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SEMIPALMATED SANDPIPER MIGRATION IN NORTH AMERICA

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ABSTRACT—Morphometric studies of adult Semipalmated Sandpipers from museum collections and banding operations show that spring and autumn routes in North America are different, and that the routes used are not the same for birds from different parts of the breeding range. In spring, breeders from Alaska and central Canadian arctic zones follow a central North American route, whereas eastern Canadian birds follow an Atlantic route. In autumn, Alaskan breeders retrace the spring route, with some possibly using more eastern corridors; central Canadian birds use an Atlantic route, with most apparently travelling far east of their spring route. Eastern Canadian breeders continue to use an Atlantic route in autumn, possibly somewhat east of their spring route.

Although the migratory movements of shorebirds across America have long been known in general terms, there is a remarkable scarcity of detailed studies of the movements of individual species. Detailed knowledge of the migration patterns and strategies of populations from different parts of the arctic is a prerequisite for the identification of sites that are of critical importance to the well-being of shorebird populations. We provide the first such account for one of the most numerous of North American shorebirds.

The Semipalmated Sandpiper (*Calidris pusilla*) breeds in a broad zone from the Alaskan Arctic coast across Canada to northern Quebec, central Baffin Island and northern Labrador, apparently in three disjunct populations (Manning, Höhn & MacPherson 1956, A.O.U. 1957, Palmer 1967). Birds from eastern parts of the breeding range have longer bills than those from western areas (Manning et al. 1956). The species is therefore well suited to comparative studies of migration strategies using morphometric studies made at stopover and wintering areas.

It has been believed for some time that the spring and autumn migration routes of Semipalmated Sandpipers are somewhat different (Loftin 1962, McNeil and Burton 1973, 1977). In this report we review and assess information on Semipalmated Sandpiper migration provided by morphometric data and indices of migrant abundance which we and others have collected. The data confirm that many Semipalmated Sandpipers use different routes for northward and southward migration. An 'elliptical' migration route involving a northward spring migration through central areas of the U.S. and Canada followed by a southward autumn migration via coastal areas along the eastern seaboard is used by many birds, particularly those from central parts of the breeding range. Birds from the extreme eastern and western parts of the range tend to migrate along the eastern and western edges of these routes, respectively, in both directions.

METHODS

In Massachusetts our studies were carried out principally at Plymouth Beach (41°55′N, 70°37′W), a 4.5 km sandy peninsula that extends into Plymouth Bay near the base of Cape Cod (Fig. 1). As many as 5500 Semipalmated Sandpipers roost on the beach during high tides in late July and early August, and the species outnumbers all others combined during most of the autumn migration period. From 1972 through 1976, shorebirds were counted while roosting at Plymouth Beach at least weekly from 1 July through 31 October, and almost daily from mid-July through September. Censuses in

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spring were less systematic, sometimes made twice weekly, but normally only once every ten days. During all censuses, individually color-marked birds and ratios of banded to unbanded birds were recorded.

Mist nets were used to capture Semipalmated Sandpipers near the outer end of Plymouth Beach. Twelve-meter long nets were erected soon after high tide, on aluminum poles sunk into sand under about 15 cm of water. Trapping was usually carried out at night, the nets being moved about every half hour as the tide fell.

Birds captured at Plymouth were held in a large, well-ventilated holding box and returned to the banding laboratory about 7 km away at the Manomet Bird Observatory for processing. Information recorded included exposed culmen length (feathers to tip of bill) to the nearest 0.1 mm, weight on a triple-beam balance to the nearest 0.1 gm, unflattened (natural) wing length to the nearest mm, and a subjective assessment of the amount of subcutaneous fat on a scale of 6. Samples of each catch were examined for molt. Banded birds were usually released at Plymouth Beach, but sometimes at Manomet: the latter were seen subsequently at Plymouth Beach as often as those that were returned to the Beach.

