RAPID COMMUNICATIONS

ESTIMATING MIGRATORY CONNECTIVITY OF GRAY CATBIRDS (*DUMETELLA CAROLINENSIS*) USING GEOLOCATOR AND MARK–RECAPTURE DATA

Thomas B. Ryder,[1,3] James W. Fox,[2] and Peter P. Marra[1]

[1]*Smithsonian Conservation Biology Institute, Migratory Bird Center, National Zoological Park, P.O. Box 37012-MRC5503, Washington, D.C. 20008, USA; and*
[2]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom*

Abstract.—Understanding the connectivity between breeding and nonbreeding populations of migratory birds is fundamental to our knowledge of biological phenomena such as population dynamics and dispersal. Moreover, our ability to quantify migratory connectivity has inevitable consequences for both conservation and management of species that utilize distinct geographic locations. Technology is rapidly advancing our ability to track birds throughout the annual cycle and to collect data on the degree of connectivity among breeding and nonbreeding populations. We combined two direct methods, mark–recapture ($n = 17$) and geolocation ($n = 6$), to estimate the migratory connectivity of breeding and nonbreeding populations of Gray Catbirds (*Dumetella carolinensis*). Data from geolocators show that birds breeding in the Mid-Atlantic overwinter in both Cuba and southern Florida. Mark–recapture data supported our geolocator results but also provided a broader spatial perspective by documenting that Mid-Atlantic and Midwestern populations occupy distinct geographic localities during the nonbreeding period. This research underscores the importance of geolocators, as well as other tools, to advance our understanding of migratory connectivity. Finally, our results highlight the potential value of U.S. Geological Survey (USGS) Bird Banding Laboratory mark–recapture data, which are often underutilized in ornithological research. *Received 6 January 2011, accepted 24 April 2011.*

Key words: *Dumetella carolinensis*, geolocators, Gray Catbird, mark–recapture, migratory connectivity.

Estimación de la Conectividad Migratoria de *Dumetella carolinensis* Mediante Datos de Geolocalizadores y de Marcado y Recaptura

Resumen.—Comprender la conectividad entre poblaciones reproductivas y no reproductivas de aves migratorias es fundamental para nuestro conocimento de fenómenos biológicos como la dinámica poblacional y la dispersión. Además, nuestra habilidad para cuantificar la conectividad migratoria tiene consecuencias inevitables para la conservación y el manejo de especies que utilizan distintas localidades geográficas. La tecnología está causando avances rápidos en nuestra habilidad para seguir aves a lo largo de su ciclo anual y para recolectar datos sobre el grado de conectividad entre poblaciones reproductivas y no reproductivas. Combinamos dos métodos directos, marcado–recaptura ($n = 17$) y geolocalización ($n = 6$), para estimar la conectividad migratoria de poblaciones reproductivas y no reproductivas de *Dumetella carolinensis*. Los datos de los geolocalizadores indican que las aves que crían en el Atlántico medio pasan el invierno en Cuba y el sur de Florida. Los datos de marcado–recaptura apoyaron nuestros resultados basados en geolocalizadores pero además brindaron una perspectiva espacial más amplia al documentar que las poblaciones del Atlántico medio y del medio oeste ocupan localidades geográficas distintas durante el período no reproductivo. Esta investigación resalta la importancia de los geolocalizadores y de otras herramientas para incrementar nuestro conocimiento sobre la conectividad migratoria. Finalmente, nuestros resultados destacan el valor potencial de los datos de marcado–recaptura del U.S. Geological Survey (USGS) Bird Banding Laboratory, que con frecuencia son subutilizados en investigaciones ornitológicas.

Migratory passerines travel annually between breeding and nonbreeding localities, and the degree to which populations are linked is termed "migratory connectivity."[1,2] Because events in the avian annual cycle are often inextricably linked,[3] migratory connectivity can have important implications for understanding complex population dynamics and can contribute to the management and conservation of migratory species.[4,5] Before the last decade, the primary source of information about large-scale movements of migratory birds was the direct method of mark–recapture, which has yielded little information for most species.[1] However, the lack of information about migratory connectivity provided by mark–recapture data may be partly attributable to

the few analyses that have drawn upon this data source. More recently, the application of indirect methods such as stable isotopes and genetic markers has begun to elucidate the extent of migratory connectivity among a variety of migratory passerines.[6,7,8,9] Despite these advances, indirect techniques are often limited to large-scale geographic inference because fine-scale genetic structure in birds is rare[10] and because the resolution of isotopes is dependent on the scale of biogeochemical variation.[11,12,13]

