupying a more black-shifted range (Fig. 1a). Furthermore, the amount of variation in male crown characteristics should be similar in absolute range within each subspecies. The black-shifted variance of the coastal subspecies would thus lead to different relationships between crown characteristics and male behavior within each subspecies (Fig. 2a). Under this hypothesis body coloration should vary between the subspecies but not between the sexes.
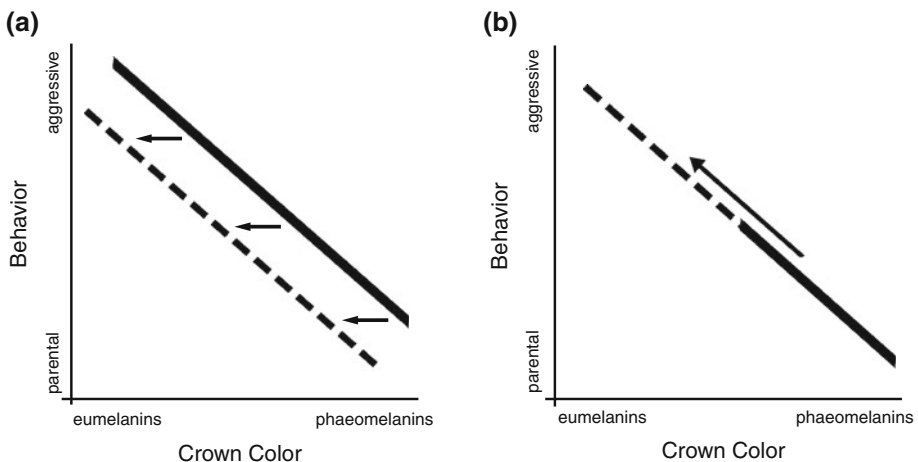

Fig. 2 Two hypothesized causes of the increased eumelanins found in male coastal plain swamp sparrow crowns (*dashed lines*) versus inland swamp sparrows (*solid lines*). **a** Natural selection favors more eumelanic male crowns directly resulting in darker crowns for each given behavioral state relative to inland birds. **b** Sexual selection favors behaviors that are associated with more eumelanic crowns resulting in a higher proportion of dark crowns

If sexual selection alone has led to crown color divergence, coastal males should possess crowns with more black than inland males and the behavioral characteristics that are associated with darker crowns for all swamp sparrows (Fig. 2b). Furthermore, as long as males possess more rust-colored crown feathers than females, sexual dichromatism should *decrease* in the coastal race, as females remain similar between the subspecies and males become less phaeomelanic (Fig. 1b). As a signal of environmental selection, body color should differ neither between the subspecies nor the sexes.

Lastly, if crown color divergence is due to natural and sexual selection, the degree of sexual dimorphism could be greater or lesser in the coastal subspecies. Under this hypothesis female color is driven primarily by natural selection for crowns with more black, whereas male crown color could settle at any point along the rust-to-black spectrum depending on the relative strength and direction of natural versus sexual selection (Fig. 1c). However, if male crown color is influenced by natural selection at any level (even as some compromise between the two selective forces), the relationship between crown color and male behavior will diverge from the inland subspecies (Fig. 2a), although to a lesser extent than if natural selection were acting alone. Finally body color under this hypothesis will vary between the subspecies (different levels of environmental selection) but not the sexes (similar levels), despite crown plumage differences by both sex and subspecies.

To test the predictions outlined above, we examined body plumage, the extent of black versus rust-colored feathers in the crown, and correlates between crown characteristics and relative male fitness within two populations: one of the coastal plain subspecies and a second of the nearest inland subspecies, *M. g. georgiana*. Within each population we tested for correlations between crown characteristics and intrasexual male competition (territory size, reaction to intrusion, vigilance, and the production of song and aggression call notes) and direct male contribution to parental care (provisioning of nestlings). We also tested for relationships between the crown and indicators of male reproductive success (breeding initiation date and annual offspring production within the social pair bond).

Materials and methods

Study site and individual measurements

We investigated the coastal subspecies at two plots in brackish (0–10 parts per thousand salinity of surface waters) *Spartina* marsh along the mouth of the Smyrna River, Delaware, USA during the 2002–2005 breeding seasons (May–August). Inland studies were conducted on two sphagnum fens on the Allegheny Plateau in Garrett County, Maryland, USA from 2004–2005 (see Olsen 2007 for detailed descriptions of study sites).

Each season we captured and banded adults and nestlings older than five days of age with a numbered, aluminum band and a unique combination of colored bands. For comparison with previous studies of this population, we classified the color of the cap into four categories based on the original analysis of sexual dichromatism in the swamp sparrow by Greenberg (1988). This classification describes the extent of rust-colored feathers, ranging from a crown completely devoid of rust with no discernable cap patch (class 1) to a crown with a cap patch that is solidly filled with only rust-colored feathers (class 4). Because melanic pigmentation is organized into two distinct patches on the crown, a black forehead and a rusty cap, we further measured the length of the forehead patch along the median line from the proximal end of the exposed culmen to the first rusty cap feathers and the length of the cap patch from the end of the forehead to the last rusty feathers.

