

and could thus produce sexual dimorphism in those structures through processes similar to those suggested for other nonavian vertebrates and invertebrate taxa (Vitt and Cooper 1985; Shine 1989; Gittleman and van Valkenburgh 1997; Thorén et al. 2005).

Comparisons between closely related taxa that differ in the degree of feeding structure dimorphism represent a powerful tool for understanding the interactions between natural and sexual selection in creating sexual dimorphism. Such studies can control for confounding effects of body size, mating system, and basic foraging ecology present in wider comparisons. We present one such contrast between 2 subspecies of the swamp sparrow (*Melospiza georgiana*), comparing a tidal marsh specialist with a sexually dimorphic bill (*M. g. nigrescens*; hereafter the “coastal” subspecies) to a freshwater-wetland subspecies that lacks such dimorphism (*M. g. georgiana*; hereafter the “inland” subspecies).

Tidal marsh sparrows as an ideal system for the study of sexual dimorphism

Recent investigations have revealed that tidal marsh sparrows as a group possess a greater degree of sexual bill dimorphism than other Emberizid sparrows (Greenberg and Olsen 2010), despite numerous, independent colonizations of the ecosystem. Tidal salt marshes are characterized by low biodiversity but high ecosystem productivity (Adam 1990). Increased intraspecific competition could therefore encourage the evolution of sex-specific foraging niches through ecological adaptation (Bolnick and Doebeli 2003). Tidal marsh birds also generally possess high territorial densities (Greenberg and Olsen 2010), however, which may increase competition for mates or territories as well as food (Olsen et al. 2010). Thus, high tidal marsh productivity could just as easily increase the strength of sexual selection on bills as signaling structures or weapons as it could encourage foraging niche divergence through natural selection.

Natural and sexual selection may both have played an important role in the evolution of bill dimorphism in swamp sparrows, specifically. Swamp sparrow song differs between the coastal and inland subspecies in ways that are consistent with bill size differences (Ballentine 2006; Liu et al. 2008), which has been suggested to be a signaling constraint due to foraging niche (Ballentine 2006). There is also increased sexual dichromatism and higher male–male competition among swamp sparrows in tidal marshes relative to those in nontidal wetlands (Olsen et al. 2010), suggesting an increase in the strength of sexual selection overall in the tidal marsh. Our objective for this study was to test whether natural selection, sexual selection, or some combination of the 2 forces is the most likely explanation for bill size dimorphism in the coastal race of the swamp sparrow.

Four hypotheses on the origin of sexual dimorphism in a trophic structure

We posit 2 hypotheses to explain how nonsexual, natural selection could produce sexual bill dimorphism and 2 hypotheses that explain how sexual selection could produce bill dimorphism (Table 1).

H1: allometry/ontogeny

Bill size dimorphism may simply be a nonadaptive consequence of body size dimorphism or ontogenetic growth patterns (as the bill may continue to grow beyond the first year of life in members of this genus; Smith et al. 1986). If either of these are the case, then bill size will correlate with either body size (Table 1: Prediction 1.1) or bird age (Table 1: P1.2) regardless of sex, but male sparrows in the tidal marsh population will be either larger (allometry) or older (ontogeny) than females.

Table 1

Predictions and summaries of support for 4 hypothesized mechanisms of the evolution of bill sexual dimorphism in swamp sparrows, *Melospiza georgiana*

Hypothesis	Supported
Nonsexual, natural selection	
H1: allometry/ontogeny	
P1.1: bill size is predicted by body size (regardless of sex) and males are larger	No
P1.2: bill size is predicted by age (regardless of sex) and males are older	No
H2: sex-specific foraging niches	
P2.1: males with larger bills are more likely to be retained in the population	No
P2.3: sexual dimorphism within the social pair bond is positively correlated with offspring production	No
P2.2: sexual dimorphism within the social pair bond is positively correlated with offspring growth	No
P2.4: individuals with large bills (regardless of sex) are adept at foraging for different items than individuals with small bills	Yes
Sexual selection	
H3: intrasexual selection on male display	
P3.1: males with larger bills are more likely to successfully defend a territory	Weak support
P3.2: male bill size is positively correlated with territory quality	No
P3.3: male bill size is positively correlated with rate of song production (controlling for breeding stage)	No
P3.4: male bill size is positively correlated with intrasexually selected plumage patch	No
H4: intersexual selection for indirect benefits	
P4.1: males with larger bills sire a greater proportion of young produced on their territories	Yes
P4.2: females prefer to mate with larger billed males	Yes
P4.3: male bill size is correlated with male quality (e.g., age)	Yes
P4.4: male bill size is positively correlated with female-selected plumage patch	Yes

Predictions are framed such that refutation of all of the predictions is required to reject each hypothesis fully, but support for more predictions is also indicative of greater support for the hypothesis. See Introduction for further elaboration.

H2: sex-specific foraging niches

Tidal marsh bill dimorphism may result from natural selection on the breeding grounds for sex-specific foraging niches. If this is the case, then either (1) larger billed coastal males should experience higher survival (P2.1: higher probabilities of retention within the breeding pool) or (2) more sexually dimorphic pairs should show increased fecundity (P2.2: in the number of offspring fledged or P2.3: in the growth rate of those offspring within the territory; Gosler 1987). Further, birds with different bill sizes (regardless of sex) will forage most effectively on different prey items (P2.4). If none of these predictions are supported, sex-specific foraging may still exist but is unlikely a strong determinant of bill size dimorphism.

H3: intrasexual selection

Alternatively, sexual bill dimorphism may have been produced by male–male competition. Under this mechanism, bill size should be related to measures of sexual selection estimated by mate acquisition (P3.1: territory occupancy in this socially monogamous species that defends all-purpose territories; Mowbray 1997) or territory quality (P3.2: territory size, assuming that small, highly contested territories are of the highest quality for mate attraction and offspring production), and lack of support for either would be

adequate evidence to reject this hypothesis. False rejection, however, is possible due to insufficiently precise estimates of territory quality.

We tested for redundant intraspecific signaling as partial insurance against inappropriate rejection. In species where males use multiple structures for signaling, these signals are often correlated (Doucet and Montgomerie 2003; Loyau et al. 2005; Martin et al. 2008), due to either a male's high quality across multiple modalities, signaling to different receivers using different structures, or the evolution of redundancy to reinforce signal reception (Møller and Pomiankowski 1993; Sullivan 1994; Rowe 1999; Candolin 2003; Bretman et al. 2011). Thus, if bill size is an intrasexually selected signal that is at least partially redundant, it may correlate with either how frequently a male displays (P3.3) or the size of sexually selected plumage badges (P3.4). We have established with prior work in these study populations that swamp sparrows possess 2 sexually selected plumage patches (Olsen et al. 2008b, 2010), the black forehead patch and the rusty cap patch, which together make up the crown. The black forehead patch in swamp sparrows is an indicator for male competitive ability assessed via male aggression, territory size, and reproductive success (Olsen et al. 2010). The rusty cap, on the other hand, predicts male parental effort and female mating preferences (Olsen et al. 2008b). A lack of support for these last 2 predictions, however, could suggest either the lack of intrasexual selection for male bill size or a lack of redundancy in male signaling structures (Doucet and Montgomerie 2003).