Satellite tracking by global positioning systems clearly provides the best approach to date for determining migratory connectivity, but units remain costly and are often too heavy for birds that weigh <100 g.[14] Although satellite tracking is limited to larger taxa, a second technology, light-level geolocators, has revolutionized our ability to directly estimate migratory connectivity for species that range in size from shearwaters to small passerine songbirds.[15,16,17] Specifically, geolocators use light sensors, data loggers, and time stamping to quantify light-transition events (sunrise and sunset) and to calculate daily latitude and longitude.[18] Although geolocators have relatively high accuracy in estimating longitude (e.g., 70 km for Purple Martin [*Progne subis*] and 110 km for Wood Thrush [*Hylocichla mustelina*][16]), latitudinal error can be large (e.g., 180 km for Purple Martin, 220–320 km for Wood Thrush[16]). Moreover, accuracy is limited by behaviors and habitats that cause variations in light attenuation. For example, recent applications of geolocators to small land birds that utilize dense vegetation suggest that increased error in latitudinal estimates was likely associated with greater shading in understory environments.[16,17] Despite their deficiencies,[19] geolocators represent a significant advance toward understanding the large-scale movement dynamics of birds.

We combined two direct methods, mark–recapture and geolocation, to estimate the migratory connectivity of breeding and nonbreeding populations of Gray Catbirds (*Dumetella carolinensis*). Breeding individuals were fitted with geolocators to determine nonbreeding locations and departure and arrival schedules. In addition, we gathered direct mark–recapture data from the USGS Bird Banding Laboratory (BBL) to estimate the extent of population connectivity across a larger spatial scale. The results presented here highlight how fine-scale measures of migratory connectivity (i.e., geolocators) can be supplemented with coarser range-wide data (i.e., BBL) to enhance our understanding of the linkages between breeding and nonbreeding populations of migratory birds.

Geolocators: Application and Findings

During the breeding season of 2009 (July) we deployed Mk10S light-level geolocators (British Antarctic Survey [BAS], Cambridge, United Kingdom) on breeding Gray Catbirds in two forested parks, Sligo Creek (SC: 38.98°N, 76.99°W) and Wheaton Parks (WP: 39.05°N, 77.03°W), located within the greater Washington, D.C., region. Light sensors were mounted on a 15-mm stalk at a 30° angle in order to clear the plumage. We deployed 22 geolocators on adult Gray Catbirds (13 males and 9 females) using size-600 Kevlar thread and the Rappole leg-loop harness attachment technique.[20] The mass of the total attachment (1.6 g) represented ~4% of average Gray Catbird body mass (mean = 35.6 ± 0.15 [SE, here and below]; *n* = 390). Geolocators were recovered from three males and three females. A fourth male fitted with a

geolocator in a previous season was also resighted but could not be captured. Although the overall return rate for birds carrying geolocators was low (7 of 23; 31.8%), it did not differ significantly from the recapture rate of birds without geolocators (88 of 294; 29.9%; $\chi^2 = 0.06$, df = 1, $P = 0.81$).

Following recovery in late May and early June 2010, light-level data were downloaded and checked for clock drift. Given that clock drift for all six units was zero, we applied no linear drift corrections. Mk10S geolocator light sensors measure light intensity every 60 s and record the maximum measurement in each 10-min interval. Light-level analyses used postdeployment calibration data (10 days) and a threshold of 5 to define light-transition events. Each light-transition event was visually assessed and assigned confidence using the program TRANSEDIT (BAS). Following Stutchbury et al.,[21] we calculated positions using only high-confidence transition events (i.e., confidence >7) such that nonlinear transition events or those with apparent light peaks caused by shading were rejected from the analysis. Consistent with previous work using geolocators on birds in forested environments, a large percentage of days were rejected because of uneven light-transition events. Specifically, an average of 62% of days were rejected because of uneven light-transition events (range: 129–208; mean = 165.8 ± 12.03), many of which occurred during migration. Therefore, given the uncertainty associated with these data, we do not present migration trajectories.

To account for unknown conditions experienced during migration and the nonbreeding period, we used the average sun-elevation angle (mean = −3.5; range: −3.18 to −3.84) from our six recovered geolocators. Variation among loggers given the same environmental conditions was ~ 0.1° (J. Fox unpubl. data). We assumed that birds were stationary during daylight hours and made no longitudinal compensations for movement. Data for 15 days before and after the spring (5 March to 5 April) and fall (7 September to 7 October) equinoxes were excluded from latitude calculations. Latitudinal and longitudinal estimates of location were plotted with BIRDTRACKER software (BAS) using the noon and midnight locations during the breeding and nonbreeding periods, but only noon locations during migration because most passerines are known to be nocturnal migrants.[22] During fall migration, Gray Catbirds with geolocators left the breeding site in Washington, D.C., in late August and early September and arrived on the nonbreeding grounds by mid-October (Table 1). During spring migration, Gray Catbirds left their nonbreeding grounds in April and arrived back at the breeding grounds in early to mid-May (Table 1).

