

MACROGEOGRAPHIC VOCAL VARIATION IN SUBSPECIES OF SWAMP SPARROW

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Abstract. Variation in song can play a central role in species and subspecies recognition among birds. The ability of individuals to distinguish between songs of their own versus songs of a different subspecies potentially strengthens local adaptation of subspecific populations. We investigated the degree of vocal divergence and discrimination between two subspecies of Swamp Sparrow (*Melospiza georgiana*) to examine how variation in song could influence behavioral response. We recorded songs of Southern (*M. g. georgiana*) and Coastal Plain (*M. g. nigrescens*) Swamp Sparrow males in Maryland and Delaware, respectively, and analyzed variation in syllable composition, repertoire size, trill rate, and frequency bandwidth. In addition to describing differences in song characteristics, we performed an estimate of local song type diversity that predicted larger population repertoires in *M. g. nigrescens*. We then broadcast recordings to evaluate male territorial responses to song and found that males reacted more strongly to songs of their own subspecies than to songs of the other subspecies. The extent of song variation and discrimination suggests the possibility of continued divergence. Further tests may determine whether such results can be generalized beyond the populations studied to the subspecies level, and whether females as well as males differentiate between songs from separate subspecies.

Key words: geographic variation, *Melospiza georgiana*, song playbacks, subspecies divergence, Swamp Sparrow, vocalizations.

Variación Vocal Macrogeográfica en Subespecies de *Melospiza georgiana*

Resumen. La variación del canto puede desempeñar un papel importante en el reconocimiento de especies o subespecies de aves. La capacidad de distinguir entre canto autóctono y alóctono puede reforzar la adaptación local de las poblaciones subespecíficas. Se investigó el grado de divergencia y discriminación vocal en dos subespecies de *Melospiza georgiana* para examinar la influencia de la divergencia vocal sobre el comportamiento de ambas subespecies. Se grabaron cantos de *M. g. georgiana* y *nigrescens* en Maryland y Delaware, respectivamente, y se analizó la variación en la composición silábica, el tamaño del repertorio, la velocidad del canto y el ancho de banda. Además de describir las diferencias en las características del canto entre las dos subespecies, se hizo un cálculo de la diversidad local del canto que predijo un repertorio colectivo más grande en *M. g. nigrescens*. Después se reprodujeron grabaciones para evaluar la respuesta territorial de los machos al canto y se encontró que la reacción era mayor ante cantos de individuos de la misma subespecie que ante aquellos de la otra subespecie. El grado de variación y discriminación entre cantos sugiere la existencia de un proceso de divergencia entre estas dos subespecies. Sin embargo, es necesario realizar más experimentos para generalizar estos resultados más allá de las poblaciones estudiadas al nivel de subespecies, y para determinar si las hembras también pueden discriminar los cantos de diferentes subespecies.

INTRODUCTION

Examining geographic vocal variation and its effects on male territorial responses offers the chance to evaluate the potential for signal evolution and discrimination in species with widespread distributions (Marler and Tamura 1964, McGregor 1980, 1983, Searcy et al. 1997). In birds with acknowledged intraspecific variation, disparate responses to local versus foreign song may be indicative of song recognition on a population level. Where the geographically

separated populations show concomitant differences in phenotypic characters, differential response to songs based on area of origin can potentially support divergence (Petrinovich and Patterson 1981, Matessi et al. 2000).

We investigated differences in song and response to song in two subspecies of Swamp Sparrow (*Melospiza georgiana*). Because of their habitat-based divergence on a relatively local scale, Swamp Sparrows provide a good opportunity for examining the influences of geographic separation on

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song variation and response. Furthermore, previous studies of their song ontogeny and structure (Marler and Peters 1982, Marler and Pickert 1984, Balaban 1988) provide considerable background information on the vocalizations of this species as a whole. The three subspecies of Swamp Sparrow (*M. g. georgiana*, *nigrescens* and *ericrypta*) probably recovered from a population bottleneck and recolonized post-Pleistocene coastal estuaries or areas in the past 10 000–15 000 years (Greenberg et al. 1998). The Southern Swamp Sparrow (*M. g. georgiana*) is a characteristic breeding species of freshwater marshes in the northeast U.S. and southern Canada. In contrast, the Coastal Plain Swamp Sparrow (*M. g. nigrescens*) nests in coastal estuaries from northern Virginia to the Hudson River (Beadell et al. 2003).

