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RESEARCH ARTICLE

Migratory connectivity of Semipalmated Sandpipers and implications for conservation

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ABSTRACT

Semipalmated Sandpiper (*Calidris pusilla*) populations have undergone significant declines at core nonbreeding sites in northeastern South America. Breeding populations have also declined in the eastern North American Arctic, but appear to be stable or increasing in the central and western Arctic. To identify vulnerable populations and sites, we documented the migratory connectivity of Semipalmated Sandpipers using light-level geolocators, deploying 250 at 8 Arctic sites across the species' breeding range from 2011 to 2015, plus 87 at a single wintering site in northeastern Brazil in 2013 and 2014. We recovered 59 units and resighted 7 more (26% return rate) on the breeding grounds, but none at the nonbreeding site. We recovered only ~3% of units deployed in 2013 at eastern Arctic breeding sites, but recovered 33% of those deployed in 2015. Overall, birds with geolocators were 57% as likely to return as those carrying alphanumeric flags. Stopover durations at prairie sites (mean: 8.7 days southbound, 6.7 days northbound) were comparable with durations estimated by local banding studies, but geocator-tagged birds had longer stopovers than previously estimated at James and Hudson Bay, the Bay of Fundy, and the Gulf of Mexico. Migration routes confirmed an eastern Arctic connection with northeastern South America. Birds from eastern Alaska, USA, and far western Canada wintered from Venezuela to French Guiana. Central Alaskan breeders wintered across a wider range from Ecuador to French Guiana. Birds that bred in western Alaska wintered mainly on the west coasts of Central America and northwestern South America, outside the nonbreeding region in which population declines have been observed. Birds that bred in the eastern Arctic and used the Atlantic Flyway wintered in the areas in South America where declines have been reported, whereas central Arctic-breeding populations were apparently stable. This suggests that declines may be occurring on the Atlantic Flyway and in the eastern Arctic region.

Keywords: geolocators, Arctic, migration, movements, nonbreeding, shorebirds, tag effects, *Calidris pusilla*

Conectividad migratoria en *Calidris pusilla* y sus implicaciones en planes de conservación

RESUMEN

Las poblaciones de *Calidris pusilla* han demostrado disminuciones significativas en los sitios principales de invernada en el noreste de Suramérica. Las poblaciones reproductivas han declinado en el oriente del Ártico norteamericano, pero parecen estables o en aumento en el Ártico central y occidental. Para identificar poblaciones y sitios vulnerables documentamos la conectividad migratoria de *C. pusilla* usando geolocalizadores de nivel de luz, desplegando 250 de ellos en ocho sitios en el área de reproducción de la especie en el Ártico entre 2011 y 2015, y 87 más en un sitio de invernada en el noreste de Brasil en 2013 y 2014. Recuperamos 59 unidades y volvimos a observar 7 más (tasa de retorno de 26%) en las áreas de reproducción, pero ninguno en el sitio de invernada. Solo recuperamos el ~3% de las unidades desplegadas en 2013 en los sitios de reproducción en el Ártico oriental, pero recuperamos el 33% de las desplegadas en 2015. En general, las aves con los geolocalizadores tuvieron sólo 57% de probabilidad de regresar que las aves que cargaban marcas alfanuméricas. La duración de las paradas migratorias en sitios en las Praderas (promedio: 8.7 días migrando hacia el sur, 6.6 hacia el norte) fue comparable a la duración estimada por estudios locales de anillamiento, pero las aves marcadas con geolocalizadores tuvieron paradas más largas a las previamente estimadas en la bahías de James y Hudson y de Fundy, y el golfo de México. Las rutas migratorias confirmaron una conexión entre el Ártico oriental y el noreste de Suramérica. Las aves del oriente de Alaska y el occidente de Canadá pasaron el invierno entre Venezuela y Guyana Francesa. Las aves que se reproducen en el centro de Alaska pasaron el invierno en un área geográfica más amplia entre Ecuador y Guyana Francesa. Las aves que se reproducen en el occidente de Alaska pasaron el invierno principalmente en la costa occidental de Centroamérica y el noroccidente de Suramérica, por fuera del área de invernada en donde se han observado las disminuciones poblacionales. Las aves que se reproducen en el Ártico oriental y usan el corredor migratorio del Atlántico pasan el invierno en las áreas en Suramérica donde se han reportado los declives poblacionales, mientras que las poblaciones del Ártico central aparentemente están estables. Esto sugiere que los declives podrían estar ocurriendo en el corredor migratorio del Atlántico y en la región del Ártico oriental.

Palabras clave: Ártico, aves playeras, *Calidris pusilla*, efectos del marcado, fidelidad al sitio, geolocalizadores, migración, movimientos, sitios de parada migratoria

INTRODUCTION

Understanding the population dynamics of migratory animals requires knowledge of migration routes and patterns of connectivity among different stages of the life cycle (Webster et al. 2002, Marra et al. 2006). Understanding migration ecology is particularly important in situations in which one population of a species is declining or where declines are present in one portion of a species' range but not others. In these cases, knowing the extent to which individuals of different populations co-occur in different seasons is essential for implementing effective conservation strategies.

The Semipalmated Sandpiper (*Calidris pusilla*) was historically one of the most widespread and numerous shorebird species in the Western Hemisphere, breeding across the North American Arctic tundra (Brown et al. 2001). Western, central, and eastern breeding populations are suspected to occur across the North American Arctic based on a stepped cline in bill length, with longer-billed forms in the east and shorter-billed forms in the west (Manning et al. 1956, Harrington and Morrison 1979, Gratto-Trevor et al. 2012a), although genetically the species appears monotypic (Miller et al. 2013). Monitoring across the breeding range has shown variable population trends, with declines occurring at some sites in the eastern Arctic, but generally stable or increasing trends in the central and western Arctic (Jehl 2007, Andres et al. 2012a,

Smith et al. 2012). Population declines have also been reported at staging sites along the east coasts of Canada and the United States (Howe et al. 1989, Morrison et al. 1994, 2001, Bart et al. 2007, Gratto-Trevor et al. 2012a, 2012b, Hicklin and Chardine 2012, Mizrahi et al. 2012). The Atlantic Flyway migration route is thought to be used by eastern Arctic breeding populations as well as by some central Arctic breeding birds. Major population-level declines have been documented in the eastern portion of the core nonbreeding range in Suriname and French Guiana since the mid-1980s (Gratto-Trevor et al. 2012b, Morrison et al. 2012).

Our current understanding of migration routes and connectivity is based on 2 major sources, bill lengths and band recoveries. A recent genetic study (Miller et al. 2013) was not useful for determining migratory connectivity between breeding and nonbreeding sites because populations were panmictic. Bill length analyses of migrating or nonbreeding birds can suggest breeding origin because of the cline in bill lengths across the Arctic (Gratto-Trevor et al. 2012a, Tavera et al. 2016). Band recoveries and resightings are available for a small proportion of the birds marked at breeding, staging, and nonbreeding sites over the past 40 yr, and connect the banding and recovery locations. Bill length data and available band recoveries suggest that most western breeders migrate south through the prairies, along with some birds from central Arctic populations (Lank 1979, 1983, Gratto-Trevor and Dickson

1994). The remaining central Arctic breeders, and all eastern Arctic birds, are thought to migrate south along the north Atlantic Coast of North America (Harrington and Morrison 1979, Gratto-Trevor et al. 2012a). Overall, western Arctic breeders appear to overwinter farther west in South America than eastern breeders, although there is considerable mixing among populations, particularly in French Guiana and Guyana (Lank 1983, Gratto-Trevor et al. 2012a). In spring, birds from the eastern Arctic usually migrate north along the U.S. Atlantic Coast. Central and western Arctic breeders primarily migrate north through the interior of North America (Morrison 1984, Gratto-Trevor et al. 2012a). Some populations exhibit elliptical migration, using western flyways for northbound migration and more easterly routes during southbound migration (Gratto-Trevor and Dickson 1994). However, knowledge of these movement patterns is incomplete because individuals have not been followed throughout the entire migratory cycle as this is not possible based on band recoveries alone, and resighting rates may be biased by the geographic distribution of banding locations or observers.

