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DARK COLOR OF THE COASTAL PLAIN SWAMP SPARROW (*MELOSPIZA GEORGIANA NIGRESCENS*) MAY BE AN EVOLUTIONARY RESPONSE TO OCCURRENCE AND ABUNDANCE OF SALT-TOLERANT FEATHER-DEGRADING BACILLI IN ITS PLUMAGE

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Abstract.—The Southern Swamp Sparrow (*Melospiza georgiana georgiana*) breeds in northeastern North America in montane, freshwater marshes and fens. Its close relative, the Coastal Plain Swamp Sparrow (*M. g. nigrescens*), breeds in northeastern North America, but in coastal salt marshes. Coastal Plain Swamp Sparrows are darker than Southern Swamp Sparrows. Darkly colored feathers are more resistant to bacterial degradation by bacilli, which are unusually salt-tolerant. We tested whether the difference in feather color of the pale montane Southern Swamp Sparrow and the dark Coastal Plain Swamp Sparrow could be an adaptive response to differences in the occurrence and activity of bacilli in habitats that differ in salinity. Southern Swamp Sparrows were caught and sampled in cranberry fens in western Maryland, whereas Coastal Plain Swamp Sparrows were sampled in salt marshes on the western shore of the Delaware River, just where it broadens into Delaware Bay. The number of birds with feather-degrading bacteria in their plumage was significantly greater among Swamp Sparrows in salt marshes than among those in freshwater fens. The number of colonies of feather-degrading bacilli per bird was also higher for salt-marsh Swamp Sparrows than for those from freshwater fens. We conclude that the dark plumage of Coastal Plain Swamp Sparrows evolved to resist feather-degradation by salt-tolerant bacilli that occur more frequently and abundantly in their plumage than in the pale plumage of the Southern Swamp Sparrow. *Received 25 July 2008, accepted 16 January 2009.*

Key words: bacilli, color, feather-degrading bacteria, *Melospiza georgiana,* Swamp Sparrow.

El Color Oscuro de *Melospiza georgiana nigrescens* Puede Ser una Respuesta Evolutiva a la Presencia y Abundancia de Bacilos Tolerantes a la Sal y Degradadores de las Plumas en su Plumaje

Resumen.—*Melospiza georgiana georgiana* cría en el noreste de América del Norte en pantanos montanos de agua dulce. Su pariente cercano, *M. g. nigrescens*, cría en el noreste de América del Norte, pero en pantanos costeros de agua salada. *M. g. nigrescens* es más oscuro que *M. g. georgiana*. Las plumas de colores más oscuros son más resistentes a la degradación bacteriana por bacilos, que son inusualmente tolerantes a la sal. Evaluamos si las diferencias en los colores de las plumas del montano y pálido *M. g. georgiana* y del oscuro *M. g. nigrescens* pueden ser una respuesta adaptativa a las diferencias en la presencia y actividad de los bacilos en ambientes que difieren en salinidad. Los individuos de *M. g. georgiana* fueron capturados y muestreados en pantanos de arándano agrio en el oeste de Maryland, y los de *M. g. nigrescens* en marismas de la costa oeste del Río Delaware, justo en donde se ensancha en la Bahía de Delaware. El número de aves que presentaban bacterias que degradan plumas en sus plumajes fue significativamente mayor entre las de las marismas que entre las de los pantanos de agua dulce. El número de colonias de bacilos degradadores de plumas por ave fue también mayor en las aves de las marismas que en las de los pantanos de agua dulce. Concluimos que el plumaje oscuro de *M. g. nigrescens* evolucionó para resistir a la degradación de las plumas por parte de los bacilos tolerantes a la sal que aparecen de modo más frecuente y abundante en su plumaje que en el plumaje pálido de *M. g. georgiana*.

