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# MIGRATORY CONNECTIVITY IN THE RUSTY BLACKBIRD: ISOTOPIC EVIDENCE FROM FEATHERS OF HISTORICAL AND CONTEMPORARY SPECIMENS

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*Abstract.* The Rusty Blackbird (*Euphagus carolinus*) has declined dramatically across its range in North America since at least the 1960s, but the causes for this decline are unknown. We measured ratios of stable hydrogen isotopes (δD) in feathers collected from Rusty Blackbirds wintering in the Mississippi Alluvial Valley ($n$ = 255 birds) and the coastal plain of South Carolina and Virginia ($n$ = 281 birds), 2005–2009, to estimate the region of origin of birds wintering west and east of the Appalachians, respectively. We also measured δD values in feathers from all available museum specimens collected from 1879 to 1990 in these same two regions ($n$ = 190 birds). Isotopic values support migratory connectivity in this species with breeding populations in the western and central boreal forest migrating through a central or Mississippi flyway and those breeding in the eastern boreal forest migrating to a winter range east of the Appalachians. We detected little long-term change in the breeding origins of modern and historical populations wintering east and west of the Appalachians. However, we found short-term temporal variability in the breeding origins of birds wintering on the coastal plain from 2007 to 2009. The migratory divide suggests that efforts at management should be tailored to at least eastern and western subpopulations on both the breeding and wintering grounds. Our approach can be applied to a broad range of migratory species in North America and on other continents.

*Key words:* *deuterium*, Euphagus carolinus, *migratory connectivity*, *Rusty Blackbird*, *stable isotopes*.

## Conectividad Migratoria en *Euphagus carolinus*: Evidencia Isotópica de Plumas de Especímenes Históricos y Contemporáneos

*Resumen.* Las poblaciones de *Euphagus carolinus* han disminuido dramáticamente en toda su distribución en América del Norte al menos desde la década de los sesenta, pero las causas de esta disminución se desconocen. Medimos los cocientes de isótopos estables de hidrógeno (δD) en plumas recolectadas entre 2005 y 2009 en el valle aluvial del Mississippi ($n$ = 255 aves) y en las planicies costeras de Carolina del Sur y Virginia ($n$ = 281 aves) para estimar la región de origen de las aves que pasaban el invierno al oeste y al este de las Apalaches, respectivamente. También medimos los valores de δD en plumas de todos los especímenes coleccionados en esas dos regiones entre 1879 y 1990 que estaban disponibles ($n$ = 190 aves). Los valores isotópicos demuestran conectividad migratoria en esta especie: las poblaciones que se reproducen en el oeste y en bosques boreales centrales migran a lo largo de un corredor central o del Mississippi, mientras que las que se reproducen en los bosques boreales del este migran a un área de invernada al este de los Apalaches. Sin embargo, encontramos variabilidad temporal de corto plazo en el origen reproductivo de las aves que pasaron el invierno en las planicies costeras entre 2007 y 2009. La división entre dos rutas migratorias sugiere que los esfuerzos de manejo deben ajustarse al menos para las subpoblaciones del este y del oeste tanto en las áreas de cría como en las de invernada. Nuestro enfoque puede aplicarse a un rango amplio de especies migratorias en América del Norte y en otros continentes.

## INTRODUCTION

The effective conservation of migratory birds that travel annually between distant breeding, stopover, and wintering sites is made difficult by a general lack of knowledge of the connectivity between these sites for specific populations of interest (Webster et al. 2002). This task is made even more difficult for those species that are distributed broadly but in low numbers over vast and remote regions. Species with broad distributions also present considerable challenges to the interpretation of global declines in populations. In such cases, knowledge of historic patterns of abundance and whether declines are disproportionate in one region versus another would assist in testing hypotheses regarding which

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FIGURE 1. Breeding and wintering ranges of the Rusty Blackbird (*Euphagus carolinus*). Dark line indicates the approximate position of the divide between the Atlantic coastal plain and Mississippi Alluvial Valley drainages along the Appalachian Mountains.

factors may have caused the decline. For broadly distributed species, however, population censuses are often limited, nonexistent, or spatially biased. Furthermore, conventional mark–recapture approaches are often poorly suited to establishing patterns of migratory connectivity and, of course, cannot be used in retrospective studies unless the appropriate data were collected in the past. Fortunately, the development of the use of endogenous markers to infer origins of migratory wildlife has provided extremely valuable tools to assist in current and retrospective studies. In particular, the measurement of the abundance of stable hydrogen isotopes (measured as δD, see Methods) in feathers of migratory birds and tissues of other wildlife has proven useful in making spatial connections among components of the annual cycle (Hobson 2005, Hobson and Wassenaar 2008).

In North America the Rusty Blackbird (*Euphagus carolinus*) is a classic example of a species whose population has declined catastrophically (Greenberg and Droege 1999) and for which interpretations of the causes of the decline are difficult because of a paucity of data from conventional mark–recapture approaches. This species has a large breeding range extending across the North American boreal forest from Maine to Alaska, where it nests in wetlands that are usually difficult to access (Avery 1995). The winter range is smaller, covering much of the eastern U.S. (Fig. 1). Within this outlined area, populations tend to be unstable, particularly in terms of how long they remain in more northern areas and how they respond to year-to-year variation in weather (Hamel and Ozdenerol 2009).