Our major objectives were to provide new and more accurate information about the migration routes of Semipalmated Sandpipers and to understand the connections between breeding and wintering areas so that causes of population declines can be studied and addressed. To effectively conserve Semipalmated Sandpipers, we need to understand the spatial and temporal relationships among nonbreeding sites, migration routes, and breeding areas (Brown et al. 2001). While geolocators cannot identify precise locations, with appropriate analytical techniques their accuracy is effective for investigating long-distance movements and for identifying the general regions used during migration and in winter by birds from different breeding locations (Porter and Smith 2013). Geolocators can provide improved information about routes and staging areas used during migration by individuals from specific breeding populations. This can allow a better understanding of how different populations may be affected by loss or degradation of habitat, hunting, and other threats occurring at particular wintering or staging sites, so that conservation efforts can be more effectively directed at key staging or nonbreeding sites used by birds from declining populations. The Arctic Shorebird Demographics Network (Brown et al. 2014), which operated study sites across the North American Arctic, provided an excellent opportunity to collect information about migration routes of birds from across the breeding range.

In addition to using geolocators to fulfil our major objectives, we also used geocator data to determine the duration of Semipalmated Sandpiper stopovers during migration. Previous measurements of stopover duration have been calculated by recapturing or resighting birds at migration sites (e.g., Dunn et al. 1988, Lyons and Haig

1995, Iverson et al. 1996, Alexander and Gratto-Trevor 1997, Warnock and Bishop 1998, Henkel and Taylor 2015), but these observations have potentially underestimated stopover durations because of the unknown amount of time that birds were present at the study site either before their first capture or after their last capture or resighting. Unbiased stopover estimates will improve population estimates based on counts at migration sites.

Our large sample of geolocators deployed over multiple years also allowed us to examine whether geolocators themselves may have detrimental effects on small migrating shorebirds. Geolocators have been successfully used to track other migratory shorebirds (Minton et al. 2010, Niles et al. 2010, Hedenström et al. 2013, Hooijmeijer et al. 2013, Smith et al. 2014, Summers et al. 2014), but none had been placed on Semipalmated Sandpipers prior to this study. Because tags have had detrimental effects on some bird species (Costantini and Møller 2013, Gómez et al. 2014, Fairhurst et al. 2015), but not on others (Conklin and Battley 2010, Petersen et al. 2015, Weiser et al. 2016), and because the weight of the tag influences the impact on the bird carrying it (Barron et al. 2010, Streby et al. 2015, Weiser et al. 2016), we investigated whether geolocators might be a handicap for Semipalmated Sandpipers. To do so, we compared return rates across our network of study sites between birds fitted with geolocators and birds marked only with alphanumeric leg flags.

METHODS

Deployment of Geolocators

We deployed 192 geolocators (W65, Migrate Technology, Cambridge, UK) on adult Semipalmated Sandpipers breeding at 8 sites on the breeding grounds across the species' Arctic breeding range in the spring of 2013 (Figure 1). An additional 29 geolocators were deployed (18 of model W65A9UJ and 11 of Mk20A, British Antarctic Survey, Cambridge, UK) on adults breeding at Nome, Alaska, USA, in 2011 and 2012, and 29 more units (model W65) on birds from Coats Island, Nunavut, Canada, in 2015, for a total of 250 units deployed at breeding sites. Nests were located using area searches and by dragging a rope along the ground between 2 people to flush nesting birds within defined study plots following methods outlined by Brown et al. (2014). Individual birds were captured at nest sites with bownet and walk-in traps, and were marked with geolocators attached to leg flags on the left tibiotarsus, and either alphanumeric leg flags or some combination of uniquely identifiable color bands on the right tibiotarsus. Leg flags are similar to traditional color bands, but have an extension, in our case either with a 3-character alphanumeric code that uniquely identified the individual bird, or to which the geocator was attached (see leg flag banding methods in Gratto-Trevor (2004), and

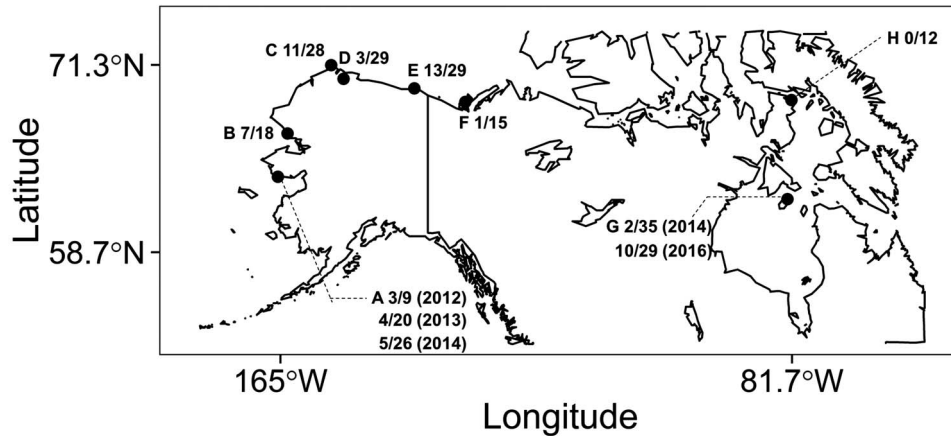


FIGURE 1. Locations of sites where geolocators were deployed on Semipalmated Sandpipers: (A) Nome, (B) Cape Krusenstern, (C) Barrow, (D) Ikpikpuk, and (E) Canning River, Alaska, USA; (F) Mackenzie Delta, Northwest Territories, Canada; and (G) Coats Island, and (H) Igloolik, Nunavut, Canada. Numbers of geolocators recovered/deployed follow site letters. All were deployed in 2013 and recovered in 2014, except at Coats Island and Nome, where recovery years and numbers are as shown.

geolocator attachment methods in Minton et al. (2010) and Niles et al. (2010)). The total weight of flag and geolocator varied among sites from 0.8 to 1.0 g, or between 3% and 4% of the average body weight of 26 g for the birds in our sample. We added a color band applied below the geolocator (spacer band) on birds from Coats Island in 2015 to help the geolocator flag move more freely and to reduce its impact.

Birds were relocated and recaptured in the year following deployment of geolocators by systematically searching areas near marked birds' previous nest locations. We sexed birds by comparing the bill lengths of adults in mated pairs, with longer-billed birds in pairs being identified as female. Within a breeding population, sexing by bill length alone is 92% accurate, and is virtually 100% if both members of the pair are measured (Gratto and Cooke 1987). When only one individual was captured, we sexed birds if possible using bill length information from Harrington and Morrison (1979) and Sandercock (1998), and otherwise considered them to be of unknown sex.

We deployed an additional 37 W65A9UJ geolocators in January, 2013, and 50 more in January, 2014, on adult birds captured at a major roosting site on the wintering grounds at Coroa dos Ovos, a site within Reentrâncias Maranhenses, a hemispherically important Western Hemisphere Shorebird Reserve Network (WHSRN) site in the state of Maranhão, Brazil. Birds were captured with mist nets at night starting 4 hr before high tide. The same roosting site was revisited in 2014 and 2015 and efforts were made to relocate and recapture birds fitted with geolocators using mist nets and a modified cannon net during 8 days of trapping each year.

The 0.65-g W65 tags were set to full level light recording in Mode 3, with a 5-min interval and minimum and

maximum temperature recording, as well as wet vs. dry count and conductivity records. The 0.8-g Mk20A units were also set to full level light recording with a 5-min interval, but with no temperature recording. Locations of birds were determined from the light-level data using the threshold methods within Bastrak software (British Antarctic Survey; see www.birdtracker.co.uk). No precalibration was conducted due to logistical constraints. Subsequent refinements were employed using the orientations of coastlines, weather, equinox equidistance, salt water conductivity, temperature, and higher thresholds in northern Canada, following techniques outlined by Porter and Smith (2013). Errors in latitude away from coastal sites are more variable due to different light characteristics, weather, topography, or the number of fixes obtained for a given position. Thus, positions of tagged birds reported from interior locations should be viewed as approximate, especially with respect to latitude. Errors in longitude may be greatly reduced by averaging across all locations in a given site, since the greatest component of error for shorebirds away from the breeding grounds is shading due to cloud cover. Shaded sunrise fixes are offset in the opposite direction from shaded sunset fixes, but across many days a shaded sunrise is likely to be offset by a shaded sunset of a different day. For a typical bird in this study, C470, the longitudes and 95% confidence intervals following the annual cycle were: Alberta, Canada, 110.1 (109.4–110.8; $n = 10$); North Dakota, USA, 100.0 (99.5–100.5; $n = 33$); Venezuela, 69.2 (68.8–69.6; $n = 28$); French Guiana, 52.0 (51.9–52.1; $n = 451$); Guyana, 59.5 (59.2–59.8; $n = 24$); and Cuba, 78.9 (78.5–79.3; $n = 14$). It is not appropriate to average latitude to improve precision because all shading dislocates the fixes in the same direction. We caution that all locations should be viewed

as approximate, and we have purposely avoided providing latitude and longitude values to prevent ascribing too much certainty to these locations. Our primary study objectives were to identify the general regions used by migrating and wintering birds and the migratory connectivity between breeding and wintering regions.