There are multiple, supported mechanisms for intrasexual selection on male bill size. Intrasexual selection for larger male bills could occur directly on the bill's use as either a weapon for male–male competition (Olsen BJ, personal observation) or as a thermoregulatory organ (Hagan and Heath 1980; Phillips and Sanborn 1994; Tattersall et al. 2009; Symonds and Tattersall 2010; Greenberg et al. 2012) allowing for higher territorial activity in the heat of the day (breeding temperatures are higher in the tidal marsh system than they are at higher elevations inland; Olsen et al. 2008a).

Alternatively, male–male competition might indirectly select for an honest indicator of male quality to avoid direct conflict (Andersson 1994; Maynard Smith and Harper 2003). As one of the only avian structures that increases in size after fledging, the bill could be used as an honest indicator of male age. Bills in male song sparrows (*M. melodia*), for example, do not reach full adult size until after the start of their first breeding season, which results in significantly larger bills in experienced versus novice breeders (Smith et al. 1986). By not reaching full adult size until the second breeding season, male bill size could signal (either directly or through its influence on song; Podos 1997; Ballentine 2006) general competitive ability and be used to decide male contests much in the same way that the delayed maturation of sexually dichromatic plumage (Hawkins et al. 2012) or adult-type songs (Germain et al. 2012) do in other bird species. Either of these potential mechanisms could explain why bill size correlates with male rank in some songbirds (Kimball 1996) and why rhamphothecal growth is sex specific in other tidal marsh sparrows (Greenberg et al. 2013). Both direct and indirect effects on competition, however, would result in higher territory occupancy rates (P3.1) and territory quality (P3.2) by larger billed males.

H4: intersexual selection

Lastly, bill size may be an indicator of male quality used in female mate choice. If this is the case, intersexual selection on bill size should be evident by predictive relationships between either bill

size and the percentage of offspring sired (P4.1) or the mating preferences of females (P4.2). Lack of support for either of these 2 predictions makes intersexual selection on bill size unlikely. We also posit 2 predictions that would provide further support for intersexual selection, if true, although lack of support for these predictions does not necessarily allow us to refute the hypothesis outright. First, bill size should correlate with male quality (P4.3: e.g., age), although this might also be true if male–male competition drives bill size evolution. Second, male bill size may correlate with the cap plumage badge (P4.4), if intersexually selected signals are at least partially redundant (Møller and Pomiankowski 1993; Candolin 2003; MacDougall-Shackleton et al. 2009). As with our prediction for redundancy in intrasexually selected signals, however, a lack of support for this last prediction could indicate either the lack of intersexual selection or simply a lack of redundancy.

METHODS

Study locations and general methods

We studied the coastal subspecies in 2 *Spartina*-dominated tidal marshes along the Delaware Bay (May–August 2002–2005) and the inland subspecies in 2 sphagnum fens, 320 km to the west on the Allegheny Plateau (May–August 2004–2005; Olsen 2007). During each breeding season, we attempted to capture all birds and find all nests on each plot. Swamp sparrows are socially monogamous, but 21% of nestlings are sired by extrapair males in our study populations (Olsen et al. 2008b). Males defend all-purpose territories and assist in provisioning offspring, whereas the female is solely responsible for nest building and egg incubation (Mowbray 1997). Male territory boundaries were delineated by the singing locations of individually marked males throughout the breeding season, and we assumed that nests within the minimum convex polygon circumscribing these locations belonged to the social mate of the territorial male. In nearly all circumstances, however, males ascribed to each nest were also captured at the nest or observed feeding nestlings. All statistical tests were completed using SAS 9.2 (SAS Institute 2008) and all reported statistical errors are standard error (SE) unless otherwise noted.

Morphometrics and tests for sexual dimorphism

We measured 3 primary bill measurements (to the nearest 0.1 mm) for each adult captured: (1) bill depth as the vertical distance in the coronal plane immediately distal to the nares, (2) bill width as the horizontal distance in the same plane, and (3) bill length as a straight-line distance in the sagittal plane following the exposed culmen from the last crown feathers to the distal tip of the upper mandible. We did not explicitly quantify measurement error by measuring the same bird multiple times during a single capture, but the standard deviation of our linear measurements for all birds measured more than once within a season was 0.2 mm. This is likely an overestimate of error, however, as it includes both measurement error and true variance in the bill size within a season (Greenberg et al. 2013). We approximated bill volume by assuming a cone with an elliptical base and a volume equal to $1/3 \pi \times (\text{width}/2) \times (\text{depth}/2) \times \text{length}$. We also measured 3 indices of body size, including tarsus (length to the nearest 0.1 mm of the tarsometatarsus from its joint with the tibiotarsus to the last complete scute before the articulation of the hallux), weight (to the nearest 0.1 g), and unflattened wing chord (to the nearest millimeter).

For brevity, we report only the results for bill volume below (the most dimorphic of our measures). We tested for differences in bill volume as a function of sparrow population (coastal vs. inland) and sex within each population. We modeled bill volume using a repeated-measures mixed model, controlling for the random effect of year within population (to control for experimenter variance, as different technicians measured birds at each site and year) with multiple measures of individuals across years. We present the results of post hoc tests comparing least squares means to explain differences among the sex by population combinations.

H1: bill dimorphism as a function of allometry or ontogeny

We tested for allometric or ontogenetic explanations of larger bills in coastal males by looking for relationships between bill volume and either body size (P1.1) or age (P1.2) with repeated-measures mixed models. For our body size prediction (P1.1), we tested for linear and log-linear effects of body size, sex, and the interaction of body size and sex on bill volume, controlling for the random effect of year and multiple measurements of individuals (PROC MIXED in SAS 9.2). Because single, univariate measures of body size are often unreliable (Freeman and Jackson 1990; Mills 2008), for this and all further tests, we used the first, population-specific, principal component constructed from the logarithms of tarsus length, wing chord, and the cube root of body weight to create an index of body size.

We tested for the effects of age (P1.2), sex, and their interaction on bill volume, controlling for the random effect of year and multiple measurements of individuals. For those adults not banded as nestlings, we assigned age on first capture as either “1-year old” or “older” by molt limits, feather wear, and feather growth bars (Pyle and Howell 1997) and then calculated the age of recaptured birds in subsequent years based on their initial assessment. Because the exact age of many birds was unknown, we treated age as a bivariate (“1-year old” or “older”) in testing for the effect of age on bill volume (coastal: $N = 431$; inland: $N = 170$). For a second, smaller group of coastal birds ($N = 145$), we tested for the effect of age as a continuous variable (2–5 years) and only included those known-age birds that were initially banded as nestlings or 1-year olds and were subsequently recaptured. This second test was only possible for the coastal population because we only marked inland birds for 2 summers.