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Southern swamp sparrows (*Melospiza georgiana georgiana*), which breed in freshwater marshes of the northeastern United States and southern Canada, are predominantly rusty brown with a brown or rusty crown. Coastal Plain Swamp Sparrows (*M. g. nigrescens*), which breed in salt marshes along the mid-Atlantic coast (Greenberg and Droege 1990), have more extensive black coloration in the crown and 40% more black feathering on the body than Southern Swamp Sparrows (Greenberg et al. 2008). The color difference in these two subspecies parallels that between the subspecies of western Song Sparrows (*M. melodia*; Zink and Remsen 1986), in which darkly colored *M. m. morphna* of the humid Northwest harbor more active feather-degrading bacilli in their plumage than pale *M. m. fallax* of the arid Southwest (Burtt and Ichida 2004). The geographic variation in the color of Song Sparrows is an example of Gloger's rule. Humid environments such as the Pacific Northwest favor bacterial growth, which may select for dark feathers that resist bacterial degradation (Goldstein et al. 2004, Gunderson et al. 2008). Because Swamp Sparrows, regardless of color, live in wet habitats, humidity is an unlikely explanation for their color variation. However, feather-degrading bacilli are unusually salt-tolerant (Claus and Berkeley 1986). Such tolerance could mean that feather-degrading bacilli are more abundant in salt-marsh habitat, where their less-tolerant microbial competitors are absent or disadvantaged. If the microbiota of salt-marsh habitat is skewed toward feather-degrading, salt-tolerant bacilli, selection should favor the evolution of melanic feathers that resist bacterial degradation. We hypothesized that the darker Coastal Plain Swamp Sparrows, which breed in coastal salt marshes, would have more, and more active, feather-degrading bacilli than the lighter Southern Swamp Sparrows, which breed in freshwater marshes and fens.

Methods

Field sampling and identification of feather-degrading bacilli.—Individual Southern and Coastal Plain swamp sparrows were captured with mist nets in late May–June 2006 at breeding sites, and their plumage was sampled for microorganisms. Coastal Plain Swamp Sparrows were studied in spartina marshes (salinity: 5–10 ppt) within state refuges near Woodland Beach, Delaware (75.6°W, 39.4°N), along the western shore of the Delaware River just north of where it expands to form Delaware Bay. Southern Swamp Sparrows were sampled at an elevation of 800 m on two plots in freshwater cranberry fens on the Allegheny Plateau in Garrett County, Maryland (79.3°W, 39.6°N).

We removed individuals from mist nets only after washing our hands with a quaternary ammonium disinfectant and rubbing or shaking them dry. We sampled microorganisms in the plumage by pressing a trypticase soy agar (TSA) plate to the back, venter, and dorsal surface of the tail. Trypticase soy agar is a rich, nonspecific agar on which most culturable bacteria (e.g., *B. licheniformis*), as well as many fungi and, occasionally, yeast, will grow. We pressed a yeast maltose agar (YMA) plate against the ventral feathers after sampling with TSA. Like TSA, YMA is a rich medium on which fungi grow particularly well but which also captures feather-degrading bacilli. After using TSA on the back, we rubbed the dorsal plumage with a mannitol salt agar (MSA) plate, which is selective for *Staphylococcus* spp. We brushed the underside of the tail across eosin-methylene blue agar (EMB), which is selective for coliforms, and stroked the primaries across actinomycetes isolation agar (AIA), which selects for *Streptococcus* spp. We used TSA first because it does not affect the viability of the microorganisms targeted by the more specialized MSA, EMB, AIA, and YMA. We sampled several different areas of the plumage to ensure a reliable estimate of the presence and abundance of plumage microorganisms.

Exposed plates were kept in coolers with ice packs until the day's end, then placed in incubators for 48 h. We incubated YMA and AIA at 28°C, and TSA, MSA, and EMB at 37°C. After incubation, we identified and counted all bacterial, fungal, and yeast colonies. Most could be identified only to general type (e.g., nonspore-forming rods), others to a broad taxonomic group (e.g., *Actinomycetes*), still others to genus (e.g., *Bacillus*), and a few to species (e.g., *Staphylococcus aureus*), the latter by using a selective medium. The combination of a selective medium and morphology enabled us to identify 23 types of culturable microorganisms in the plumage.

