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Source: Waterbirds, 35(1):83-95. 2012.
Published By: The Waterbird Society
DOI: http://dx.doi.org/10.1675/063.035.0109
URL: http://www.bioone.org/doi/full/10.1675/063.035.0109

Migratory Connectivity of Semipalmated Sandpipers: Winter Distribution and Migration Routes of Breeding Populations

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Abstract.— The Semipalmated Sandpiper (*Calidris pusilla*) is a small, abundant shorebird that breeds primarily in sub-Arctic to mid-Arctic habitats across the Nearctic and winters principally along the northern and central coasts of South America. No subspecies have been described and little is known concerning their genetics. However, birds show a cline in bill length across the Arctic, with longest bills in the east and shortest in the west. There appear to be several 'steps' in the cline, suggesting a division into eastern, central and western breeding populations. Since females average longer bills than males in a breeding population, there is considerable overlap of bill lengths at migration staging areas. Based on bill length patterns and sightings and recoveries of marked individuals, most western breeders migrate south through the prairies, along with some birds from central Arctic populations. The remaining central Arctic breeders, and all eastern Arctic birds, migrate south through the north Atlantic Coast of North America, particularly the Bay of Fundy. Western Arctic breeders appear to winter farther west in South America than eastern breeders, although there is considerable mixing among populations in French Guiana and Guyana. In spring, birds from the eastern Arctic migrate north through the U.S. Atlantic coast, including Delaware Bay. Central and western Arctic breeders primarily migrate north through the interior of North America. Therefore, central Arctic breeders in particular demonstrate an elliptical migration pattern. *Received 27 December 2010, accepted 2 December 2011.*

Key words.—bill length**,** *Calidris pusilla,* migration, populations, Semipalmated Sandpiper.

Waterbirds 35(1): 83-95, 2012

Effective conservation of migratory birds depends on knowledge of nonbreeding sites used by different breeding populations, including migratory stopovers and wintering sites (Myers *et al.* 1987; Gauthreaux 1996; Webster *et al.* 2002). Linkages among breeding, staging, and wintering sites can aid in assessing which breeding populations will be affected by gradual habitat loss and degradation or by catastrophic events (such as hurricanes or oil spills) at specific nonbreeding sites. These linkages, recently referred to as 'migratory connectivity', can be made in different ways, including morphometrics (e.g. Harrington and Morrison 1979; Engelmoer and Roselaar 1998), banding (e.g. Stucker *et al.* 2010), radio or satellite telemetry (e.g. Iverson *et al.* 1996; Haig *et al.* 2002), data loggers (e.g. Conklin and Battley 2010), genetics (e.g. Haig *et al.* 1997), and stable isotopes (e.g. Farmer *et al.* 2003); each technique has advantages and disadvantages for different species. For small shorebirds that migrate large distances over a broad range and for which useful telemetry devices are too large or logistics of recovering devices are too difficult, color marking is commonly used.

Semipalmated Sandpipers (*Calidris pusilla*) are small migratory shorebirds that breed in the sub-Arctic to mid-Arctic across northern Canada and Alaska and winter primarily in northern and central coasts of South America (Hicklin and Gratto-Trevor 2010); very few

winter in the United States and few in the West Indies (Phillips 1975). They are one of the most common shorebirds in North America during migration, particularly in the east (Hicklin and Gratto-Trevor 2010), but also through the North American Midwest (Skagen *et al.* 1999). There has been evidence of population declines, both in North America (Morrison *et al.* 2001, 2006) and South America (Ottema and Spaans 2008; Morrison *et al.* 2012). No subspecies has been named, but morphometrics, particularly bill length, vary across the breeding range (Harrington and Morrison 1979). An early genetics analysis using random amplified polymorphic DNA found that the genetic identity of individuals from different breeding areas overlapped extensively (Haig *et al.* 1997).

Semipalmated Sandpipers arrive on the Arctic breeding grounds in late May to early June. Birds pair monogamously, both parents share in incubation for 19-21 days (Hicklin and Gratto-Trevor 2010), and chicks fledge in 16-19 days (Safriel 1975; Gratto-Trevor 1991). Females usually desert the brood earlier than their mates, earliest if nests hatch late in the season (Ashkenazie and Safriel 1979; Gratto-Trevor 1991). Most Semipalmated Sandpipers do not attempt to breed until two years of age (Spaans 1984; Gratto 1988). Generally, non- or failed breeders migrate south first, followed by adult females. Successful males follow in a few days, then juveniles several weeks later (Morrison 1984).

The marking studies of McNeil and Burton (1973, 1977) demonstrated that spring and fall migration routes of Semipalmated Sandpipers were different for at least some populations. Harrington and Morrison (1979) reviewed dates and relative abundances of Semipalmated Sandpipers in different regions during spring and fall migration and examined morphometrics of birds in various breeding and migration areas to propose migratory routes used by different breeding populations. Their analysis of bill length coefficients of variation (CV) suggested that fall migrants at specific staging sites had originated from a larger geographic area than birds at spring staging areas, since CVs of mixed populations will be higher than those of samples drawn from a restricted part of the breeding range. Other studies of Semipalmated Sandpiper migration routes followed, including Lank (1983), Morrison (1984), Hicklin (1987), Gratto-Trevor and Dickson (1994), among others, which are discussed later. The purpose of this study is to combine published and unpublished information with North American Bird Banding Office recoveries to produce an updated review of geographic differences in bill length, migration routes and wintering areas of breeding populations of Semipalmated Sandpipers.