H2: bill dimorphism as a function of sex-specific foraging niches

To test for natural selection gradients (sensu Lande and Arnold 1983) on bill volume dimorphism, we created 3 multivariate models to predict survival (P2.1) and fecundity (P2.2 and 2.3). We examined the effect of male bill volume on interannual retention in the breeding pool (a proxy for interannual survival) using a logistic regression (returned vs. did not return) with the logarithms of body size, age (1-year old or older), the cube root of bill volume, and cap plumage patch size (because of our results presented here showing correlations between cap plumage patch and bill size) as predictors. Birds we counted as “not returned” include both males that died (survival) and males that dispersed off our study plots (emigration). This potential error likely overestimates the strength of selection because emigrated birds may not have dispersed out of the local breeding population. If, however, bill volume is linked to the

probability of local emigration, this test may still reflect underlying selective processes due to the combined effects of emigration and survival.

For our examination of nonsexual natural selection on bill volume due to differences in fecundity, we compared the degree of dimorphism within mated pairs to the number of young produced within a territory (P2.2). If dimorphism is ecologically selected because of the advantages provided by within-pair bill dimorphism to the provisioning of young (Gosler 1987; Mariano-Jelicich et al. 2007), then pair bill dimorphism should predict territorial fecundity ignoring the parentage of the young, which partially differentiates the effect of pair dimorphism from individual genetic quality. We compared adult bill differences (the absolute value of male bill volume minus female volume) with the cumulative number of young fledged on a territory using quantile regression at the 90th percentile. Quantile regression is appropriate here because offspring production can be limited by many factors, yet only those pairs with the greatest bill dimorphism should be able to raise the most young if sex-specific foraging niches assist in offspring production (i.e., the negative residuals should have a much higher variance than the positive residuals). For this model, we tested for the effects of population (because clutch size varies by population; Olsen et al. 2008a) and bill dimorphism within the social pair, nested within population. The reported confidence intervals and P values were calculated using the “sparsity” method in PROC QUANTREG (SAS 9.2), as bootstrap resampling methods are unstable for smaller data sets.

We also tested for the ecological selection gradient of nestling quality due to bill dimorphism within pairs, using the slope of the nestling growth curve as a proxy (P2.3). To determine nestling growth slopes, we weighed any nestlings on the plots that were younger than 8 days posthatch (we ceased weighing nestlings older than this to prevent early fledging) every third calendar day. This resulted in data from a variety of nestling ages over multiple broods within each territory. The slope of nestling growth was calculated with a general linear mixed model by plotting chick weights for each territory over the entire season (transformed using the logistic growth curve method described by Ricklefs 1967), controlling for broodmate interdependence with nesting attempt as a random variable. This parameter estimate is thus an index of the ability of a sparrow social pair (with a given degree of bill size dimorphism) to provision offspring within their territory over a season.

We used quantile regression again to test for a relationship between bill volume dimorphism and territory-specific nestling growth rate. We regressed bill dimorphism against the 90th percentile of offspring growth, assuming that if offspring growth rate is related to parental dimorphism (P2.3), then pairs with less dimorphism should show a lower, maximum nestling growth rate. We assume that offspring growth can be limited by many factors (i.e., any brood can have low growth rates for reasons that are independent of parental bill size), but only the most dimorphic pairs should achieve the highest nestling growth rates during any given season if dimorphism provides provisioning advantages. For this model, we again tested for the effects of population (because nestling growth rate varies by population; Olsen et al. 2008a) and bill dimorphism within the social pair, nested within population.

To test for sex-specific foraging niches as a function of bill size (P2.4), we sampled the gastrointestinal contents of breeding adults that were not provisioning young using gastric lavage throughout each breeding season (methods formally reviewed and approved by the Conservation and Research Center’s Institutional Animal

Care and Use Committee of the Smithsonian National Zoological Park under proposal #04-10). Adults were gavaged until (1) we had used 5 mL of distilled water, (2) the bird had evacuated both stomach and intestinal contents, or (3) defecation yielded only water (whichever occurred first). Gastrointestinal contents were stored in a 70% ethanol solution and later identified to genus (plant seeds) or order (invertebrates). We identified most invertebrates using chitinous remains (which unfortunately precluded us from measuring prey size, mass, or nutritional content), and the individual counts we present here represent minimum estimates. For gastropods, we were only able to record presence or absence due to our inability to estimate the minimum number of individuals from shell fragments.

We tested for the effect of bill volume on sparrow diet using 6 repeated-measures generalized linear models (PROC GENMOD in SAS 9.2), including a test to predict the amount of total invertebrates consumed, a test for each of the 3 most commonly consumed invertebrate orders (Coleoptera, Diptera, and Araneae), a test for the total number of seeds consumed (including *Vaccinium* sp., *Amelanchier* sp., and *Schoenoplectus americanus*), and a test to predict the presence or absence of gastropod fragments in the sample. For the 5 models for arthropods, we used a repeated-measures (controlling for multiple measures of birds across years), Poisson regression. The distribution of the number of consumed items for any given bill volume should approximate a Poisson distribution, as foraging at the maximum rate over the complete time interval represented by the gastrointestinal sample should be a rare event (e.g., males spend some time defending territories, females spend some time incubating). For the model of seeds consumed, we used zero-inflated Poisson regression because many birds (especially in the coastal population) did not consume any seeds, and for the gastropod model, we used logistic regression. We included 5 predictor variables for all 6 of these models: (1) population (coastal or inland), (2) conic bill volume within population (to test for bill by foraging relationships separately within the dimorphic and nondimorphic populations), (3) sex within population (to control for sex-related foraging patterns unrelated to bill size), (4) year within population, and (5) Julian date (to control for prey availability across time). For the zero-inflated Poisson regression, we used these same candidate predictors for the nonzero model and set the zero-model parameter to population type (coastal vs. inland) for all models. We also conducted post hoc contrasts comparing the diet of coastal males to coastal females for each model with the effect of bill volume removed because prey selection should differ by sex on average in coastal birds if bill dimorphism is a function of niche divergence.

H3: intrasexual selection on male bill volume

We estimated (*sensu* Lande and Arnold 1983) the size and significance of the intrasexual selection gradient within each population (P3.1), using a multiple logistic regression to predict territory occupancy (male defended a known territory or did not) as a function of logarithm-transformed bill volume, logarithm-transformed forehead plumage patch size, and logarithm-transformed body size. Each year, we caught and banded numerous males (especially during the first nesting attempts of the population) within the territories of other males. These trespassing males were never seen displaying, and we assume that at least some had failed to obtain a territory (although this group may also include birds trespassing from territories off our plots, which biases our estimate of the selection gradient downward). Anecdotally, territorial males that disappeared from our study plots (1–3 times a year per population) were quickly replaced by males we had never seen defending a territory

(although sometimes these males had been captured previously while trespassing). Indirectly, this suggests that there is a surplus of males and some males fail to obtain breeding territories.

We also tested for 2 correlations between male bill volume and competitive ability. First (P3.2), we looked for a relationship between male bills and territory area (which is negatively correlated with territory quality; Olsen 2007; Olsen et al. 2010). We tested for this relationship with a repeated-measures mixed model with logarithm-transformed territory area as our dependent variable, bill volume nested within population and population alone as fixed effects, and year within population as a random effect.