Southern and Coastal Plain Swamp Sparrows are generally distinguishable by morphology. Differences in physical traits of *M. g. nigrescens*, such as grayer and darker plumage and larger bill size, are thought to be evidence of ecological adaptation to the unique conditions of tidal marshes (Greenberg and Droege 1990). The absence of consistent differences in mitochondrial DNA markers suggests that divergence between the taxa is very recent and that genetic drift probably does not explain phenotypic differences (Greenberg et al. 1998). Instead, either selection for a few specific, heritable, and evolutionarily labile traits is the driving force for this rapid divergence, or the differences are a result of environmental pressures (or a combination of the two factors).

A study of the subspecific differences in song and their effects on song response should provide further insight into the process underlying divergence. Some distinctions among the three subspecies' songs have already been noted (Mowbray 1997), and Ballentine (2006) has compared song traits between *M. g. nigrescens* and *georgiana*. Despite these reports, there has been no study coupling a description of song with an experimental test of vocal discrimination in these two subspecies. We therefore describe in greater detail the nature of variation in the songs of *M. g. nigrescens* and *georgiana* and examine whether such variation is sufficient to evoke distinct responses in members of these subspecies. Specifically, we address two questions. First, do songs from *M. g. nigrescens* and *georgiana* differ qualitatively or quantitatively? Second, do male Swamp Sparrows distinguish between songs of same versus different subspecies in a territorial context?

METHODS

SONG RECORDING

We conducted recordings and song playback experiments in coastal Delaware and western Maryland. We recorded male *M. g. nigrescens* in the Delaware Department of Fish and Wildlife's Woodland Beach Wildlife Area, near the Smyrna and Delaware Rivers in Kent County, Delaware. Two plots within the area, about 1 km from each other, contained

breeding *M. g. nigrescens* and were studied throughout the summer of 2005. We also recorded three individuals near Port Mahon, a site south of Woodland Beach within the Little Creek Wildlife Area and adjacent to the Delaware Bay. *M. g. georgiana* males were recorded in two plots in or near Garrett County, Maryland. The multiple sites within each state were chosen to allow for variation across individuals from different field sites, thereby generalizing the validity of the results. However, because sites within a subspecies' range were relatively close to one another, all *M. g. nigrescens* males were treated as one population and all *M. g. georgiana* males as another.

We recorded birds daily from 27 May to 3 June 2005 (Delaware) and 4 June to 13 June 2005 (Maryland) from 06:00 to 14:00 EST, using a TC-D5M portable cassette recorder (Sony Corporation of America, New York, New York) and AT815b shotgun microphone (Audio Technica, Stow, Ohio). The majority of birds at both sites were color-banded. We mapped territory boundaries using either song posts observed in the field or GPS waypoints recorded previously by other researchers studying the same population. To secure the complete repertoire of an individual, we recorded each bird for at least 30 min, a time period known to be sufficient for capturing entire repertoires in this species (Ellis 1980). In total, we obtained complete repertoires from 16 *M. g. nigrescens* and 12 *M. g. georgiana* individuals.

SONG ANALYSIS

We digitized and analyzed recordings using SIGNAL/RTSD (Beeman 1996). After creating spectrograms for each song, we analyzed trill rate (song speed), frequency bandwidth (the difference between the minimum and maximum frequencies), and syllable composition. Swamp Sparrow songs follow a predictable syntax in which one syllable is repeated throughout the entire song. Syllables can be further broken down into individual note types that are classifiable into six categories (Marler and Pickert 1984; Fig. 1). We defined a song type as a song consisting of a syllable with a visually distinct note type sequence. Finally, we used recordings to determine individual repertoire sizes and predict local song type diversity.

Of the 89 song types categorized by eye (48 from *M. g. nigrescens* and 41 from *M. g. georgiana*), we used the 10 best-quality exemplars of each to calculate frequency bandwidth and trill rate. These two characteristics are inversely related to each other due to the physical constraints that prevent maximal vocal performance in both traits (Podos 1997, 2001, Podos and Nowicki 2004, Ballentine et al. 2004, Ballentine 2006). They are also ideal characteristics to examine because they measure concrete quantitative traits of vocal performance with which different song types can be compared.

