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DO ARCHIVAL LIGHT-LEVEL GEOLOCATORS AND STABLE HYDROGEN ISOTOPES PROVIDE COMPARABLE ESTIMATES OF BREEDING-GROUND ORIGIN?

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ABSTRACT.—Migratory connectivity for small migratory passerines has been quantified primarily with stable hydrogen isotopes in feathers ($\delta^2\text{H}_f$) because, until recently, we lacked the technology to track small organisms over long distances. Direct tracking of small passerines throughout the annual cycle is now possible with archival light-level geolocators. Our objective was to evaluate whether $\delta^2\text{H}_f$ and geolocators produce similar breeding-origin assignments for the same individual birds sampled during the non-breeding season. We estimated breeding origin with geolocators and $\delta^2\text{H}_f$ and validated those estimates using a population of Ovenbirds (*Seiurus aurocapilla*) from a known breeding location at Hubbard Brook Experimental Forest, New Hampshire. We also deployed geolocators on Ovenbirds in Jamaica and Florida during March 2010–2011. We performed stable hydrogen isotope analysis on feathers of birds whose geolocators we recovered (Jamaica: $n = 9$; Florida: $n = 3$). Probabilistic assignments of $\delta^2\text{H}_f$ that accounted for regional variation in feather-isotope discrimination predicted breeding origins that agreed with kernel density estimates of origin derived from geolocators. By contrast, assignments of $\delta^2\text{H}_f$ using the common assumption of a consistent feather-isotope discrimination across space predicted breeding origins that overlapped minimally with those from geolocators. Finally, Bayesian analyses that incorporated prior information of Ovenbird abundance across the breeding range yielded more accurate assignments for both site-independent and site-specific discrimination factors. Our findings suggest that creating more detailed feather isoscapes by increasing the number of validation locations and sampling underrepresented portions of species distributions could increase the accuracy of geographic assignments using $\delta^2\text{H}_f$. Received 27 February 2013, accepted 15 March 2013.

Key words: Bayesian, deuterium, discrimination, migratory bird, Ovenbird, *Seiurus aurocapilla*, solar geocator, stable isotopes.

¿Son Comparables los Estimados de Sitios Reproductivos de Origen Obtenidos Mediante Geolocalizadores Basados en Niveles de Luz y Mediante Isótopos Estables de Hidrógeno?

RESUMEN.—La conectividad migratoria de los paserinos migratorios de tamaño pequeño ha sido cuantificada principalmente mediante isótopos estables de hidrógeno ($\delta^2\text{H}_f$) presentes en las plumas debido a que, hasta hace poco, carecíamos de la tecnología para seguir organismos pequeños por distancias largas. El rastreo directo de paserinos pequeños a través de todo el ciclo anual ahora es posible con geolocalizadores basados en niveles de luz. Nuestro objetivo fue evaluar si los $\delta^2\text{H}_f$ y los geolocalizadores producen una asignación similar del lugar original de reproducción para las mismas aves individuales muestreadas durante la temporada no reproductiva. Estimamos el lugar original de reproducción con geolocalizadores y $\delta^2\text{H}_f$ y validamos esos estimados usando una población de *Seiurus aurocapilla* de una localidad de reproducción conocida ubicada en Hubbard Brook Experimental Forest, New Hampshire. También acoplamos geolocalizadores a individuos de Jamaica y Florida en marzo de 2010 y 2011. Hicimos el análisis de isótopos estables de hidrógeno en las plumas de las aves cuyos geolocalizadores pudieron ser recuperados (Jamaica: $n = 9$; Florida: $n = 3$). Las asignaciones probabilísticas de los $\delta^2\text{H}_f$ que tuvieron en cuenta la variación regional en la discriminación de los isótopos de las plumas predijeron sitios originales de reproducción que estuvieron de acuerdo con los estimados de densidad de *kernel* del sitio de origen derivados de los geolocalizadores. En contraste, las asignaciones de los $\delta^2\text{H}_f$ basados la suposición común de que la discriminación plumas-isótopos es consistente a través del espacio, predijo sitios originales de reproducción que se superponían mínimamente con los predichos por los geolocalizadores. Finalmente, análisis bayesianos que incorporaron información previa de la abundancia de *S. aurocapilla* a través de su distribución reproductiva resultaron en la asignación más exacta del sitio original de reproducción, tanto para factores de discriminación independientes como específicos para cada sitio. Nuestros resultados sugieren que la creación de paisajes de isótopos más detallados al incrementar el número de localidades de validación y al muestrear porciones pobremente representadas de la distribución de las especies, podría incrementar la exactitud de la asignación geográfica usando $\delta^2\text{H}_f$.

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LONG-DISTANCE MIGRATION IS A common avian behavior, yet the degree to which populations are geographically linked throughout the annual cycle remains poorly understood for thousands of species (Webster et al. 2002, Marra et al. 2006). Such uncertainty impairs our capacity to study and manage migratory bird populations and, thus, emphasizes the need for accurate information about migratory connectivity (Marra et al. 2011). Progress has been especially challenging with passerines because the small body size of most species precludes the use of satellite telemetry (Clegg et al. 2003, Robinson et al. 2010). In addition, the value of long-term band-recovery data sets has been limited by low recapture rates (e.g., Ryder et al. 2011).