We identified *Bacillus* spp. on the basis of colony morphology, as described by Claus and Berkeley (1986). We transferred a representative colony of putative *Bacillus* spp. from each culture plate on which it occurred to a test tube of nutrient broth, alkaline salts (pH 7.7 and 7.0% NaCl; Burtt and Ichida 1999). These cultures were incubated in a shaking incubator at 50°C and 125 rpm for seven days. If the broth remained clear, we discarded it and noted that the colony was not a species of *Bacillis*. If the broth became turbid, we used a sterile loop to remove a drop of medium and cross-streak it on TSA plates to isolate colonies of *Bacillus* spp. From each plate, we subcultured a single colony to a TSA slant, incubated the slant at 37°C for 48 h, and stored the slant at 4°C for later use in feather-degradation experiments. If the isolated colony was a feather-degrader, we considered all colonies of *Bacillus* on the original plate feather-degraders, on the basis of their identical morphology.

Measurement of the rate of feather degradation.—We quantified *in-vitro* feather degradation by measuring the concentration of oligopeptides released into the feather medium when bacterial keratinase degrades β-keratin (Goldstein et al. 2004). We performed all bacterial transfers in a laminar flow hood, using aseptic technique to prevent contamination. We transferred our isolated strains of bacilli from the TSA slants on which they were stored to nutrient broth, which was incubated at 37°C and 125 RPM for ~18 h. This allowed the cells to reach their stationary growth phase before use for feather degradation. We transferred 5 mL of each liquid culture to a sterile centrifuge tube with a sterile disposable pipette. We centrifuged the culture to create a pellet of cells, decanted the nutrient broth, resuspended the cells in a small amount of sterile saline, and transferred the cell suspension to a sterile disposable glass test tube. We added saline to this suspension until the turbidity of the suspension visually matched a 0.5 McFarland Standard. This produced a cell density of approximately 1.5×10^8 cells mL^{-1} (Chapin and Lauderdale 2003).

We used 25 × 150 mm test tubes for the feather-degradation analyses. To each test tube, we added 0.06 g of white feather barbs, cut from secondary feathers of Domestic Geese (*Anser anser*). We prepared feather medium as described by Williams et al. (1990): 0.5 g NH_4Cl, 0.5 g NaCl, 0.3 g K_2HPO_4, 0.4 g KH_2PO_4, 1 g $MgCl_2$, $6H_2O$, and 0.1 g of yeast extract per liter of deionized water. We added 20 mL of medium to the feather barbs in each tube

TABLE 1. Comparison of the microbiota of the plumage of Southern and Coastal Plain swamp sparrows, with emphasis on feather-degrading bacilli.

	Southern Swamp Sparrow in freshwater fens (mean ± SD)	Coastal Plain Swamp Sparrow in salt marshes (mean ± SD)	Statistic and probability that the means are equal
Proportion of sparrows with feather-degrading bacilli	18/45 (40%)	33/40 (82%)	$\chi^2 = 3.96$ df = 1 $P < 0.05$
Number of types of plumage microorganisms individual^{-1}	9.20 ± 1.84	9.46 ± 0.71	$U = 1{,}499.5$ df = 37 and 40 $P = 0.94$
Mean species diversity of plumage microorganisms	1.58 ± 0.33	1.58 ± 0.29	$t = 0.03$ df = 75 $P = 0.97$
Mean abundance of all types of microorganisms in plumage	152.08 ± 178.37	371.51 ± 230.51	$t = -4.21$ df = 75 $P < 0.001$
Mean abundance of feather-degrading bacilli in individuals with one or more feather-degrading bacilli	2.00 ± 0.86	97.89 ± 78.20	$U = 41$ df = 37 and 40 $P = 0.0025$

before autoclaving the tubes at 121°C and 17 psi for 15 min. After the tubes cooled, each was inoculated with 2 drops (0.1 mL) of the prepared saline suspension. We incubated the tubes at 37°C and 125 rpm for five days.