We determined the trill rate of a given song by taking the inverse of the mean duration of the first clear individual syllable and subsequent intersyllable interval, and we measured the frequency bandwidth by calculating the difference between

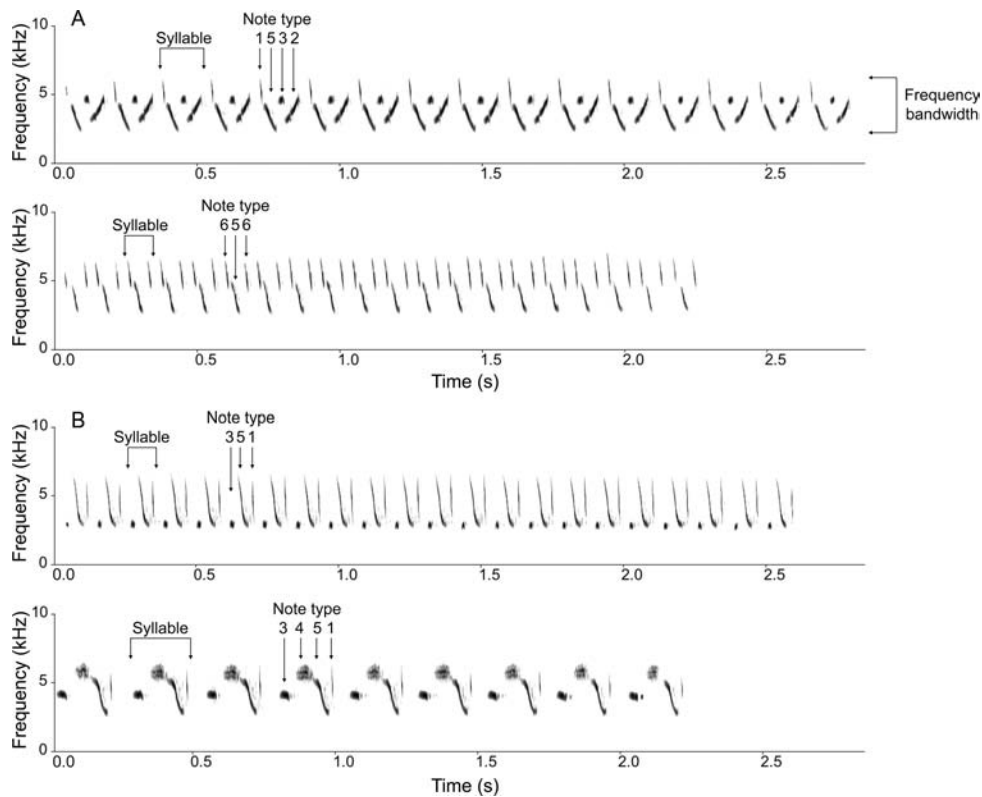


FIGURE 1. Spectrograms of typical (A) *Melospiza georgiana nigrescens* (Woodland Beach Wildlife Area, Delaware, 2005) and (B) *M. g. georgiana* (Garrett County, Maryland, 2005) trilled songs, with relevant acoustic variables labeled. The top spectrogram in each pair depicts the most frequently recorded song type for each subspecies. Numbers refer to the six note-type categories identified by Marler and Pickert (1984).

the maximum and minimum frequency at -30 dB relative to the peak amplitude of the song. Measuring bandwidth in this way enabled us to obtain a frequency range sufficiently wide to capture the variation in bandwidth without including excessive background noise.

To calculate the mean individual repertoire size, we divided the total number of recorded song types by the number of sampled individuals in each subspecies. We then used EstimateS (Colwell 2005), a biodiversity assessment program, to generate song type accumulation (i.e., Mao Tau) curves and predict the size and confidence limits of each subspecies' collective repertoire using the Chao1 richness estimator (Chao 1987). These curves allowed us to approximate the expected song diversity independent of whether we had obtained the total number of song types in the field.

PLAYBACK PROTOCOL

We assembled the complete repertoires for all males and inspected each to identify the best-quality exemplars of every song type. Out of the 28 birds we recorded, we chose songs of 21 males to use as stimulus songs and additionally included six samples from a Pennsylvania *M. g. georgiana* population (B. Ballentine, Smithsonian Migratory Bird Center,

pers. comm.). We created multiple sets of pairwise stimuli to encompass a broad range of songs from each population and to avoid the risk of pseudoreplication during playbacks (Kroodsma 1989). Each playback tape was composed of two song types (i.e., a song pair) from a recorded male. To control for possible effects of trill rate on response, we broadly classified song types of each bird's repertoire into slow and fast songs, defined by their relative trill rates, and then chose one slow and one fast song type to constitute the song pair. If a bird had more than two song types in its repertoire, we selected the slow and fast song types with the highest signal-to-noise ratio. Songs from the Pennsylvania population were similarly paired into three slow-fast song pairs, resulting in a total of 24 stimulus tapes. Song playbacks were divided such that 12 tapes contained songs of *M. g. nigrescens*, while the other 12 contained songs of *M. g. georgiana*, allowing for a possible sample of 12 males at each site.