Banding and Bill Lengths

Bill length refers to exposed culmen (from feathers at the base of the bill to the tip of the bill, in mm; Prater *et al.* 1977; Gratto-Trevor 2004). We obtained Semipalmated Sandpiper bill length measurements from live birds and specimens from breeding, staging, and wintering areas across the range (Tables 1-3). Engelmoer and Roselaar (1998) found that bill lengths decrease by approximately 1% in dried specimens, so that field measurements of live birds may not be directly comparable with those from museum specimens. However, Prater *et al.* (1977) did not find the difference significant, and measurements were not adjusted here.

Recoveries of banded birds were retrieved from North American Bird Banding Office records, with a few additional resightings of birds marked in or seen at breeding areas, primarily from published literature, plus a few additional records from enquiries to individual researchers. Recoveries were often not in the same year the bird was banded. We divided recoveries as follows: winter was considered to be between November and February, spring between March and May in nonbreeding areas, summer in breeding area locations from May to July, and fall in nonbreeding areas between July and October. Many of the South American recoveries, especially in the Caribbean and Guyana, are from areas where the birds are hunted, whereas most North American recoveries are recaptures of live birds.

Bill Lengths and Breeding Distribution

There is a geographic cline in average bill lengths from east to west, with the shortest bill

lengths in the west (Fig. 1, Table 1). There appear to be distinct steps in the cline; bill lengths in the western part of the range (Alaska) average 17.8 to 18 mm, those of central Arctic breeders (western Arctic Canada) range from 18.6 to 19.1, and birds in the eastern Arctic (eastern Baffin Island/western James Bay and east) average from 20.1 to 20.6 mm. Within each Semipalmated Sandpiper breeding site, there is overlap between the sexes in bill length, although female bill length averages about 10% greater than males (Table 2).

Average bill length in spring is greater in the U.S. mid-Atlantic coast (e.g. Delaware Bay) compared to areas farther south on the Atlantic coast (Fig. 2, Table 3), suggesting that western breeders on northwards migration arrive in North America at points farther south along the Atlantic coast than eastern-breeding birds. A greater percentage of females to males farther north on the coast might also produce this pattern, but this has not been tested and would be unlikely to completely explain these bill length differences. The short average bill lengths of birds in the interior in spring suggest that central Arctic breeders migrate north primarily through the interior. In the fall, bill lengths of sandpipers migrating through the interior are shorter than in spring, suggesting a western breeding origin of migrants there. Long average bill lengths in the northeast suggest that eastern and perhaps central Arctic breeders migrate south through the eastern seaboard. In South America, birds with the shortest average bill lengths (presumably western and perhaps some central Arctic breeders) are found on the west coast, and longest bill lengths (eastern Arctic breeders) are found in Brazil. Averages in Suriname and French Guiana are intermediate. In Suriname, average bill length of adult Semipalmated Sandpipers is longest during both south- and northbound migration periods, compared to the winter or summer periods (Spaans 1984), which suggests movements of longer-billed birds (birds from more eastern breeding areas) from Suriname and French Guiana in spring and fall, leaving birds from farther west or a mix of birds from various breeding areas in Suriname and French Guiana in winter.

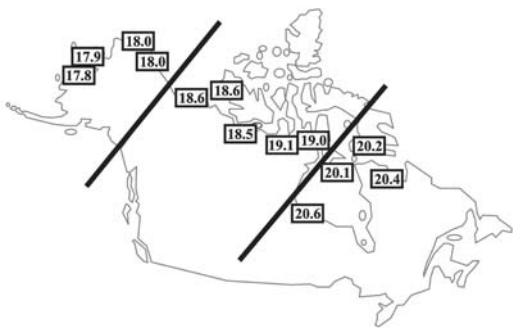

Figure 1. Geographic variation in average bill length (exposed culmen, mm) of Semipalmated Sandpipers across the breeding range. Solid black lines separate steps in the bill length cline; potentially separate breeding populations: West (Alaska), Central (Yukon to western Baffin Island/northwestern Hudson Bay), East (eastern Baffin Island/southwestern Hudson Bay and eastwards). See Table 1 for sources of data.

Recoveries and Resightings of Marked Birds

Relatively few (28) marked Semipalmated Sandpipers have been observed both in breeding areas and at other locations. Of those reported, almost all involve birds from Alaska (Fig. 3a and 3b). Only 225 Semipalmated Sandpipers (many of them chicks) have been marked in central Arctic breeding areas, and of those, none has been recovered elsewhere. In spring, western breeders migrated north through the interior of North America (e.g. Kansas), while eastern breeders staged in more easterly (often coastal) locations (Fig. 3a). Fall/winter resightings/recoveries of western breeders are primarily interior, with a few reports from the southeast Atlantic coast and the Gulf of Mexico, but none from the northeast Atlantic coast where over 64,000 Sandpipers have been banded (Fig. 3b). The only two recoveries of known eastern breeders were birds nesting at La Pérouse Bay, Manitoba, previously marked at James Bay during fall migration (Morrison 1984). Alaskan birds were marked or found in both north-central and western parts of the wintering range, including Suriname, Guyana, Venezuela and Ecuador (Fig 3b).

Overall winter - spring connections (individual birds marked during spring migration or during winter and recovered

Table 1. Average bill length (exposed culmen, mm) of Semipalmated Sandpipers across the breeding range, from west to east. Measurements are from live birds unless noted otherwise.