To determine northbound and southbound migration stopover sites, we mapped tracks and evaluated them one fix at a time to determine periods when a bird was traveling vs. stationary. Periods of travel were identified by consistent directional movement and distances between consecutive fixes of >200 km. We assumed that a bird had stopped at a new location when there was an absence of consistent directional change in latitude and longitude, and distances between consecutive fixes were <200 km. We plotted direct connections between stopover sites, but actual travel routes may have deviated from direct-line paths. Our approach allowed us to discern the start and end of each stopover or travel period with a resolution of 0.5 to 1.0 day.

Effects of Geolocators on Return Rates

We compared the 1-yr return rates of the birds carrying geolocators with those of a control group captured at the same breeding sites. The control group consisted of Semipalmated Sandpipers that were individually marked with an alphanumeric flag, but not fitted with geolocators. Aside from application of the geocator, both groups of birds were subject to similar capture and handling effects and were captured at nests in the same study plots at our field sites. Control birds included those captured in 2010–2013 and resighted the next year in 2011–2014 at all sites, and birds captured in 2015 and resighted in 2016 on Coats Island. No control birds were banded on Coats Island in 2013, the first year of geocator deployment, so the control group for birds fitted with geolocators on Coats Island in 2013 consisted of birds without geolocators that were marked in 2004 and 2005, and resighted in 2005 and 2006. We used birds marked with flags in 2015 as controls for the birds marked with geolocators on Coats Island in the same year. All Semipalmated Sandpipers captured at Igloodik, Nunavut, Canada, received a geocator, so this site did not have a control group. At other sites, resighting effort was similar between groups, although observers may have been more likely to pursue and accurately record resightings of birds carrying geolocators relative to control birds.

For each group of birds at each site, we estimated the 1-yr return rate as the proportion of marked birds that were resighted or recaptured 1 yr after initial capture in systematic searches of the areas in each site in which geolocators were deployed. We did not include any resighting records from subsequent years because at most sites we had only a single year of resighting data for birds

with geolocators (deployed in 2013, resighted in 2014). Return rates are the product of 4 probabilities, and a marked bird not seen in the year after capture could have died, dispersed to breed elsewhere, skipped a year of breeding, or been overlooked by observers.

We tested for an overall effect of geocator and other potential covariates on return rates with a generalized linear mixed-effects model (GLMM, with a binomial link function). The other covariates (sex, nest success, timing of capture relative to season or incubation, body mass upon capture, whether or not an alphanumeric leg flag was applied) were included in case the birds fitted with geolocators represented a biased sample with respect to some factor that may have affected return rates. We also included a random effect of year on the intercept, and a random effect of site on both the intercept and slope of the geocator effect. Our model thus controlled for effects of year and site while still testing for an overall effect of geocator that was interpretable for the species as a whole.

To make effect sizes comparable across covariates with different scales, we standardized explanatory covariates by centering on the mean and dividing by 2 standard deviations with the `standardize` function in R package `arm` (Gelman and Su 2013). We tested all possible submodels of this full model using the `dredge` function in R package `MuMIn` (Bartoń 2013), and considered any model with a difference from the top model in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c) <2 to be a competitive model. Controlling for other potential covariates required using subsets of the data, so if a factor did not have an important effect on return rates (see below), we excluded it and repeated the model-selection procedure. Once all remaining covariates were included in the top model set, we used model averaging (Burnham and Anderson 2002) with function `model.avg` in package `MuMIn` to estimate effect sizes for variables in the top model set while accounting for model uncertainty. We made inferences from the averaged model. Return rates varied among sites, so we also compared return rates between groups within each site with a Fisher's exact test. We concluded that there was a site-specific effect of geolocators when the 95% confidence interval of the odds ratio (probability that a bird fitted with a geocator returned / probability that a control bird returned) did not include 1.0.

RESULTS

We recovered 59 geolocators from Semipalmated Sandpipers that returned to the breeding grounds where they were tagged the previous year (Figure 1). We also recovered 3 geolocators from dead birds or remains prior to fall migration in the year that they were deployed (2 at

TABLE 1. Wintering regions of Semipalmated Sandpipers equipped with geolocators at 7 breeding sites in the Arctic (see Figure 1 for breeding site locations) by sex. Western South America includes Peru, Ecuador, Colombia, and Venezuela; northeastern South America includes Suriname, French Guiana, and Brazil.

Breeding site	Sex (F, M, U) ^a	Breeding region	Percentage and sex of birds wintering in each area ^a				Total geolocators
			Central America	Western South America	Caribbean	Northeastern South America	
Nome	5, 4, 2	Western	27%, 2F, 1M	73%, 3F, 3M, 2U	0	0	11
Cape Krusenstern	1, 6, 0	Western	33%, 2M	67%, 1F, 3M	0	0	7 ^b
Barrow	3, 5, 2	Western	10%, 1M	40%, 3F, 1M	10%, 1U	40%, 3M, 1U	10
Ikpikpuk	1, 1, 1	Western	50%, 1F	50%, 1U	0	0	3 ^b
Canning River	6, 7, 0	Western	0	8%, 1F	15%, 2F	77%, 3F, 7M	13
Mackenzie Delta	0, 1, 0	Central	0	0	0	100%, 1M	1
Coats Island	3, 9, 0	Eastern	0	0	0	100%, 3F, 9M	12

^a F = female, M = male, U = Unknown.

^b The wintering location of one male from each of the Cape Krusenstern and Ikpikpuk breeding sites could not be identified due to geolocator failure.

Mackenzie Delta, Canada, and 1 at Nome), but had no information about the cause of death. Two of the 59 returned units had malfunctioned and recorded no useful light data, so we had migration tracks for 57 birds captured at sites across their Arctic breeding range. One bird at Nome was recovered 2 yr after deployment, and its geolocator had recorded both a round trip and an additional southbound trip. Not all recovered geolocators had recorded a full year of light data, and only 46 had recorded full northbound tracks, which affected the sample sizes of some analyses. Geolocator tags recorded movement data for an average of 329 ± 73.3 SD days. Of the birds with recovered functioning geolocators, 19 were classified as female, 33 as male, and 5 as unknown sex (Table 1). We also identified an additional 7 birds with geolocators that returned to the breeding grounds, but were not recaptured, using their unique color band combinations or alphanumeric flags, and these individuals were included in the 26% return rate calculated across all breeding sites.

Of the 37 birds fitted with geolocators in Brazil in January, 2013, at least 5 were observed again at their wintering location and 3 were observed during migration, but although they were uniquely identified using their color bands, none were recaptured. One bird was observed at Squaw Creek, Missouri, USA (40.08°N, 95.27°W), in May, 2013, a second at Wells, Maine, USA (43.31°N, 70.57°W), in July, 2013, and a third at Mispillion Harbor, Delaware, USA (38.95°N, 75.31°W), in May, 2014. Thus, it appears that 1 of these birds used the Central Flyway during northbound migration, 1 used the Atlantic Flyway during northbound migration, and 1 used the Atlantic Flyway during southbound migration. None of the 50 birds fitted with geolocators in January, 2014, were recaptured or resighted on the wintering grounds, or during northbound or southbound migration.