We conducted six paired, single-speaker playback tests at the Maryland field sites and 11 at the Delaware sites between 2 July and 7 August 2005 from 06:00 to 11:00. During each playback experiment, a male heard 6 min of song: the first song type was repeated nine times over 1.5 min (a rate of six songs per min), followed by the second song type nine times at

the same rate, followed by the first song type nine times, and ending with the second song type nine times. Song rate was selected to mimic the natural rate of song delivery in Swamp Sparrows (Ellis 1980).

Subject males each heard two playback tapes: one of *M. g. nigrescens* and one of *M. g. georgiana*, each on a different day. Order was randomized within each site such that half the birds at a site were played the tape with *M. g. nigrescens* songs first, while the other half were played the tape with *M. g. georgiana* first. Out of each of these two subsets of six tapes each, three tapes featured the fast song first, while the other three featured the slow song first. We performed experiments blind to whether an *M. g. nigrescens* or *georgiana* song was broadcast.

Playback trials with a given male consisted of a 3-min pre-playback silent period, the 6-min playback broadcast, and a 6-min post-playback silent period. Behavioral observations were recorded during the entire 15-min experiment. We broadcast tapes through a camouflaged mounted speaker (model SC-A70, Saul Mineroff Electronics Inc., Elmont, New York) placed at the edge rather than the center of the male's territory to highlight any subtleties between his reaction to stimulus songs. We placed distance flags at 4-m intervals out to 16 m on either side of the speaker to measure the male's position to within 2 m during a trial and dictated all observations into a handheld cassette recorder. Response measures were average distance to the playback speaker, time spent within 10 m of the speaker, number of flights, and number of songs produced by the male.

Playback trials sometimes failed because of interference by a neighbor or poor visibility. Because of the pairwise design of the experiment, both trials for an individual had to be successful for data to be used. If the first failed, we returned after 48 hr to attempt the trial again; if either the second attempt at a first trial failed, or the attempt at the second trial in the pairwise design failed, we excluded that subject from the analysis. No bird was played its own songs or those of an audible neighbor as stimulus songs (Temeles 1994). Adjacent neighbors also were not tested within 24 hr of a trial. Because of the relatively conservative criteria we established to ensure that differences in response were based on the broadcast songs only, we ultimately discarded data from eight of 19 *M. g. nigrescens* and seven of 13 *M. g. georgiana* playbacks.

STATISTICAL ANALYSES

We conducted paired *t*-tests with SigmaStat (Systat Software Inc., 2003) to determine whether mean individual repertoire size and frequency bandwidth differed between *M. g. nigrescens* and *georgiana*. Trill rate data could be neither square-root- nor log-transformed to fit the assumptions of normality and equal variance and were analyzed instead with a Mann-Whitney *U* test. For playback trials, we used data during and after playbacks to perform paired *t*-tests on each variable to evaluate differences in response to songs of

same versus different subspecies. Because response variables may be intercorrelated, we then pooled results from all four variables and subjected them to a principal components analysis using Systat (Systat Software Inc., 2004) to generate a composite measure of playback response. We then compared factor scores from the first principal component of these composite responses in a paired *t*-test. Values reported are means \pm SE, and significance levels were set at $\alpha = 0.05$.

RESULTS

VARIATION IN SONG

Individual males sang one to four different song types. Sixteen distinct song types were recorded from 16 *M. g. nigrescens* males and seven song types from 12 *M. g. georgiana* males. A single *M. g. nigrescens* "two-parted" trill composed of two song types (Podos et al. 1999, Ballentine 2006) was excluded, as both song types were represented in the repertoires of other males. Song types were unique to each population; that is, no note sequence in an *M. g. nigrescens* song was found in a song of *M. g. georgiana* and vice versa (Fig. 1). In addition, note type 4, as defined by Marler and Pickert (1984), was found exclusively in songs of *M. g. georgiana*.