For our second competitive ability test (P3.3), we examined song production rate with a similar approach. We estimated song rate during 1-h observation periods for each male. For our mixed model, we tested for the fixed effect of bill volume nested within population and the interaction between bill volume and territory area (to control for the effect of bill volume in territories of varying quality) nested within population on the rate of song production. Year within population, time of observation, and calendar date were all set as random effects.

Assessing relationships with sexually selected plumage patches (P3.4 and 4.4)

To look for evidence of male bill size as a possible signal of male quality, we tested for correlations between bill volume and either the black forehead patch or the rusty cap patch. We digitally photographed male crowns and measured the size of each plumage patches. We used patch length and patch area (with Carnoy 2.0; Schols 2001) to construct a single principal component for each plumage badge. We used principal components because variable amounts of nonrusty (cap patch) or nonblack (forehead patch) feathers can be found within each patch's boundary, thus preventing a simple geometric relationship between patch length and area (Pearson's correlation between forehead patch length and black feather area: $r = 0.46$; between cap patch length and rusty feather area: $r = 0.42$). For all statistical tests, we used the first principal component constructed for each patch, which were the only components with eigenvalues >1.0 and represented 73.1% (forehead patch) and 71.1% (cap patch) of the variance in the initial measures.

To test for correlation between plumage dimorphism and bill dimorphism, we used 2 repeated-measures mixed models (1 for forehead patch and 1 for cap patch) that examined the fixed effects of bill volume within population and population alone on plumage patch size. Year within population was set as a random effect, and we repeatedly measured individuals across years.

H4: female choice for male bill volume

Fertilizations outside of the social pair bond in swamp sparrows are controlled by female preference for male traits (Olsen et al. 2008b). To determine whether bill size divergence might be driven by female choice, we genotyped adults (putative parents captured while provisioning offspring) and offspring (those that survived to at least 5 days of age) at 6 polymorphic, DNA-microsatellite loci using electrophoresis (64 alleles total across all loci; Olsen et al. 2008b). We sized genotypes with GeneScan 3.7 and scored alleles with Genotyper 2.5 (Applied Biosystems, Inc., Foster City, CA). All loci met Hardy–Weinberg equilibrium assumptions within each population, and there was no evidence for linkage disequilibrium among loci (Olsen et al. 2008b). We conducted a simple paternal exclusion analysis (i.e., did the social male sire each nestling) assuming

Mendelian inheritance and no egg dumping by extrapair females. Our results thus represent a minimum estimate of extrapair young. Full descriptions of genetic methods and the results of a power analysis for parental exclusion using Cervus 2.0 (Marshall et al. 1998) are described by Olsen et al. (2008b).

To estimate the strength and direction of selection due to female choice (sensu Lande and Arnold 1983), we constructed models to predict the percentage of young sired within each territory by the defending male (P4.1) and whether or not the female obtained extrapair fertilizations (P4.2). We estimated the strength of the selection gradient due to the percentage of young sired within the territory for each population with a repeated measures-generalized linear model, repeatedly measuring territory pairs across nesting attempts within a season. We estimated selection gradients due to whether or not the female obtained extrapair fertilizations with a repeated-measures logistic regression for each population. For all of these estimates, we modeled extrapair young as a function of relative bill volume, the relative size of the cap plumage patch (which is correlated with female choice; Olsen et al. 2008b), male age (1-year old or older), and body size (as calculated above). We calculated both bill volume and plumage patch size relative to those of immediate neighbors within 95.3 m, or twice the mean territory width ($[\text{focal male bill} - \text{smallest neighboring bill}] / [\text{largest neighboring bill} - \text{smallest neighboring bill}]$) based on both our previous finding that female choice appears to operate along a “best of N ” rule in regard to male cap size in these populations (Olsen et al. 2008b) and that nearby territory holders are most often the extrapair mates in a variety of songbirds (Stutchbury et al. 1994; Langefors et al. 1998; Dickinson 2001; Mennill et al. 2004). To avoid overfitting these models given our small sample sizes within each population (coastal = 27; inland = 35), we also estimated selection gradients with the 2 lowest performing variables (as judged by test statistics) removed in a stepwise manner.

RESULTS

Sexual dimorphism in bill volume varies by population

Of all 4 of our bill measurements, bill volume showed the greatest difference between our 2 populations (Figure 1), and the pattern was the same as that of the 3 linear measurements. There

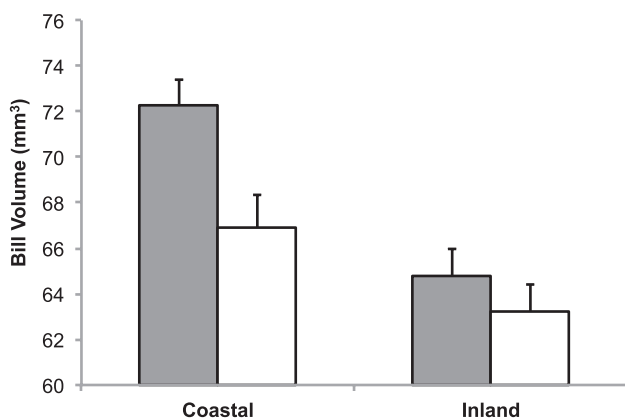


Figure 1

Least squares means + SEs for bill volume for male (filled columns) and female (open columns) swamp sparrows in 2 populations: the coastal *Melospiza georgiana nigrescens* and the inland *M. g. georgiana*.

was a significant effect of sex within populations ($N = 488$, $F_{2,480} = 11.2$, $P < 0.0001$), but no additional additive effect of population ($F_{1,480} = 0.1$, $P = 0.75$). The bills of coastal males ($N = 231$) were $9.6\% \pm 2.1\%$ ($6.2 \pm 1.3 \text{ mm}^3$) larger than those of coastal females ($N = 125$) on average ($t = 4.6$, $P < 0.0001$), but there was no significant difference between the sexes inland (78 males and 69 females, $t = 1.0$, $P = 0.34$) or between coastal females and either inland females ($t = 0.2$, $P = 0.87$) or males ($t < 0.01$, $P > 0.99$).

P1.1: increased male bill volume is not due to allometric scaling

In the coastal population, there was no linear relationship between bill volume and body size overall ($N = 343$, $F_{1,336} = 2.6$, $P = 0.11$), although there was a significant interaction between body size and sex ($F_{1,336} = 6.5$, $P = 0.01$; Supplementary Figure A) due to a scaling relationship within females ($N = 120$, $F_{1,115} = 8.1$, $P = 0.005$) but not within males ($N = 223$, $F_{1,218} = 0.3$, $P = 0.57$). The pattern was similar for the log-linear model with no relationship between bill volume and body size overall ($N = 343$, $F_{1,336} = 1.7$, $P = 0.20$), but an interaction between sex and log body size on log bill volume ($F_{1,336} = 4.4$, $P = 0.04$), due to a relationship between body and bill size among females ($N = 120$, $F_{1,115} = 6.0$, $P = 0.02$) but not among males ($N = 223$, $F_{1,218} = 0.08$, $P = 0.78$). The estimated slope of the female relationship in both models, however, was negative (linear = -2.9 ± 1.0 ; log-linear = -0.12 ± 0.05), which is counter to more conventional patterns of allometry but resoundingly precludes allometric scaling as a possible explanation for larger bill volume in males due simply to their larger body size.