We estimated geolocator accuracy at the breeding deployment sites by averaging point locations for each individual from June to August, when the birds were expected to remain stationary. Breeding latitude ranged from 37.56° to 39.62°, and longitude ranged from 75.37° to 77.38° (mean latitude: SC, 38.72 ± 0.14°; WP, 39.62 ± 0.53°; mean longitude: SC, 76.85 ± 0.09°; WP, 76.93 ± 0.28°). Point location error was assessed using the differences between the true deployment location and geolocator locations. Latitudinal error ranged from 2 to 156 km (mean = 58.2 ± 22.81 km), and longitudinal error ranged from 1 to 140 (mean = 40.0 ± 21.05 km). Some of this error may have resulted from the use of an average sun-elevation angle, but additional sources of error include subtle variation in logger light sensitivity (see above) and differences among territories in topography and vegetation structure.

Table 1. Estimated departure and arrival dates and mean winter latitude and longitude (± SE) for six Gray Catbirds fitted with geolocators in Washington, D.C.

ID	Sex	Fall migration		Spring migration		Winter latitude	Winter longitude
		Depart	Arrive	Depart	Arrive		
7764	♂	>1 September	19 October	>5 April	16 May	20.25 ± 0.22°	80.51 ± 0.09°
7717	♂	>6 September	16 October	>5 April	2 May	23.49 ± 0.21°	81.47 ± 0.09°
7821	♂	>3 September	10 October	>21 April	15 May	27.53 ± 0.28°	79.44 ± 0.18°
7704	♀	>14 August	14 October	>21 April	8 May	18.89 ± 0.34°	77.04 ± 0.14°
7711	♀	>21 August	8 October	>11 April	2 May	22.56 ± 0.65°	79.56 ± 0.34°
7714	♀	>26 August	9 October	>22 April	15 May	26.83 ± 0.40°	79.68 ± 0.26°

To determine geographic locations during the nonbreeding period, we estimated fixed kernel densities based on point data from November to March with the spatial analyst tool in program ARCMAP, version 10.0 (ESRI, Redlands, California). Following Bächler et al.,[17] we set the search radius at 200 km and the grid size at 2 km. We selected the 200-km search radius to encompass point estimates at the upper bound of our observed error (see Table 1). For each individual, we present kernel densities encompassing 50%, 75%, and 90% of the maximum density. In addition to the kernel-density approach, we also present mean locations for the same data (Table 1 and Fig. 1).

Data from our recovered geolocators show that birds from the Washington, D.C., region spent the nonbreeding period in Florida, Cuba, and possibly Jamaica. Specifically, fixed kernel-density estimates showed that one male (7821) and one female Gray Catbird (7714) overwintered along the eastern coast of Florida (Fig. 1B, C). By contrast, one female (7711) and two males (7764 and 7717) overwintered in central and southern Cuba (Fig. 1A–C). The final female (7704) overwintered in either southern Cuba or northern Jamaica, given that the 50% kernel density overlapped both locations. Although our kernel densities were largely consistent with the mean localities (Table 1), subtle differences underscore that analysis methods can influence estimated nonbreeding locations (Fig. 1).

Mark–Recapture: Larger-scale Patterns

We obtained BBL mark–recapture data for Gray Catbirds banded throughout the United States from 1914 to 2009 (*n* = 8,774) to provide a range-wide view of migratory connectivity. We filtered the data to include only birds captured during the breeding season (May–August; *n* = 7,347) and recaptured during the sedentary portion of the nonbreeding season (November–March; *n* = 56). Finally, to ensure that connectivity estimates represented known breeding populations, we included only after-hatch-year individuals (*n* = 17). This represents a 0.2% yield, given the starting data set. We grouped mark–recapture events into regional populations by lumping birds that bred in the Mid-Atlantic and Northeast into a group (hereafter "Mid-Atlantic") and birds that bred across the northern Midwest into another ("Midwest"). Specifically, the mark–recapture data showed that birds from the Midwest (*n* = 7) overwintered exclusively in Central America and birds from the Mid-Atlantic (*n* = 10) overwintered in Florida and the Caribbean (Fig. 2).