The Rusty Blackbird is the passerine most closely tied to boreal forest wetlands for breeding (Erskine 1977, Spindler and Kessel 1980). It nests near open water (Kennard 1920) and feeds primarily on the adults and aquatic larvae of wetland insects (Ellison 1990). Several changes in the availability and quality of boreal wetlands may be contributing to the species' population decline (Greenberg and Droege 1999). Disturbance regimes of wetlands and rates of population decline of blackbirds, however, do not appear to be uniform across the vast boreal region of North America. In the northwestern portion of the breeding range in Alaska, boreal wetlands are drying widely from climate warming (Klein et al. 2005, Riordan et al. 2006) with shrinkage of wetlands resulting in changes in water chemistry, concentration of nutrients, and decreases in the abundance of macroinvertebrates (Corcoran et al. 2009). Resource development is widespread or increasing along the southern edge of the boreal forest, and acid rain and mercury contamination have affected wetlands in the eastern part of the boreal forest (Greenberg et al. 2011).

Anthropogenic disturbances in the boreal forest may be having broad effects, as several species breeding only in boreal wetlands are among the most rapidly declining birds in the continent. In addition to the Rusty Blackbird, severe long-term declines have been documented across all or major portions of the breeding ranges of the co-occurring Lesser Scaup (*Aythya affinis*), White-winged (*Melanitta fusca*) and Surf (*M. perspicillata*) Scoters, Horned Grebe (*Podiceps auritus*), Lesser Yellowlegs (*Tringa flavipes*), and Solitary Sandpiper (*T. solitaria*) (North American Waterfowl Management Plan 2004, Sauer et al. 2007, U.S. Fish and Wildlife Service 2009). These species migrate and winter in different habitats and areas, so parsimony argues that events on the breeding grounds are at least in part responsible for their declines. If a similar suite of factors operating on the breeding grounds is contributing to the declines of these species, the Rusty Blackbird may be particularly sensitive to its effects, as among these birds it has declined most precipitously (−12.5% per year range-wide, Sauer et al. 2007).

On the wintering grounds, Rusty Blackbirds are strongly associated with wooded wetlands but use other forested habitats with mast (such as pecan orchards), partially flooded impoundments, and feedlots. Although the species winters broadly throughout the eastern U.S., the greatest concentrations are in the Mississippi Alluvial Valley and adjacent areas to the north and east (Niven et al. 2004), as well on as the Atlantic coastal plain (particularly South Carolina and Georgia; Hamel and Ozdenerol 2009). Rusty Blackbirds appear to need relatively warm conditions for feeding on arthropods in the sod in and around temporary pools and continue to move south in November and well into December, probably to avoid frozen ground. Threats to winter habitat include loss of forested wetlands to agriculture and perhaps loss of areas with intermittent flooding to water management (Greenberg et al. 2011). At this point, it is not clear if habitat loss and degradation have been more severe in the Mississippi Alluvial Valley than along the coastal plain (Hamel et al. 2009).

Most of the hypothetical causes of decline should result in a distinct geographic pattern in the decline. But establishing these predicted patterns first requires an understanding of the connectivity of breeding and wintering populations. In this study we estimated the breeding origins of Rusty Blackbirds wintering across the southeastern U.S. to (1) identify connectivity between breeding and wintering populations and (2) determine if the distribution of breeding origins may have changed historically and through the period of major decline. We did this by comparing measurements of stable hydrogen isotope ratios in feathers of museum specimens (1879–1990) and of wintering Rusty Blackbirds recently (2005–2009) captured live. Our intention was to identify regions where the change in breeding distribution is greatest in order to gain insight into possible mechanisms causing the species' decline.

## METHODS

### FEATHER SAMPLING

We obtained historical feather samples from Rusty Blackbirds collected 1879–1990 in several museums (see acknowledgments). These feathers were removed from study skins by museum staff, and all collection information was noted (information available from the senior author). Detailed examination of live birds captured in the field and specimens held in museums reveals that the species undergoes a pre-alternate molt restricted to feathers around the head and nape (Mettke-Hofmann et al. 2010). Our feather samples avoided these areas and instead included either flight feathers or buff or rusty-tipped contour feathers (feathers molted in winter lack these) from the flank or belly. We obtained modern samples by trapping birds in mist nets on their wintering grounds in (1) the Mississippi Alluvial Valley near Greenville, Mississippi (33° 29′ 40″ N, 90° 5′ 5″ W), near Johnson, Arkansas (36° 8′ 2″ N, 94° 9′ 57″ W), and at Tensas River National Wildlife Refuge (NWR), Louisiana (32° 9′ 48″ N, 91° 26′ 51″ W) between 2005 and 2009 and (2), the Atlantic coastal plain near Donnelly Wildlife Management Area, South Carolina (32° 40′ 30″ N, 80° 37′ 54″ W), Conestee, South Carolina (34° 46′ 3″ N, 82° 20′ 52″ W), and Williamsburg, Virginia (37°16′ 14″ N, 76° 43′ 2″ W) between 2007 and 2009. We also sampled feathers from available museum specimens of birds collected on the breeding grounds. These were augmented with feathers from breeding Rusty Blackbirds captured at nest sites in Anchorage, Alaska (61° 17′ 14″ N, 149° 44′ 25″ W) in 2007 (Matsuoka et al. 2010). We obtained these samples of known origin opportunistically to test how well they corresponded to values of δD in feathers that we predicted from values of δD in precipitation (see below).