P1.2, 2.1, and 4.3: bill size differs by age in the sexually dimorphic population

In the coastal population, bill volume was smaller for 1-year-old individuals than it was for older birds ($N = 431$, $F_{1,425} = 5.1$, $P = 0.02$); however, there was an interaction between sex and age such that older males had significantly larger bills than younger males ($N = 288$, $F_{1,283} = 5.7$, $P = 0.02$), whereas older females did not ($N = 143$, $F_{1,138} = 0.6$, $P = 0.46$). There were no significant decreases, however, in the overall variance of male bill volumes with age (1-year-old coefficient of variation [CV] = 27.6, older CV = 22.0). This was also the case for the 3 components of volume: length (18.0, 13.1), width (10.9, 9.6), and depth (12.0, 10.0). In fact, the smallest 1-year-old male bill ($N = 77$) was 25.5% of the volume of the largest 1-year-old male bill (24.1 vs. 94.6 mm³), and the smallest older male bill ($N = 211$) was 26.4% of the volume of the largest older male bill (32.8 vs. 124.2 mm³).

These patterns were repeated with the smaller data set using only known-age birds. Again, male bill volume was positively, linearly related to age ($N = 96$, $F_{1,91} = 7.6$, $P = 0.007$), but female bill volume was not ($N = 49$, $F_{1,44} = 0.6$, $P = 0.45$), and the maximum bill volume increased within each male age group (1-year old = 94.6 mm³, 2-year old = 104.2 mm³, older = 121.0 mm³), despite decreasing sample sizes (1-year old = 83, 2-year old = 7, older = 6). The smaller data set, however, was heavily weighted toward young birds due to the low rate of return, especially in females, and we may have lacked the statistical power to detect age-related patterns for females (Figure 2). Considering intraindividual (instead of cohort) change among all of the known-age, coastal birds that were measured in multiple years, bill volume increased in every instance for

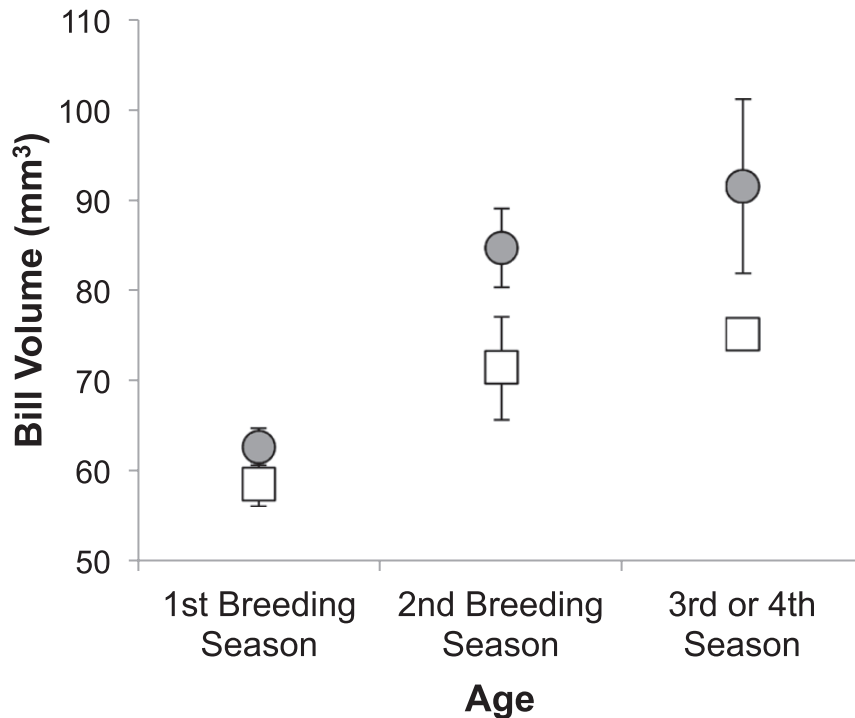


Figure 2

Means (\pm SEs) of bill volume for coastal male (filled circles) and female (open squares) swamp sparrows (*Melospiza georgiana nigrescens*) captured during their first ($N = 45$ females and 83 males), second ($N = 3$ females and 7 males), or third/fourth ($N = 1$ female and 6 males) breeding season in tidal salt marsh.

both males (mean increase \pm SE = 24.6 ± 5.0 mm³; $N = 11$) and females (17.3 ± 5.0), although the female sample size ($N = 3$) is too low to make any conclusions. Among inland birds, there were no bill size differences between the 2 age groups ($F_{1,165} = 0.5$, $P = 0.49$). Likewise, there was no interaction between age and sex ($F_{1,165} = 0.9$, $P = 0.36$).

P2.1–2.3: no evidence for nonsexual, natural selection for bill dimorphism

Bill volume did not predict male return rate to the breeding grounds on the next year (apparent survival) in either population. Bill volume did not significantly predict male return in either the coastal ($N = 116$, $\chi^2_{1,110} < 0.01$, $P = 0.95$) or inland ($N = 33$, $\chi^2_{1,27} = 2.2$, $P = 0.13$) populations, after we controlled for the size of the cap plumage patch, body size, and age (Table 2).

Controlling for differences in nestling growth rate between the 2 populations, dimorphism in bill volume between mated pairs was negatively related to nestling growth rate in the inland, monomorphic population ($\beta \pm$ SE = -0.005 ± 0.002 , $N = 13$, $t = -2.6$, $P = 0.01$) but unrelated in the dimorphic, coastal population ($N = 33$, $t < 0.01$, $P > 0.99$; Supplementary Figure B). The inland pattern, however, was driven by the nestling growth rate of a single, mated pair. If this datum was removed, the negative relationship disappeared ($N = 12$, $t = -0.8$, $P = 0.46$).

Bill volume dimorphism was negatively associated with offspring production in both the inland ($N = 79$, $\beta = -0.19$, $t = -3.4$, $P = 0.0009$) and the coastal ($N = 217$, $\beta = 0.09$, $t = -2.2$, $P = 0.03$; Figure 3) populations, controlling for population-specific fecundity. Post hoc analyses indicated that the negative slope between bill volume dimorphism and offspring production was similar (Figure 3) in the 2 populations ($t = 1.4$, $P = 0.16$).

P2.4: no evidence for niche divergence by sex along the coast because of bill volume

We tested (1) for a relationship between bill volume and coastal foraging patterns and (2) divergence in foraging niche by sex as 2 pieces of evidence to support the hypothesis that dimorphism results from ecological causes (H2). We found evidence for the first of these patterns in 2 dietary categories. For both the total number of arthropods consumed ($N = 77$, $\chi^2 = 8.5$, $P = 0.004$) and the total number of dipterans consumed ($N = 77$, $\chi^2 = 8.2$, $P = 0.004$), bill volume predicted consumption rates in the dimorphic, coastal population ($\beta \pm$ SE for total arthropods = 0.02 ± 0.01 ; dipterans = -0.04 ± 0.01), and neither pattern was present in the non-dimorphic, inland population (total arthropods: $N = 21$, $\chi^2 = 2.4$, $P = 0.12$; dipterans: $N = 21$, $\chi^2 = 1.1$, $P = 0.29$). Despite this, however, males did not consume significantly more total arthropods ($N = 56$, $\chi^2 = 0.07$, $P = 0.80$) or fewer dipterans ($N = 56$, $\chi^2 = 0.6$, $P = 0.45$) when we tested for sex-biased diets among coastal birds without controlling for bill volume.