Our understanding of migratory connectivity in passerines was revolutionized by the analysis of stable hydrogen isotope ($\delta^2\text{H}$) ratios in feathers (Chamberlain et al. 1997, Hobson and Wassenaar 1997). These ratios, which are incorporated into growing feathers from local food webs and become metabolically inert, have been used to estimate both breeding (e.g., Kelly et al. 2005, Boulet et al. 2006) and non-breeding (e.g., Pain et al. 2004, Mazerolle et al. 2005) locations. However, this approach has three important constraints. First, although $\delta^2\text{H}$ in growing-season precipitation ($\delta^2\text{H}_p$) is strongly correlated with latitude in many parts of the Northern Hemisphere, it does not show a clear relationship with longitude (Hobson 1999, Bowen et al. 2005), which limits geographic inferences based on $\delta^2\text{H}$ in feathers ($\delta^2\text{H}_f$) alone. Second, the heavy fraction of hydrogen in nature varies in relation to other factors, including elevation (Clark and Fritz 1997, Hobson et al. 2003), diet (Lott et al. 2003), distance from coastlines (Hobson et al. 2000, Lott et al. 2003), foraging guild (Hobson et al. 2012), bird age, and habitat type (Haché et al. 2012), all of which can complicate assignment of origin. Lastly, some birds molt at multiple times and locations each year (Butler et al. 2002, Leu and Thompson 2002, Rohwer et al. 2005), which can further confound geographic assignment. Accurately assigning individuals to breeding origin using $\delta^2\text{H}$ requires an understanding of the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$. Currently, much of our understanding of migratory connectivity comes from assignments based on $\delta^2\text{H}_f$ where the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ is assumed to be similar throughout the breeding range (e.g., Kelly et al. 2005, Hobson et al. 2012). In addition, various factors can influence the magnitude of isotopic discrimination between long-term average $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ (Hobson et al. 2012), but these discrimination relationships require further refinement.

Direct tracking of birds throughout their annual cycle is the most accurate way to quantify migratory connectivity and has recently become possible for small passerines with the advent and miniaturization of archival light-level geolocators (e.g., Shaffer et al. 2006, Stutchbury et al. 2009). Geolocators provide much-improved spatial resolution in both latitude and longitude compared with $\delta^2\text{H}_f$ but are expensive per bird compared with isotope analyses. Moreover, geolocators have a low recovery rate, require that individuals be recaptured, and may alter behavior and survival (Bowlin et al. 2010).

Direct and indirect tracking methods therefore remain valuable tools for assessing migratory connectivity. The accuracy of geographic assignments derived from $\delta^2\text{H}_f$ measurements, however, has not been fully validated. Here, we compare assignments of breeding-ground origin determined by $\delta^2\text{H}_f$ values and geolocators for the Ovenbird (*Seiurus aurocapilla*), a small

Neotropic–Nearctic migratory passerine. The Ovenbird is well suited for our study because it is widely distributed throughout North America during the breeding season and throughout the Caribbean Basin during the non-breeding season (Van Horn and Donovan 1994). Also, it annually molts its flight feathers before fall migration (Pyle 1997) and is large enough to carry a geocator. We captured Ovenbirds in the eastern United States during the breeding season to validate the relationship between estimates of origin derived through $\delta^2\text{H}_f$ values and breeding estimates provided by geocator data at a known breeding location. We then captured individuals on Caribbean non-breeding areas to compare the agreement between $\delta^2\text{H}_f$ values and geocator data in assigning overwintering birds to unknown breeding locations.

METHODS

Field work was conducted from 2010 to 2012 on the breeding grounds at the Hubbard Brook Experimental Forest (HBEF) in central New Hampshire (41°30'N, 71°73'W), in Everglades National Park in southern Florida (25°13'N, 80°95'W), and at Font Hill Nature Preserve, St. Elizabeth Parrish, Jamaica (18°04'N, 77°94'W). We captured Ovenbirds with simulated territorial intrusions and passive mist-netting techniques (Faaborg and Arendt 1984, Hobson et al. 2004), fit archival light-level geolocators (British Antarctic Survey, models MK12 [1.0 g] and MK20SALT [0.9 g]) to individuals whose mass was ≥ 19.0 g using a leg-harness technique (Naef-Daenzer 2007), and plucked a single tail feather (rectrix R3) for stable isotope analysis. A single tail feather was sampled from each Ovenbird captured to determine whether individuals with geolocators were representative of the capture population. We deployed 51 geolocators on Ovenbirds breeding at HBEF (2010, $n = 17$ [16 males and 1 female]; 2011, $n = 34$ [all male]) and 46 geolocators on birds on the non-breeding areas in Florida ($n = 18$ [12 males, 1 female, and 5 of unknown sex]) and Jamaica (total $n = 28$; 2010, $n = 11$ [4 males, 3 females, and 4 of unknown sex]; 2011, $n = 17$ [10 males, 1 female, and 6 of unknown sex]). We recaptured returning birds in subsequent years, removed geolocators (HBEF: $n = 20$ [all male]; Florida: $n = 3$ [all male]; Jamaica: $n = 9$ [5 males, 2 females, and 2 of unknown sex]; Table S1, available with the online version of this article; see Acknowledgments), and collected another tail feather (rectrix R3) for stable isotope analysis.

Geocator analysis.—Light data were transformed into latitude and longitude using BASTRAK, versions 18 and 19 (British Antarctic Survey). Each sunrise and sunset was scored by the same observer (M.T.H.) using a threshold of 5, with TRANSEdit software (British Antarctic Survey). Light transition events from stationary geolocators indicated smooth transitions during sunrise and sunset. Transition events that indicated smooth transitions were scored as high-quality transitions (69 ± 9 [SE] of 190 transitions between 1 May and 31 July; $36.1 \pm 0.10\%$), whereas those that included shading during light transitions were scored as low-quality and were removed from all analyses (McKinnon et al. 2013). These low-quality transition events were excluded because they would have increased uncertainty associated with sunrise and sunset estimates used to generate location data. Both midnight and noon locations were used to estimate breeding location. Locations within 15 days of spring and fall equinox were excluded from analyses (spring equinox period = 5 March–4 April; fall

equinox period = 7 September–8 October) because of unreliable location data due to day length being similar everywhere. Sun elevation angles were determined by locator aid (BASTRAK) using the latitude and longitude of deployment for geolocators recovered at HBEF and by using calibration from stationary geolocators placed on the forest floor at HBEF (-1.82°) as well as geolocators deployed on Ovenbirds at HBEF ($-1.75 \pm 0.14^\circ$). For all geolocators recovered during the non-breeding season, our analyses assumed a sun elevation angle of -1.75° based on 1,034 transition events prior to fall migration collected from 20 geolocators on Ovenbirds breeding at HBEF. A single sun elevation angle was used for all geolocators recovered during the non-breeding season because the true sun elevation angle at the breeding location was unknown and the variation in sun elevation angle between geolocators deployed at the same location and between individual geolocators was small (HBEF: $-1.75 \pm 0.14^\circ$, $n = 20$; Florida: $-3.31 \pm 0.07^\circ$, $n = 3$; Jamaica: $-3.53 \pm 0.13^\circ$, $n = 9$).