### STABLE-ISOTOPE ANALYSIS

We cleaned all feathers of surface oils in a solvent consisting of a 2:1 ratio of chloroform to methanol and, following drying under a fume hood, prepared them for analysis of stable hydrogen isotopes at Environment Canada's stable-isotope laboratory in Saskatoon, Saskatchewan. Analyses of stable hydrogen isotopes in feathers used calibrated keratin isotope reference materials and the comparative equilibration method described in detail by Wassenaar and Hobson (2003). We measured ratios of stable hydrogen isotopes on $H_2$ derived from high-temperature flash pyrolysis of feathers by using continuous-flow isotope-ratio mass spectrometry. All δD values are expressed in the typical delta notation, in units of per mil (‰) and normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation scale. Repeated analyses of hydrogen isotope inter-comparison material IAEA-CH-7 (−100 ‰) and our calibrated keratin reference materials yielded an external repeatability of better than ± 3.2 ‰, based on the distribution of within-autorun residuals of accepted versus measured values for the reference materials.

### STATISTICAL ANALYSIS

We first examined factors influencing δD values of feather samples. We considered a potential migratory divide between origins of birds wintering on the Atlantic coastal plain versus those wintering in the Mississippi Alluvial Valley since the Appalachians could represent a natural barrier. Furthermore, the subspecies *E. c. nigrans*, which is restricted to breeding in Atlantic Canada, is thought to winter in North Carolina and Georgia (Avery 1995). We therefore tested for mean differences in feather δD values by wintering population (Mississippi Alluvial Valley versus coastal plain) and time period (historic versus modern) with a full-factorial, two-way analysis of variance (ANOVA). We tested the assumption of homogeneity of variance with Levene's test and examined the data and residuals for normality both graphically and by the Kolmogorov–Smirnov test. Our data showed only a slight departure from normality; however, variance was greater in the Mississippi Alluvial Valley than in the coastal plain ($F_{3,724} = 11.3$, $P < 0.001$). Because variances were heterogeneous, we checked our results with a Kruskal–Wallis test. We used SPSS version 17.0 (SPSS 2008) for all analyses.

*Establishing blackbird origins*. In order to assign birds to geographic origins, we first converted the δD values in feathers (hereafter $\delta D_f$) to corresponding values of expected growing-season δD in precipitation (hereafter $\delta D_p$; Bowen et al. 2005). We treated values of $\delta D_f$ from passerines and waterfowl of known source in North America as predictors regressed against $\delta D_p$ estimated from a GIS model of $\delta D_p$ (Bowen et al. 2005, Clark et al. 2006). Since there is error associated with both the analytical measurement of isotope values and the geospatial models of $\delta D_p$, we used reduced major-axis regression (Bowen et al. 2005). We ran the regression on the mean values of $\delta D_f$ at each site to control for both pseudoreplication among individuals sampled at same site and differences in sampling effort among sites. Parameter estimates for this regression were similar to those reported for other passerines (see references in Hobson 2008), with the relationship defined as $\delta D_p = 24.92 + 1.04\delta D_f$ ($r^2 = 0.95$, df = 18, $P < 0.001$). We also examined this relationship from the feathers of breeding Rusty Blackbirds that we sampled from museum specimens (19 specimens, 1896–1988) and a recent field study (17 nesting individuals from Anchorage, Alaska, 2007). Using these birds of known source, we used the regression equation above to convert the observed $\delta D_f$ values to $\delta D_p$ values and then contrasted these with the values of growing-season $\delta D_p$ predicted from the GIS model by ordinary least-squares regression.

Assigning birds to their geographic origins on the basis of $\delta D_f$ is complicated by differences in physiology among birds growing feathers at the same site, analytical error, and errors associated with the isotope surface to which birds are being assigned (Wunder and Norris 2008, Wunder 2010). Therefore, it is not reasonable to assume that measured values of $\delta D_f$ can be mapped directly to a GIS-based model of $\delta D_p$. Therefore, prior to assignment of probable origins, we propagated errors associated with both $\delta D_f$ and $\delta D_p$. Using data reported by Clark et al. (2006), we calculated the standard deviation (SD) of $\delta D_f$ values among wetland- and upland-associated birds at each of the 20 sites across North America ranging from 31.0° to 67.4° N latitude. We used maximum likelihood and fit a gamma distribution to the 20 observed SDs within each population to estimate the nature of the distribution (Venables and Ripley 2002). Using this distribution, we then propagated errors by simulating 1000 new expected $\delta D_p$ values for each measured $\delta D_f$ value. Each corresponding $\delta D_p$ value was simulated with a mean equal to the calculated $\delta D_p$ value, and a standard deviation was drawn at random from the derived gamma distribution with a shape parameter of 7.156 and scale of 1.322. For each blackbird population of interest (Mississippi Alluvial Valley historical and recent; coastal plain historical, winter 2007, and winter 2008–2009), we used the simulated $\delta D_p$ dataset to calculate a probability density function with the MASS library in R version 2.6.2 (R Development Core Team 2008). The probability densities were normalized to the largest observed probability density within each blackbird population of interest.