Breeding Location	Latitude, Longitude	N	Mean	SD	Source
WEST					
Cape Espenberg, AK	66°32'N, 163°36'W	—	17.8	—	D. M. Tracy, unpublished data
Nome, AK	64°20'N, 164°56'W	201	17.9	—	Sandercock 1998
Barrow, AK	71°17'N, 156°47'W	77	18.0	1.0	R. Lanctot, unpublished data
Prudhoe Bay, AK	70°19'N, 148°42'W	419	18.0	—	D. Troy, unpublished data
CENTRAL					
Mackenzie Delta, NT	69°20'N, 135°05'W	11	18.6	0.6	C. Gratto-Trevor, unpublished data
Banks Is., NT	73°00'N, 121°30'W	12	18.6*	—	Harrington and Morrison 1979
Mackenzie district, NT	~68°N, 100-135°W	9	18.5*	—	Harrington and Morrison 1979
Rasmussen Lowlands, NU	68°26'N, 94°45'W	10	19.1	1.4	C. Gratto-Trevor, unpublished data
Keewatin district, NU	~67°N, 80-100°W	26	19.0*	—	Harrington and Morrison 1979
EAST					
La Pérouse Bay, MB	58°44'N, 93°25'W	284	20.6	1.2	C. Gratto-Trevor, unpublished data
Coats Island, NU	65°51'N, 82°29'W	50	20.1	1.4	P. Smith, unpublished data
East Baffin Island, NU	~65°N, 68°W	29	20.2*	—	Harrington and Morrison 1979
Belcher Is./E Hudson Bay, QC	~56°N, 76-79°W	31	20.4*	—	Harrington and Morrison 1979

*museum specimens

or resighted in winter or spring) indicate that birds migrating farther to the east in spring wintered farther to the east (Fig. 3c). Recoveries from fall to winter were primarily in north-central South America, including birds marked during fall migration in northeastern North America, James Bay, Saskatchewan and Kansas (Fig. 3d). On the whole, fall recoveries are generally farther to the northeast than those in spring (Fig. 3c and 3d), reflecting the elliptical migration of some populations (Spaans 1984; Gratto-Trevor and Dickson 1994). There are a few anomalies, includ-

Table 2. Average bill length differences between male and female Semipalmated Sandpipers during breeding and migration. Sex difference was calculated by: (average female bill length – average male bill length)/average male bill length.

			Female			Male			Sex
Location	Popn	Season	N	Mean	SD	N	Mean	SD	difference
Barrow, AK[a]	West	Breeding	11	19.1	0.6	22	17.3	0.8	10%
Nome, AK[b]	West	Breeding	106	18.7	0.9	95	17.1	0.8	9%
La Pérouse Bay, MB[c]	East	Breeding	149	21.5	0.8	135	19.8	0.7	9%
North Dakota[d]	Mix	Spring	44	20.2	1.1	53	18.3	0.8	10%
Saskatchewan[e]	Mix	Spring	5	20.0	0.6	8	18.1	0.9	10%
Saskatchewan[e]	Mix	Fall	12	18.9	1.0	8	17.6	0.6	7%
James Bay, ON[f]	Mix	Fall	67	20.2	1.1	44	18.4	0.8	10%
Bay of Fundy, NB[g]	Mix	Fall	304	21.5	1.2	151	19.6	0.9	10%
Bay of Fundy, NS[h]	Mix	Fall	71	21.0	1.4	79	19.6	1.4	7%
Grand Manan, NB[i]	Mix	Fall	27	20.5	1.0	55	19.3	1.1	6%
Plymouth Bay, MA[j]	Mix	Fall	27	20.7	1.3	18	18.7	1.0	11%
Suriname[k]	Mix	Fall/Winter	15	20.5	1.2	33	18.9	0.8	8%

[a]MacLean 1969 (sexed by dissection).
[b]Sandercock 1998 (sexed by pair differences in size).
[c]Gratto-Trevor unpubl. (sexed by behavior such as male flight displays, pregnant females).
[d]Krapu et al. 2006 (sexed by dissection).
[e]Alexander and Gratto-Trevor 1997 (sexed by dissection).
[f]Morrison 1984 (sexed by dissection).
[g]Hicklin and Gratto-Trevor unpubl. (sexed by dissection).
[h]Boates 1980 (sexed by dissection).
[i]White 1985 (sexed by dissection).
[j]Harrington 1982 (sexed by dissection).
[k]Spaans unpubl. (sexed by dissection).