Geocator location data collected during the breeding season were used for direct comparison with $\delta^2\text{H}_F$ values to validate both tools. A longitudinal range for the months of June and July was created for every bird captured in Jamaica and Florida. A longitudinal range was created because arrival information from HBEF indicated that all birds are present before 1 June if they attempt to breed (M. T. Hallworth et al. unpubl. data); however, the true breeding location was not known for Jamaica and Florida birds. Location data were classified as breeding locations once the geocator locations fell within the June–July longitudinal range (arrival date range: 2–23 May), at which point we assumed that migration had ceased and individuals attempted to breed. The longitudinal range was used to determine when individuals arrived at breeding locations because changes in latitude could result from migratory movements or uncertainty associated with sunrise and sunset transitions caused by a number of factors (Lisovski et al. 2012). For geolocators recovered from HBEF, location points generated during July of the deployment year, and those generated between the date of arrival at HBEF and the date of recapture during the subsequent recovery year, were used to test the accuracy of geolocators for estimating the breeding location of birds at HBEF.

Stable hydrogen isotopes.—Isotope analysis was performed at the Smithsonian Institution's Stable Isotope Mass Spectrometry Laboratory in Suitland, Maryland. Tail feathers were washed of debris and surface oils with a 2:1 chloroform:methanol solution and air dried for 48 h under a fume hood. Feathers were allowed to equilibrate with the local atmosphere at the laboratory for 72 h. A small distal sample (non-breeding: 0.345 ± 0.005 mg, $n = 151$; HBEF: 0.346 ± 0.003 mg, $n = 92$) of feather was clipped and loaded into a silver capsule. The feather samples were combusted in an elemental analyzer (Thermo TC/EA; Thermo Scientific, Waltham, Massachusetts) and introduced to an isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage) via a ConFlo IV interface. One in-house standard was run for every two unknowns to measure the accuracy and precision during sampling. Analytical error (\pm SD) was 2‰, based on replicate analysis of the same feather ($n = 20$). The non-exchangeable hydrogen was determined by linear regression with calibrated in-house keratin standards (spectrum keratin: $-121.6 \pm 0.88\%$, $n = 20$; CBS: $-197.3 \pm 1.20\%$, $n = 20$; KHS: $-54.1 \pm 0.91\%$, $n = 20$; Wassenaar and Hobson 2003). To minimize any potential systematic errors caused by

exchangeable hydrogen, we ran all samples within 7 days of one another and included an approximately equal number of samples from Florida and Jamaica for each run (Wassenaar and Hobson 2003). We report isotope ratios for non-exchangeable hydrogen in δ notation in relation to Vienna Standard Mean Ocean Water.

The $\delta^2\text{H}_p$ values were determined using the interpolated amount-weighted mean $\delta^2\text{H}$ during the growing season from the Global Network of Isotopes in Precipitation database (Bowen et al. 2005). We used two approaches to convert from this $\delta^2\text{H}_p$ isoscape to a $\delta^2\text{H}_F$ isoscape that accounted for isotopic differences between precipitation, Ovenbird prey, and feathers. First, adult (after-second-year) breeding Ovenbirds were captured throughout the eastern portion of their breeding range in Maryland ($n = 5$), Michigan ($n = 5$), Missouri ($n = 5$), New Hampshire ($n = 10$), North Carolina ($n = 5$), Vermont ($n = 5$), and West Virginia ($n = 5$). We used a linear mixed model that included capture location as a random intercept to determine a site-specific discrimination equation (hereafter $\delta^2\text{H}_{F\text{site-specific}}$) that allowed for potential regional variation in isotopic discrimination (Table 1). Second, we converted $\delta^2\text{H}_p$ values into $\delta^2\text{H}_F$ values using the calibration relationship derived by Hobson et al. (2012) for ground-foraging Neotropical migratory birds (hereafter $\delta^2\text{H}_{F\text{site-independent}}$). The site-specific intercept was determined using location data obtained with geolocators. If the 75% kernel density estimate (KDE) derived from geolocators (see below) deployed during the non-breeding season overlapped one of the sampling locations used to create the site-specific calibration relationship ($n = 10$), we chose the intercept for that site to convert $\delta^2\text{H}_p$ into $\delta^2\text{H}_F$ (Table 1). None of the 75% KDEs overlapped more than one sampling location. A site-specific intercept was not used when a KDE did not overlap any of the sampling locations ($n = 2$ birds, 1 in Florida and 1 in Jamaica), and those individuals were excluded from analyses comparing assignment accuracy of site-specific intercepts versus site-independent intercepts. For birds breeding at HBEF, we used the site-specific intercept for New Hampshire to determine $\delta^2\text{H}_{F\text{site-specific}}$.

Statistical analyses.—To compare $\delta^2\text{H}_F$ of Ovenbirds with and without geolocators and between non-breeding locations, we used a two-way analysis of variance including individual as

TABLE 1. Site-specific discrimination intercepts used for converting $\delta^2\text{H}_p$ to $\delta^2\text{H}_F$ isoscapes for geographic assignment of Ovenbirds to breeding origin. Geographic coordinates (latitude, longitude) of the study locations are given for the states in which Ovenbirds were captured. Site-specific intercepts were determined using a linear mixed model incorporating capture site as a random variable. Feather isoscapes were created using a site-independent ($\delta^2\text{H}_{F\text{site-independent}} = -27.09 + 0.95 * \delta\text{H}_p$; Hobson et al. 2012) and a site-specific ($\delta^2\text{H}_{F\text{site-specific}} = \text{site-specific intercept} + 1.15 * \delta\text{H}_p$) discrimination equation.