To map the probability of breeding or natal origins of wintering Rusty Blackbirds, we used ArcGIS version 9.1 and Spatial Analyst (ESRI 2005), to reclassify the GIS-based model of $\delta D_p$ (Bowen et al. 2005) into a probability surface. We accomplished this reclassification by (1) multiplying the probability-density values for a given GIS grid cell (0.33°, Bowen et al. 2005) by $10^7$ to provide the integer values required by ArcGIS, (2) reclassifying these transformed values into the $\delta D_p$ surface with Spatial Analyst, (3) converting the reclassified grid to a floating-point grid, and (4) dividing the values in the floating-point grid by $10^7$ to obtain a probability grid with values ranging from 0 to 1.

TABLE 1. Summary statistics for δD values (‰) in feathers of Rusty Blackbirds captured on their wintering grounds in the Mississippi Alluvial Valley and east of the Appalachians on the Atlantic coastal plain. Historic samples (1879–1990) were obtained from museum collections and current samples were obtained from birds captured in the winter from 2000 to 2009.

| | Historic | | | 2000–2007[a] | | | 2008–2009[b] | | |
|---|---|---|---|---|---|---|---|---|---|
| Population | *n* | Mean | SD | *n* | Mean | SD | *n* | Mean | SD |
| Mississippi valley | 101 | −131.1 | 24.7 | 169 | −133.1 | 20.4 | 86 | −135.9 | 19.4 |
| Coastal plain | 92 | −109.1 | 14.0 | 67 | −84.2 | 16.5 | 213 | −114.7 | 12.3 |

[a]Mississippi valley sampled 2000–2007, coastal plain sampled only in winter of 2007.
[b]Both populations sampled during this period.

## RESULTS

The ANOVA examining factors influencing $\delta D_f$ explained 30% of the variance in the data. Our results support the hypothesis of a migratory divide between the populations wintering in the Mississippi Alluvial Valley and Atlantic coastal plain because there was a significant effect of wintering population on $\delta D_f$ ($F_{1,724} = 216.8$, $P < 0.001$). A Kruskall–Wallis test yielded similar results (Kruskal–Wallis $\chi^2 = 223.4$, df = 1, $P < 0.001$). Values of $\delta D_f$ did not differ by time period ($F_{1,724} = 0.2$, $P > 0.1$) nor with the interaction between time period and wintering population ($F_{1,724} = 1.9$, $P > 0.1$). However, within the coastal-plain sample, there was substantial short-term temporal variation in the $\delta D_f$ values (Table 1), which remained constant from 1879 to 1990, increased in 2007, and then shifted back to historical values in 2008–2009 (Fig. 2). The 2007 coastal-plain sample came exclusively from South Carolina; $\delta D_f$ values for this sample were not consistent with those for other samples collected in South Carolina in other years or with samples from birds in neighboring states (Fig. 3).

Our derived probability-density function for the population wintering on the coastal plain suggested that in 2007 the breeding origins of that population shifted south and possibly east of

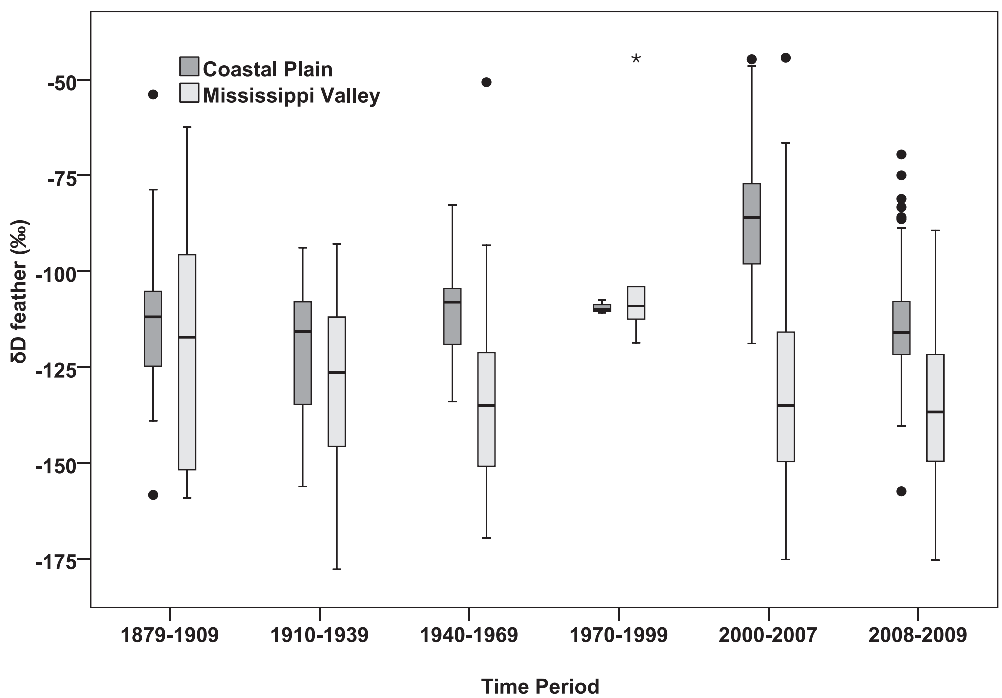


FIGURE 2. Temporal patterns of δD values in feathers of Rusty Blackbirds captured in their winter range in the Atlantic coastal plain and Mississippi valley, 1879–2009. Boxes represent upper and lower quartiles, heavy horizontal lines represent medians, whiskers represent ranges of nonoutlier values, and open circles indicate outliers. Sample sizes are given below the whiskers. More negative values represent origins at higher latitudes.