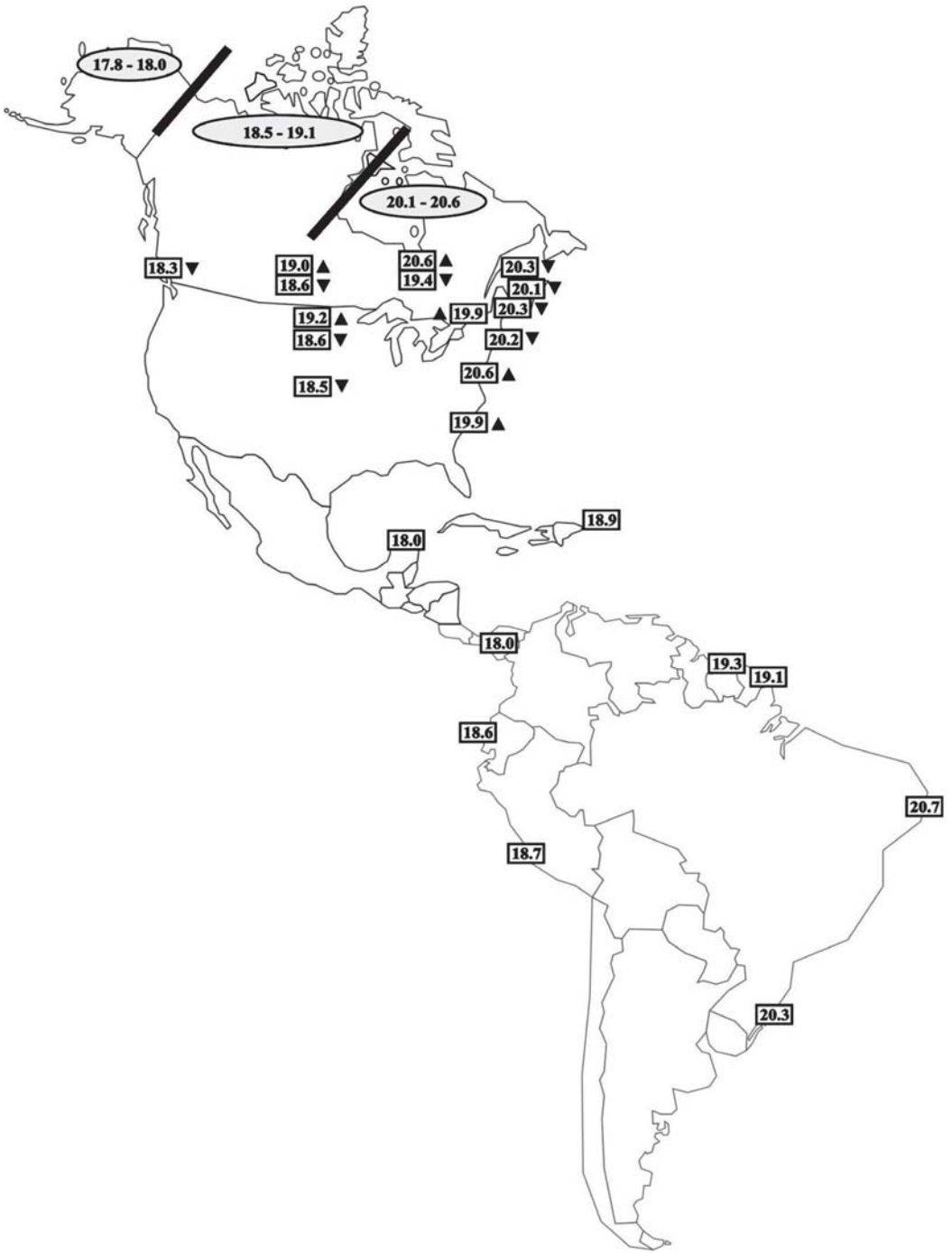

Figure 2. Geographic variation in average bill length (exposed culmen in mm) of Semipalmated Sandpipers during migration and on the wintering grounds. Arrows indication direction of migration at staging sites (upwards spring, downwards fall). Circled values represent average of bill lengths on the breeding grounds for western, central and eastern populations (see Fig. 1). See Table 3 for data sources.

ing a bird marked in fall on the Fraser River Delta, BC, recovered in Guyana, one marked in fall in southern Ontario recovered on the west-central coast of Mexico, and one banded in the Bay of Fundy, New Brunswick, in fall recovered in Ecuador

Table 3. Average bill length (exposed culmen in mm) of Semipalmated Sandpipers during migration and on the wintering grounds, from west to east in each country. Measurements are from live birds except for frozen specimens in spring North Dakota.