Capture location	Coordinates	Site-specific intercept	95% CI
Maryland	38.54, -73.20	11.92	07.95 to 15.87
Michigan	44.65, -84.13	-23.38	-27.34 to -19.42
Missouri	38.35, -93.55	-09.69	-13.65 to -05.73
New Hampshire	41.30, -71.73	21.35	17.40 to 25.32
North Carolina	35.49, -82.99	06.55	02.59 to 10.52
Vermont	44.54, -73.20	-14.76	-18.72 to -10.80
West Virginia	44.65, -84.13	08.01	04.04 to 11.97

TABLE 2. The amount of overlap between breeding $\delta^2\text{H}_\text{F}$ assignments reclassified using a 3:1 odds ratio for site-independent and site-specific discrimination equations and geolocator estimates of Ovenbirds captured in Jamaica and Florida. The amount of overlap was quantified in two ways: (1) a binary approach, whereby the 75% KDE determined by geolocators was classified as either overlapping or not overlapping any portion of the 3:1 odds ratio assignment (see supplemental materials with the online version of this article); and (2) a percentage of overlap, whereby the 3:1 odds ratio assignment was classified as overlapping >25% or <25% of the 75% KDE determined by geolocators. The observed (Obs.) and expected (Exp.) numbers of individuals using a 3:1 odds ratio are shown for each scenario. The *P* value from a Fisher's exact test is indicated under the corresponding data.

	Without breeding bird abundance				With breeding bird abundance			
	Site-independent		Site-specific		Site-independent		Site-specific	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Overlap	11	9	10	7.5	12	9	10	7.5
No overlap	1	3	0	3.5	0	3	0	2.5
Significance	<i>P</i> = 0.59		<i>P</i> = 0.47		<i>P</i> = 0.22		<i>P</i> = 0.47	
>25%	5	9	7	7.5	11	9	10	7.5
<25%	7	3	3	2.5	1	3	0	2.5
Significance	<i>P</i> = 0.21		<i>P</i> = 0.99		<i>P</i> = 0.59		<i>P</i> = 0.47	

a random effect. We used a normal probability density function (Royle and Rubenstein 2004) to determine breeding origin, where the likelihood that each $\delta^2\text{H}_\text{F}$ value, y^* , originates from a given location is

$$f(y^*|\mu_b, \sigma_b) = \frac{1}{\sqrt{2\pi}\sigma_b} \exp\left[-\frac{1}{2\sigma_b^2}(y^* - \mu_b)^2\right]$$

where μ_b is the specific cell in a given feather isoscape and σ_b is the standard deviation of the residuals from the calibration equation. We used $\sigma_b = 16.40\text{‰}$ for both feather isoscapes because the standard deviation of residuals for calibration relationships were similar and it was the most conservative. We then incorporated Ovenbird abundance from Breeding Bird Survey routes sampled between 2006 and 2010 (Sauer et al. 2011) as prior information using Bayes's rule:

$$f(b|y) = \frac{f(y|b)f(b)}{\sum_{b=1}^B f(y|b)f(b)}$$

where $f(y|b)$ is the likelihood of assignment to breeding locations and $f(b)$ is the probability that Ovenbirds occur in each breeding location throughout their breeding range. Breeding Bird Survey data were obtained from Patuxent Wildlife Research Center's website (see Acknowledgments). We reclassified each raster cell (approximately 35×35 km) within the breeding-origin assignments into likely (1) or unlikely (0) origin using a 3:1 odds ratio (Chabot et al. 2012). Breeding assignments based on $\delta^2\text{H}_\text{F}$ values were created and reclassified into binary assignments using the "raster" package (Hijmans and van Etten 2011) in R (R Development Core Team 2012).

Kernel density estimates (50%, 75%, and 95%) were created using geolocator location data for each individual during the breeding season, using least-squares cross validation (Barg et al. 2005) to estimate the bandwidth or smoothing parameter with Geospatial Modelling Environment software (Beyer 2012). From these three KDEs, we chose the 75% KDE for subsequent analyses because 19 of 20 individuals (95%) overlapped the true breeding

origin with this approach when the breeding location was known (i.e., HBEF: 50% KDE = 14 of 20 [70%]; 95% KDE = 20 of 20 [100%]). Moreover, the 75% KDE was directly comparable with the probability of correct assignment for $\delta^2\text{H}_\text{F}$ under a 3:1 odds ratio. In addition, a single KDE (75% KDE) was created using geolocator data from all birds captured at HBEF. We used Fisher's exact test to evaluate whether the two methods of assignment using $\delta^2\text{H}_\text{F}$ predicted the same origin estimated using geolocators. The amount of overlap between geolocators and assignment using $\delta^2\text{H}_\text{F}$, both site-independent and site-specific discrimination equations, was quantified in two ways. First, if the 75% KDE produced from geolocator data overlapped any portion of the reclassified posterior probability using a 3:1 odds ratio, it was classified as overlapping. Second, the percentage of the 75% KDE that overlapped the reclassified posterior probability was enumerated. The percentage of overlap was classified into >25% and <25% overlap to be consistent with both the 3:1 odds ratio reclassification of $\delta^2\text{H}_\text{F}$ and the 75% KDE produced with geolocator data. All statistical analyses were conducted in R, version 2.15.0 (R Development Core Team 2012). Results are presented as means \pm SE.