Banding studies in James Bay were carried out in 1975, 1976 and 1977 at North Point (51°29′N, 80°27′W), on the southwest coast of James Bay, approximately 27 km northeast of Moosonee, Ontario (Fig. 1). The coast is very flat, with extensive marshes. Mist-netting was the principal trapping technique, although cannon nets were used when appropriate conditions occurred. From 70–150 mist nets were erected in lines of up to 17 nets over a 2 km stretch of coast at the junction of the saltmarsh and tidal flats, to intercept flight lines of birds moving to high tide roosts. Nets were checked continuously during suitable weather on a 24-hour basis using all terrain tricycles. Birds were returned 1 km to the camp for processing, which included measurement of wing (maximum length stretched and flattened to the nearest mm), bill (exposed culmen to 0.1 mm), weight (Pesola spring balance to 0.5 g), examination for molt, and color dyeing and color-banding. They were returned to the coastal marsh for release near the place of capture.

Bill (exposed culmen) and wing (flattened and/or unflattened) measurements were also made on a large number of museum specimens. All birds showing damaged or molting distal primaries were excluded. To enable comparison of wing lengths measured by the two authors to be made, each measured a series of either the same (live) or directly comparable (specimens) birds. The difference (RIGM = BAH + 2 mm for museum specimens, RIGM = BAH + 6.8 mm for live birds) has been allowed for in discussing comparisons of wing measurements and in calculating bill/wing ratios, as noted in Tables 2 and 3. No difference was found between bill measurements made by the two authors. Unless noted, measurements of live or fresh specimens were not compared with those of dried museum specimens owing to problems caused by shrinkage (e.g. Vepsalainen 1968, Prater et al. 1977). Last, unless noted measurements from juveniles are excluded from analyses owing to problems of comparability including, for example, the facts (i) that museum specimens from breeding areas include juveniles with incompletely grown bills, and (ii) that juveniles caught at stopover areas tend to have shorter wings than adults of comparable bill length.

The coefficient of variation (CV) has been used to compare the variability of bill measurements between different seasons and places where samples have different means, as well as to compare the variability between measurements of museum specimens and live birds, since the CV is independent of the units of measurement (Simpson, Roe and Lewontin 1960). Statistical differences between CV's were tested using the *t*-test described by Dow (1976). Analysis of variance was used to test the statistical significance of differences between sets of measurements, and frequency data were compared using a chi-square test (Sokal and Rohlf 1969).

RESULTS

Regional Status During Migration

Spring migration

Palmer (1967) noted that most of the spring migration of Semipalmated Sandpipers in the coterminous United States occurs in the middle two weeks of May. While this is generally true, regional variations seem to exist. In Louisiana (Lowery 1974) and northern Florida (Loftin 1960, 1962), Semipalmated Sandpipers are most common in late April/early May, but have gone by late May/early June