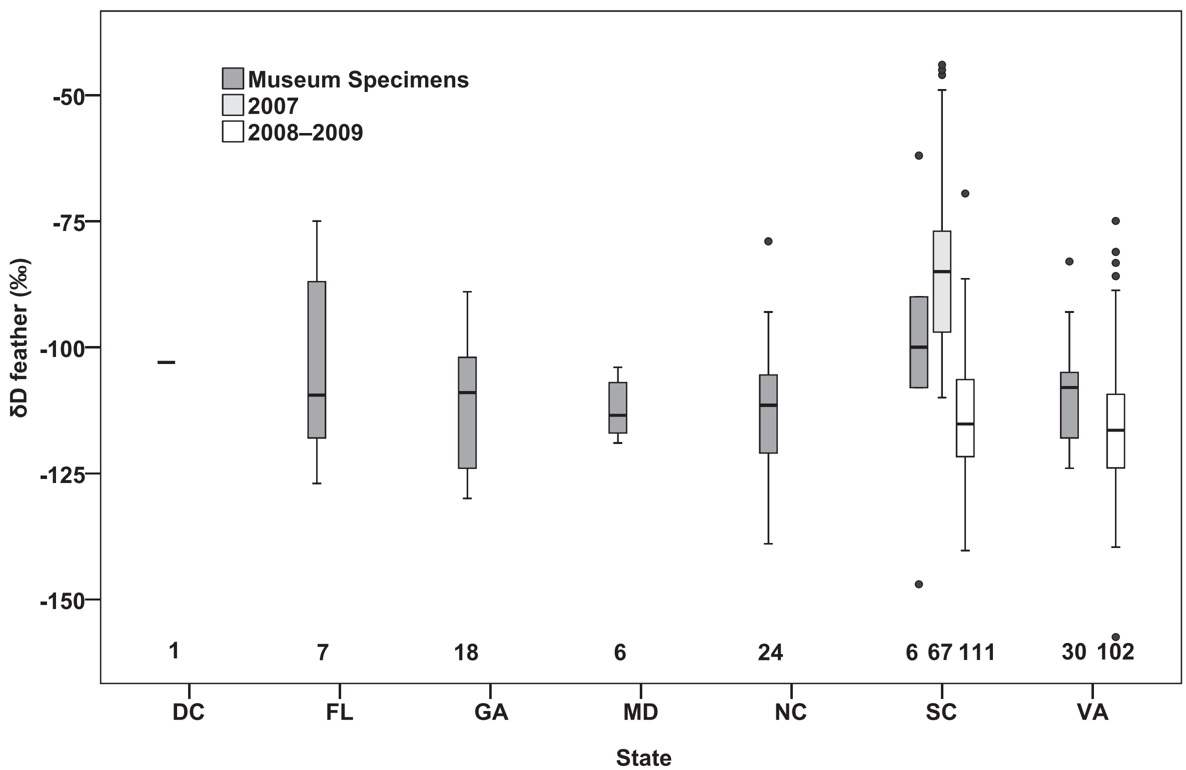


FIGURE 3. Geographic variation of δD values in feathers of Rusty Blackbirds captured on the Atlantic coastal plain, 1879–2009. Boxes represent upper and lower quartiles, heavy horizontal lines represent medians, whiskers represent ranges of nonoutlier values, and open circles indicate outliers. Sample sizes are given below the whiskers. More negative values represent origins at higher latitudes.

its historic area (Fig. 4a and Fig. 5a vs. 5b). The isotopic values of the historic population of birds wintering in the coastal plain corresponded to a band stretching from the mid-boreal zone of Manitoba through the Hudson Bay lowlands of Ontario and northeast toward the boreal shield of Labrador (Fig. 5a). The winter 2007 sample likely originated from the extreme southeastern portion of the breeding range (Fig. 5b), but the 2008–2009 sample was consistent with the likely origins of the more broadly distributed historical population (Fig. 5c vs. Fig. 5a). In contrast, the historic and current Mississippi Alluvial Valley populations had similar probability-density functions, so the current population likely originated from areas similar to those of the historic population (Fig. 4b). Birds wintering in the Mississippi Alluvial Valley potentially originated from a broad region from Labrador west to Alaska (Fig. 5d–f), an area largely northwest of the probable current geographic origins of the coastal-plain population (Figure 5a-c).

Finally, we examined the relationship between $\delta D_f$ and $\delta D_p$ for Rusty Blackbirds of known origin. We considered this relationship by using all specimens except for three outliers. The relationship without outliers (observed $\delta D_p = -9.5 + 0.9 \times$ predicted $\delta D_p$; $r^2 = 0.41$, $n = 33$, $P < 0.001$) provides some confidence in our overall approach and supports the contention that this relationship did not change during the last 100 years.