RESULTS

Twenty geolocators (40%) were recovered from Ovenbirds breeding at HBEF (deployed in 2010: $n = 3$; deployed in 2011: $n = 17$). Forty-six percent of Ovenbirds with geolocators returned to HBEF, which is similar to return rates of Ovenbirds without geolocators ($53 \pm 1.85\%$; M. T. Hallworth et al. unpubl. data). Three individuals returned carrying geolocators but could not be recaptured (2011: $n = 1$; 2012: $n = 2$), and one returned during 2011 without a geolocator attached. The mean number of locations used to determine breeding-origin estimates for birds captured at HBEF was 34 ± 4 ($54.5 \pm 0.6\%$ of location points). Mean $\delta^2\text{H}_\text{F}$ values of Ovenbirds known to have bred at HBEF varied among years (2010: $-70.4 \pm 1.7\text{‰}$; 2011: $-67.4 \pm 1.2\text{‰}$; 2012: $-61.3 \pm 3.0\text{‰}$). The $\delta^2\text{H}_\text{F}$ profiles of individual birds captured in multiple years also showed annual variation (2010–2011: mean difference = 4.54‰ , $t = 2.11$,

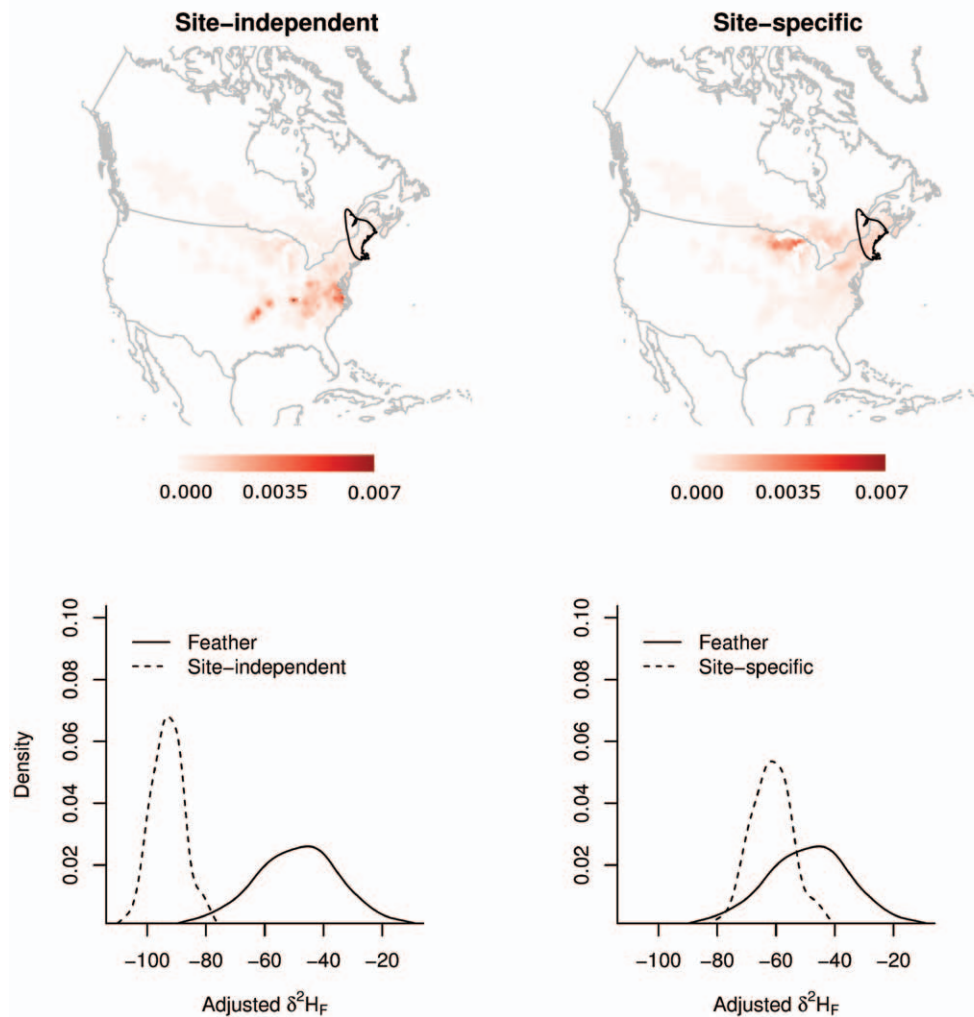


FIG. 1. Posterior probability of origin using $\delta^2\text{H}_F$ and bird relative abundance with site-independent and site-specific discrimination equations for Ovenbirds breeding at Hubbard Brook Experimental Forest (HBEF), New Hampshire. The 75% kernel density estimate (KDE), represented by the black polygon, includes locations from all 20 geolocators recovered during the breeding season. The color ramp indicates the posterior probability of assignment using $\delta^2\text{H}_F$ and bird relative abundance. The bottom panels show the normal distribution around the mean $\delta^2\text{H}_F$ value of birds fitted with geolocators breeding at HBEF (solid line) with a standard deviation of 16.40‰, which was used to create breeding assignments. The density of values under the curve is represented by the y-axis. Also shown is the adjusted $\delta^2\text{H}_F$ value after including relative abundance of breeding birds in assignment under the 75% KDE using the site-independent and site-specific discrimination equations to create the feather isoscape (dotted line). The map projection is North American Lambert Conformal Conic.

$df = 28, P = 0.044$; 2011–2012: mean difference = 8.60‰, $t = 3.46$, $df = 18, P = 0.003$; 2010–2012: mean difference = 12.86‰, $t = 4.03$, $df = 9, P = 0.003$). The $\delta^2\text{H}_F$ values did not differ between birds with geolocators and those without geolocators breeding at HBEF ($t = 0.17, df = 45, P = 0.86$).