Country	Location	Latitude, Longitude	Season	N	Mean	SD	Source
Canada	Fraser River Delta, BC	49°04'N, 122°55'W	fall	16	18.5	1.0	S. Franks and B. Schwarz, unpublished data
	Little Quill Lake, SK	51°55'N, 104°00'W	spring	725	19.0	1.1	Gratto-Trevor and Dickson 1994
	Little Quill Lake, SK	51°55'N, 104°00'W	fall	88	18.6	1.4	Gratto-Trevor and Dickson 1994
	James Bay, ON	51°23'N, 80°24'W	spring	354	20.6	—	Morrison 1984
	James Bay, ON	51°23'N, 80°24'W	fall	22,875	19.4	—	Morrison 1984
	Ottawa, ON	45°24'N, 75°41'W	fall	56	19.9	1.3	T. & J. Dean, C. Gratto-Trevor, unpublished data
	Magdalen Is., QC	47°26'N, 61°47'W	fall	858	20.3	1.4	Y. Aubry, unpublished data 1983
	Dorchester Cape, NB	45°52'N, 64°29'W	fall	1,225	20.1	1.4	P. Hicklin, unpublished data 1982
	Kent Island, NB	44°35'N, 60°27'W	fall	1,161	20.3	1.5	Lank 1983
United States	Stutsman/Kidder Co., ND	46°52'N, 99°45'W	spring	97	19.2	—	Krapu et al. 2006
	Sibley Lake, ND	45°57'N, 99°43'W	fall	617	18.5	1.2	Lank 1983
	Kansas	38°30'N, 98°38'W	fall	355	18.5	1.6	S. Franks, unpublished data
	Plymouth, MA	41°57'N, 70°38'W	fall	1,929	20.2	1.6	Harrington 1982
	Delaware Bay, NJ	39°11'N, 75°05'W	spring	9,136	20.6	1.5	D. Mizrahi, unpublished data
	Georgetown, SC	33°20'N, 79°09'W	spring	1,542	19.9	1.4	J. Lyons, unpublished data
Mexico Yucatan		21°18'N, 88°20'W	winter	8	18.0	1.4	S. Franks, B. Schwarz and J. Carrea, unpublished data
Panama		8°58'N,79°29'W	winter	11	18.0	1.6	S. Franks and B. Schwarz, unpublished data
Puerto Rico		1 7°56'N, 67°06'W	fall/winter	106	18.9	1.1	Rice et al. 2007
Ecuador		2°13'N,80°58'W	winter	67	18.6	1.2	B. Schwarz and B. Haase, unpublished data
Peru		17°06'N,71°54'W	winter	—	18.7	—	Morrison and Myers in Morrison 1984
Suriname		5°54'N,54°55'W	winter	776	19.3	1.4	D. Mizrahi, unpublished data
Suriname		5°55'N,55°19'W	winter	995	19.4	1.4	A. L. Spaans, unpublished data
French Guiana		5°44'N,53°54'W	winter	1,326	19.1	1.5	D. Mizrahi, unpublished data
Brazil	Rio Grande do Sul	31°21'S, 50°00'W	winter	57	20.3	1.5	Resende *et al.* 1989
	Lagoa de Peixe	31°20'S, 51°00'W	winter	11	19.4	1.3	Harrington *et al.* 1986
	Coroa do Aviao	7°40'S, 34°50'W	winter	251	20.7	1.5	de Azevedo and Larrazabel 1999