At intervals of 24, 48, 72, 96, and 120 h, we removed a 1-mL sample from each of the test tubes to a fresh microcentrifuge tube. The samples were centrifuged at 14,000 rpm for 10 min to remove any cells and pieces of feather from the suspension. We transferred the supernatant to a fresh microcentrifuge tube and centrifuged a second time. We transferred the second supernatant to a fresh microcentrifuge tube. We transferred the supernatant to a quartz cuvette and measured absorbance at 230 nm with a UV-Vis Spectrometer (Beckman DU 530). We used autoclave-sterilized feather medium as the blank control and rinsed the cuvette between samples with autoclave-sterilized Milli-Q water. If needed, we diluted the samples with autoclave-sterilized feather medium.

In feather medium that has been inoculated with feather-degrading bacilli, degradation of the feather by bacterial enzymes produces protein fragments called oligopeptides, and the concentration of these fragments is proportional to absorbance of the medium at 230 nm (Goldstein et al. 2004). Greater absorbance indicates that there are more oligopeptides in the medium. Greater absorbance and more oligopeptides mean that more feather keratin has been degraded by bacterial enzymes, and the more quickly oligopeptides appear in the medium, the more quickly the feather is being degraded (Goldstein et al. 2004).

Statistics.—Because we sampled different numbers of individuals of the two subspecies (Table 1), we used the chi-square test for independence to compare the proportion of individuals of each subspecies that had one or more feather-degrading bacilli in their plumage. From the number of different types of microorganisms in the plumage of each Swamp Sparrow, we calculated the average species richness of plumage microbes in the two populations. We calculated the average Shannon-Weiner diversity index for every individual in both populations on the basis of the number of types of microbes and abundance of each type. We also calculated the mean total number of microbial colonies in the plumage of the two populations and the number of colonies of feather-degrading bacilli in the plumage of Southern and Coastal Plain swamp sparrows.

We realize that the variances in total abundance of plumage microbes and in abundance of feather-degrading bacilli are large (Table 1). The variance ratio test (Zar 1984) indicated nonsignificant differences when comparing means of total abundance ($F = 1.68$, df = 39 and 44, $P > 0.05$) or microbial species diversity ($F = 1.30$, df = 39 and 44, $P > 0.05$) in the two populations of Swamp Sparrows. Therefore, we used the *t*-test for independence to compare these means. Variances were significantly different for means of species richness ($F = 3.68$, df = 39 and 44, $P < 0.001$) and abundance of feather-degrading bacilli ($F = 8{,}377$, df = 39 and 44, $P < 0.001$) in the plumage. These means were compared with the Mann-Whitney *U*-test. All analyses were completed with MINITAB 15 (Minitab, State College, Pennsylvania).

RESULTS

We isolated feather-degrading bacilli from the plumage of 18 of 45 adult Southern Swamp Sparrows captured in freshwater fens in the mountains of Maryland (Table 1). We isolated feather-degrading bacilli from the plumage of 33 of 40 adult Coastal Plain Swamp Sparrows captured in the salt marshes of the lower Delaware River (Table 1). Significantly more individuals from the salt marshes had feather-degrading bacilli in their plumage than did those from the freshwater fens (Table 1).

The abundance of feather-degrading bacilli per individual, as estimated from the number of colony-forming units (CFUs) counted on all TSA and YMA plates, was significantly higher in individuals from salt marshes than in those from freshwater fens (Table 1). Several Coastal Plain Swamp Sparrows had almost 500 CFUs of feather-degrading bacilli per individual (Fig. 1). By contrast, one Southern Swamp Sparrow had 27 CFUs, another 26, and the remaining 16 that had bacilli in their plumage sample had ≤12 CFUs.

Coastal Plain Swamp Sparrows were not only more likely to have feather-degrading bacilli in their plumage, and more of them, than Southern Swamp Sparrows; they also had significantly higher loads of plumage microorganisms overall (Table 1). However, the number of types of culturable microorganisms in the plumage was similar for the two populations of Swamp Sparrows (Table 1), as was the diversity (Table 1).