Seed consumption was also predicted by bill volume (Figure 4), but only in the nondimorphic inland population ($N = 77$, $\chi^2 = 24.0$, $P < 0.0001$). There was no similar pattern among coastal birds ($\chi^2 = 0.01$, $P = 0.94$). Seed consumption, however, was much more common inland than it was along the coast ($\chi^2 = 4.4$, $P = 0.04$; Figure 4), which may have impacted our ability to detect a coastal pattern. Among inland birds, the number of seeds consumed (among birds that did consume seeds) was more than twice as high for males on average (mean seeds consumed \pm SE = 25.2 ± 15.7) than for females (11.8 ± 5.2), even after controlling for the bill volume pattern ($\chi^2 = 15.1$, $P = 0.0001$), suggesting that the inland pattern is produced by mechanisms related to both bill size and sex (independent of bill size). This result, however, was due to the leverage of a single

Table 2
Log-linear selection gradient estimates on male swamp sparrows, normalized by means for direct comparison

State	Normalized selection gradient estimates ± SEs				Sample size ^d
	Bill volume ^a	Cap patch size ^a	Body size ^b	Age ^c	
Retained in the breeding pool					
Coastal	-0.2 ± 3.7	8.8 ± 3.2**	-0.05 ± 0.07	0.1 ± 0.5	116 (40)
One-year olds	-2.4 ± 6.8	6.4 ± 5.8	-0.2 ± 0.2	na	32 (9)
Older	0.4 ± 4.6	10.0 ± 4.0*	-0.02 ± 0.07	na	84 (31)
Inland	15.4 ± 10.7	-8.9 ± 7.7	-0.2 ± 0.3	-1.6 ± 0.9	33 (17)
Obtained breeding territory					
Coastal	5.2 ± 2.9	-0.4 ± 0.3	0.02 ± 0.05	-0.6 ± 0.4	179 (97)
Inland	-0.8 ± 7.4	0.4 ± 1.0	0.8 ± 0.3**	-0.5 ± 0.6	70 (46)
Sired all young in the territory					
Coastal	82.1 ± 57.3 (74.4 ± 36.2*)	25.7 ± 14.6 (24.0 ± 14.9)	0.1 ± 0.2	0.1 ± 1.7	27 (14)
Inland	-1.7 ± 12.7 (-1.3 ± 6.2)	0.8 ± 21.0 (1.3 ± 8.8)	-0.06 ± 0.1	-1.1 ± 1.0	35 (19)
Sired greater percentage of young in territory					
Coastal	1.7 ± 0.5*** (1.8 ± 0.4****)	1.1 ± 1.1 (1.2 ± 0.9)	0.001 ± 0.01	0.07 ± 0.2	27
Inland	-3.4 ± 2.0 (-2.9 ± 14.5)	4.3 ± 2.8 (3.2 ± 20.8)	-0.002 ± 0.02	-0.1 ± 0.1	35

^aRelative to neighboring territorial males within 2 mean territory diameters, calculated as (focal male morphology - smallest neighboring morphology)/(largest neighboring morphology - smallest neighboring morphology).

^bThe first principal component of mass, tarsus length, and wing chord.

^cOne-year old or older.

^dSample sizes in parentheses are the number of individuals that achieved each state out of the population sampled.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, and **** $P < 0.0001$.

male that consumed 85 seeds, and with this point removed the pattern vanishes (males = 10.0 ± 5.2 ; females = 11.8 ± 5.2).

Gastropod shell fragments were the only dietary category that showed evidence of sex-biased foraging in the coastal population (without controlling for bill volume: $N = 77$, $\chi^2 = 5.6$, $P = 0.02$). There was no evidence, however, that this pattern was related to bill volume, as the sex-specific foraging pattern remained ($\chi^2 = 4.8$, $P = 0.03$) after bill volume was added to the model, and bill volume itself did not explain significant variation in coastal diets in this model ($\chi^2 = 0.5$, $P = 0.46$). Coastal females were 2.3 (SE = 1.1) times more likely to consume gastropods than coastal males, whereas there was no difference in the probability of consumption between the sexes inland ($\chi^2 = 1.8$, $P = 0.18$).

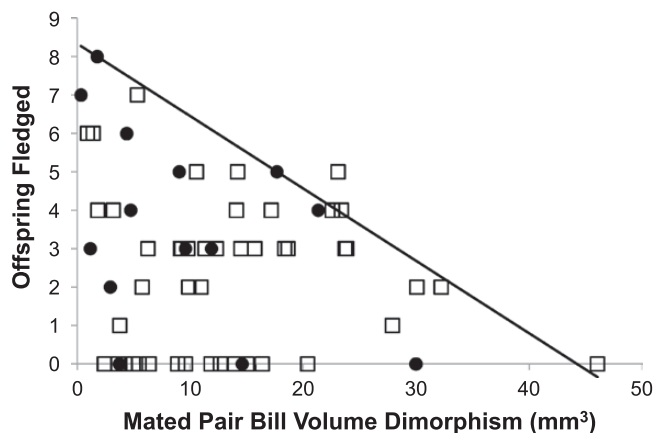


Figure 3
 The quantile regression (90th percentile) of the number of offspring fledged in a complete breeding season versus the relative difference in the bill volumes of social pairs (absolute value of male minus female bill volume) for coastal (open squares) and inland (filled circles) swamp sparrows.

P3.1–3.4: coastal dimorphism is not a result of intrasexual selection

Male bill volume was not intrasexually selected in the inland population due to competition for territory occupancy ($N = 70$, $\chi^2 = 0.01$, $P = 0.92$), after controlling for the selection gradients due to an intrasexually selected forehead plumage patch, male body size, and age (Table 2). Likewise, there was no statistically significant selection gradient for male bill volume due to territory defense in the coastal population ($N = 179$, $\chi^2 = 3.3$, $P = 0.07$), although the size estimate of the gradient was much higher here than inland (Table 2), and the

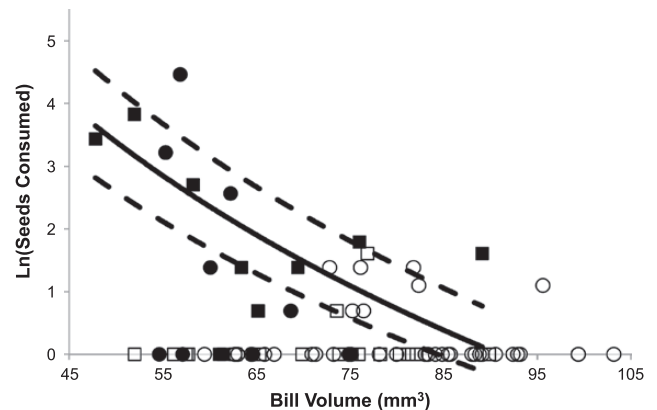


Figure 4
 The natural log of the number of seeds consumed versus the bill volume of inland (*Melospiza georgiana georgiana*) females (filled squares) and males (filled circles) versus coastal (*M. g. nigrescens*) female (open squares) and males (open circles). The solid and dashed lines represent the ln-transformed regression line and 95% confidence intervals for the nonzero values of the inland population only (there was no significant relationship for the coastal population alone, although the nonzero coastal values fall within the 95% confidence interval of the inland Poisson regression).