Finally, to develop a more complete quantitative overview of crown patch pigmentation, we photographed the relaxed crowns of all adults, digitally selected and isolated rusty (versus black or brown) cap feathers and black (versus brown or gray) forehead feathers using Adobe Photoshop 5.5 (Adobe Systems Inc. © 1999), and determined the area of these patches using Carnoy 2.0 (Schols 2001). To test for a correlation between crown and body coloration, we digitally analyzed the dorsal body contour feathers between the nape and rump patches of a randomly selected subset of individuals to determine the percentage cover of black (versus brown, buff, or gray) feathers among non-crown, body-contour feathers. This value was then compared to the percentage of black feathers in the complete crown (including both the cap and forehead patches). Percentages were used instead of absolute area to control for differences in individual body size and to eliminate variation due to wing posture and precise dorsal plumage area delineation.

To examine possible age-related aspects of plumage and condition-related aspects of behavior, we aged adults based on banding returns and feather wear (Pyle and Howell 1997) and determined mass to the nearest tenth of a gram and tarsus length to the nearest tenth of a millimeter. Almost all males were captured after territory establishment, and a significant number were measured during or very shortly after the initial nesting attempt. We used mass divided by tarsus as a measure of condition.

Since reported correlations between male behavior and melanin-based plumage badges have occurred almost exclusively with a badge's size or extent rather than its chroma, brightness, or hue (e.g. Rohwer 1975; Siefferman and Hill 2003; Bókony and Liker 2005; Dunn et al. 2008; but see Sætre et al. 1994), we have used similar measurements here. For ease of communication we have used terms like "rustier" or "blacker" throughout, but these should be interpreted as increases in the *extent* of rusty or black feathers rather than differences in the spectral characteristics of these feathers.

Reproductive and territoriality measurements

We located nesting attempts of banded individuals from the first of May until either the end of August or the cessation of breeding. Because we used female nest-departure calls (McDonald and Greenberg 1991) to find nests, we typically located nests early during the nest cycle (mean ± standard error = 3.4 ± 0.3 days after clutch completion). The earliest clutch was completed on the ninth of May on the coast and the tenth of May inland. Nests were monitored daily until they failed or offspring fledged. In 2005, we observed 31 nests (15 coastal and 16 inland) with chicks of at least 3 days of age from a camouflaged location for 2 h or six feeding trips (whichever occurred first) to assess relative male provisioning rate. The sex of the provisioning parent was determined by colored-band identification. For each territory we defined 'nest-initiation date' (a measure of pairing success) as the Julian date of clutch completion during the initial nesting attempt. For initial attempts that were not found during the nest-building or egg-laying phase, dates were assigned based on the date of egg hatch, assuming that females incubated eggs for the population-specific average of 11 (coastal) or 12 (inland) days (Olsen 2007).

We delineated territories with minimum convex polygons around male singing locations during the active breeding season. Territory area was calculated in ArcMap 8.3 (ESRI 2002). We defined the territorial neighbors for each male as all birds with singing locations that were less than a distance of two mean territory diameters from the center of the male's territory. To assess relative male-male aggression, we observed males from 45 territories (27 coastal and 18 inland) for 1 h to record the baseline rates of song, aggressive 'growl' notes (Reinert and Golet 1979; Ellis 1980), and perch changes (as a measure of territory

vigilance). Observation occurred between sunrise and 1100 hours on males paired to incubating females (males do not incubate eggs) or males without an active nest (either prior to their initial nesting attempt or between attempts).

After this hour of observation, we presented each male with a subspecies-specific, taxi-dermied, adult male with a category four crown (completely rusty cap patch), accompanied by a single, subspecies-specific song, recorded within 4 km of our study plots (but not on our plots). The recording consisted of 4 min of silence, followed by 4-min of a single song type with ten seconds between each song to match natural song frequency (Ellis 1980), followed by 4 min of silence. During this 12-min period we recorded the length of time males actively responded to the mount, including both aggression and mobbing call notes, wing-flashes (Stefanski and Falls 1972), rapid perch-changes within 2 m, and physical contact.

Twice each for 11 additional banded males (3 inland and 8 coastal), we simulated intrusion in 2005 using broadcast song only (via the methods described by Searcy et al. 1997) to control for the effect of badge differences between the mount and the focal male on his behavioral response (Garamszegi et al. 2006). Detailed descriptions of the methods of this experiment are described in Liu et al. (2008). One of twelve song tapes were randomly selected for broadcast from a camouflaged, mounted speaker placed at the territory edge as determined by previously observed singing locations of the territorial male. From the start of the 6-min broadcast to an additional 6 min after the end of the recording, we noted the male's distance from the speaker in 15-s intervals, the time spent within 10 m of the speaker, and the rate of song production.

Statistical analysis

We used SAS 9.1.3 (SAS Institute 2005) for all statistical analysis. For our continuous measures of the crown (patch lengths and areas), we tested both for the relationship between crown characteristics and age, controlling for subspecies, and for crown as a function of sex, subspecies, and their interaction with two analyses of variance, subsampling individuals among years. We tested similar models for crown class as an output variable, using multinomial logit regression.

Crown color differed among males such that the rusty cap or black forehead patches could include a varying degree of non-rusty or non-black feathers (respectively) within its borders. Thus, while the length and area of the two crown patches were significantly correlated (Cap area vs. length: $n = 229$, $r = 0.62$, $P < 0.0001$; Forehead area vs. length: $n = 174$, $r = 0.49$, $P < 0.0001$), the two measurements were not completely dependent upon each other and both long patches with small areas and short patches with relatively large areas were possible. Given these relationships among our crown measurements, we constructed two principal components for male crown characteristics, one describing the rusty cap and the other the black forehead. The first component (hereafter Cap-PC) was created from cap patch length, cap patch area, and crown class and captured 63% of the variation in these variables (eigenvalue = 1.9). The second component (hereafter Fore-PC) was comprised of forehead patch length and area and captured 76% of their variation (eigenvalue = 1.5). Both principal components were positively correlated with all component variables such that high values of Cap-PC indicate a large cap patch containing mostly rusty feathers, and increasing Fore-PC values indicate larger forehead patches containing mostly black feathers. We tested for a tradeoff between male cap and forehead patch characteristics using a simple linear regression between the two principal components.