Frequency bandwidth and trill rate of all songs fell along an inverse continuum, as first described by Podos (1997). Songs of *M. g. nigrescens* showed a faster trill rate and narrower frequency bandwidth than songs of *M. g. georgiana* (*M. g. nigrescens*: bandwidth = 4070 ± 65 Hz, trill rate = 8.5 ± 0.4 Hz; *M. g. georgiana*: bandwidth = 4683 ± 92 Hz, trill rate = 7.4 ± 0.3 Hz; Fig. 2), although differences in trill rate were not significant (bandwidth: $t_{87} = -5.6$, $P < 0.001$; trill rate: Mann-Whitney $U = 1670$, $P = 0.08$, $n = 89$).

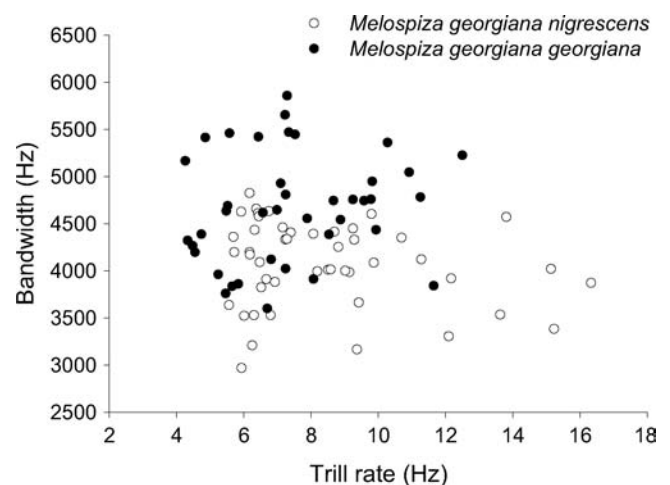


FIGURE 2. Scatterplot of frequency bandwidth versus trill rate for the 89 distinct song types recorded from *Melospiza g. nigrescens* (Woodland Beach Wildlife Area, Delaware, 2005) and *M. g. georgiana* (Garrett County, Maryland, 2005) males. Each point represents the mean values for one song type.

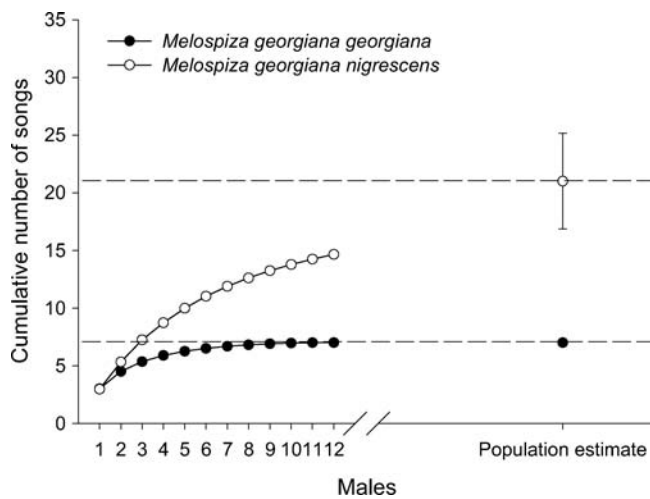


FIGURE 3. Cumulative song curves of expected population repertoire size in *Melospiza georgiana nigrescens* (Woodland Beach Wildlife Area, Delaware, 2005) and *M. g. georgiana* (Garrett County, Maryland, 2005). Estimates were limited to 12 individuals, the sample size obtained from Maryland. Dotted lines indicate predicted maximum repertoire size.

Individual males in the two populations did not possess significantly different repertoire sizes (*M. g. nigrescens*: 3.0 ± 0.2 song types, *M. g. georgiana*: 3.4 ± 0.2 , $t_{26} = 1.3$, $P = 0.19$, $n = 28$). However, the total population repertoire size for the *M. g. georgiana* population was estimated to be 7.0 ± 0.3 song types, while the population repertoire size for *M. g. nigrescens* was estimated to be 21.0 ± 4.2 distinct song types. This projection of population repertoire size was significantly higher for *M. g. nigrescens* than for *M. g. georgiana* (the 95% confidence intervals of each curve did not overlap with the means of the opposite curve; Fig. 3).