Discussion

We estimated migratory connectivity using two direct methods, mark–recapture and geolocation, which vary in both geographic and temporal scope. Geolocator data that were collected over 1 year showed that Gray Catbirds breeding in Washington, D.C., typically overwinter in Florida and the Caribbean. Bird Banding Laboratory data collected over a 90-year period supported our fine-scale findings and also provided information about range-wide patterns of migratory connectivity. Regardless of the methods, both suggest strong connectivity, with eastern populations overwintering in Florida and the Caribbean, and Midwestern populations overwintering in Central America. Our results (1) support the importance of using geolocators to map migratory connectivity, (2) point to the usefulness of archived BBL data, and (3) emphasize that (at least under the current scheme) the use of mark–recapture alone is limited because it requires data gathered over a long period (e.g., ~90 years) and is unlikely to yield information about migration or nonbreeding-season movements.

The degree of migratory connectivity among Gray Catbird populations is consistent with two previous studies of small Nearctic–Neotropical migratory birds that used isotopes and genetics to demonstrate that Midwestern populations overwinter in Central America whereas Eastern populations overwinter in the Caribbean.[7,23] Moreover, these results further corroborate the presence of east–west winter divides in several Nearctic–Neotropical migrants.[24] Despite nonbreeding-site differences between populations on an east–west gradient, our data do not enable us to determine where breeding populations sort into distinct overwintering localities. Although we found some mixing on the winter grounds among birds that bred in the Mid-Atlantic, the strength of connectivity is surprising given the breadth of the Gray Catbird wintering range (see Fig. 2). Hypotheses to explain strong connectivity include historical biogeographic events, migration costs, and prevailing wind patterns.[7,25,26,27] Regardless of the mechanisms that maintain migratory connectivity, the application of geolocator technology will enhance our ability to document the linkages between breeding and nonbreeding ranges of migratory species.

Understanding the movement patterns and connectivity across periods of the annual cycle in migratory species has remained a challenge in migration biology. Geolocation using ambient light-level recording represents a significant advance in our ability to track migratory taxa throughout the annual cycle. Although this technology clearly improves our understanding of
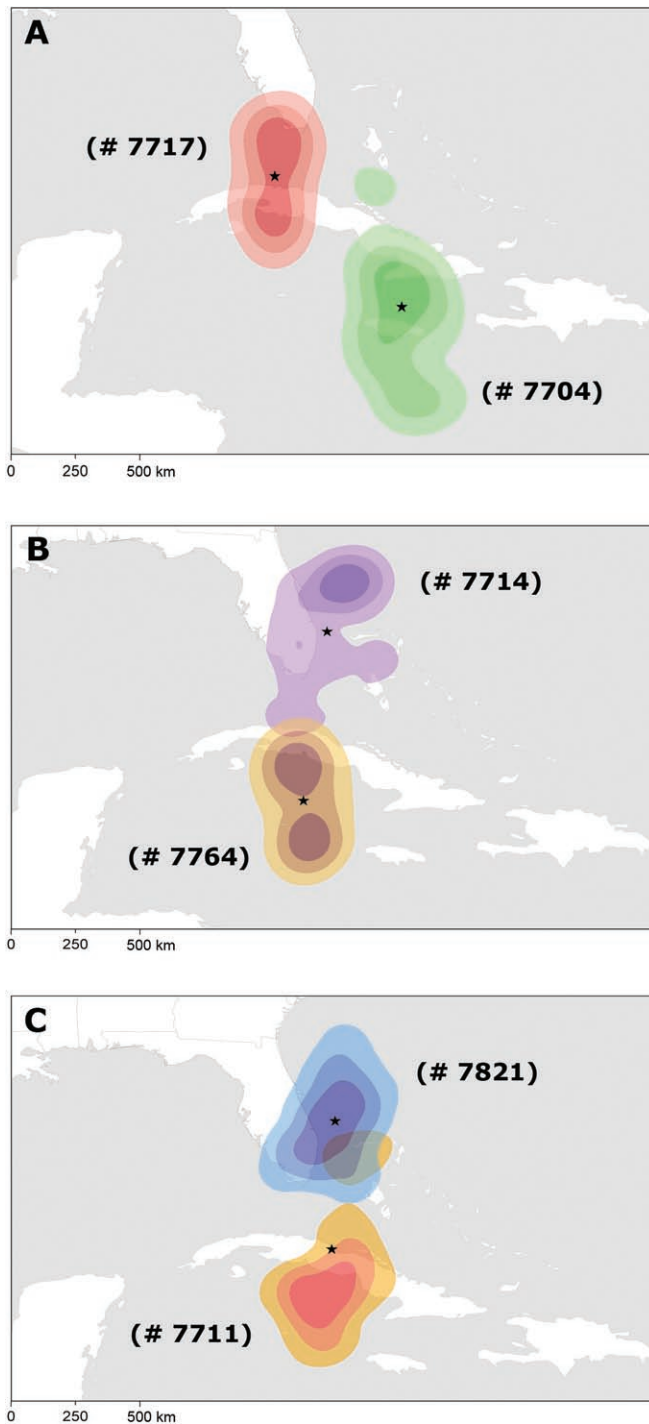
FIG. 1. Kernel density estimates and means (stars) for estimated overwinter localities of six Gray Catbirds fitted with geolocators. Each panel depicts two individuals and the associated error (50%, 75%, and 90% kernel density) for overwinter location estimates. (A) After-hatch-year (AHY) male (7717) and female (7704). (B) AHY male (7764) and female (7714). (C) AHY male (7821) and female (7711). Each kernel density estimate is displayed as a color gradient (darkest shade = 50%, intermediate shade = 75%, lightest shade = 90%).
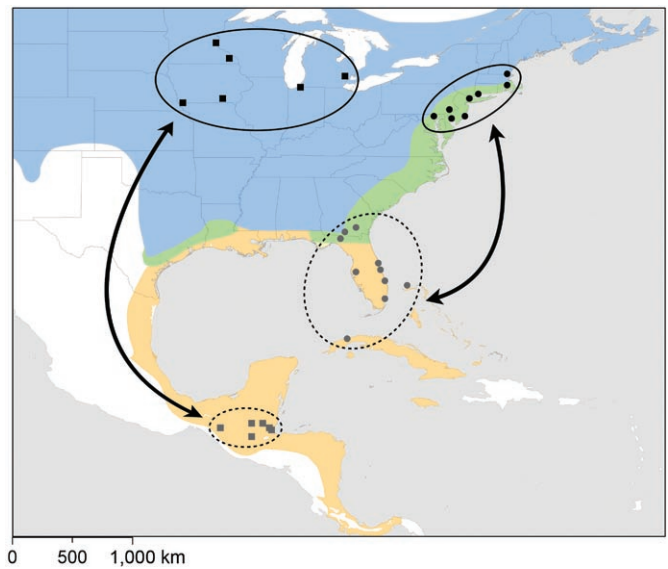