We also tested for sex and subspecies differences in the percentage of black feathers in the body contour plumage with an ANOVA, taking the natural log of the ratios to

transform the data to meet assumptions of normality. Candidate independent variables included sex, subspecies, and their interaction. To investigate whether blacker crowns result simply from high, body-wide, melanin production, we tested for correlations between the percentage of black body contour feathers and the percentage of black crown feathers, using simple linear regression for each sex by subspecies combination. We followed the same methods to test for the relationship between the principal components describing the percentage of black feathers in the male forehead versus cap patches.

Due to differences in clutch size (Greenberg and Droege 1990; Olsen et al. 2008b), nesting phenology, and territory size between the subspecies (which may have diverged for reasons other than sexual selection: Olsen 2007), we tested within each population for correlations between crown coloration and estimates of male fitness using multiple linear regression. Candidate predictors for offspring production included Cap-PC, Fore-PC, body condition, age, territory area, and nest-initiation date (to control for territory establishment and pairing success). Similar models were constructed for nest-initiation date and territory area with the same candidates.

To examine relationships between crown color and behavior, we tested for variation in song rate, perch changes per minute (during the 1-h male observation period), and mount engagement length (during the mount with song playback experiment) using three multiple linear regressions with each behavior as a dependent variable. Candidate independent variables included territory area, the Julian date and time of day of our observation, the number of territorial male neighbors, male condition, age, indicator variables for subspecies and nesting period, Cap-PC, and Fore-PC. Similar candidate variables were tested for two more regressions for the mean distance to the speaker and time spent within 10 m of the speaker during the audio playback experiment. We used forehead and cap patch lengths instead of the two principal components for these last two tests, however, as we only had photographs of four of the males from our trials (and therefore could not calculate either patch area or the principal components for the majority of trials). Further, we conducted trials on each male twice (Liu et al. 2008), thus we tested for effects on approach distance and time spent near the playback speakers using a repeated-measures ANOVA controlling for the trial type within each individual. Given the small sample size of these trials and the model's nested structure, we constrained model selection to include only those models with two or fewer independent variables. Models predicting the occurrence of growl notes were tested using multiple logistic regression (one, two, or three growls produced) and the same candidate independent variables as the linear models.

Final models with categorical variables were analyzed *post hoc* for interaction terms with subspecies using the general linear model procedure in SAS (Proc GLM). Multiple and simple linear regression model selection was based on Mallow's Cp, and multiple logistic regression and ANOVA models were chosen using stepwise selection with entrance and exit criteria set to $\alpha = 0.15$. All residuals were tested for normality and homogeneity of variance where appropriate, and we log-transformed territory area to meet assumptions. All means given are $\pm$ standard error (SE), and means and standard errors reported for models with multiple predictors are corrected means using least squares.

Results

Subspecies divergence in plumage color

Across all crown characteristics, coastal birds possessed fewer rusty and more black-colored feathers than inland birds, and males were rustier and less black than females.

Variation in the extent of rust in the male crown was not related to bird age. Controlling for the effect of subspecies, age had no effect on crown class ($n = 93$, $\chi_{1,\,90} = 0.4$, $P = 0.51$), cap patch length ($n = 93$, $F_{1,\,90} = 0.7$, $P = 0.39$), cap patch area ($n = 93$, $F_{1,\,90} = 1.0$, $P = 0.32$), forehead patch length ($n = 93$, $F_{1,\,90} = 0.7$, $P = 0.41$), or forehead patch area ($n = 93$, $F_{1,\,90} = 2.7$, $P = 0.11$).

The extent of rust in the entire crown varied significantly by subspecies and sex. Crown class was predicted by subspecies ($n = 476$, $\chi_{1,\,472} = 77.0$, $P < 0.0001$), sex ($\chi_{1,\,472} = 127.2$, $P < 0.0001$) and the interaction of the two ($\chi_{1,\,472} = 9.6$, $P = 0.002$). Inland birds possessed more rusty feathers than costal birds; Males possessed more rusty feathers than females, and the difference between the sexes was greatest among coastal birds (average crown class: 3.19 ± 0.05 for coastal males, 1.62 ± 0.06 for coastal females, 3.64 ± 0.06 for inland males, and 2.70 ± 0.10 for inland females; Fig. 3).