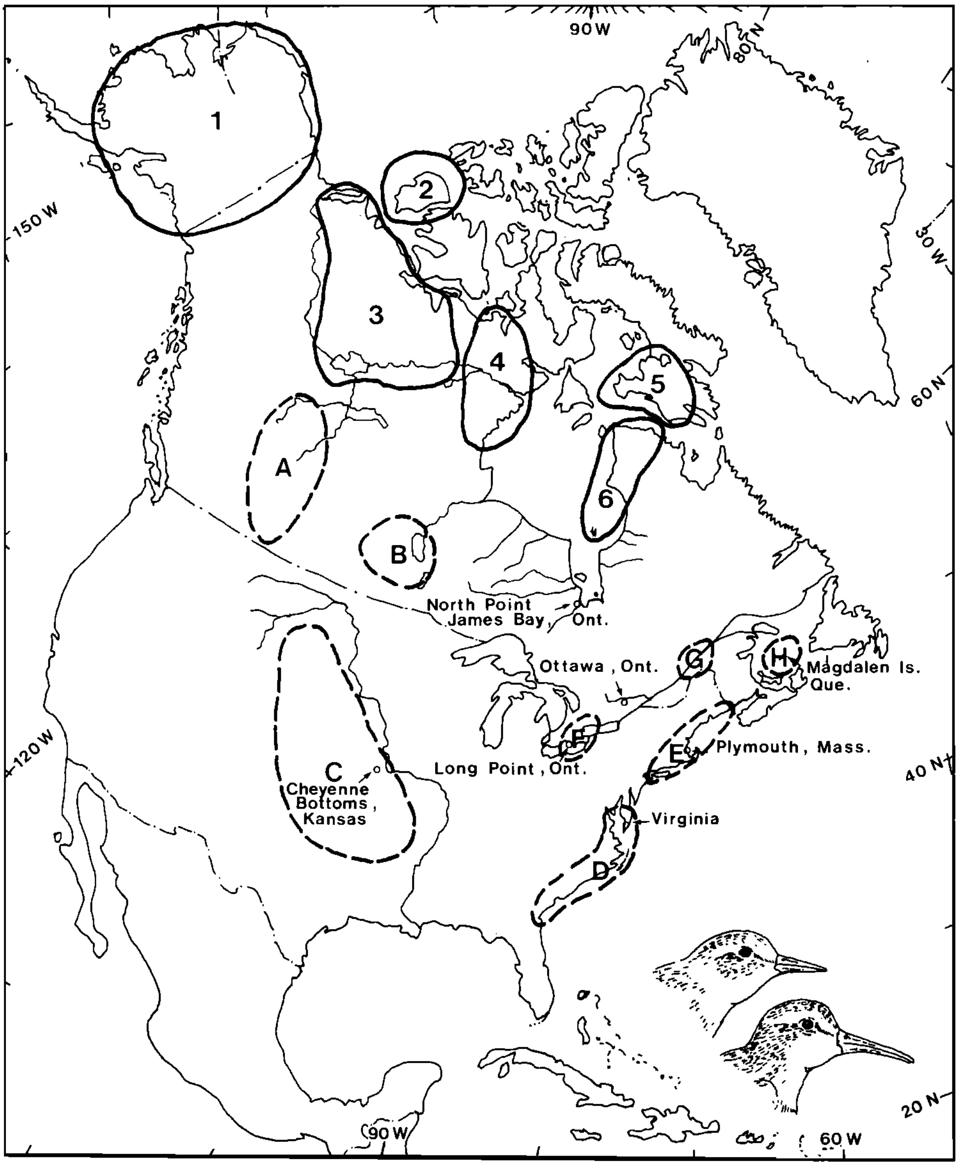

FIGURE 1. North America, showing locations of banding studies referred to in the text and in Table 4, and areas from which measurements of museum specimens were collected for morphometric studies (Tables 2 and 3).

Breeding areas (solid lines, numbers, see Table 2): 1. Alaska, 2. Banks Island, N.W.T., 3. Mackenzie district, N.W.T., 4. Keewatin district, N.W.T., 5. West Baffin Island, N.W.T., 6. Belcher Islands, N.W.T., and East Hudson Bay, Quebec.

Migration areas (broken lines, letters, see Table 3): A. Alberta, B. Saskatchewan/Manitoba, C. Central U.S., areas between the Mississippi River and the Rocky Mountains, D. Maryland to Georgia, E. New York to Maine, F. Southern Ontario, areas between Toronto and Long Point, G. Kamouraska, St. Lawrence River, Quebec, H. Magdalen Islands, Gulf of St. Lawrence, Quebec.

Heads of the short-billed and long-billed forms of the Semipalmated Sandpiper from western and eastern arctic breeding areas, respectively, are illustrated.

(Loftin 1962). In Oklahoma (Oring and Davis 1966), Kentucky (Mengel 1965), Ohio (Trautman 1940) and central Kansas (Parmelee et al. 1969), highest counts also occur between late April and late May. In the Drumheller area of Alberta, the main passage occurs in the latter half of May (Kondla et al. 1973), as it does in northern Saskatchewan (Houston and Street 1959).

On the east coast the seasonal pattern is somewhat different, especially in the northeast where peak counts are found in late May or early June. At Daytona Beach, Florida, Longstreet (1934) did not find Semipalmated Sandpipers in April, they were abundant in May, and they were virtually absent in June. In Maryland, the species is most common in May (Stewart and Robbins 1958), but moderate numbers also occur in the first third of June. In New Jersey, peak spring counts are in mid-May (Urner and Storer 1949), but high numbers are still found in early June. In New York, spring maxima occur in the latter half of May and early June (Bull, 1974).