## DISCUSSION

### POPULATION STRUCTURE

Our isotopic analysis of feathers from modern and historical wintering populations of the Rusty Blackbird revealed a strong difference in the breeding origins of birds wintering on the east and west sides of the Appalachians. On the basis of both historic and modern samples, birds wintering to the west of the Appalachians, in the Mississippi Alluvial Valley, originated across a broad span of the boreal forest from Alaska to Labrador. The origins of birds wintering on the coastal plain, however, appeared to be much more restricted to eastern regions of the breeding range. While by no means definitive, our results support the hypothesis of a migratory divide in breeding origins of birds wintering to the east and west of the Appalachians. Migratory divides have been documented in other boreal-forest songbirds, such as Wilson's Warbler (Kelly et al. 2002) and Swainson's Thrush (Ruegg 2008), but these are located at the interface of the cordilleran forests of the Rockies and the low-elevation boreal belt. If a migratory divide exists in the Rusty Blackbird, its location in the center of the boreal belt is a region lacking any obvious underlying physiographic division. Barriers to mixing on the wintering grounds might be a more likely mechanism

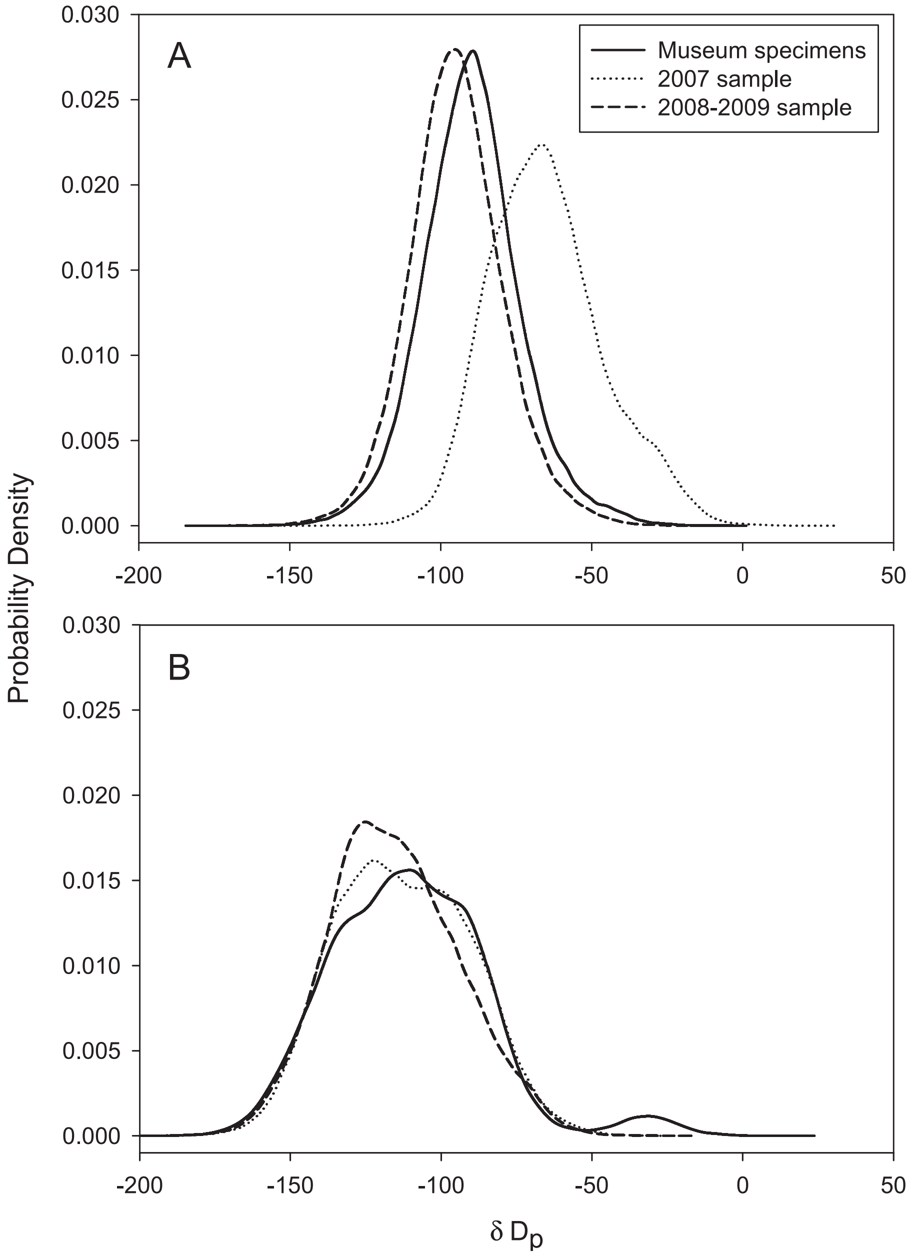


FIGURE 4. Probability-density distributions of Rusty Blackbird populations wintering in the southeastern U.S. in the (A) Atlantic coastal plain and (B) Mississippi Alluvial Valley based on δD analysis of feathers. The coastal-plain sample consisted of feathers from 91 museum specimens and birds captured in the field in 2007 ($n = 68$) and 2008–2009 ($n = 213$). The Mississippi Alluvial Valley sample consisted of feathers from 99 museum specimens and birds captured in the field in 2007 ($n = 169$) and 2008–2009 ($n = 86$). Probability distributions result from fitting probability-density functions to propagated errors associated with isotope values. Feather isotope values were converted to expected δD precipitation values with a reduced major-axis regression of birds of known source (see Methods).

for the creation of such a migratory divide. Recent analyses of Christmas Bird Counts by Hamel and Ozdenerol (2009) suggest that the Appalachians may create a gap in the Rusty Blackbirds' winter distribution. Similarly, band recoveries suggest that only a small proportion of birds crosses the Appalachians (Hamel et al. 2009). Regardless, the strong migratory connectivity between breeding and wintering regions to the east and west of the Appalachians has important implications for management.