The 75% KDE for 19 of 20 birds (95%) with geolocators breeding at HBEF overlapped HBEF, indicating that the 75% KDE accurately predicted true breeding origin and, thus, provided an unbiased baseline for evaluating the accuracy of assignments made with $\delta^2\text{H}_F$ for individuals captured during the non-breeding season (Fig. 1). Assignments of $\delta^2\text{H}_F$ done with a site-specific intercept in the feather-isotope discrimination equation showed strong concordance with 75% KDEs derived from geolocators (Table 2 and Figs. 2, S1, and S2; Figs. S1 and S2 are supplemental materials

available with the online version of this article; see Acknowledgments). By contrast, $\delta^2\text{H}_F$ assignments made with the commonly used site-independent fractionation equation (i.e., Lott et al. 2003, Mazerolle et al. 2005, Van Wilgenburg and Hobson 2011) overlapped minimally with KDEs from geolocators. Bayesian analyses that incorporated prior information of Ovenbird abundance across the breeding range yielded posterior probabilities of assignment that more closely matched 75% KDEs calculated from geocator data for both site-independent and site-specific discrimination factors (Table 2 and Figs. 2, S1, and S2).

We deployed 46 geolocators during the non-breeding seasons of 2010 and 2011. Twelve geolocators were recovered (Florida, 2011: 3 [17%]; Jamaica, 2010: 3 [27%]; 2011: 6 [35%]), 8 from males, 2 from females, and 2 from individuals of unknown sex (Table S1).

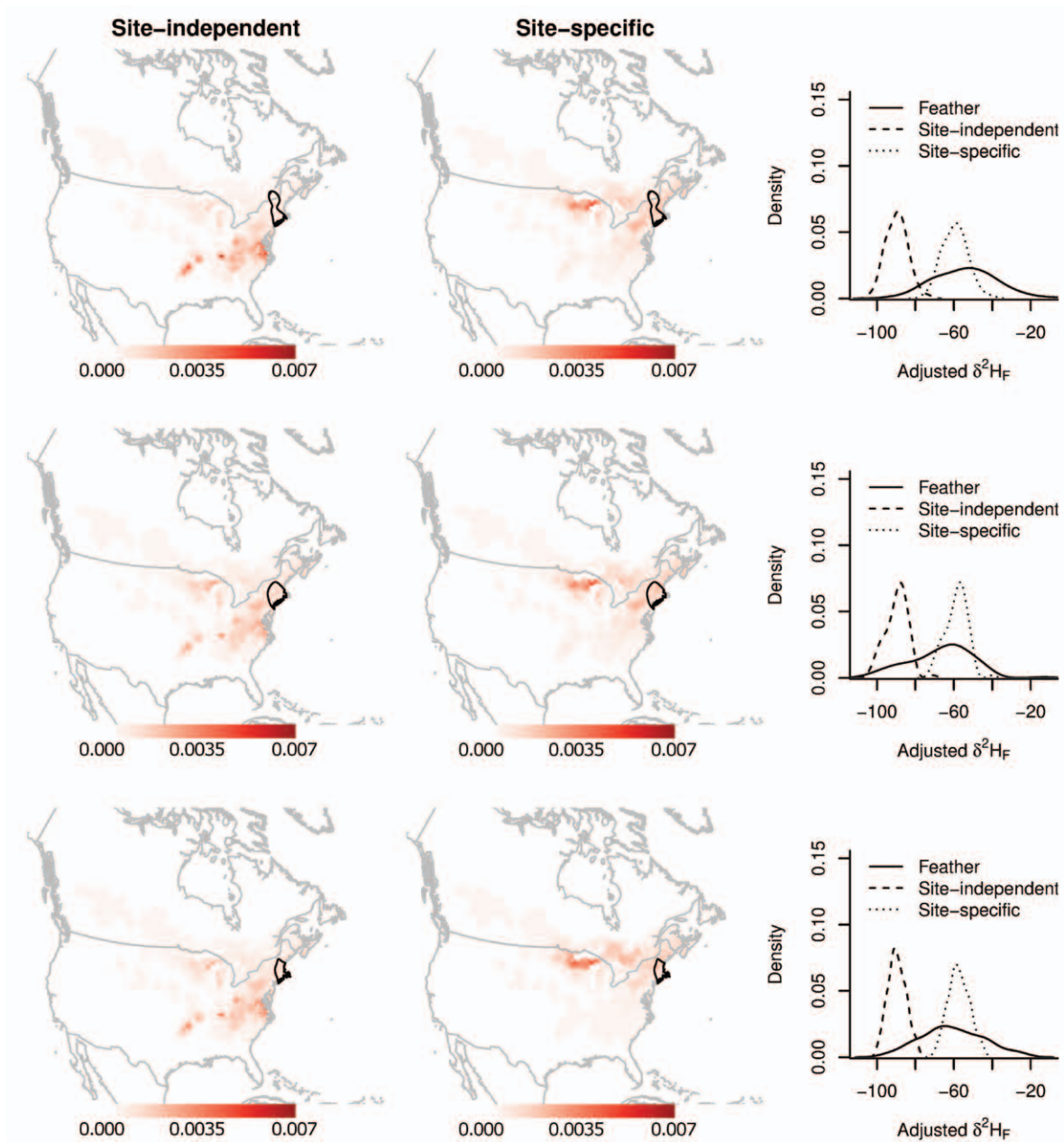


FIG. 2. Posterior probability of origin using $\delta^2\text{H}_F$ and bird relative abundance with site-independent and site-specific discrimination equations for 3 of 9 birds fitted with geolocators captured at Font Hill Nature Preserve, St. Elizabeth Parish, Jamaica, during the non-breeding season (see Fig. S1, available with the online version of this article). Each row corresponds to a different individual fitted with a geocator. The right column shows the normal distribution around the mean $\delta^2\text{H}_F$ value from feathers collected upon recapture (solid line; $\text{SD} = 16.40\%$), which was used to create breeding assignments (see Fig. 1 caption). Also shown is the adjusted $\delta^2\text{H}_F$ value after including relative abundance of breeding birds in assignment under the 75% kernel density estimate using the site-independent discrimination equation (hashed line) and the site-specific discrimination equation (dotted line) to create the feather isoscape. The map projection is North American Lambert Conformal Conic.

The number of geocator fixes used to estimate breeding origin between May and 31 July ranged from 44 to 95 (69 ± 9 , $36.1 \pm 0.1\%$).