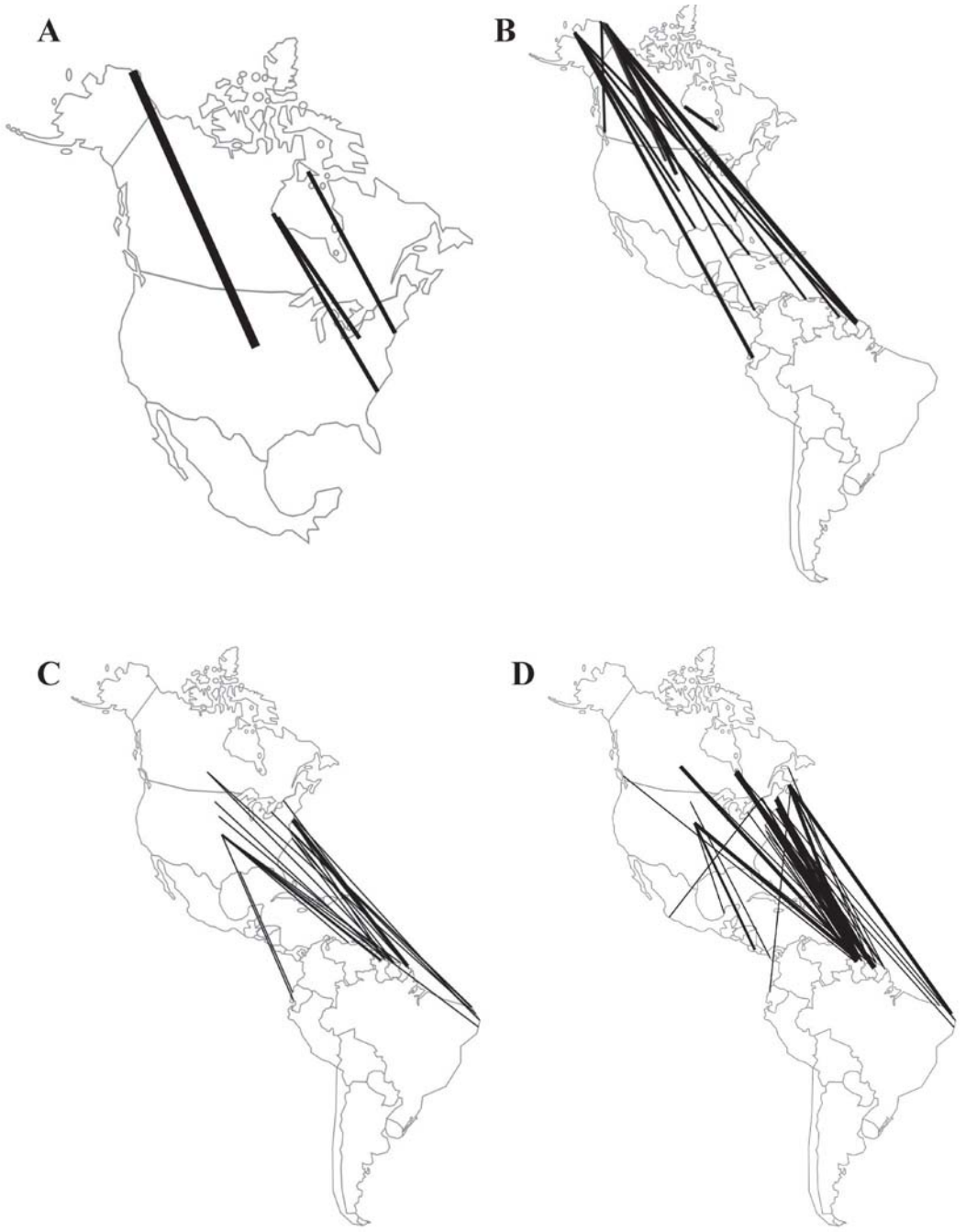

Figure 3. Recoveries of marked Semipalmated Sandpipers. Observations connected by lines were not necessarily from the same year. Data were obtained from North American Bird Banding Recoveries, Martinez 1974, Morrison 1984, Sandercock *et al.* 2000, C. Gratto-Trevor unpublished data, D. Lank unpublished data, D. Troy unpublished data. A: Spring to breeding area recoveries. The thinnest line represents one bird; thicker lines two individuals. B: Breeding area to fall and winter recoveries. The thinnest line represents one bird; thicker lines two to four individuals. C: Winter to spring recoveries. The thinnest line represents one bird; the thicker the line the more individuals (up to a maximum of eleven birds). D: Fall to winter recoveries. The thinnest line represents one bird; the thicker the line the more individuals (up to a maximum of 101 birds).

(Fig. 3d). Fall-marked birds recovered in the Caribbean came from a wide variety of locations, including eastern Canada (primarily the Bay of Fundy and the Magdalen Islands), New England, James Bay, North Dakota, Kansas, and North Carolina, and in spring in New Jersey and Kansas (North American Banding Office recovery data). Overall, the banding and morphometric analyses provide consistent interpretations of the routes taken by western, central and eastern breeding populations of Semipalmated Sandpipers.

MAJOR BANDING AND MIGRATION ROUTE STUDIES AT SPECIFIC STAGING SITES

Magdalen Islands, Quebec Fall versus Venezuela Spring

Fall migrants from the Magdalen Islands in eastern Canada (47°26'N, 61°47'W) had higher energy reserves than those initiating spring migration from northeastern Venezuela (10°41'N, 63°46'W), suggesting a longer nonstop trans-ocean flight in fall from eastern Canada to northern South America for many birds, compared to the shorter flights of the northward migration when birds use an interior route in spring (McNeil and Cadieux 1972; McNeil and Burton 1977).

New Brunswick Fall versus North Dakota Fall

Lank marked Semipalmated Sandpipers during fall migration at Kent Island, New Brunswick, in the Bay of Fundy, Canada (44°35'N, 60°27'W), and at Sibley Lake, Kidder County in east-central North Dakota, USA (45°57'N, 99°43'W; Lank 1979, 1983). Interior birds had shorter bills and a western Arctic origin, whereas eastern migrants had longer bills and bred in more eastern areas. Resightings of marked birds showed that Semipalmated Sandpipers caught in the interior were seen farther west (and farther south on the Atlantic coast of North America) than those from the Bay of Fundy. Western birds were found farther west on the wintering grounds, although there was some mixing in north-central South America, and one bird marked in July 1977 in New Brunswick was recovered in Ecuador in March 1979 (see Fig. 3d).

James Bay, Ontario

Approximately 40,000 Semipalmated Sandpipers were marked on the southwest coast of James Bay, Canada (51°23'N, 80°24'W), between 1974 and 1982, primarily during fall migration (Morrison 1984). Birds dispersed to the eastern coast of North America, from the Bay of Fundy to Pennsylvania, with a concentration in the Bay of Fundy. In winter they were observed in Guyana, Suriname, French Guiana and Brazil. A comparison of CVs of James Bay birds to those of samples from the breeding grounds indicated that fall migration birds at James Bay originated from a relatively small part of the breeding range. Morrison (1984) noted a decline in average bill length over the fall migration season. He considered that the slightly earlier migration of females (with their longer bills) than males might explain part of the trend, but that it was also due to birds from farther west arriving at James Bay later in the fall migration season.

Saskatchewan Spring versus Fall

Semipalmated Sandpipers were marked during both spring and fall migration at Little Quill Lake, Saskatchewan, Canada (51°55'N, 104°00'W; Gratto-Trevor and Dickson 1994, Alexander and Gratto-Trevor 1997). Resightings of these birds verified the elliptical migration of some populations. On average, longer billed birds (central plus western Arctic breeders) migrated through Saskatchewan in the spring. In the fall, smaller billed (western) birds migrated south through the same area, some of which had been marked there in the spring, while other spring migrants (presumably central Arctic breeders) staged in eastern Canada and the northeastern U.S. Both spring and fall migrants were seen in northeastern South America.

French Guiana

From 1994 to 1998, over 2,000 Semipalmated Sandpipers were banded in coastal French Guiana during fall and winter (5°10'N, 52°38'W; Hansen-Chaffard 2000; E. Hansen-Chaffard; A. LeDreff and P. Hicklin, unpublished data). Resightings and recoveries of marked birds were from many areas of Canada and the U.S., from the Atlantic coast (New Brunswick to South Carolina) to the interior (Saskatchewan), and one in British Columbia. The longer average bill length of birds captured during early fall migration in French Guiana (August through October) indicated an eastern/central Arctic breeding origin, whereas shorter average bill lengths later in the season (October, November), suggested those birds originated from breeding areas farther west. Two birds marked in Brazil (December and February) were observed in French Guiana between August and October, demonstrating southeastern movements of fall migrants. One bird from Chile was seen in French Guiana in February.