The eastern wintering population appeared to shift breeding origins to more southeastern locations in 2007. However, the 2008–2009 sample was indistinguishable from the historical distribution. Currently, we do not know if this change represented a shift in the breeding distribution that year or

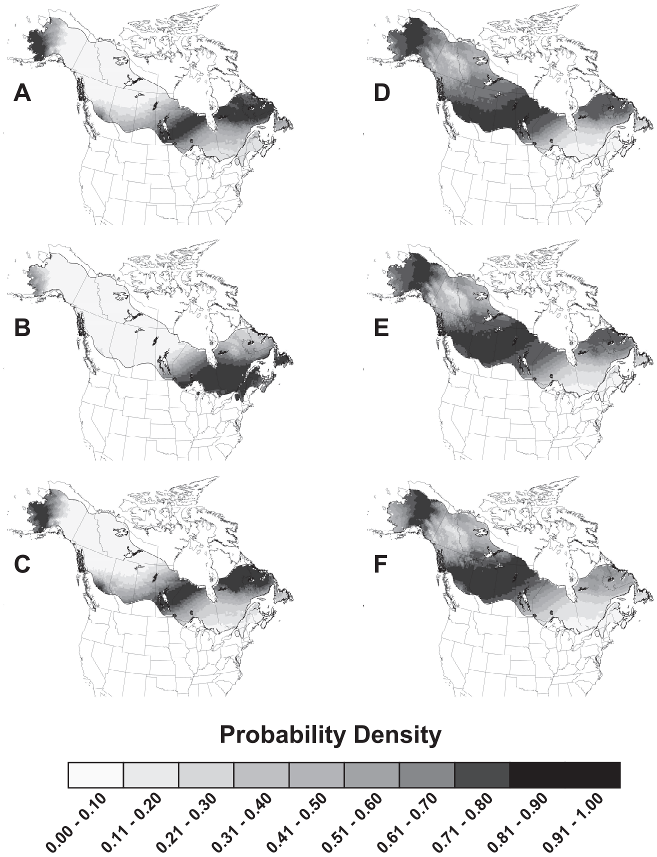


FIGURE 5. Probable breeding origins of Rusty Blackbirds wintering in the southeastern U.S. along the Atlantic coastal plain based on (A) museum specimens collected 1879–1990 and from live captures from (B) winter 2007 and (C) winter 2008–2009; probable breeding origins of Rusty Blackbirds wintering in the Mississippi Alluvial Valley from (D) museum specimens and live captures from (E) winter 2007 and (F) winter 2008–2009. Probable origins are inferred from probability densities fit to δD values in feathers and incorporating propagated errors associated with isotope signatures (see Methods). Probability densities were relativized to maximum values and then mapped to a GIS-based model of δD in precipitation (Bowen et al. 2005), after feather values were converted into expected precipitation values on the basis of a reduced major-axis regression of birds of known source (see Methods). Maps depict the full isotopic solution space encompassing the Rusty Blackbird's entire breeding range; however, birds wintering in the Atlantic coastal plain more likely originate from eastern portions of the breeding range.

if it was an artifact of sampling. In winter, Rusty Blackbirds are difficult to trap, particularly where they occur in low densities. Wintering blackbirds undoubtedly change locations from year to year (Hamel and Ozdenerol 2009), and it is currently unclear how populations may be further structured on the wintering grounds with respect to breeding origin. Our results underline the need to sample as broadly as possible when isotopic methods are used in an attempt to infer distributional changes in a broadly distributed species like the Rusty Blackbird. Alternatively, our data may indicate higher variability in recruitment from source breeding populations to the wintering grounds in the east. Although surveys in the southeastern breeding ground indicate a range contraction (Hodgman and Hermann 2003, Hodgman and Yates 2007) and a steep decline in breeding pairs (Sauer et al. 2007; Maritime Breeding Bird Atlas, unpubl. data), no equivalent data are available from the northernmost part of the breeding range in the east. Several studies suggest that habitat conditions in the northern boreal regions have changed (Klein et al. 2005, Riordan et al. 2006, Savignac 2006). A fruitful avenue of research would be to identify possible historical changes in wetland health such as wetland size, water quality (degree of acidification, contamination), and food-web structure between these different source areas.

The more restricted area of the Atlantic coastal plain suggests that attention be paid to the conservation of wintering habitat in that region since Rusty Blackbirds wintering there likely represent the small remaining population breeding in New England and the Maritime Provinces. Stronger connectivity between eastern breeding and wintering populations also allows more direct testing of factors affecting population regulation there. For example, if wetland conditions or other components of suitability of breeding habitat in the east could be improved, we would expect to see a measurable response in populations wintering in the coastal plain. A lack of response would point more to population limitation on the wintering grounds or at stopover sites en route.