In general, $\delta^2\text{H}_F$ assignments of overwintering birds in Florida and Jamaica to unknown breeding origins were similar to the geocator assignments under both site-specific and site-independent discrimination equations, although the mean $\delta^2\text{H}_F$ values of Ovenbirds captured in Florida differed from those

sampled in Jamaica (Florida: $-45.6 \pm 2.5\%$; Jamaica: $-52.1 \pm 1.4\%$; $t = -2.76$, $\text{df} = 108$, $P = 0.007$). Similarly, the $\delta^2\text{H}_F$ values of birds fitted with geolocators did not differ from those without geolocators at the same non-breeding capture location ($t = -1.18$, $\text{df} = 14$, $P = 0.26$). Both site-specific and site-independent methods produced overlap with 75% KDEs of breeding origin in the same individuals (Table 2), but the site-specific discrimination

factor overlapped with more 75% KDEs than the conventional site-independent approach, although the difference was not statistically significant (Table 2). For birds overwintering in Jamaica, the site-specific discrimination resulted in a higher probability of assignment to breeding locations predicted by geolocators in 5 of 8 individuals (Figs. 2 and S1), and for Florida birds, the site-specific discrimination relationship indicated a higher probability of assignment to breeding origins suggested by geolocators in 2 of 3 individuals (Fig. S2). Bayesian assignment of $\delta^2\text{H}_F$ values that incorporated range-wide variation in Ovenbird abundance reduced the differences in predicted breeding origin made using the site-independent and site-specific discrimination relationship by 50% and 30%, respectively.

DISCUSSION

Although archival light-level geolocators represent an important advance in our ability to track movement and destinations of migratory birds, indirect methods, such as stable isotopes, continue to provide valuable information and are likely to remain in the migratory-connectivity toolbox for many years. Validating the use and assumptions of these indirect techniques to infer breeding origins is therefore essential. We examined how geolocators and stable hydrogen isotopes compared in their ability to assign Ovenbirds to known and unknown breeding origins, and our results indicate that (1) breeding-origin assignments that use $\delta^2\text{H}_F$ values of unknown origin would be improved substantially by incorporating $\delta^2\text{H}_F$ values of known breeding birds sampled from the area of potential origin, because of regional differences in isotopic discrimination between $\delta^2\text{H}_p$ and $\delta^2\text{H}_F$; and (2) incorporating relative abundance of breeding birds into probabilistic origin assignments using a Bayesian approach (Royle and Rubenstein 2004) provided more accurate breeding assignments than using probabilistic assignments alone. Below, we discuss the implications of these findings.

Accurately assigning individuals to breeding origin using $\delta^2\text{H}_F$ values depends on the ability of feather isoscapes to encompass sources of the heavy fraction of hydrogen variation in nature. Assignments to breeding origin done with $\delta^2\text{H}_F$ values are characterized by a high degree of uncertainty because the discrimination between $\delta^2\text{H}_p$ and $\delta^2\text{H}_F$ varies in relation to diverse factors (Lott et al. 2003; Hobson et al. 2000, 2012; Haché et al. 2012). Despite rigorous feather-sampling efforts across the breeding range, isoscape values are interpolated across substantial geographic areas and, therefore, may not accurately depict local isotopic variation. Consistent with this idea, we found that the site-independent discrimination equation, the approach commonly used to assign $\delta^2\text{H}_F$ values to breeding origin (i.e., Lott et al. 2003, Kelly et al. 2005, Mazerolle et al. 2005, Van Wilgenburg and Hobson 2011), led to assignments that differed markedly from the geocator estimates of breeding origin. Conversely, the site-specific discrimination equation, which accounted for regional differences in discrimination, led to assignments that were more concordant with geocator estimates.

Geolocators enabled us to incorporate site-specific discrimination equations into $\delta^2\text{H}_F$ assignments. Although location estimates from geolocators can have high uncertainty because of variation in habitat features, bird behavior, and weather (Fudickar

et al. 2012, Lisovski et al. 2012), our geocator estimates for Ovenbirds encompassed the true breeding location for 95% of individuals when deployed and recovered from a known breeding location at HBEF. Geolocators also provided longitudinal estimates of breeding origin, unlike $\delta^2\text{H}_F$. However, other intrinsic markers such as genetic markers provide longitudinal information (e.g., Kelly et al. 2005, Chabot et al. 2012) and, in combination with $\delta^2\text{H}_F$, may improve assignment.

Developing a calibration relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_F$ to create feather isoscapes with general linear models may be misleading because of regional differences in isotopic discrimination. Instead, building in random effects for different sites (Wunder et al. 2005), like the approach we applied here, may be necessary to determine the accurate origin for individual feathers using $\delta^2\text{H}_F$. Assigning single individuals to breeding origin may not reflect the origins of an entire population. Here, however, it was necessary to assign individuals to compare the estimates of origin derived from $\delta^2\text{H}_F$ and geolocators for the same individual. The site-independent discrimination may not have performed as well as the site-specific equation because few validation locations were used to create the isotopic basemap of the area where our sample population bred (Hobson et al. 2012). In addition, a coastal effect (Lott et al. 2003) may have influenced $\delta^2\text{H}_F$ values, especially for individuals breeding east of the Appalachian Mountains in North America. Coastal areas are known to have higher $\delta^2\text{H}_F$ values and relationships between $\delta^2\text{H}_p$ and $\delta^2\text{H}_F$ that differ from those found inland because of the marine influence on the prey base (Lott et al. 2003, Kelly et al. 2005). Refining feather isoscapes for individual species by increasing the number of validation locations will likely increase the accuracy of assignments to breeding origin. In addition, including other intrinsic markers that provide longitudinal information such as genetic markers (i.e., Kelly et al. 2005, Chabot et al. 2012) in combination with $\delta^2\text{H}_F$ may also improve assignment.