In Massachusetts the peak of spring migration is usually between 25 May and 7 June (Bailey 1955). Highest numbers occur in eastern parts of the state, e.g., on Cape Cod where estimates of as many as 25,000 have been made on 30 May (Hill 1965) and 35,000 on 1 June 1957 (Bailey 1968), about double the maximum numbers found in the same area during autumn migration. At Plymouth, small flocks normally appear in mid-May, but peak numbers (about 1500 birds) do not occur until late May or, more often, in early June. Counts of as many as 5500 birds are made at Plymouth in autumn migration.

At points north and east of Massachusetts, adult Semipalmated Sandpipers are much less common in spring than autumn. In Maine they are "common" in spring from the middle of May to the end of the first week in June, and "abundant" in autumn (Palmer 1949). At Mary's Point, New Brunswick, on the upper Bay of Fundy, the species is much more numerous in autumn than spring, the northward passage occurring during the latter part of May and early June (D. S. Christie, Maritimes Shorebird Survey observations, pers. comm.). In Nova Scotia, Tufts (1973) describes the Semipalmated Sandpiper as rare in spring, but common in autumn. In Newfoundland they are absent in spring, yet regular in autumn (Godfrey 1966).

In the Great Lakes area, passage dates of Semipalmated Sandpipers are generally in late May. At Kingston, Ontario, arrival dates average 22 May with most birds gone by 30 May (Quilliam 1973), and at Point Pelee on Lake Erie, the passage occurs at the end of May (Stirrett 1973). In the Cleveland Region, peak passage dates are in the last ten days of May (Newman 1969). At Ottawa, Ontario, and Montreal, Quebec, the peak passage occurs at the very end of May and early June (P. Hamel, pers. comm., S. Holohan, pers. comm.).

Autumn migration

In Newfoundland there are no July records of Semipalmated Sandpipers and highest counts, most from the southwestern part of the province, do not occur until late August or the first half of September (Peters and Burleigh 1951). The main passage of migrants in Labrador does not occur until about the third week in August (Austin 1932). This is long after maximum numbers of adults occur at James Bay and Plymouth, but is when highest numbers of juveniles are seen at these sites (Table 1), as well as in the Maritime Provinces (Morrison 1976).

TABLE 1
NUMBERS OF SEMIPALMATED SANDPIPERS CAUGHT DURING AUTUMN MIGRATION

Sampling site	Age	July		August		September
		1–15	16–31	1–15	16–31	1–15
North Point, James Bay (1976)	Adults	369	3001	2778	661	3
	Juveniles	0	0	605	2381	473
Plymouth, Mass. (1973–77)	Adults	0	582	1001	319	27
	Juveniles	0	0	8	137	213

In New England and southeastern Canada the autumn migration of Semipalmated Sandpipers is more protracted than in spring, beginning in early July and continuing until early October. In the Montreal region, the peak of adults occurs at the very end of July, with the main passage of juveniles occurring around 20 August (S. Holohan, pers. comm.). In the upper Bay of Fundy at Mary's Point, N.B., numbers rise rapidly from mid-July and usually reach a peak at the end of July or in the first few days of August, remaining high into the first week of August (Morrison 1976). In Nova Scotia and Maine, small flocks arrive between early and mid-July, and numbers increase until the second week of August, when a sharp decline begins (Tufts 1973, Palmer 1949, Morrison 1976). The pattern of numbers at Plymouth, Mass., is apparently representative of northeastern sites in the U.S., with peak counts occurring in late July/early August. Highest numbers in New Jersey have been reported at the very end of July (Urner and Storer 1949, Kane 1976).

In the southeastern United States, peak counts of Semipalmated Sandpipers during autumn migration tend to be later and of lower numbers than at sites to the northeast, suggesting the possibility that many of the birds are juveniles. In Louisiana, peak numbers occur after early September (Lowery 1974), and in October/November in eastern Florida (Longstreet 1934). In northwestern Florida, Weston (1965) found practically no movement of Semipalmated Sandpipers during autumn, even though there is a very large westward movement along the Gulf Coast in spring. At Athens, Georgia, Burleigh (1958) rarely found the species in autumn, but found it comparatively often in spring.

Although abundant during autumn migration in the midwest, Semipalmated Sandpipers are less common than during spring (Oring and Davis 1966, Ferguson 1962, E. F. Martinez, pers. comm.).