Migration Routes

The Semipalmated Sandpipers marked in this study wintered across the species' entire wintering range, with varying levels of connectivity between breeding and wintering areas (Figure 2, Table 1). Birds captured at breeding sites at Nome and Cape Krusenstern, Alaska, USA (western Arctic breeding population), wintered primarily on the west coast of South America (Ecuador, Colombia, and Peru) as well as at sites in Central America (Guatemala, Honduras, Nicaragua, and Panama; Figure 2A, Table 1). Birds from Barrow and Ikpikpuk, Alaska (western Arctic breeding population), wintered across almost the entire nonbreeding range of the species, from Peru to French Guiana (Figure 2B, Table 1). Birds from the Canning River, Alaska (western Arctic breeding population), and Mackenzie Delta, Canada (central Arctic breeding population), primarily wintered on the northeastern coast of South America (Suriname and French Guiana), as well as in western South America (on the Caribbean Coast of Colombia) and the Caribbean (Figure 2C, Table 1). The 12 birds from Coats Island, Nunavut, Canada (eastern Arctic breeding population), also wintered in northeastern South America (Suriname, French Guiana, and Brazil; Figure 2D, Table 1). The migration routes of western breeders went through the interior of North America for both northbound and southbound migrations, often staging in the Canadian prairies or the Dakotas, USA (Figures 2, 3, Table 2). All birds from Alaska and the Mackenzie Delta stopped on the coasts of Texas and Louisiana, USA, during northbound migration, often for several weeks, but only 40% used these areas during southbound migration (Figures 2, 3, Table 2).

All 12 of the eastern-breeding Coats Island birds stopped at James or Hudson Bay, Canada, during southbound migration (Figure 2D, Table 2). One bird flew directly from James Bay (after staging there for 31 days) to

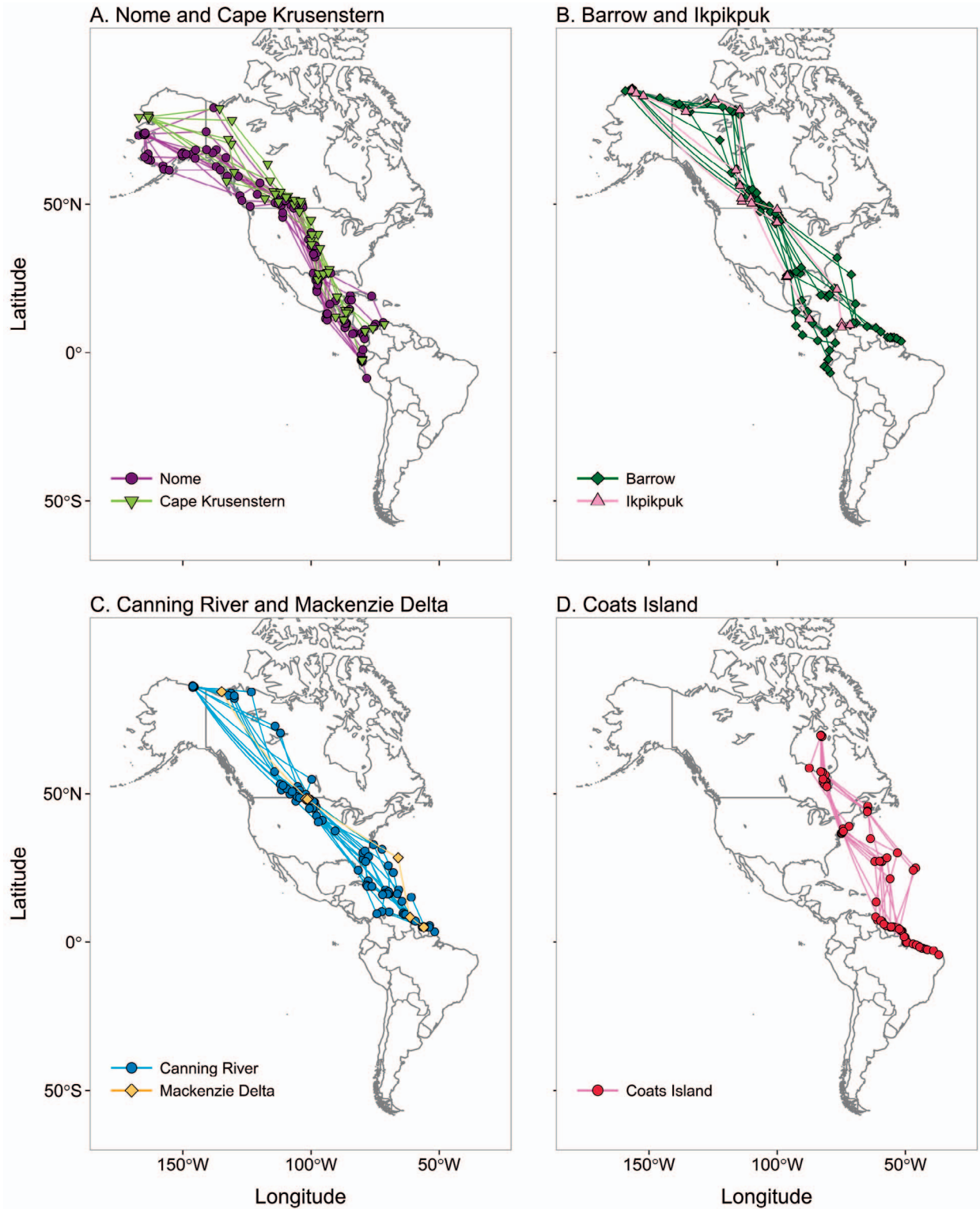


FIGURE 2. Southbound movement patterns of 57 geolocator-tagged Semipalmated Sandpipers from 7 Arctic breeding sites in 2011, 2012, 2013, and 2015. Different symbols represent location fixes obtained for birds from different breeding sites. Lines show direct connections between stopover sites, not paths taken by birds.