nonsignificance was marginal. There was no relationship between bill volume and territory area in either the coastal ($N = 147$, $t = -0.6$, $P = 0.59$) or inland populations ($t = 1.0$, $P = 0.34$). Similarly, there were no relationships between bill volume and male singing rate in either population (coastal: $N = 32$, $t = 0.7$, $P = 0.47$; inland: $t = -1.1$, $P = 0.27$) or between bill volume and a sexually selected plumage badge that indicates male competitive ability (coastal: $N = 158$, $t = 0.07$, $P = 0.94$; inland: $t = 0.6$, $P = 0.55$).

P4.1, 4.2, and 4.4: male bill volume predicts female choice

We detected a significant, positive selection gradient on coastal male bill volume due to mate choice in the form of extrapair fertilizations (Table 2). Coastal males that possessed larger bill volumes relative to their territorial neighbors were less likely to be cuckolded overall ($\beta \pm SE = 32.1 \pm 15.6$, $N = 27$, $\chi_{1,23} = 2.1$, $P = 0.04$) and sired a greater percentage of the young produced on their territory ($\beta \pm SE = 0.76 \pm 0.19$, $N = 27$, $\chi_{1,23} = 4.1$, $P < 0.0001$), after controlling for the size of a known plumage

badge used in female mate choice. Reflecting this, all of the males that avoided cuckoldry had both bills and plumage patches that were larger than those of their neighbors, and all males who had either the smallest cap patch or the smallest bill volume in their local vicinity (regardless of the size of their other characteristic) were cuckolded (Figure 5A). Male age was not significant when added to either of these models (probability of cuckoldry: $\chi = 0.4$, $P = 0.73$; percentage of extrapair young: $\chi = 0.4$, $P = 0.69$). Among inland males, however, bill volume did not predict whether a male was cuckolded ($N = 35$, $\chi_{1,31} = -0.02$, $P = 0.84$) or the degree of cuckoldry ($N = 35$, $\chi_{1,31} = -1.6$, $P = 0.12$), despite a similar rate of extrapair fertilization to the coastal population (Figure 5B).

Male bill volume in the coastal population was positively correlated with a principal component describing the size of the cap plumage patch preferred by females ($N = 158$, $t = 2.7$, $P = 0.008$), controlling for differences in cap patch size between the populations. There was no similar relationship, however, in the inland population ($t = 0.07$, $P = 0.94$).

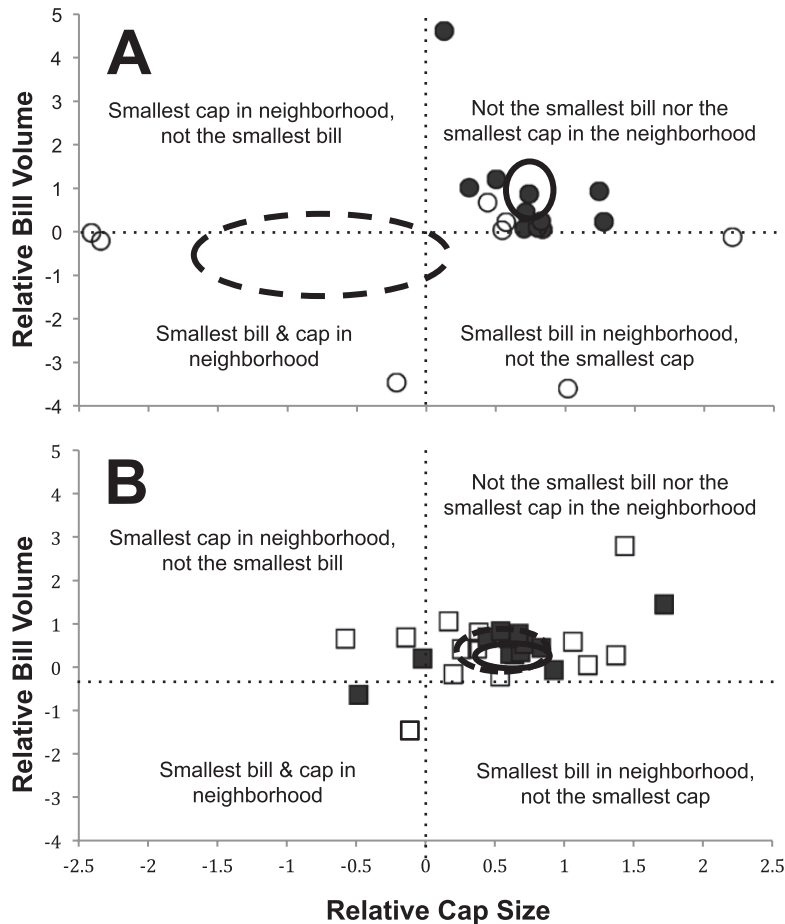


Figure 5

The relative sizes of the male bill and the rusty plumage cap in swamp sparrows that sired all of the offspring located in their defended territories (filled symbols) or failed to do so (open symbols) for (A) the tidal marsh nesting *Melospiza georgiana nigrescens* and (B) the inland, freshwater marsh nesting *M. g. georgiana*. The ovals in each graph indicate the 95% confidence intervals for mean bill and cap sizes for males that sired all their territorial offspring (solid) and those that were cuckolded (dashed). Relative bill and cap sizes were defined as the difference between the size of each focal male’s feature bill and the smallest neighboring bird divided by the size range of the feature within the neighborhood (2 mean territory diameters from the focal male). The stippled horizontal and vertical lines, therefore, divide each graph into 4 quadrants that indicate whether a male possessed the smallest bill or cap locally (negative values), possessed the largest bill or cap (values greater than 1), or possessed some intermediate value (values between 0 and 1).