Similarly, cap patch area (full model: $n = 291$, $F_{3,\,287} = 62.5$, $P < 0.0001$) was related to subspecies ($F_{1,\,287} = 66.7$, $P < 0.0001$), sex ($F_{1,\,287} = 121.7$, $P < 0.0001$), and the interaction between subspecies and sex was nearly significant ($F_{1,\,287} = 3.6$, $P = 0.06$). Inland birds and males had larger caps than coastal birds and females, respectively, and there was again a greater degree of sexual dimorphism in the coastal population (coastal male mean cap area: 150.7 ± 8.2 mm^2, coastal female: 19.3 ± 4.2 mm^2, inland male: 214.5 ± 10.8 mm^2, and inland female: 121.6 ± 12.2 mm^2). For cap patch length (full model: $n = 507$, $F_{3,\,503} = 189.3$, $P < 0.0001$) there was also a significant effect of sex ($F_{1,\,503} = 145.7$, $P < 0.0001$), subspecies ($F_{1,\,503} = 223.3$, $P < 0.0001$), and a sex by subspecies interaction ($F_{1,\,503} = 67.4$, $P < 0.0001$). Rusty cap patches were shorter in coastal birds, in females versus males, and the sexual difference was again significantly larger among coastal birds (coastal males: 11.7 ± 0.2 mm, coastal females: 4.3 ± 0.3 mm, inland males: 14.1 ± 0.4 mm, and inland females: 12.7 ± 0.4 mm).

The forehead patch was also different between both the sexes and the subspecies. Forehead patch length (full model: $n = 506$, $F_{3,\,502} = 181.6$, $P < 0.0001$) differed by subspecies ($F_{1,\,502} = 297.2$, $P < 0.0001$), sex ($F_{1,\,502} = 72.8$, $P < 0.0001$), and their interaction ($F_{1,\,502} = 93.6$, $P < 0.0001$). Coastal birds had longer patches than inland birds, and coastal females had longer patches than coastal males, although there was no
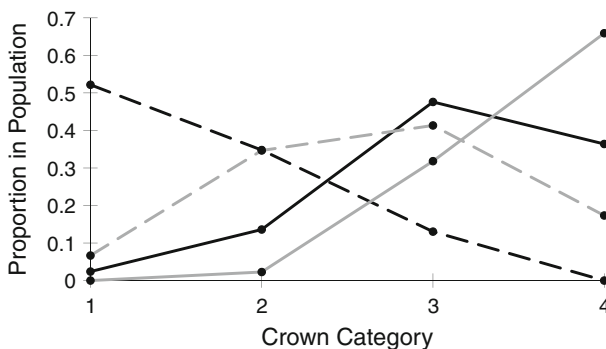

Fig. 3 The proportion of individuals that possessed four crown types for males (*solid lines*) and females (*dashed lines*) from populations of coastal *Melospiza georgiana nigrescens* (*black lines*) and inland *M. g. georgiana* (*gray lines*) swamp sparrows (1 = black crown with gray or brown median stripe, 2 = cap patch present and includes >0 and <50% rusty feathers, 3 = cap patch includes >50 and <100% rusty feathers, and 4 = 100% rusty feathers). Data was taken from the crowns of 388 coastal birds (138 females, 250 males) and 163 inland birds (75 females, 88 males)

significant difference between the sexes inland (coastal males: 7.2 ± 0.1 mm, coastal females: 10.4 ± 0.1 mm, inland males: 5.8 ± 0.2 mm, and inland females: 5.6 ± 0.2 mm). Forehead patch size (full model: $n = 79$, $F_{3, 75} = 33.4$, $P < 0.0001$) differed by subspecies ($F_{1, 76} = 50.2$, $P < 0.0001$), and sex ($F_{1, 76} = 17.3$, $P < 0.0001$). The addition of the interaction term did not improve the model ($F_{1, 75} = 0.6$, $P = 0.45$). Again, coastal birds possessed more black feathers than inland birds and females were likewise darker than males (coastal male black forehead patch size: 68.1 ± 3.9 mm^2, coastal females: 86.9 ± 3.9 mm^2, inland males: 44.0 ± 3.8 mm^2, and inland females: 57.1 ± 3.7 mm^2).

The percentage of black coloration among dorsal, non-crown, body-contour feathers differed by subspecies alone ($n = 78$, $F_{1, 76} = 81.0$, $P < 0.0001$). Neither sex ($F_{2, 75} = 0.4$, $P = 0.53$) nor the interaction of sex and subspecies ($F_{3, 74} = 1.1$, $P = 0.36$) were significant when added to this model. Dorsal body plumage of both coastal sexes contained more black feathers than in inland individuals of either sex (coastal males: $46.3 \pm 2.4\%$ black body contour feathers, coastal females: $48.4 \pm 2.4\%$, inland males: $28.4 \pm 2.4\%$, and inland females: $25.1 \pm 2.4\%$). The percentage of black, dorsal plumage correlated positively with the percentage of black plumage in the entire crown across all females of ($n = 39$, $r^2 = 0.43$, $F_{1, 37} = 28.1$, $P < 0.0001$) and within inland males ($n = 20$, $r^2 = 0.22$, $F_{1, 18} = 5.0$, $P = 0.04$). There was no relationship, however, between the amount of black on the body versus the crown of coastal males ($n = 19$, $r^2 = 0.09$, $F_{1, 17} = 1.7$, $P = 0.21$). Among all males, there was a significant negative correlation between Cap-PC and Fore-PC ($n = 117$, $r^2 = 0.20$, $F_{1, 115} = 28.5$, $P < 0.0001$; Fig. 4).