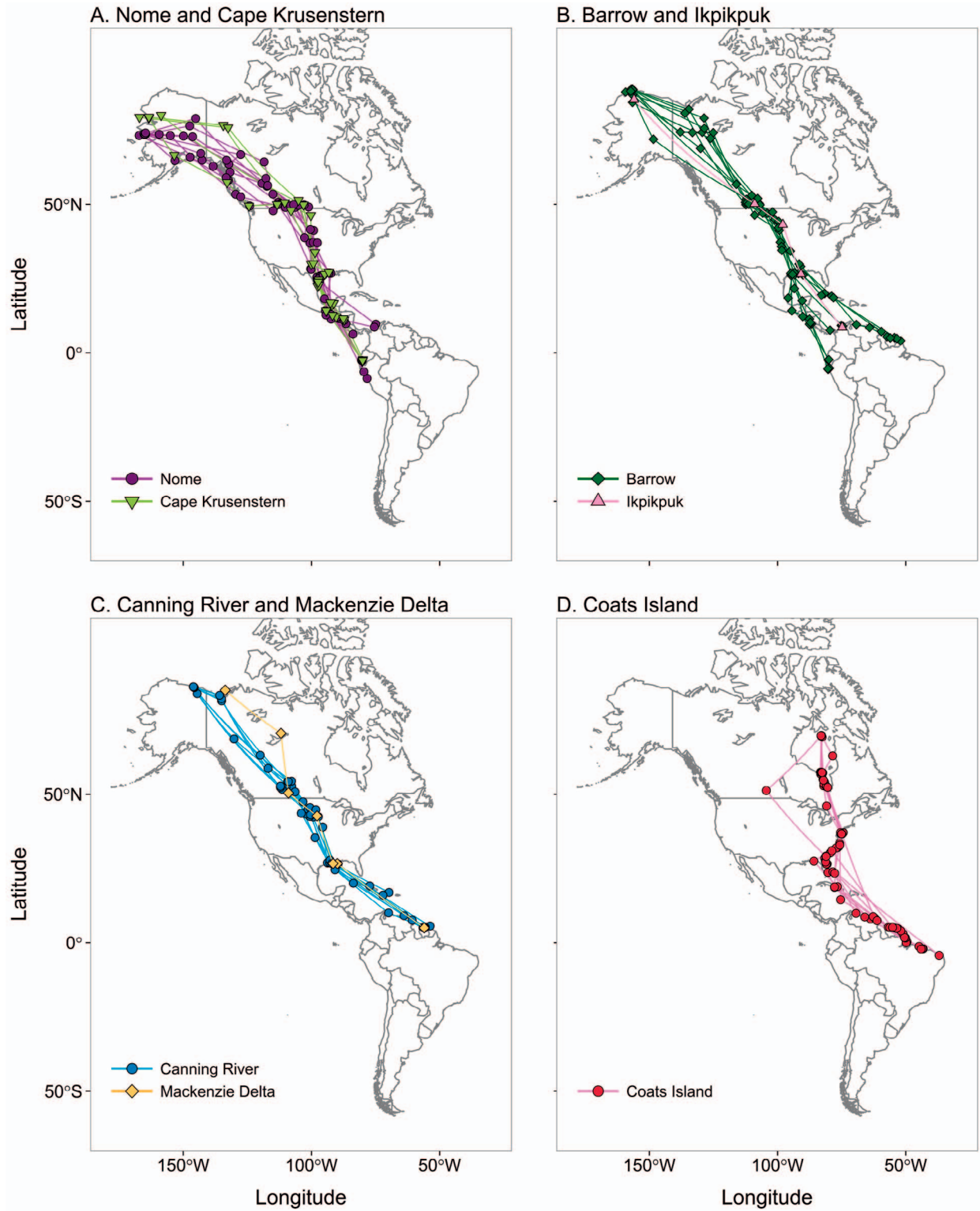


FIGURE 3. Northbound movement patterns of 46 geolocator-tagged Semipalmated Sandpipers from 7 Arctic breeding sites in 2012, 2013, 2014, and 2016. Symbols and lines as in Figure 2.

TABLE 2. Duration of northbound and southbound migration in days (d) for the entire migration (All) and for specific staging areas of Semipalmated Sandpipers equipped with geolocators at 7 breeding sites in the Arctic. Sample sizes vary based on the number of birds using an area.

Staging area	Northbound				Southbound				<i>t</i> ^a	<i>P</i>
	<i>n</i>	Range (d)	Mean (d)	SD	<i>n</i>	Range (d)	Mean (d)	SD		
All	42	24–79	43.9	12.1	54	23–104	50.9	18.0	–2.27	0.02
Gulf USA	32	1–29	12.3	8.4	19	4–27	14.5	6.1	–1.08	0.15
Texas	14	2–29	12.4	9.6	14	4–27	14.2	7.0		
Louisiana	18	1–28	12.2	7.7	6	4–17	12.8	5.0		
Prairies	23	1–18	6.7	3.0	39	1–41	8.7	7.7	–1.44	0.08
North Dakota	4	1–10	5.2	4.0	17	2–16	9.9	4.0		
Southern Saskatchewan	10	3–18	6.5	4.2	23	1–24	5.6	5.8		
Southern Alberta	12	3–10	5.7	1.7	13	1–7	3.2	2.0		
Delaware Bay	9	3–15	8.6	3.6	7	15–30	23.0	5.1	–6.65	0.001
James and Hudson Bay	9	6–12	8.9	2.4	12	6–31	16.8	7.3	–3.51	0.002

^a *t*-values are for one-tailed tests (as northbound migration is expected to be faster than southbound migration).

Venezuela's Orinoco River Delta region, a distance of approximately 5,270 km, and then flew to the Amazon Delta region of Brazil. One bird stopped north of the Bay of Fundy, Canada, for 25 days, and 3 stopped in the Bay of Fundy (for 18, 27, and 31 days) before departing for the southern over-ocean flight. The remaining 7 birds stopped for 15–30 days at Delaware Bay, New Jersey, USA, before departure. All but 1 followed their arrival in South America with movements eastward to wintering locations (Figure 2D); 1 moved west from French Guiana to Suriname. All of the northbound tracks recorded from Coats Island birds (Figure 3D) followed the U.S. Atlantic coast, except for 1 that included the Florida panhandle, USA, and 1 that stopped in Georgia, USA, and then went as far inland as Saskatchewan, Canada, on the return trip to Coats Island. All but the bird that went to Saskatchewan stopped in James or Hudson Bay on the way north.

The duration of northbound and southbound migration varied greatly among individual birds, but was significantly longer on average during southbound migration (Table 2). Migration rates averaged 201.0 ± 66.2 SD km per day ($n = 57$), and total round-trip migration distance averaged $17,854 \pm 4,424$ SD km ($n = 42$). The influence of migratory direction on length of stay at common North American

stopover sites differed among sites (Table 2). Length of stay along the Gulf Coast of the U.S. and on the North American prairies (western breeders) was similar between northbound and southbound migrants, but was longer for southbound than northbound migrants at Delaware Bay and James or Hudson Bay (eastern breeders; Table 2).

Females and males showed no significant differences in initiation date of northbound migration or arrival at the breeding site, nor were there significant differences in duration of northbound or southbound migration (Table 3). However, females started migrating south significantly earlier than males (Table 3). Among birds of known sex, females wintered throughout the entire range of the species, but no confirmed males were among the 3 birds found in the Caribbean region (Table 1).

Effects of Geolocators on Return Rates

To compare return rates between birds with geolocators and birds carrying leg flags only, we analyzed 247 capture events of individuals in the geolocator group and 1,070 capture events of 978 individuals in the control group. We excluded 3 individuals from the geolocator group that were found dead without having left the breeding site. We encountered 66 (26%) birds with geolocators and 408

TABLE 3. Timing and duration (in days; d) of migration for male and female Semipalmated Sandpipers equipped with geolocators at 7 breeding sites in the Arctic.

	Females			Males			<i>t</i> ^a	<i>P</i>
	<i>n</i>	Mean	SD (d)	<i>n</i>	Mean	SD (d)		
Start southbound migration	19	8 July	6.6	33	13 July	4.9	5.49	0.001
Southbound migration length (days)	19	47.9	19.6	30	54.3	17.3	1.21	0.23
Start northbound migration	14	17 April	17.0	27	22 April	15.3	0.97	0.34
Northbound migration length (days)	13	46.1	14.2	25	41.9	11.5	–0.98	0.33
Arrival at breeding site	13	4 June	6.3	25	5 June	7.8	–0.04	0.97

^a 2-tailed *t*-tests.

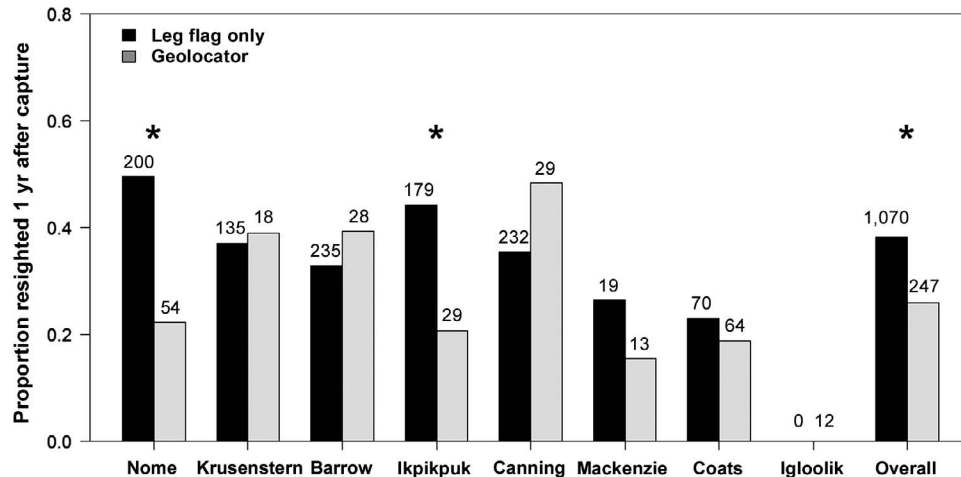


FIGURE 4. Proportion of Semipalmated Sandpipers that were resighted in the year following capture across their range. Sites are ordered from west to east across the North American Arctic (see Figure 1). Sample size (number of birds marked with geolocators or with uniquely coded leg flags) is shown above the corresponding bar for each site. Sample sizes for birds marked with geolocators at the Nome and Mackenzie sites differ from those in Figure 1 because 3 birds with geolocators were found dead prior to migration. An asterisk indicates a significant difference in return rate ($P < 0.05$; Table 4).