DISCUSSION

Among our 4 hypotheses for the evolutionary origin of sexual bill dimorphism in swamp sparrows, intersexual selection due to female mate choice received the strongest support (Tables 1 and 2). In the sexually dimorphic coastal population (Figure 1), male bill volume was positively correlated with both age (Figure 2) and a plumage patch previously shown to be under intersexual selection (Olsen et al. 2008b, 2010). Neither of these patterns existed in the nondimorphic population. More telling, females from the dimorphic coastal population but not the monomorphic inland populations were more likely to cuckold social mates if they possessed a smaller bill than neighboring males (controlling for plumage patch size differences; Figure 5), which resulted in positive sexual selection for larger billed males due to mate choice (Table 2). We found no evidence that bill dimorphism was simply a function of body size dimorphism and little evidence for the role of intrasexual selection in causing bill dimorphism. Diet was related to bill volume in both populations (Figure 4), but correlation alone is not evidence for ecological causation, as diet could easily be either the cause of bill size dimorphism or the effect of bill size dimorphism that evolved due to sexual selection. None of the 6 tests for diet by sex supported ecological causation for bill dimorphism. Two of the dietary categories showed no relationship with bill size (Coleoptera and Araneae); two did show a bill size relationship but failed to show sex-specific niches independent of bill size (Diptera and total arthropod consumption); one category showed a clear sex-specific niche but no relationship with bill size (Gastropoda), and the last showed clear relationships with both sex and bill size but only in the monomorphic inland population (seeds). Further, larger billed males were not more likely to be retained in the coastal breeding pool, and there was no fitness advantage (as measured by offspring growth or fledgling production) gained by increased bill dimorphism within coastal social pairs (Figure 3). The weight of evidence supports sexual selection via female choice as an important driver of bill volume dimorphism in an Emberizid sparrow. We find it unlikely that prey selection has been the primary cause of sexual size dimorphism, but the clear correlations between bill volume and diet do suggest that bill size, regardless of sex, still experiences nonsexual natural selection.

Sexual selection for trophic-structure dimorphism

As additional (although not irrefutable) evidence of female mate choice as the driving force behind male bill size, mate choice for a condition-dependent trait can result in the evolution of a highly variable trait, whereas ecologically based natural selection (in a consistent direction) reduces trait variance (Pomiankowski and Møller 1995). The CVs we report here for coastal male bill lengths are >60% higher (range: 60–450%) than any of the 37 songbird species reported by Groth (1988). For comparison, the inland males possessed typical bill length CVs for songbirds (1-year old = 4.5, older = 5.7). For this pattern to be produced by nonsexual natural selection, the direction of selection would have to be significantly more variable in the tidal salt marsh than any of the other 37 species reported by Groth (1988), which, although not impossible, seems unlikely.

The relationships we report here among male bill volume, age, and female mating behaviors in the coastal, dimorphic population suggest a potential mechanism for the evolution of female preference for larger bills. First, male age did not predict female

mate choice directly, only male bill volume did. Thus females, if they value older males, appear not to assess age directly. By choosing larger billed males, however, females increase the probability of mating with older birds due to the correlation between bill volume and male age. Females that prefer larger billed males are likely to receive either direct benefits from the social mate (parental care and territory quality from experienced breeders) or indirect benefits from extrapair matings (genetic correlates of survival), although we only found direct evidence of the later. How females perceive differences in male bill size remains open to speculation, but the shape of the male bill influences song (Podos 1996, 1997, 2001; Fletcher and Tarnopolsky 1999; Hoese et al. 2000; Herrel et al. 2009), and correlations between male song and age have been reported recently in swamp sparrows (Ballentine 2009). Together, this opens the possibility that females could judge male bill size indirectly through vocal displays, although this hypothesis remains untested.

No strong case for ecological niche divergence by sex

We did not find strong evidence that sexual dimorphism in coastal swamp sparrow bills was a result of niche divergence, as has been posited both for this species (Ballentine 2006) and other birds with sexually dimorphic bills (Selander 1972; Shine 1989). Although there were correlations between diet and bill volume within each of the populations and divergent diets between coastal and inland swamp sparrows (Figure 4), we only found evidence for sex-specific foraging niches in gastropod consumption, which was unrelated to bill volume (but may be linked to calcium demand by females during egg-laying).

For those prey items whose consumption was predicted by bill size in the sexually dimorphic population, the absence of dietary differences between the sexes was due likely to the large overlap in male and female bill sizes and our heavier dietary sampling of male sparrows. Although large-billed coastal birds (those individuals with bill volumes greater than the population median) were almost always male (82% of 28 birds sampled), small-billed birds were relatively evenly divided between the sexes (57% of 30 birds sampled were male). Given this sampling distribution and our results, we can conclude that small-billed males consume items similarly to females with similarly sized bills but differently to larger billed males.

We can thus reject the hypothesis that males fundamentally consume different prey than females, but males with larger bills are more adept at this strategy than smaller billed males (conditions that would cause ecologically driven sexual dimorphism). We cannot reject, however, the hypothesis that males consume different items at different ages, and sex-specific dietary niches exist only when comparing older, larger billed males with smaller billed birds of both sexes. Sample size restrictions with known-aged birds prevented us from testing this hypothesis explicitly. Additionally, we cannot reject the hypothesis that sex-specific foraging niches exist at an invertebrate taxonomic level lower than order. We failed to detect, however, any fitness advantages (via increases in offspring production or growth rates) for the most sexually dimorphic pairs, which would be expected if either of these 2 alternative hypotheses were true.

Seed consumption was related to both bill volume and sex but only in the nondimorphic, inland population. Our results support the general ecosystem pattern, where tidal marsh vertebrates rely more heavily on invertebrate prey than their freshwater relatives (reviewed in Grenier and Greenberg 2006). Although we did not find direct evidence that a coastal diet can lead to sex-specific foraging niches, a more exclusively invertebrate diet may release coastal bills from the size and sex-specific relationships with seed consumption that we

witnessed among inland birds and therefore allow sexual selection to play a larger role in the evolution of bill dimorphism.

It should be noted that we have only examined the effects of bill dimorphism on reproductive fitness. Coastal sparrows also winter in a different habitat than inland birds (Greenberg et al. 2007), and bill divergence may increase survival by allowing mixed flocks of males and females to coexist on brackish marshes in the nonbreeding season when food is severely limited (Danner 2012). The bills of other tidal marsh sparrows, however, suggest that bill dimorphism in the entire group is most extreme during the breeding season (Greenberg et al. 2013), and any advantage given by increased winter survival would need to compensate for the losses in offspring production reported here for the most dimorphic pairs (Figure 3).

Little evidence for intrasexual selection on male bill volume

Selection for bill volume via intrasexual selection for territory defense was not statistically significant, but it was nearly so in the coastal population. Our method for assigning male territoriality status admittedly biases our estimate of the strength of intrasexual selection low (because we very likely called some territorial males nonterritorial but called no nonterritorial males territorial), and as such, this weak pattern may hint to something stronger and should be tested more explicitly. Bill volume, however, did not correlate with other indicators of territorial aggression, and larger billed males were not more likely to occupy territories in the most contested areas of the marsh. A single hour of morning observation, however, may not be the best indicator of male singing ability (although we did only observe mated males with incubating females to control for breeding stage and success). Therefore, we tentatively reject the hypothesis that dimorphism arises primarily from sexual selection on male bills as a result of male–male competition.

CONCLUSIONS

Among our 4 hypothesized mechanisms, female mate choice appears the most likely cause for the evolution of sexual bill dimorphism in 1 subspecies of the swamp sparrow. These results emphasize that sexual selection can be a powerful force on vertebrate morphology, even in structures that have been traditionally considered constrained by foraging efficiency. Females may gain indirect benefits in mate choice due to the correlation between bill size and male age. It remains unclear, however (1) by what mechanism females select large-billed males and (2) whether interannual bill rhamphothecal growth and wear (Greenberg et al. 2013) can be influenced by male condition to make bill size an informative indicator for mate choice even within age cohorts.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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