Reproductive success and parental investment

Among inland birds the best model for the number of chicks fledged ($n = 47$, $r^2 = 0.23$, $F_{2, 44} = 6.4$, $P = 0.004$) included a positive correlation with Cap-PC ($t_{1, 60} = 2.1$, $P = 0.04$) and a negative correlation with the date of nest initiation ($t_{1, 60} = -2.8$, $P = 0.007$), indicating that males that nested earlier and possessed caps with more rusty feathers fledged the most young (Fig. 5a). For coastal sparrows, however, the best model
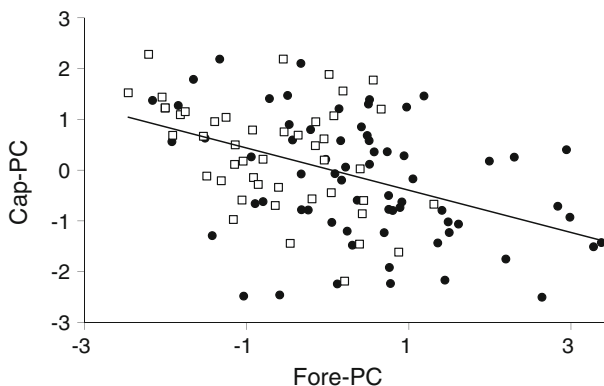

Fig. 4 The relationship between a principal component describing the rustiness of the cap patch (Cap-PC) and a principal component describing the blackness of the forehead patch (Fore-PC) in male, coastal *Melospiza georgiana nigrescens* (*black circles*) and inland, *M. g. georgiana* (*white squares*). Principal components are positively correlated with the extent of either rust- or black-colored feathers (Cap-PC and Fore-PC, respectively). The regression line is based on all points

($n = 58$, $r^2 = 0.23$, $F_{3, 54} = 5.4$, $P = 0.003$) included a positive correlation with Fore-PC ($t_{1, 54} = 2.3$, $P = 0.03$) and negative correlations with both nest-initiation date ($t_{1, 54} = -2.5$, $P = 0.02$) and log-transformed territory area ($t_{1, 54} = -2.9$, $P = 0.005$). These patterns remain even if the two most successful males (each with seven offspring produced) are omitted from the analysis, although the relationship with nest-initiation date then becomes only marginally significant ($P = 0.06$). Along the coast, earlier nesting males with more black feathers in their foreheads and smaller territories produced more young (Fig. 5b).

For inland birds the best model predicting nest-initiation date included a positive relationship with only log-transformed territory area ($n = 43$, $r^2 = 0.08$, $F_{1, 41} = 4.3$, $P = 0.05$), suggesting that birds on smaller territories bred earlier. For coastal birds, however, early nesting was best explained by a low Cap-PC ($n = 72$, $r^2 = 0.07$, $F_{1, 70} = 5.6$, $P = 0.02$). Thus males with fewer rusty feathers in their cap patches nested earlier. For both subspecies, Cap-PC alone was the best predictor of the proportion of feeding trips made by males ($n = 30$, $r^2 = 0.33$, $F_{1, 28} = 13.6$, $P = 0.001$). Thus, males with larger rusty caps fed nestlings more (Fig. 6). Subspecies had no significant explanatory power when added to this model ($n = 30$, $r^2 < 0.01$, $F_{1, 31} = 0.3$, $P = 0.60$).

Territory size and baseline aggressive behavior

Among coastal males, log-transformed territory area was best predicted (full model: $n = 109$, $r^2 = 0.52$, $F_{2, 106} = 57.6$, $P < 0.0001$) by study plot ($t_{1, 106} = 10.4$, $P < 0.0001$) and increasing male condition (mass adjusted for body size: $t_{1, 106} = 2.8$, $P = 0.006$), such that the size of territories in the densest coastal plot were positively

Fig. 5 The mean value ($\pm$ SE) of the principal component describing **a** the rusty cap patch of inland, male *Melospiza georgiana georgiana* (controlling for initial nest completion date and log-transformed territory area) and **b** the black forehead patch of coastal, male *M. g. nigrescens* (controlling for initial nest completion date), calculated for each number of fledglings produced within the social pair bond. *Italicized* values above each point are the sample sizes for that mean
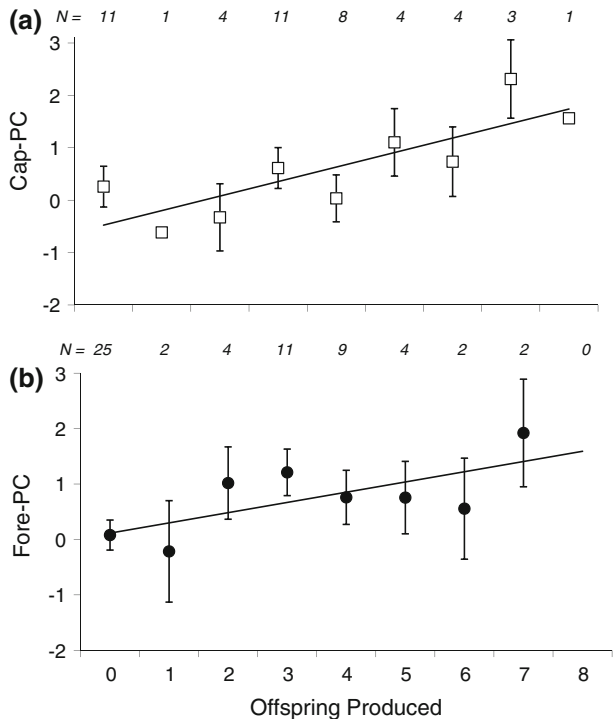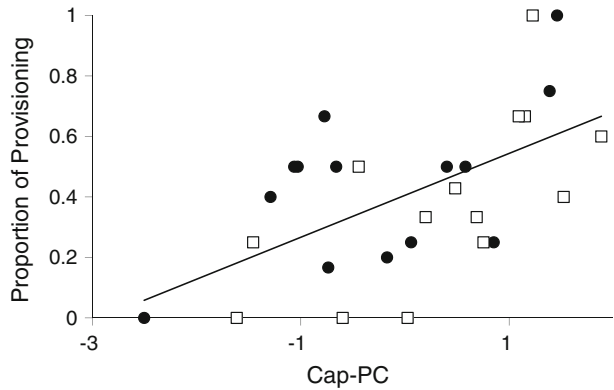
Fig. 6 The proportion of offspring provisioning trips made by the male versus a principal component describing the extent of rust-colored feathers in the cap patch of inland (*white squares*) and coastal (*black circles*) swamp sparrows