Consistent with the results of Royle and Rubenstein (2004), our findings suggest that incorporating breeding bird abundance into probability-based assignments may alleviate the need to incorporate site-specific intercepts when validation locations do not occur throughout the entire breeding range or when prior knowledge of breeding location is not known. Specifically, incorporating breeding bird abundance increased the accuracy of origin assignments, especially where Ovenbirds are abundant. Assignments that incorporated breeding bird abundance accurately assigned 100% of birds when using a site-specific discrimination and 91.7% when the site-independent discrimination was used. In comparison, only 70% and 41.7% of birds were accurately assigned when using the site-specific and site-independent discrimination, respectively, without accounting for spatial variation in breeding bird abundance. Unfortunately, few isotopic studies have incorporated variation in breeding bird abundance into probabilistic breeding assignments (Royle and Rubenstein 2004, Norris et al. 2006).

A major assumption of assigning breeding origin with $\delta^2\text{H}_F$ is that birds molt where they breed (e.g., Chabot et al. 2012, Studts et al. 2012), which occurs frequently but may not always be the case (Butler et al. 2002, Leu and Thompson 2002). One of our Ovenbirds equipped with a geocator (male captured in Jamaica 2011) made a long-distance movement (~800 km) in the middle

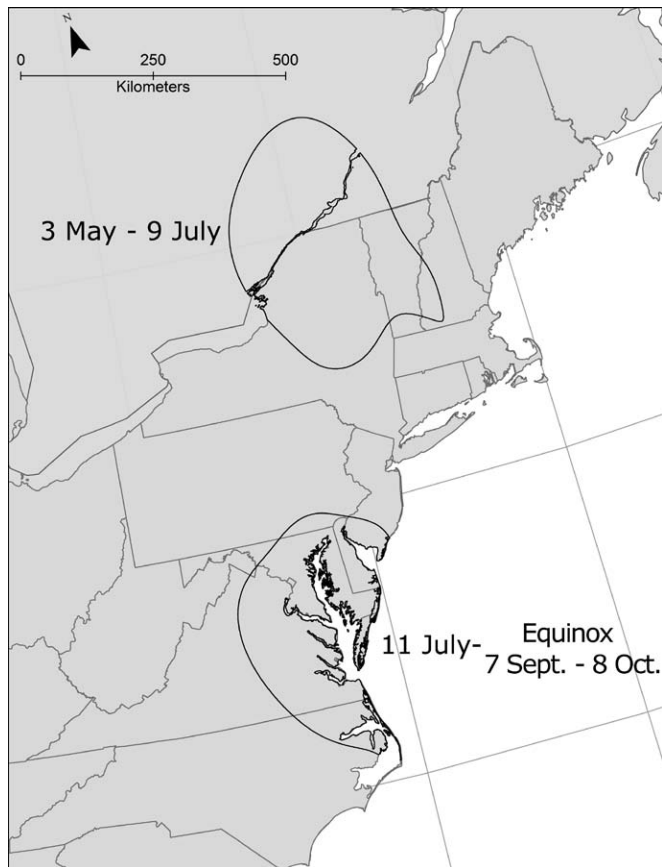


FIG. 3. Movement of a male Ovenbird, determined by geolocator data during the summer of 2011. The polygons represent the 75% kernel density estimate of geolocator points during generated from 3 May until 31 July. The bird arrived at the northern location on 3 May and migrated to the second location on 10 July, where it remained until the period around fall equinox (7 September–8 October), where latitude estimates determined by geolocators are not reliable (see text).

of the summer, perhaps to a southern staging area or to a second breeding location (Fig. 3; also see Rohwer et al. 2009). Consistent with the geolocator data, the $\delta^2\text{H}_F$ value suggests that it molted at the second, more southerly location. Relying solely on $\delta^2\text{H}_F$ would have resulted in missing the first location completely, even though the individual arrived at the northern location on 3 May and departed for the southerly location on 9 July, providing enough time at the more northerly location to reproduce successfully (Van Horn and Donovan 1994, M. T. Hallworth et al. unpubl. data). Although sample sizes are generally small for studies that use geolocators (e.g., Ryder et al. 2011, Stutchbury et al. 2011), our results suggest that the use of stable hydrogen isotopes alone may miss some rare, large-scale movements within the breeding season. Individuals that molt in areas different from those used by the rest of the population will increase variation of $\delta^2\text{H}_F$ sampled during the non-breeding season. As a consequence, increased variation in $\delta^2\text{H}_F$ within a non-breeding population will reduce the precision and accuracy of probabilistic assignments when assigning non-breeding populations to breeding origin. We were not able to assess how often such broad-scale movements occur during the breeding season, given our small sample size of geolocators

recovered from Ovenbirds. Even if large-scale movements during the breeding season are rare, they will likely have important implications for interpretations of the ecology and evolution of migratory birds, such as the possibility of “double breeding” (Rohwer et al. 2009) or dispersal dynamics. Further direct comparisons between stable isotopes and geolocators may provide additional insights into the frequency of this phenomenon.

Conclusions.—Our geolocator- and isotope-based estimates of origin were not statistically different (Table 2), despite low overlap of estimates for most birds (Figs. 1, 2, S1, and S2). This discrepancy is due in part to the uncertainty of site-independent and site-specific location estimates, even after incorporating range-wide relative Ovenbird abundance into our assignment models. Converting probabilistic, $\delta^2\text{H}_F$ -based assignments of location into binary assignments and using a 3:1 odds ratio (Chabot et al. 2012) yielded low statistical power to detect differences between geolocator and isotope methods, despite our relatively large sample size. Indeed, >85% of our birds would have to have been misclassified for this Fisher’s exact test to have acceptable power (i.e., $1 - \beta \geq 0.8$; $\alpha = 0.05$) to detect a statistically significant difference between assignment methods (Cohen 1988). Therefore, using only $\delta^2\text{H}_F$ values to assign breeding origin, especially with a site-independent isoscape model, could have led to an erroneous interpretation of migratory connectivity for the Ovenbird. Additional studies that compare geolocator and $\delta^2\text{H}_F$ assignments of origin are needed to determine the generality of our findings for other migratory bird species.

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