Bay of Fundy, New Brunswick

Central and eastern Arctic birds migrate to wintering areas in north-central and eastern South America via the Bay of Fundy, Canada. At the Bay of Fundy, individuals stage for 7-12 days to deposit fat reserves in order to accomplish the non-stop flight over the Atlantic Ocean. Long-billed eastern arctic breeders are the first to arrive in the Bay of Fundy during fall migration, and are the first to leave (Hicklin and Gratto-Trevor 2010). Eight Semipalmated Sandpipers color-marked near Dorchester Cape, Bay of Fundy (45°52'N, 64°29'W) were seen along the coast of Suriname the same year they were banded (P. Hicklin, unpublished data), and 16 marked adults were recaptured in French Guiana (Hansen-Chaffard 2000; see Hicklin and Gratto-Trevor 2010). One adult Semipalmated Sandpiper banded in the Bay of Fundy was captured in Maranhão, Brazil (Rodrigues 2000), and two other adults banded in Brazil were recaptured in the Bay of Fundy (P. Hicklin, unpublished data; Hicklin and Gratto-Trevor 2010). Both adults and juveniles marked in the Bay of Fundy were observed in Caribbean countries (A. Lartiges, personal communication) and captured in regions farther south and east (A. Levesque, personal communication), although juveniles are more commonly seen on the Caribbean islands than in areas farther south (A. Levesque, personal communication). Few migrants stage in the Bay of Fundy in spring (Hicklin 1987).

Suriname

Of 7,041 Semipalmated Sandpipers marked in Suriname (5°55'N,55°19'W) during January to May 1976 and 1977, more than 170 were resighted or recovered elsewhere (Spaans 1984, 2003). This indicated that birds did not depart for North America before early May and arrived in their breeding areas from late May to mid-June. Birds began to leave breeding areas in the first ten days of July, with a migration peak through North America from late July to early August. Shortly after that period, recoveries from North America decreased sharply, with the first reports of marked birds from the Caribbean and South America at that time. Most sightings and recoveries occurred in the interior of the U.S. during spring migration and in eastern Canada and the U.S. during fall migration, which suggests an elliptical migration for most central Arctic breeders and perhaps some western breeders. In one year, 22 birds marked at James Bay during fall migration were seen later in Suriname (Morrison and Spaans 1979). Many of the birds arriving in Suriname in late summer or early fall migrated farther southward to winter in French Guiana and Brazil. From the drop in average bill length in Suriname after this migration, most of these migrants were apparently eastern breeders. Only 0.1% of marked yearlings (marked in their first winter) were reported from outside Suriname during the year of banding compared to 1.3% of older birds during the year of banding, indicating that few juveniles returned to North America the following summer. Many remained in tropical wintering grounds the entire year.

Delaware Bay, New Jersey, Spring

Birds marked during spring at Delaware Bay, New Jersey, USA (39°11'N, 75°05'W), were resighted in spring in North Carolina (1), Del-

aware (1), Wisconsin (1), and Michigan (1), and in fall in eastern Canada (New Brunswick 2, Quebec 1), New England (Massachusetts 4, Maine 4, Connecticut 3), New York (2), New Jersey (1), Florida (1), and James Bay, Ontario (1) (D. Mizrahi, unpublished data). Eight birds marked in fall in New Brunswick were seen at Delaware Bay, New Jersey, in spring. A Semipalmated Sandpiper marked in New Jersey in the spring was observed in Florida in February. Six spring New Jersey birds were reported from the Caribbean (Guadeloupe 3, Puerto Rico 2, Grand Turks 1), and 28 from South America (French Guiana 25, Brazil 2, Guyana 1), while one bird from Brazil and two from Suriname were seen at Delaware Bay in spring. This supports the primarily eastern and perhaps central Arctic origin of spring Delaware Bay migrants, which generally returned south farther north on the Atlantic coast.

CONCLUSIONS

Owing to the cline in bill length across the breeding range, we can use average bill lengths obtained during migration or on the wintering grounds to give some indication of the breeding population(s) in those nonbreeding areas. Interpretation of geographic origin is complicated not only by the overlap in bill length among breeding populations, but also by the sex differences in bill length discussed above (e.g. sizes of bills of eastern males overlap with those of western females). Semipalmated Sandpipers cannot be identified to sex by plumage, thus unsexed migrants are an unknown mixture of sexes and breeding populations. Nonetheless, in staging and wintering areas where sexes have been identified, females still average longer bill lengths than males, and thus sex ratio skews cannot entirely drive geographical patterns.

Our data further establish the geographic cline in bill length of Semipalmated Sandpipers previously described by Manning *et al.* (1956) and Harrington and Morrison (1979). However, average bill length does not decrease uniformly from east to west. Harrington and Morrison (1979) noted an apparent step in the cline in the area of Southampton Island, and H. Ouellet (*in* Morrison 1984) suggested a further step in the cline in the extreme west of the range in Alaska. This may suggest up to three genetically differentiated populations or subspecies. Here, with more data from live birds in different parts of the breeding range, there appears to be no difference in average bill length within Alaska, but a step in the cline around the border of Alaska and the Yukon/Northwest Territories, and a second step in the area of eastern Baffin Island/western James Bay, thus forming three major populations. Whether these three populations are separate subspecies will require further genetic analysis.