(38%) control birds at breeding sites in the year after capture. Return rates varied among sites and tended to be lower at sites in the eastern part of the breeding range (Figure 4). Overall, Semipalmated Sandpipers fitted with a geolocator were 57% as likely as those without a geolocator to return to breeding sites (Table 4). Two submodels were included in the top model set ($\Delta AIC_c < 2$; Table 5). Averaging the 2 models resulted in final estimates of a strong negative effect of carrying a geolocator, a negative effect of carrying an alphanumeric flag, and a positive effect of having previously been banded at the capture site (Table 5).

Site-specific tests indicated that geolocators had a significant negative effect on return rates at 2 sites: Nome

TABLE 4. Site-specific Fisher's exact tests for the difference in return rates between Semipalmated Sandpipers fitted with geolocators ($n = 247$) and control birds without geolocators ($n = 1,070$). The odds ratio is the proportional return rate of birds with vs. without a geolocator, and a value of 1 indicates no difference (e.g., in Nome, 0.293 birds with a geolocator returned for every 1 bird without a geolocator). Sites with a significant effect of geolocator are shown in bold font (see Figure 1 for site locations). Igloodik could not be tested because there were no data for birds without geolocators.

Site	Odds ratio (95% CI)	P-value
Nome	0.293 (0.132–0.607)	<0.001
Cape Krusenstern	1.081 (0.333–3.287)	1.00
Barrow	1.326 (0.534–3.173)	0.53
Ikpikpuk	0.332 (0.105–0.891)	0.02
Canning River	1.704 (0.723–3.997)	0.22
Mackenzie Delta	0.520 (0.042–3.973)	0.67
Coats Island	0.780 (0.305–1.952)	0.67
Overall	0.568 (0.409–0.780)	<0.001

and Ikpikpuk (Table 4). Field crews at Nome and Ikpikpuk applied geolocators only to birds that had not been previously banded, but had some control birds that had been marked in prior years. At the other study sites, both treatment groups included a mix of previously banded and unbanded birds. In our dataset, previously unbanded birds were less likely to return, which could partially explain why fewer birds marked with geolocators returned to Nome and Ikpikpuk. However, when we looked at only these 2 sites and used a subset of the data that included only previously unbanded birds in both the geolocator ($n = 83$) and control groups ($n = 340$), the negative effect of geolocator remained strong and significant (GLMM with random effects of site and year: intercept = -0.50 ± 0.08 , geolocator effect = -0.91 ± 0.25 , $P < 0.001$). Therefore, banding history did not explain the negative effects of carrying a geolocator at these 2 sites.

TABLE 5. Standardized effect of each covariate on 1-yr return rates of Semipalmated Sandpipers across all sites in the North American Arctic in 2012, 2013, 2014, and 2016. Values are on the logit scale and were obtained by averaging the top model set ($\Delta AIC_c < 2$), which included 2 models: geolocator + alphanumeric flag + previously banded ($w_i = 0.505$, $\Delta AIC_c = 0.00$), and geolocator + previously banded ($w_i = 0.364$, $\Delta AIC_c = 0.65$). Each model included random effects of year (on intercept) and site (on intercept and geolocator effect).

Covariate	Mean	SE	Relative importance
Intercept	-0.67	0.30	—
Geolocator	-0.62	0.23	1.00
Previously banded	0.48	0.16	1.00
Alphanumeric flag	-0.26	0.29	0.58

DISCUSSION

Our study provides the first large-scale analysis of migratory connectivity for Semipalmated Sandpipers among breeding, stopover, and nonbreeding sites. Our results confirm and refine the previous general understanding of population-specific migratory movements based on resightings, band recoveries, and bill length measurements (Harrington and Morrison 1979, Lank 1979, 1983, Gratto-Trevor and Dickson 1994, Gratto-Trevor et al. 2012a). Going well beyond current knowledge from prior studies, deploying geolocators simultaneously across the entire breeding range of this species provided unprecedented information about the timing of migration and clarified specific connectivity among breeding, migration, and nonbreeding areas, which will help to assess the relative conservation importance of sites and regions for Semipalmated Sandpipers.

Migration Routes and Connectivity

Geolocators recovered from Coats Island showed movements consistent with previous data suggesting that birds that breed in the eastern Arctic overwinter in the areas of northern South America where large population declines have been observed, including Suriname, French Guiana, and Brazil. Connectivity between these sites suggests that declines documented in northern South America may be linked to population declines in the eastern Arctic. On the other hand, at least some birds from the northwestern part of the breeding range also wintered in northern South America, including birds from the northern coast of Alaska as far west as Barrow and the Canning River. Birds from these sites spread out across the entire wintering range from Ecuador to Brazil. In contrast, all of the birds breeding in far western Alaska spent the boreal winter in South America in areas no farther east than western Venezuela.

Birds from breeding sites farther east also generally wintered farther east in South America (Table 1), which is consistent with the results of previous studies (Harrington and Morrison 1979, Lank 1979, 1983, Morrison 1984, Gratto-Trevor and Dickson 1994, Gratto-Trevor et al. 2012a). Previous work demonstrated that some Alaskan breeders wintered in northeastern South America, but our results indicate that these birds are primarily from sites in northeastern rather than far western Alaska. Birds from Barrow were scattered among virtually all wintering sites, and those from western Alaska concentrated instead in more western South American and Central American sites. Our data showed no obvious differences between the sexes in wintering locations, in contrast to the latitudinal pattern found in the closely related Western Sandpiper (*Calidris mauri*; Nebel et al. 2002).

We also detected differences in the migration routes used by birds breeding in the eastern and western portions of the Arctic (Figures 2, 3). Western breeders from sites west of Canning River followed similar routes during both northbound and southbound migration, stopping over throughout the prairies of the Central Flyway. Birds breeding at Canning River and Mackenzie Delta also used the prairies of the Central Flyway, but tended to migrate farther east during southbound migration. In contrast, the eastern breeders from Coats Island tended to show more of an elliptical migration, with stopovers in James Bay during southbound migration before flying over the Atlantic Ocean to reach South America, and return routes along the Atlantic Coast. Most birds carrying geolocators that wintered in northeastern South America (Suriname, French Guiana, and Brazil) first arrived in Venezuela or Guyana and then moved farther west. The observed routes add detail to our previous understanding of movements based on morphometric analyses (Spaans 1978, 1984, Morrison 1984, Hansen-Chaffard 2000, Hicklin and Gratto-Trevor 2010, Gratto-Trevor et al. 2012a).

The eastern and western populations both showed high migratory connectivity, with disjunct breeding ranges, migration routes, and nonbreeding areas from each other. Thus, in theory, these populations could be demographically distinct from each other with respect to population effects occurring during any part of the annual cycle. Eastern birds had the highest overall connectivity because their migration routes were distinct from the other sampled populations, which could add to connectivity generated by their partially disjunct wintering grounds. In practice, detecting such demographic independence would be complicated by movements from the intervening North Slope and Mackenzie Delta based breeding populations, which show substantially lower connectivity in both migration routes and wintering ranges, strongly with each other, but also with the extreme eastern and western populations.

Our results provide an approach for starting to distinguish the geographical distribution of potential drivers of declines. For example, if hunting of birds on the Caribbean and northern South American wintering grounds is driving declines (Ottema and Spaans 2008, Andres 2011, Morrison et al. 2012), then we would expect to see the greatest declines in the eastern Arctic breeding population, lesser declines in central and eastern Alaskan populations, and little to no decline in the western Alaskan population. Breeding trend data support this conclusion to some extent, although trends in the central and western populations appear to be similar (i.e. stable to increasing; Smith et al. 2012). Alternatively, if declines are being driven by factors along the northern Atlantic Flyway, perhaps at staging sites such as Delaware Bay where horseshoe crab egg availability is an issue (Atkinson et al.

2007, Mizrahi et al. 2012), then we would expect only the eastern Arctic breeding population to be affected, which is consistent with the observed pattern in breeding population trends. However, if declines are being driven by factors in the eastern Arctic breeding range, we would also expect only the eastern breeding population to be affected. Further information on the productivity and survival of individual birds wintering in northeastern South America and breeding in different portions of the Arctic is needed to fully determine the most likely locations of factors causing declines.