Maximum and minimum degradation rates of *B. licheniformis* from the plumage of Southern Swamp Sparrows and Coastal Plain Swamp Sparrows were almost identical (Fig. 2). Thus, feather-degrading bacilli, whether from the plumage of Swamp Sparrows in freshwater fens or those in salt marshes, pose the same threat to the individual's feathers. However, a Swamp Sparrow in the Delaware salt marshes was twice as likely to have feather-degrading bacilli in its plumage (82% of individuals sampled) as a Swamp Sparrow from the Maryland fens (40% of individuals sampled). Furthermore, the number of colonies of feather-degrading bacilli

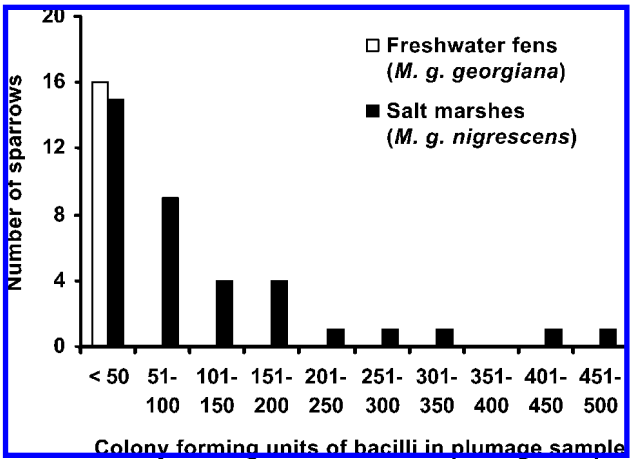

Fig. 1. A plot of the number of Swamp Sparrows with one or more colony-forming units of feather-degrading bacilli in their plumage shows that more salt-marsh Swamp Sparrows have feather-degrading bacilli in their plumage and that they have many more bacilli than Swamp Sparrows from freshwater fens.

in the plumage of salt-marsh Swamp Sparrows was 50× greater than in the plumage of Swamp Sparrows in freshwater fens.

Discussion

Both Song Sparrows (Arcese et al. 2002) and Swamp Sparrows (Mowbray 2000) have dark and light subspecies that occur in different habitats. Like Song Sparrows (Burtt and Ichida 2004), the differently colored subspecies of Swamp Sparrow face different exposure to feather-degrading bacilli. Unlike in Song Sparrows, the feather-degrading bacilli from the plumage of dark and light Swamp Sparrows degrade feathers at similar rates. However, individuals of the dark subspecies are significantly more likely to have feather-degrading bacilli in their plumage and have significantly more bacilli.

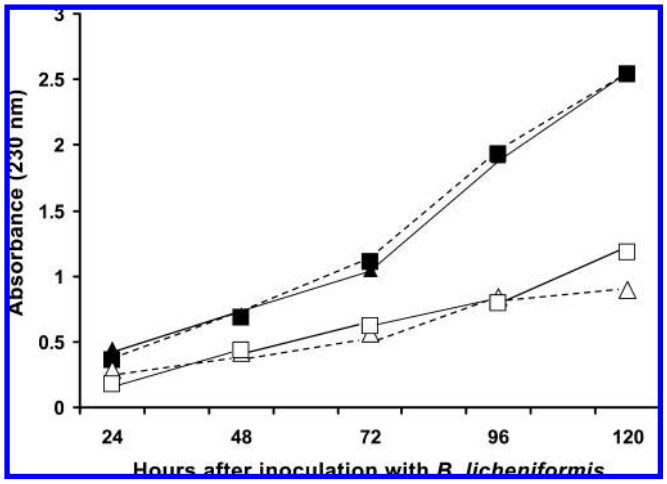

Fig. 2. The increasing absorbance of the supernatant from the feather medium indicates the increasing degradation of the feather. The maximum (filled symbols) and minimum (open symbols) mean absorbance for supernatant from cultures of bacilli isolated from Southern Swamp Sparrows (squares) and from Coastal Plain Swamp Sparrows (triangles) indicate that the rate of feather degradation is the same, regardless of whether the bacilli come from Swamp Sparrows living in salt marshes or in freshwater fens.