FIG. 2. The combination of USGS Bird Banding Laboratory mark–recapture data and the breeding (blue), year-round (green), and wintering (orange) distributions of Gray Catbirds provide a range-wide perspective of migratory connectivity. Mark–recapture patterns suggest strong regional connectivity, with Mid-Atlantic populations (n = 10) wintering in Florida and the Caribbean and Midwest populations (n = 7) wintering in Central America.

migratory timing, routes, and nonbreeding localities, there are limitations. For example, the estimation of point locality depends on high-quality light data, which can be challenging to obtain for species that spend a significant portion of their time on the ground, under dense vegetation. We hope that future iterations of geolocator technology and analysis techniques will more accurately estimate both latitude and longitude.

A second potential limitation of geolocators is their possible effects on individual survival and behavior. Any attachment that protrudes outside of the normal space occupied by a bird will increase both load and drag, which could negatively influence survival probability and subsequent return rates.[28] Although we found no differences in return rates for Gray Catbirds with and without geolocators, all future studies should be cognizant of this possibility. Lastly, there are challenges with the subjectivity of the current geolocator analysis techniques. Analyzing geolocator data is far from an exact science. For example, users subjectively quantify light transition-event quality, make decisions about pre- and postcalibration, and decide on the use of unique versus averaged sun-elevation angles. Although the development of computer analysis algorithms may present new analytical challenges, it would move us toward a much-needed objective approach to the analysis of these data.

Direct mark–recapture has been the primary tool used by avian ecologists to understand movement and survival. Despite the vast number of birds captured annually in the United States, return rates are often too low between independent sites to provide estimates of both fine (e.g., natal dispersal and recruitment) and large-scale movement dynamics (e.g., migratory

connectivity). Here, the congruence between geolocators and BBL mark–recapture data suggests that the long-term banding data sets may be more valuable than previously thought. In-depth analyses of more species from the BBL are needed to better assess the value of these data for quantifying migratory connectivity. Although these data may lack the resolution required for understanding fine-scale patterns of connectivity, the BBL data can provide important information at larger spatial scales.

Ultimately, combining multiple technologies and data sources will help refine estimates of migratory connectivity. Regardless of the technologies we apply, future studies that adequately sample across the entire nonbreeding or breeding range are needed to provide a more comprehensive understanding of migratory connectivity in Nearctic–Neotropical migrant birds.

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