Finally, the high connectivity of the populations at the eastern and western extremes of the breeding range raises questions about the low level of genetic differentiation found by Miller et al. (2013). This may have occurred in part because the few samples available from the Seward Peninsula, far western Alaska ($n = 6$), were pooled with North Slope birds into a single "Western" sample; there was in fact an indication of greater allelic diversity within the Seward Peninsula sample. If the current situation reflects long-established patterns, our results suggest that allelic differences between the 2 geographically and morphologically extreme populations should produce a stronger contrast than the data available to Miller et al. (2013) showed.

Stopover Locations

Geolocator data identified stopover areas not previously known to be used by Semipalmated Sandpipers, and not currently part of the Western Hemisphere Shorebird Reserve Network (WHSRN). Two general regions within Venezuela were identified as worth further investigation: the Orinoco Delta region in the east, and the Gulf of Venezuela region, including Lake Maracaibo, in the west. Additional information on the magnitude of passage through these 2 areas is required to understand their relative importance to Semipalmated Sandpipers, and to shorebirds more generally. The Pacific Coast of northern Central America (southernmost Mexico to Nicaragua) also appears to be used during southbound migration by Semipalmated Sandpipers that overwinter on the Pacific Coast of South America. Relatively little attention has been paid to the importance of coastal wetlands in Central America for providing stopover and nonbreeding habitats. However, recent ground surveys here have revealed sites of global conservation importance for shorebirds, in particular within the Gulf of Fonseca, including the Estero del Delta Real in Nicaragua (S. Morales personal communication), where 1 bird carrying a geolocator appeared to winter, and 4 stopped during migration.

It is surprising that only 2 Semipalmated Sandpipers were recorded in the vicinity of the Upper Bay of Panama: 1 bird wintered there and another passed through the area during southbound migration. The Upper Bay of Panama

is a WHSRN Site of Hemispheric Importance and thought to receive major use by nonbreeding populations of small shorebirds, with an estimated 1.3 million birds passing through on southbound migration (Angehr 2003). However, the numbers of Semipalmated Sandpipers that winter in the Bay are low compared with Least (*Calidris minutilla*) and Western sandpipers (Watts 1998). The bird that wintered in the Upper Bay of Panama first stopped in the vicinity of Parita Bay, close to where another bird wintered. Parita Bay has the second-highest abundance of migratory shorebirds among sites in Panama (Angehr 2003).

We also found geolocator evidence that a number of the Alaskan breeders used previously unknown stopover sites in northern Alberta and Saskatchewan. The short length of stopovers, the large number of areas used, and the remoteness of these areas would have made prior sightings of birds difficult, allowing the birds to go largely unnoticed. The ability of the species to use many different sites may reflect the ephemeral nature of stopover sites in this region.

It is surprising that only 3 of 12 eastern breeders stopped in the Bay of Fundy, which was historically thought to host up to 95% of the global Semipalmated Sandpiper population during southbound migration (Hicklin 1987, Mawhinney et al. 1993). It is possible that conditions there have changed since the 1980s (decreases in food availability or increases in predators), or that birds using the Bay of Fundy are from different breeding areas farther east and were not covered by this study. We need more information from additional eastern breeding areas such as Baffin Island and Quebec to decipher the consistency of this pattern. However, the geolocator data did underscore the importance of Delaware Bay (a Hemispheric WHSRN site) and James and Hudson Bay staging sites to eastern breeders.

Migration Duration and Length of Stay

Northbound migration in shorebirds is generally of shorter duration than southbound migration, even when considering only adults (Jehl 1979, Senner and Martinez 1982, Alerstam and Lindström 1990, Colwell 2010), but no previous studies have estimated the total duration of migration for individual Semipalmated Sandpipers. Even at specific sites, little previous information is available to allow comparison of average length of stay during different migration periods. Our results, with accurate measurement of migration duration, found that southbound migration was significantly longer than northbound migration. This difference was inconsistent across important stopover sites, but generally more evident in eastern breeders than birds breeding in the western and central Arctic. Interestingly, our estimates of average prairie site stopover durations of 6.2 days during

northbound and 8.8 days during southbound migration are remarkably similar to previous estimates (Skagen and Knopf (1994): 3.4–9.7 days on northbound migration; Alexander and Gratto-Trevor (1997): 4–6 days northbound and 8–9 days southbound migration), despite potential bias in earlier estimates, which used traditional methods (Iverson et al. 1996, Warnock and Bishop 1998) based on birds captured an unknown amount of time after arrival. However, most other estimates of length of stay based on resightings or radio-transmitters were considerably shorter than estimates from the geolocator data; e.g., Gulf USA spring mean of 6.5 days (Henkel and Taylor 2015) vs. geolocator mean of 12.3 days; James and Hudson Bay fall mean of 6.5 days (Pollock et al. 2012) vs. geolocator mean of 16.8 days; Bay of Fundy fall average of 15.0 days (Hicklin 1987) and Maine fall mean of 11.0–13.7 days in different years (Dunn et al. 1988) vs. Bay of Fundy and New Brunswick geolocator mean of 25.2 days. Our more accurate measures of length of stay will support unbiased calculations of the sizes of populations using these sites during migration for use in monitoring programs.

We found no significant differences between the sexes in the initiation date of northbound migration, in the duration of northbound or southbound migration, or in arrival dates on the breeding grounds. This last result is somewhat unexpected, since displaying males are typically observed setting up territories several days before females are seen (Hicklin and Gratto-Trevor 2010). The complete lack of evidence in the geolocator data for earlier male arrival suggests that sex-biased resightings, rather than true (if small) arrival time differences, drive the perception of sex-biased arrival dates, but sufficient data to allow tests within individual sites would be needed to robustly test this hypothesis. Females usually desert broods earlier than their mates, so it is not surprising that we found an earlier onset of southbound migration in females (Morrison 1984, Gratto-Trevor 1991).

Sites and Movements within South America

Until now, insights into the movement patterns of Semipalmated Sandpipers after arrival in South America have been based on an extremely limited number of recaptures of banded birds or resightings of individuals marked with leg flags with alphanumeric codes, and clarifying the use of wintering sites was a major part of our objective to increase the understanding of migratory connectivity for this species. Our geolocator data dramatically increased the information available about movements within South America, and showed that Venezuela was the first entry point during southward migration for 12 of the 27 individuals that wintered in northeastern South America. These birds moved eastward from Venezuela to winter in Suriname, French Guiana, or Brazil, following

stopovers of up to 23 days (range = 1–23 days, mean = 12.0 \pm 3.6 SE days). Another individual appeared to make first landfall in Guyana, not far from the Venezuelan border, and stayed for 4 days before moving east to winter in Suriname. Four other individuals appeared to fly directly to Suriname after stopovers in the Greater Antilles, with 1 moving farther east to winter in French Guiana.

On northbound migration, only 2 individuals that wintered in the northeastern region of South America retraced their routes through Venezuela, while 1 individual that did not stop in Venezuela on its way south did so on its return trip. Two other individuals traveled as far west as Guyana before departing South America. Eight individuals that wintered in Suriname, French Guiana, and Brazil for which we had northbound tracks appeared to leave directly for stopover sites in Cuba ($n = 3$) or along the Gulf of Mexico in Louisiana ($n = 5$).

Collectively, our movement data suggest that Venezuela is frequently used by birds wintering along the northeastern coast of South America, especially during southbound migration. Specifically, the Orinoco Delta region, in the eastern part of the country, and the Gulf of Venezuela, including the area around Lake Maracaibo in westernmost Venezuela, appear to be key stopover areas for Semipalmated Sandpipers traveling to and from the breeding grounds. The same areas of Venezuela are known to be major conduits for other migratory shorebirds, including Red Knots (*Calidris canutus*; Niles et al. 2010).

Semipalmated Sandpipers that wintered in northwestern South America exhibited relatively limited movements after arrival on the continent compared with birds breeding in the northeastern region. A number of individuals made landfall in Ecuador (8), Peru (1), and Colombia (1) and moved little thereafter. Two other individuals arrived first in Colombia and, after short stopovers, traveled to Ecuador to winter. In contrast, 2 individuals first stopped in Venezuela, stayed for >130 days, and then moved to wintering areas in Colombia. However, no individuals that wintered in northwestern South America used Venezuela as a starting point for their northward migrations. One bird that overwintered in Peru was near Faclo Grande, the site with the highest Semipalmated Sandpiper abundance among nonbreeding sites in the north of the country, as recorded during a recent coast-wide survey (Senner and Angulo Pralongo 2014).