The western wintering population almost certainly derives from a much larger and broader-based breeding population. Our data suggest that little has changed historically in the distribution of origins of these birds. Anecdotally, the southern limit of the Rusty Blackbird's range appears to be retracting across the continent, yet populations have been more stable in the northwestern segment of the range in Canada and Alaska (Machtans et al. 2007, Greenberg et al. 2011). However, the geographic broadness of the isotopic contours related to growing-season precipitation, particularly across the east-to-west bands of the boreal forest, may have obscured changes across the central and western portions of the breeding range. More research is now required to improve our understanding of connectivity between breeding and wintering populations within this region. Consideration of differences in wetland conditions in the western and eastern sections of the boreal forest and between those on the boreal shield in the east and those to the south appears to be the most parsimonious direction for future research. One additional consideration is that the populations wintering in the Mississippi Alluvial Valley consist of birds that migrate, on average, much farther than those wintering along the Atlantic coast, which should have implications for both demographic constraints and conservation strategies.

The broad decline of the species on both sides of the migratory divide (Greenberg and Droege 1999) indicates that several factors are likely responsible. In the western breeding range, a likely candidate is wetland drying, which needs to be studied in more detail (Greenberg et al. 2011). Even though destruction and alteration of winter habitat are a likely cause for the historic decline of the species, it is less likely that these are the cause for the continuing decline as afforestation programs, particularly in the Mississippi Alluvial Valley, have increased the wooded area available to the species (Hamel et al. 2009, Greenberg et al. 2011). Nonetheless, attention should be paid to possible changes in food availability or increased contamination in this region. In the eastern breeding range, acid rain in combination with methylmercury contamination (Edmonds et al. 2010) and logging (Powell et al. 2010) may be suppressing the population. Data about habitat availability, habitat quality, and food availability are urgently needed there. Finally, almost no information is available about resource requirements and limiting factors during migration. Habitat destruction and alteration may have a significant effect on both western and eastern populations of the Rusty Blackbird.

### STABLE ISOTOPES, CONNECTIVITY, AND CONSERVATION

The stable-isotope approach we have demonstrated here provides an advance in the way we can examine population connectivity and limitation in a migratory species that is dispersed broadly and in low numbers across its breeding range. Several authors are now applying this approach to examine pressing conservation problems (Hobson 2005, Greenberg et al. 2007, Perez and Hobson 2007, Wunder and Norris 2008, Hobson et al. 2009). This approach is especially useful for generating new and testable hypotheses that would be difficult or impossible through any other means. Nonetheless, it is productive in all such applications to consider the assumptions inherent in this approach and to examine possible alternative hypotheses to explain the isotopic results (Hobson and Wassenaar 2008, Wunder et al. 2009).

We adopted a statistical approach to assigning breeding origins of migratory birds that (1) accounts for errors in both $\delta D_f$ and $\delta D_p$ on the basis of reduced major-axis regression between $\delta D_f$ and $\delta D_p$ for birds from known breeding locations (Clark et al. 2006) and (2) propagates population-level errors via simulation. However, our method did not account for errors associated with the long-term Global Network of Isotopes in Precipitation (GNIP) dataset used to generate the mean surface of $\delta D_p$ averaged over the growing season (Bowen et al. 2005). Currently, an error surface is not available for the GNIP dataset (G. J. Bowen, pers. comm.). Another basic assumption in the analysis of stable-isotope data for temporal trends is that the baseline isotopic surface of $\delta D_p$ has not changed appreciably over the period of retrospective comparison, about 100 years in our case. We assumed all changes in feathers' isotope values to be associated with changes in the distribution of origin of individuals and not to changes in the base map of precipitation. Anecdotally, we note that there was no long-term trend in $\delta D_f$ values in Rusty Blackbirds wintering in either the Mississippi Alluvial Valley or Atlantic coastal plain. In addition, other authors who have used museum specimens of birds in North America report no effect of date on $\delta D_f$ values (Kelly et al. 2002, Lott and Smith 2006). So, our assumption of no major change in the $\delta D_p$ surface is reasonable. In addition, our birds of known origin collected on the breeding grounds provided a reasonable fit to our algorithm linking values of $\delta D_f$ and $\delta D_p$.

Several authors have emphasized the critical importance of establishing population connectivity between breeding, stopover, and wintering sites of migratory birds and other animals (Webster et al. 2002, Webster and Marra 2005). Knowledge of migratory connectivity will allow a more informed analysis of population demography and trends and the effects of seasonal interactions (Marra et al. 1998, Sillett et al. 2000, Gunnarsson et al. 2005, Holmes 2007). While the concept of protecting populations throughout their annual cycle seems obvious, our ability to make connections among populations within a species has been restricted overwhelmingly to game species that are amenable to band recoveries and satellite telemetry (Hobson 2003). Our study has emphasized the potential of the stable-isotope approach as a means of quickly and efficiently establishing patterns of migratory connectivity in a declining but broadly distributed species. We also have shown the value of museum specimens for isotopic analysis as a means of retrospectively examining factors that may be linked to long-term declines in a species (Smith et al. 2003). Importantly, our approach has served to quickly narrow down research questions associated with the potential recovery of the Rusty Blackbird. For example, we now suggest a focus on long-term population trends for the populations wintering in the Mississippi Alluvial Valley and Atlantic coastal plain. We also suggest that more scrutiny be directed toward understanding Rusty Blackbirds breeding in the southern boreal forest of central and western Canada since the Christmas Bird Count shows population trends for the Mississippi Alluvial Valley and Atlantic coastal plain to be equally negative despite the migratory divide (Niven et al. 2004). Finally, an examination of historical landscape change and wetland quality east and west of the Appalachians is now warranted.

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