PLAYBACK RESPONSES

Males approached the speaker more closely ($t_{16} = -2.4$, $P = 0.03$, $n = 17$; Fig. 4A), spent more time within 10 m of the speaker ($t_{16} = 2.8$, $P = 0.01$; Fig. 4B), and sang a greater

TABLE 1. Loadings of the four response variables on the first principal component for playback response of male *Melospiza georgiana georgiana* and *M. g. nigrescens* during trials conducted in 2005 at Woodland Beach Wildlife Area, Delaware and Garrett County, Maryland. Measurements from all playbacks, regardless of treatment, were considered in the analysis. Three of four response variables loaded strongly onto the first component.

Response variable	Loading
Average distance to speaker	0.90
Time within 10 m of speaker	0.88
Number of songs	0.65
Number of flights	0.33

number of songs ($t_{16} = 2.4$, $P = 0.03$; Fig. 4C) when exposed to songs of their own subspecies than when exposed to songs of the other subspecies. Number of flights, while not significant, was also greater in response to songs from the same versus the other subspecies ($t_{16} = 1.9$, $P = 0.08$, Fig. 4D).

To determine whether these responses were consistent within as well as across subspecies, we analyzed playback responses within the *M. g. nigrescens* population alone. We found that *M. g. nigrescens* males displayed a stronger response to local song, though not significantly so (distance to speaker: $t_{10} = -1.1$, $P = 0.30$; number of songs: $t_{10} = 1.6$, $P = 0.15$; number of flights: $t_{10} = 1.5$, $P = 0.16$; time spent within 10 m of the speaker: $t_{10} = 1.8$, $P = 0.10$, $n = 11$). An *M. g. georgiana*-only analysis was not attempted due to the small sample size from that population.

Distance to speaker, number of songs and time spent within 10 m of the speaker aggregated along a single principal component with an eigenvalue > 1 (2.10), explaining 53% of variance (Table 1). A *t*-test on principal component scores detected a significantly stronger response to same-subspecies song ($t_{16} = 2.7$, $P = 0.02$).

DISCUSSION

Comparisons of song variation and response to song in populations of *M. g. nigrescens* and *georgiana* revealed significant differences in vocal traits and local song type diversity as well as subspecies-specific song discrimination. Given the geographic and ecological separation in these subspecies, these differences suggest a level of subspecies recognition that may play an important role in the signal evolution, reproductive behavior, and subspecies divergence of Swamp Sparrows.

VARIATION IN SONG

Song types of *M. g. nigrescens* and *georgiana* were unique to each subspecies, although some similarities in syllable composition occurred (e.g., note sequences 125 in *M. g. nigrescens* and 251 in *M. g. georgiana* involved the same note types, but in a different order, within a syllable). Whether such similarities are coincidental or informative about the nature of the subspecies' divergence remains to be tested. A study of song types in the contact zone of the two subspecies in northern New Jersey and New York (Greenberg and Droege 1990) may be particularly informative, with assessment of the degree of dissimilarity proportional to geographic separation. This comparison could be achieved by recording songs from increasingly remote sites in both directions relative to this zone and characterizing them with the same vocal traits as in the present study.

Songs of *M. g. nigrescens* and *georgiana* also differed in acoustic characteristics, dividing them into separate distributions along the frequency bandwidth–trill rate continuum. While the majority of *M. g. nigrescens* songs displayed a narrower frequency bandwidth and faster trill rate, most