related to male condition, although this was not true for any other plot (less dense coastal plot: $F_{1, 29} = 0.1$, $P = 0.76$; denser inland plot: $F_{1, 14} = 3.0$, $P = 0.10$; less dense inland plot: $F_{1, 29} = 0.5$, $P = 0.50$). Among inland sparrows log-transformed territory area was predicted by increasing Cap-PC ($t_{1, 34} = 2.1$, $P = 0.05$) and decreasing Fore-PC ($t_{1, 34} = -2.1$, $P = 0.04$), such that males defending the smallest territories possessed both larger forehead patches and decreased percentages of rust in the cap ($n = 37$, $r^2 = 0.19$, $F_{2, 34} = 4.0$, $P = 0.03$).

Coastal males were more aggressive overall during the 1-h observation period. Coastal males sang more (full model: $n = 45$, $r^2 = 0.13$, $F_{1, 43} = 6.7$, $P = 0.01$), producing 57.2 ± 9.3 songs compared to 21.4 ± 11.7 songs by inland males. Subspecies alone was the best predictor of song rate during the observation period. The best model (full model: $n = 39$, $r^2 = 0.52$, $F_{4, 34} = 9.4$, $P < 0.0001$) for movements around the territory (a likely reflection of vigilance) included subspecies ($t_{1, 34} = 2.7$, $P = 0.01$), an indicator variable for the incubation period ($t_{1, 34} = 2.6$, $P = 0.01$), time of day ($t_{1, 34} = -3.1$, $P = 0.004$) and male age ($t_{1, 34} = 1.9$, $P = 0.07$). Both subspecies were more vigilant during incubation than in periods when there was no active nest, coastal males were more vigilant than inland males, vigilance was higher earlier in the day, and older males were more vigilant than younger males. Coastal males changed perch much more frequently, averaging 17.2 ± 1.8 times per hour compared to 5.8 ± 2.3 moves per hour by inland males.

Finally coastal males produced more aggressive 'growl' notes during the 1-h observation period. Coastal males growled 0.9 ± 0.2 times per hour compared to 0.2 ± 0.2 growls per hour by inland males. The best model for growling frequency (full model: $n = 32$, $\chi_2^2 = 13.2$, $P = 0.001$) included time of day ($\chi_1^2 = 6.7$, $P = 0.01$) and Cap-PC ($\chi_1^2 = 7.6$, $P = 0.006$). Males growl more frequently earlier in the day, and males with fewer rusty cap feathers are more likely to growl than those with rustier caps. Subspecies was not significant, however, when added to this model ($\chi_1^2 = 1.0$, $P = 0.31$), suggesting that the difference between the subspecies is explained by the subspecific difference in cap characteristics. This is more easily visualized by examining both the mean Cap-PC scores for birds that produced the same number of growl notes and the percentage of each subspecies in each group (Fig. 7).

Intrusion simulations

The best model ($n = 27$, $r^2 = 0.34$, $F_{2, 24} = 6.3$, $P = 0.006$) for the length of time males engaged the mount during a simulated territorial intrusion included Cap-PC ($t_{1, 24} = -3.0$,

$P = 0.007$) and condition ($t_{1, 24} = 2.7$, $P = 0.01$). Males with smaller cap patches and those in better condition mobbed the mount for the longest period of time. The effect of subspecies was not significant when added to this model ($t_{1, 23} = 0.2$, $P = 0.81$).

Birds with larger black forehead patches were more aggressive during the audio playbacks in both populations. Unfortunately we did not take photographs for these males (thus could not calculate patch area or the principal components) and instead used patch length as a surrogate. The best model for average distance to the playback speaker included a negative correlation with forehead patch length alone ($r^2 = 0.41$, $F_{1, 19} = 18.4$, $P = 0.0004$), such that males with large forehead patches approached the speakers closer (Fig. 8). Subspecies was not significant when added to this model ($t_{1, 18} = -0.8$, $P = 0.42$). The best regression model explaining the amount of time males spent within 10 m of the speaker also included forehead patch length alone ($r^2 = 0.30$, $F_{1, 19} = 11.1$, $P = 0.004$). Again, subspecies was not significant when added to this model ($t_{1, 18} = -0.2$, $P = 0.83$). The number of songs produced over the audio trials was best correlated with increasing male age ($r^2 = 0.51$, $F_{1, 19} = 25.7$, $P < 0.0001$) with second year birds producing 23.0 ± 5.1 songs during the trial and older birds producing 46.1 ± 4.5 songs. These results should be interpreted with caution considering the relatively few inland birds sampled.