In both Song Sparrows and Swamp Sparrows, the subspecies with darker plumage faces a greater threat of bacterial degradation of its feathers. Melanin, which darkens the feathers, also retards bacterial degradation (Goldstein et al. 2004, Gunderson et al. 2008). Thus, subspeciation in Song and Swamp sparrows may be driven, in part, by the greater risk of bacterial degradation to the plumage of the darker subspecies. The darker Coastal Plain Swamp Sparrows were twice as likely to have feather-degrading bacilli in their plumage as the paler Southern Swamp Sparrows, and the bacilli were one to two orders of magnitude more abundant in their plumage. Such a difference would seem to constitute a considerable selection pressure for dark plumage that can resist bacterial degradation.

In the Song Sparrow, dark coloration and increased bacterial activity are correlated with the humidity of the habitat (Burtt and Ichida 2004). The dark color of populations in humid habitats is widespread and well documented (Zink and Remsen 1986, Burtt and Ichida 2004). The correlation is known as "Gloger's rule." Several explanations have been offered for Gloger's rule (see review in Burtt and Ichida 2004), all of them mutually compatible, but none explains the color difference observed in Swamp Sparrows. Both light and dark populations of Swamp Sparrow occupy wet habitats in which all the suggested explanations for the color difference described in Gloger's rule would apply to both populations. However, 40% of light Southern Swamp Sparrows from the freshwater fens have feather-degrading bacilli in their plumage, whereas 82% of dark Coastal Plain Swamp Sparrows have feather-degrading bacilli in their plumage and, if there, the bacilli are vastly more abundant (97.89 ± 78.20 CFUs) than in the plumage of Southern Swamp Sparrows (2.00 ± 0.86 CFUs).

The fens of western Maryland are cooler than the salt marshes of upper Delaware Bay. The heat of the salt marshes and the high humidity that goes with such heat promote bacterial growth. The difference in heat and humidity may account for the greater overall microbial load in the plumage of Coastal Plain Swamp Sparrows than in the plumage of Southern Swamp Sparrows of the mountain fens (Table 1), but this does not explain the difference of almost two orders of magnitude in the abundance of feather-degrading bacilli.

The cranberry fens of western Maryland have a far lower salinity than the salt marshes at the head of Delaware Bay (0 vs. 5–10 ppt). Few bacteria are as salt-tolerant as *B. licheniformis* (Claus and Berkeley 1986) and related bacilli. Indeed, we isolate them from other bacteria by growing them in a 7.7% salt solution (Burtt and Ichida 1999). The salt tolerance of bacilli may account for their abundance in the plumage of Coastal Plain Swamp Sparrows. With such bacilli abundant in the plumage and surrounded by a damp habitat in which the feathers are often wet, selection for resistance to bacterial degradation of the feathers could be intense. Melanization of the feathers, as has happened in the Coastal Plain Swamp Sparrow, increases their resistance to bacterial degradation (Goldstein et al. 2004, Gunderson et al. 2008).

The marked color difference between salt-marsh and inland populations of Swamp Sparrows despite their genetic similarity prompted Greenberg et. al. (1998) to suggest that either (1) there is strong selection and sufficient heritable variation or (2) the color differences are environmentally induced (Von Bloeker 1932, James 1983, Zink and Remsen 1986). We suggest that the "strong selection" hypothesized by Greenberg et al. (1998) is provided by the high probability of acquiring feather-degrading bacilli and the abundance of such bacilli in the plumage of affected Coastal Plain Swamp Sparrows (*M. g. nigrescens*). Furthermore, the occurrence and distribution of eumelanin (gray to black), as opposed to pheomelanin (buff to rust), in the plumage appear to be under strong genetic control in birds (Smyth 1990). This would account for the "heritable" aspect of Greenberg et al.'s (1998) hypothesis. That the color difference between subspecies of Swamp Sparrows is substantially less than the difference between the subspecies of Song Sparrows (Burtt and Ichida 2004) may be the result of the recent expansion of Swamp Sparrows into habitat that was tundra as recently as 15,000 years ago, during the Pleistocene glaciation (Jacobsen et al. 1987, Cox and Moore 2005). The strength of selection for melanic colors that resist bacterial degradation and the recency of the Swamp Sparrow's evolutionary response to such selection are indirectly supported by the frequent grayish or blackish color of tidal populations of other terrestrial vertebrates—the "salt marsh melanism" noted by Grinnell (1913) and Von Bloeker (1932).

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