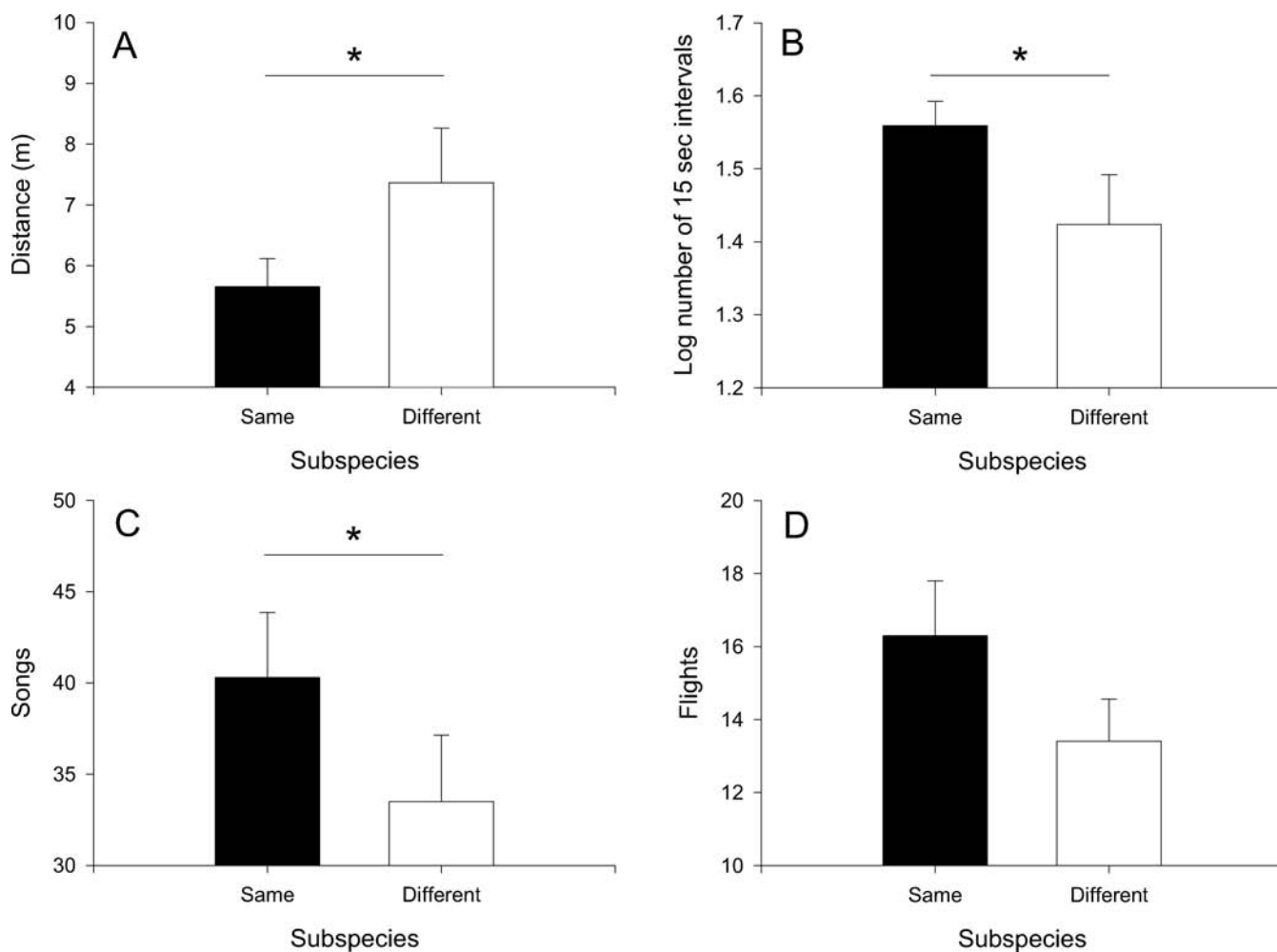


FIGURE 4. Male Swamp Sparrows (*Melospiza georgiana georgiana* and *M. g. nigrescens*, $n = 17$) tended to respond more strongly to playback of songs from their own versus other subspecies. An asterisk indicates a significant difference (paired t -test). (A) Average distance of approach to speaker; closer approach indicates a stronger response. (B) Duration of close approach. Y -values are log-transforms of the number of 15-sec intervals spent within 10 m of the speaker during and after taped playback. Longer duration indicates a stronger response. (C) The number of songs sung by males in the 12 min during and after the playback. Higher number of songs indicates a stronger response. (D) The number of times males changed perches in the 12 min during and after the playback. Higher number of flights indicates a stronger response.

M. g. georgiana songs possessed instead a broader frequency bandwidth and slower trill rate. Ballentine (2006) found the same trend in populations of *M. g. nigrescens* and *georgiana* in coastal New Jersey and northwestern Pennsylvania, respectively. Taken together, these data suggest that such song properties may be generalized beyond populations to the level of subspecies. An analysis of songs from *M. g. georgiana* populations, combined with work on other *nigrescens* populations for the same suite of traits, could further establish the generality of these distinctions between the two subspecies.

Individual repertoire size between populations was slightly greater in *M. g. georgiana* than *nigrescens*, but not significantly so. This finding differs from the results of Ballentine (2006), who reported that *M. g. nigrescens*

had significantly greater individual repertoires than *M. g. georgiana*, though the magnitude of this difference was not large (3.68 versus 3.06 song types per individual). In contrast to individual repertoires, estimates of collective repertoire size were significantly greater for *M. g. nigrescens* than *georgiana*. Higher local song type diversity in *M. g. nigrescens* corresponds with the hypothesis that the vocal constraints imposed by larger bills (and consequent decrease in vocal performance) may be the primary driving force behind greater song complexity (Podos and Nowicki 2004, Ballentine 2006).