Patterns of migratory connectivity between breeding, migration and wintering grounds based on bill morphometrics agree with those demonstrated from movements of individually-marked birds. In general, as reported previously, an east-west cline in bill lengths transferred southward from breeding to nonbreeding areas. Although we established that western breeders migrate northward farther to the west (through the interior of North America) and south of more eastern breeding birds, and migrate southward again through the interior of North America, the extent to which the Pacific coast of Canada and the United States is used by migrant Semipalmated Sandpipers is less obvious. In Washington State, Semipalmated Sandpipers are rare in spring, and in fall are more common in the eastern part of the state than along the coast (Weber 1981). In British Columbia, this species is locally abundant, but greatly outnumbered by other small Calidrids, although it was the third most common 'peep' caught when banding on the Fraser River Delta during summer (Campbell *et al.* 1990). The latter observation, in combination with a sighting of twelve yearlings (marked in Saskatchewan the previous fall as juveniles) in spring on the Fraser River Delta (Gratto-Trevor and Dickson 1994), and their generally late arrival in spring plus variable migration strength in British Columbia (Campbell *et al.* 1990), suggest that many of the spring west coast migrants may be nonbreeding yearling Semipalmated Sandpipers. Most Semipalmated Sandpipers do not breed as yearlings (Spaans 1984; Gratto 1988).

As for most shorebirds, adults precede juveniles during fall migration (e.g. Morrison

1984). The first wave of adults during fall migration at James Bay contained a higher percentage of yearlings (14% of all adults in mid-July declining to 9% by mid-August; Morrison 1984). Yearlings are more likely than older birds to be non-breeders (Spaans 1984; Gratto 1988), which explains their earlier fall migration. Females migrated slightly earlier than males in fall (Morrison 1984), presumably because males normally remain longer than females with the brood (Gratto-Trevor 1991). In addition to differences between age groups in timing of fall migration, juveniles of some populations apparently use different routes than adults. For example, Gratto-Trevor and Dickson (1994) noted that their marked juvenile (western breeding) Semipalmated Sandpipers were not observed in Tennessee, although fall marked adults were seen there in some numbers. They suggested that adults staging in Saskatchewan in fall might migrate south in more inland locations than Saskatchewan juveniles, as the latter appeared to migrate down the Atlantic coast. Morrison (1984) noted that a greater percentage of juveniles than adults were recovered from the Caribbean, suggesting either a decreased flight range capability of juveniles compared to adults or departure points farther south along the Atlantic coast, possibly as part of an anti-predator migration strategy (Lank *et al.* 2003). Gratto-Trevor and Dickson (1994) also suggested that western breeding adults might winter farther east on the South American wintering areas as compared to juveniles.

Most Semipalmated Sandpipers winter in northern and central coasts of South America along the coasts of Suriname, French Guiana and Guyana (Morrison and Ross 1989), although significant numbers also winter in Brazil (Morrison and Ross 1989; Resende *et al.* 1989; de Azevedo and Larrazabel 1999). Although western breeders, on average, winter farther west in South America than eastern or central Arctic breeders, there is considerable mixing (Lank 1979, 1983; Morrison 1984; Gratto-Trevor and Dickson 1994; Fig. 3b-3d). Most adults staging in northeastern Venezuela migrate farther, probably southward, at the end of September (McNeil 1970). The decline in numbers of birds in Guyana during November to March suggests that birds are moving through to other areas (Morrison 1984), and phenology of movements in Suriname and French Guiana also suggests birds moving farther east in the fall and returning in the spring (Spaans 1978; Hansen-Chaffard 2000). Numbers in Suriname peak later than in Venezuela (early November) and later still in Maranhão, Brazil, further suggesting movement of birds from northwest to east and south in South America (Spaans 1978; Rodrigues 2000; Hicklin and Gratto-Trevor 2010). Average bill length in Suriname is longer during these spring and fall migration periods than during the winter, and the difference is apparently (from analysis of banding casualties) not due to sex differences but to longer-billed eastern breeders moving into Brazil (Spaans 1984).

While a considerable body of work exists on Semipalmated Sandpiper migration routes, much less is known about differences among breeding populations in wintering areas and routes, and whether there are, as for some other shorebird species (e.g. Myers 1981; Nebel 2006), age and/or sex differences in wintering and migration. Since resighting rates may be biased by the geographic distribution of both banding locations and observers, newer techniques such as data loggers or genetics may eventually provide improved information on sex or age-related migration routes and staging areas of specific breeding populations. Such information would allow a better understanding of how specific breeding populations would be affected by habitat degradation or loss at particular wintering or staging sites or by a catastrophic event, such as a major oil spill or hurricane. As discussed in later papers in this volume, at least some Semipalmated Sandpiper populations (e.g eastern breeders; Hicklin and Chardine 2012) are thought to be in decline. Conservation efforts could be particularly concentrated on 'at risk' staging or wintering sites used by birds from declining populations.

Acknowledgments

We acknowledge the Canadian Bird Banding Office for compiling lists of Semipalmated Sandpiper banding and recoveries, and the banders themselves, especially B. Harrington, R. McNeil, E. F. Martinez, and S. Skagen. Also, we thank those who provided unpublished data

(primarily average bill length), including S. Franks, Y. Aubry, J. Chardine, J. Correa, T. Dean, J. Dean, B. Haase, R. Lanctot, J. Lyons, B. Sandercock, B. Schwarz, P. Smith, D. M. Tracy, and D. Troy. B. Harrington, N. Warnock, and B. Andres provided comments on an earlier version of this manuscript. Finally, we acknowledge the Science and Technology Branch and the Canadian Wildlife Service, Environment Canada, for logistical support.

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