Discussion

Natural selection on crown feathers

Paralleling the general trend found among all tidally endemic sparrows (Greenberg and Droege 1990), the crowns of coastal plain swamp sparrows contained more black and fewer rusty feathers overall, with lower crown classes (*sensu* Greenberg 1988), smaller rusty cap patches, and larger black forehead patches. Differences between the two subspecies existed for both females and males, but they were larger for females, and thus sexual dimorphism was greater in the coastal population. We propose that the crown is a sexually selected signal, such that changes in male crown color are meaningful to territory establishment, the date of pairing, and offspring production. Furthermore, sexual selection on coastal males has prevented the degree of eumelanization found in coastal female crowns, which are subject more exclusively to natural selection. The dorsal plumage of

Fig. 7 The mean value ($\pm$ SE) of a principal component describing the extent of rust-colored feathers in the cap patch for male coastal (*Melospiza georgiana nigrescens*) and inland (*M. g. georgiana*) swamp sparrows that uttered between zero and three aggressive 'growl' notes during 1 h of observation. The pie chart at each point shows the percentage of birds in the coastal (*black*) and inland (*white*) subspecies. *Italicized* values above each point indicate sample size
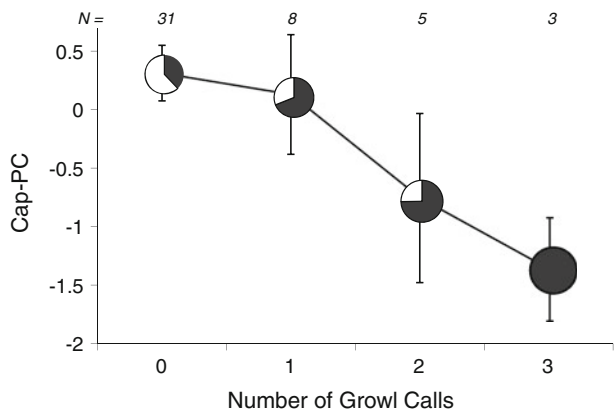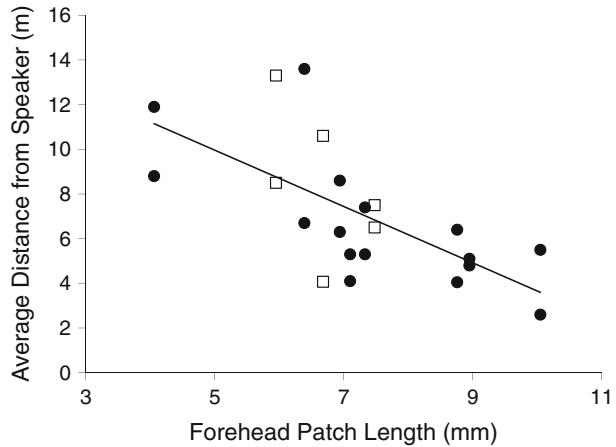
Fig. 8 The mean distance from the playback speaker versus the length of the black forehead patch during playback of non-neighbor song among inland (*white squares*) and coastal (*black circles*) swamp sparrows

both sexes of coastal birds, which presumably is subject only to natural selection, contains more black feathers than is found among inland birds, but it is not sexually dichromatic in either population. We can conclude therefore that natural selection is operating similarly on both male and female coastal sparrows. Furthermore, in both subspecies the extent of black in female crowns was correlated with black in the dorsal plumage, suggesting that the crown experiences similar selection pressure to the body when sexually selection is removed. In coastal males, however, there was no correlation between the percentage of black feathers in these two plumage areas, further supporting the supposition that male crown color is controlled by sexual selection and not sex-specific natural selection.

Biologists have long speculated that the degree of sexual dimorphism is due as much to natural selection on females as to sexual selection on males (Wallace 1889), and there has been some quantitative evidence to support this (e.g. Björklund 1991; Irwin 1994; Martin and Badyaev 1996; Bleiweiss 1997; Gotmark et al. 1997; Burns 1998; Badyaev and Hill 2003). Among coastal swamp sparrows both sexes are likely under strong natural selection for eumelanistic crowns, but only coastal females are released from the impact of inter and intrasexual signaling on crown color. The difference in body plumage between the sub-species but not the sexes, while crown plumage differs by both subspecies and sex fulfills our prediction for the action of both natural and sexual selection on overall plumage color. Given the correlations between crown color and behavior and the patterns of sexual dimorphism, however, we propose that male crown color is determined by sexual selection alone.

Sexual selection on crown color

In both subspecies we found evidence of complex signaling involving the crown. The extent of black in the forehead related to territorial aggression, and the extent of rust in the male cap related to parental contributions. Forehead patch size in both subspecies was directly related to two measures of aggression (average distance from the playback speaker, and time spent close to the speaker), which agrees with investigations of black melanin patches in other species (reviewed in Senar 1999). Males with larger rusty caps provisioned young more, regardless of subspecies, and cap size was negatively related to two measures of aggression (aggressive call notes and mount mobbing length).

The difference in crown coloration between inland and coastal males is best explained by variation in sexual selection alone, through environment-specific solutions to the

tradeoff between male parental care and aggression. The variation in crown characteristics are related to behavioral differences similarly within and between the subspecies, and three different measures of territoriality are predicted best by crown melanization without a subspecies effect. This fulfills our prediction for the action of only sexual selection on the male crown (Fig. 2b). However, our initial prediction also inferred that such a change would be accompanied by a *decrease* in sexual dichromatism in the coastal population, since the action of only sexual selection would shift male crown color more toward the female mean phenotype. Instead, we witnessed an *increase* in sexual dichromatism. We propose that swamp sparrow plumage color is controlled by both natural and sexual selection (Fig. 1c), but that natural selection is the predominant force acting on female crowns and both male and female body plumage (increasing eumelanization for either camouflage or as a defense against bacterial degradation), while sexual selection is the predominant force acting on male crowns (increasing the size of the black forehead badge as an indication of increased territorial aggression).