PLAYBACK RESPONSES

Male Swamp Sparrows responded more aggressively to songs of their own subspecies than to songs of the other subspecies.

This finding is consistent with previous studies that have documented a stronger response in males to local song (Northern Cardinal, *Cardinalis cardinalis*, Lemon 1967; Corn Bunting, *Emberiza calandra*, McGregor 1983; Song Sparrow, *Melospiza melodia*, Searcy et al. 1997; Yellow-naped Amazon, *Amazonia auropalliata*, Wright and Dorin 2001; Golden Bowerbird, *Prionodura newtonia*, Westcott and Kroon 2002, reviewed by Catchpole and Slater 1995, Nelson 1998). Coupled with data from other Swamp Sparrow populations (Searcy et al. 1985, Ballentine 2006), our results support the hypothesis that these subspecies recognize and discriminate between songs of same versus different subspecies. However, the mechanism by which this differential response occurs is unclear.

The observed difference in reaction to song may reflect either an ability simply to discriminate between local versus foreign songs, or it may suggest distinct responses on a subspecies scale. While playback responses in our study are not necessarily stronger than what would be found between any two geographically separated Swamp Sparrow populations, other studies provide some support for the prediction that this discrimination may be a subspecies-level phenomenon. For example, Searcy et al. (1985) reported that *M. g. georgiana* males from a Pennsylvania population did not distinguish between songs from their population and those recorded from a New York population, suggesting little or no variation in response to songs within a single subspecies. Further studies between other *M. g. nigrescens* and *georgiana* populations would help determine whether the observed responses within and between subspecies are universal. Reciprocal playback tests using opposite-subspecies songs, paired with same-subspecies songs from different populations separated by a similar distance, could distinguish between a local or subspecific scale of discrimination. Results from these tests would clarify whether differences in response are due to vocal variation present in populations, or whether they are indeed a behavioral effect of subspecies divergence.

In a prior study examining genetic and song variation in Swamp Sparrows, Balaban (1988) found that male Swamp Sparrows approached speakers playing songs from other populations more quickly than they approached speakers playing songs from their own population. Several differences between the present study and that of Balaban (1988), however, may account for the apparent incongruity in results. First, in contrast to our playback procedure, that of Balaban (1988) involved separate treatment types, with some subjects exposed to local versus foreign songs (as in the present study) and others hearing songs from two areas that were both foreign to them. The use of songs from different populations introduces the question of discrimination between multiple geographic variants (Searcy et al. 2002), an issue not addressed in our study. Second, the stronger response to foreign song was not uniform across playback trials. When results were analyzed according to syllable type (i.e., three- or four-note syllables), males

were shown to react more strongly to foreign three-syllable songs but to not distinguish between local and foreign four-syllable songs, suggesting that acoustic or syntactical features unrelated to song recognition could have influenced the intensity of their response. Most importantly, males in Delaware may not have been exclusively of the subspecies *nigrescens* at the time of song recording in this earlier study, as songs were obtained in mid-April, when migrants of both subspecies are known to occur along the mid-Atlantic coast (Greenberg and Droege 1990). The uncertain identity of subject males thus makes direct comparisons difficult with results of later studies.

Measuring response to song via playback trials in females as well as males could test the idea that vocal discrimination facilitates reproductive isolation. Furthermore, because assortative mating ultimately affects the extent of gene flow between populations, female preferences may play a stronger role than male song recognition in determining the rate of signal evolution within subspecies (Ratcliffe and Otter 1996, Nowicki et al. 2001). Evaluating the ability of young birds to detect subspecies-level song differences could also clarify the implications of vocal variation, as this sensitivity may surface at a relatively young age during an individual's development and persist until song crystallization (Nelson 2000). An innate preference in Swamp Sparrow chicks toward subspecies-specific song could contribute to signal divergence by reinforcing present differences found in song variation well before the onset of song learning.

Our results support the hypothesis that Swamp Sparrows recognize and differentiate between songs of same and different subspecies. The extent of song variation and discrimination found in the present study provides behavioral evidence to suggest vocal divergence between *M. g. nigrescens* and *georgiana*, especially with regard to signal production and perception. Combined with future tests, these findings may clarify the consequences of vocal differences in subspecies divergence, particularly when considered under the broader contexts of assortative mating and cultural evolution.

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