Six birds appeared to winter in the area of the Guayas Estuary in southwestern Ecuador. The estuary is an extensive area of mangroves and mudflats within the Gulf of Guayaquil. Morrison and Ross (1989) recorded surprisingly low numbers of shorebirds within the estuary (1,714 small shorebirds), and the area has not been highlighted as critical for shorebirds in subsequent priority site assessments, despite being considered globally significant for

other waterbird species (Freile and Santander 2005). However, Ridgely and Greenfield (2001) noted thousands of shorebirds wintering in the Guayas estuary. Recent fieldwork has confirmed the continued presence of flocks of thousands of Semipalmated Sandpipers (A. Agreda personal communication). Two Ramsar Convention sites and several protected areas exist within the estuary, but extensive construction of shrimp ponds has occurred, with significant pressure on remaining mangrove habitats to be converted to shrimp farms or used for urban expansion (Freile and Santander 2005).

Factors Underlying Observed Population Declines

Anthropogenic harvest on the wintering grounds and alteration of habitat at major migration stopover areas have been suggested as possible causes for population declines of Semipalmated Sandpipers (Mizrahi et al. 2012, Morrison et al. 2012, Watts et al. 2015), although the impacts of these activities are unclear. For example, shorebirds are harvested throughout many parts of the Caribbean and northern South America for subsistence, recreation, and market hunting (Andres 2011). Such harvest may impose population-level constraints for some species (Zöckler et al. 2010), although knowledge of which shorebird populations use areas with harvest would allow a better assessment of the potential impact of harvest (Watts et al. 2015). In addition, anticipated sea level rise may affect mangrove communities in Suriname, French Guiana, and northern Brazil, and expanding shrimp aquaculture is reducing salt flat and mangrove habitats that are used by foraging and roosting shorebirds, respectively (Carlos et al. 2010). Shrimp farming may also expose shorebirds to harmful chemicals, but this is only beginning to be studied. Locating the areas in which birds from declining wintering populations spend the remainder of their life cycle is necessary to assess possible causes of declines outside wintering areas and to devise appropriate conservation actions.

When evaluating factors underlying apparent population declines in Semipalmated Sandpipers, it is important to consider recent information about the potential adverse effects of illegal or poorly regulated hunting on shorebirds during migration or overwintering periods (Ottema and Spaans 2008, Watts et al. 2015). Although specific information about hunting pressure or the magnitude of mortality across Semipalmated Sandpiper migration and wintering ranges is incomplete, the data that do exist have conservation implications. Ottema and Spaans (2008, p. 344) reported that “several tens of thousands” of shorebirds, primarily Semipalmated Sandpipers and Lesser Yellowlegs (*Tringa flavipes*), were trapped or shot each year in Suriname. Importantly, coastal Suriname supported the greatest abundance of Semipalmated Sandpipers in coastal South America in the 1980s, with estimates of

~1.35 million birds (Morrison and Ross 1989). Morrison et al. (2012) reported a nearly 80% decline in Semipalmated Sandpiper populations wintering in Suriname and French Guiana between the mid-1980s and the mid-2000s. The authors suggested that the most conservative estimate of removal from hunting described by Ottema and Spaans (2008), of 20,000 birds annually, when applied to a population of 2 million individuals, the estimate for Semipalmated Sandpipers wintering in Suriname and French Guiana combined, could cause a significant population decline (~26%) in the species. Patterns of connectivity from our geolocator study suggest that populations that breed along the eastern portion of Alaska’s North Slope and in Canada’s Mackenzie Delta and northern Hudson Bay winter in the Guianas or pass through the region during migration to and from northern Brazil. Additionally, Semipalmated Sandpipers that winter in the Guianas often pass through the Caribbean basin. Although surveys of resource managers across the region suggest that Semipalmated Sandpipers are not a target species for hunters, unintended or unreported mortality from hunting could be occurring (B. Andres personal communication).

Many other potential causes of decline merit further investigation. For example, Pfister et al. (1992) noted that disturbance of birds at migration stopover sites, which is common along the Atlantic Flyway, can lower survival rates. Henkel et al. (2014) explored impacts from the Deepwater Horizon oil spill in the Gulf of Mexico and noted potential negative effects on shorebirds from long-term exposure to toxins, degraded habitats, and altered food chains. Exposure to contaminants in the Gulf of Mexico may be important given the migration routes shown here, and the use of the Gulf region as a stopover site by birds from many breeding and wintering areas. Habitat loss and degradation have also been severe along the Atlantic Flyway, including the decline in horseshoe crab eggs used as a major food source during spring migration (Mizrahi and Peters 2009), and have been suggested as a major cause of shorebird population declines (Brown et al. 2001), but relative impacts are difficult to measure given the large number of potentially affected stopover sites. Parks et al. (2016) noted that while populations declined in Puerto Rico between the 1980s and 2014, body condition did not change over that time, suggesting the population declines were not caused by habitat conditions there.

Effect of Geolocators on Return Rates

Geolocators decreased the return rates of Semipalmated Sandpipers, both overall and at 2 of 7 sites that had control groups for comparison. Across all sites, birds carrying geolocators were 57% as likely to return as control birds, indicating a substantial impact on these birds that is much

stronger than what has been observed in most other, larger shorebird species (Pakanen et al. 2015, Weiser et al. 2016). Resighting effort was sometimes higher for birds with geolocators than for control birds, so additional site-specific negative effects of geolocators, and/or larger overall negative effects, could have been masked by underestimated return rates for the control groups. The impact of geolocators appeared to be greater in the 2013 season than the 2015 season at Coats Island, and greater for birds from the eastern Arctic than from other sites in the 2013 season, which may indicate that year effects such as severity of storms during migration, or other impacts on survival rate or site fidelity, vary among years. It is also possible that the spacer band reduced the impact of carrying the geocator in 2015, so we recommend use of this technique. The mechanisms of reduced return rates should be investigated further in the future, but our findings indicate that application of alphanumeric flags along with geolocators should be avoided, and that applying geolocators to previously banded birds with proven site fidelity may help to improve recovery of geolocators.

While our study may have caused mortalities associated with attachment of geolocators, Semipalmated Sandpipers are an abundant species, with an estimated total population size of 2.26 million birds (Andres et al. 2012b). Our study is unlikely to have affected the species on a population level, and the movement data gained can be applied to direct future research and conservation efforts. However, our return rate data suggest that there are impacts on individuals carrying geolocators, in addition to the many other cumulative stressors facing migratory shorebirds, so caution should be used when applying geolocators, especially to small shorebirds.

Conclusions

Our results confirm that Semipalmated Sandpipers that breed in the eastern Arctic and use the Atlantic Flyway also use the areas in South America where population declines have been detected, suggesting that declines may be concentrated in populations along the Atlantic Flyway and in the eastern Arctic. However, because some birds from sites as far west as Barrow also used the areas in northeastern South America where declines have occurred, further work is necessary to localize the geographic areas used by declining populations, and therefore the potential causes for the declines. We identified several new stopover and wintering areas, where implementing conservation actions to preserve the habitats used by Semipalmated Sandpipers could contribute to protecting the species. We measured a larger impact of geolocators on return rates than has been observed for larger shorebirds, indicating that caution should be used when working with small shorebirds, and that potential new information gains

from additional geocator studies should be weighed against expected impacts on individual survival. Our data provided new insights into stopover ecology and duration of stay in various areas, which could be useful to studies that measure and monitor the total size of populations using these sites. Understanding the migratory connectivity of these populations of a widespread yet declining shorebird can help future studies to identify the causes of declines and ensure the effectiveness of targeted conservation efforts.

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Author contributions: S.B., R.B.L., B.K.S., and R.P. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). All authors performed the experiments (collected data, conducted the research). S.B., C.G.-T., R.P., E.L.W., D.M., M.B., R.C., M.-A.G., E.K., S.S., P.S., A.T., B.W., B.K.S., and R.B.L. wrote the paper (or substantially edited the paper). R.P., R.B.L., and E.L.W. developed or designed methods. R.P., E.L.W., S.B., R.B.L., C.G.-T., E.K., and S.F. analyzed the data. All authors contributed substantial materials, resources, or funding.

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