Therefore, this divergence in the mean size of the plumage badges without a change in the correlation between badge size and behavior suggests that there is increased selection for aggressive behavior among coastal males. The relative importance of territorial defense has thus diverged between males of the two subspecies, although the signal values indicating aggression have remained similar both within and between subspecies (Fig. 2b). Greater importance of territorial aggression in the coastal environment is suggested by a higher singing rate and a higher frequency of perch changes among coastal birds, although the later might also be explained by increased vigilance for nest predators (nest-predation rate is higher in the salt marsh: Olsen et al. 2008b). These two behaviors appear to operate independently of plumage badges, but have nonetheless diverged (either genetically or through plastic shifts in behavior) in the direction predicted by behavioral changes tied to crown color.

The greater importance of aggression in the coastal environment is also supported by plumage correlates of offspring production. Controlling for pairing success (via nest-initiation date), coastal males with more black in their crowns produced the most offspring, while among inland males those with larger rusty cap patches did. This suggests that the ability to maintain territories in high quality habitat is more important in the salt marsh while the ability to provide high levels of parental care is more important inland. There was a negative relationship between territory size and offspring production among coastal males, such that males in the smallest territories produced the most offspring (following Fretwell and Lucas 1970 and Fretwell 1972). We suggest that in the salt marsh, the best quality habitat is highly contested, resulting in smaller territories and favoring the most aggressive males. Among inland males we propose that the ability to maintain territories in highly contested habitats is still tied to the forehead patch, as evidenced by both the behavioral experiments and the negative relationship between forehead patch and territory size, but its importance for male fitness is reduced as the offspring production of inland pairs was not predicted by male forehead patch size. Finally we suggest that selection for the defense of habitat is driven by intrasexual selection on aggression, of which the forehead patch is a signal, while selection for male parental contribution may be driven by female choice on the rusty cap. Admittedly however, although breeding initiation dates suggest female choice, we did not specifically test for mating preferences and such tests are warranted. Despite this, intrasexual selection appears to be the stronger determinant of offspring production among coastal males, while intersexual selection appears to operate more strongly on inland males.

Male competition versus female choice

Nest-initiation date, a measure of pairing success, was predicted by the extent of rust col-
oration in coastal males, suggesting that female choice may maintain that badge charac-
teristic. Additionally, cap size in both subspecies (relative to neighbors) is an important
predictor of extra-pair young (Olsen et al. 2008a), suggesting that swamp sparrow females
use the rusty cap in mate selection for both social and extra-pair bonds and value both the
parental care of social males and the genes for parental care in extra-pair males. However,
coastal females have been shown to pair preferentially not only with rustier-crowned males
but also with males defending smaller territories in high quality habitat (Olsen 2007). The
ability of males to establish and defend territories in highly contested areas (where nests are
initiated earlier) is related to aggression, of which the black forehead is a signal. In both
populations therefore, female choice may be indirectly selecting for black forehead patches
through selection on habitat while directly selecting for rusty caps and male parental con-
tribution at the same time. It is the relative strength of the direct versus indirect relationships
that we propose has shaped the crown characteristics of each population, with coastal males
benefiting more (in terms of offspring production) from territorial maintenance and inland
males more from parental care. Thus, the two-part melanin badge of swamp sparrows can
serve as an indication of the relative strength of direct female choice versus the combined
strength of male-male competition and female habitat preference in each population.

    We propose that selection for increased size in both crown patches in breeding male
swamp sparrows is limited by head size (especially available head area that is visible
during face-to-face interactions). The negative relationship between the size of the fore-
head and cap patches suggests a tradeoff between the production of one signal over the
other and an inability to produce large signals for both aggression and parental care
simultaneously (Fig. 3). These two plumage signals echo the tradeoff between parental
care and territorial aggression reported in other species (e.g. Wingfield et al. 1987;
Ketterson et al. 1992; Stoehr and Hill 2000; Duckworth 2006). Whether the variance in the
morphological tradeoff reflects an underlying endocrinological tradeoff between these
behavioral states is unknown, but one can imagine the honesty of these signals being
reinforced by such morphological limitations.

Conclusions

The crown coloration of the tidal, salt-marsh endemic subspecies of the swamp sparrow
(relative to inland subspecies) is best explained by sexual selection on aggressive versus
parental behaviors in males and natural selection for darker feathers over the entire dorsal
plumage for both males and females (Fig. 1c). Both sexes of the coastal plain swamp
sparrow show greater body plumage eumelanization, a pattern which converges across a
wide variety of tidal salt marsh vertebrates and suggests a strong natural selection regime
(Greenberg and Droege 1990; Greenberg and Maldonado 2006; Peele et al. 2009). The
sexes differ, however, in the eumelanization of the crown plumage, and the extent of black
in the crown correlates with dorsal body plumage color only in females. Increased sexual
dichromatism in coastal birds relative to those inland is caused by more black feathers in
female crowns due to natural selection and more black feathers in male crowns (although
less than in coastal females) due to sexual rather than natural selection. The interplay
between male-male competition (selecting for black pigmentation), female choice (for
rusty pigmentation), and environmental selection (for greater eumelanins overall)

represents a clear example of the importance of the interactions between sexual and natural selection in subspecies divergence.

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