MORPHOMETRIC STUDIES OF ADULT SEMIPALMATED SANDPIPERS

Bill and wing measurements

Breeding grounds.—Male Semipalmated Sandpipers tend to have shorter bills and wings than females (Ridgway 1919, Manning et al. 1956, Ouellet et al. 1973). Our own measurements of adults from a number of Canadian and United States museum collections (Table 2) confirm that males have shorter bills ($P < 0.01$) and shorter wings ($P < 0.01$) than females from the same area, and that Semipalmated Sandpipers from eastern breeding grounds tend to have longer bills than those from western areas. There is thus geographic as well as sexual variation in size, complicating morphometric analysis of data from live birds of unknown sex.

TABLE 2
MEASUREMENTS OF MUSEUM SPECIMENS OF SEMIPALMATED SANDPIPERS FROM VARIOUS PARTS OF THE BREEDING RANGE[a]

	Males				Bill/wing ratio		Females			
District[b]	$\bar{x}$[c]	N	(S^2)	CV	Males	Females	$\bar{x}$	N	(S^2)	CV
Bill length										
1. Alaska	17.27	23	0.53	4.24	.1853	.1964	18.92	9	0.17	2.18
2. Banks Island	17.53	7	0.95	5.56	.1859	.1980	19.68	5	0.44	3.36
3. Mackenzie district, NWT	17.76	5	0.46	3.81	.1881	.2037	19.20	4	0.53	3.78
4. Keewatin district, NWT	18.21	21	0.31	3.05	.1903	.2067	19.68[d]	5	0.71	4.87
5. W. Baffin Island	19.30	22	1.05	5.32	.2011	.2088	21.03	7	0.35	2.82
6. Belcher Is./E. Hudson Bay	19.99	20[e]	0.53	3.63	.2091	.2212	21.54	11[e]	1.11	4.88
Wing length										
1. Alaska	93.22	23	3.72	2.07			96.33	9	3.25	1.87
2. Banks Island	94.29	7	2.24	1.59			99.40	5	10.3	3.23
3. Mackenzie district, NWT	94.40	5	2.80	1.77			94.25	4	13.6	3.91
4. Keewatin district, NWT	95.67	9	3.25	1.88			95.20[d]	5	1.20	1.15
5. W. Baffin Island	95.95	22	4.43	2.19			100.71	7	0.57	0.75
6. Belcher Is./E. Hudson Bay	95.58	12	6.45	2.66			97.38	8	5.13	2.33

[a] All measurements by RIGM, except where noted.
[b] Numbers refer to collection areas illustrated in Figure 1.
[c] $\bar{x}$ = mean, N = sample size, S^2 = variance, CV = coefficient of variation.
[d] Measured by BAH; add 2 mm to wings to compare with measurements by RIGM.
[e] Includes measurements by BAH.

Spring migration.—Bill lengths of museum specimens collected at spring stopover areas (Table 3) in central and midwestern North America are shorter than those from eastern sites. For example, the average for 23 males from central and western areas (A, B, and C, Fig. 1, Table 3) is 17.9 mm, significantly shorter ($P < 0.01$) than the average (19.5 mm) for 56 males from eastern areas (E, F, and G, Fig. 1, Table 3). The same trend exists among females (Table 3). Reference to measurements of museum specimens from known breeding areas indicates that central and eastern migrants would be predominantly from western/central and eastern breeding areas, respectively.

Bill lengths of birds banded during spring migration followed the same trends as museum specimens, with lower averages at central and midwestern sites than at eastern sites (Table 4). For example, the average bill length in Kansas was 18.6 mm, much shorter than the comparable 21.1 mm from Massachusetts. The averages are statistically different ($P < 0.01$) for any of the comparisons possible between the spring samples in Table 4. Reference to museum measurements again indicates that migrants from the central U.S. breed in western/central areas, and eastern migrants breed in the eastern arctic.

The average wing length measurements of museum specimens increase from western to eastern breeding areas (Table 2), and in spring from western to eastern stopover sites (Table 3). Wing measurements from autumn migration sites were not compared because of the small number of specimens measured from central and midwestern locations.

Autumn migration.—As in spring, there is a trend for longer-billed birds to be found in eastern areas and for shorter-billed birds to be further west during

TABLE 3

MEASUREMENTS OF MUSEUM SPECIMENS OF SEMIPALMATED SANDPIPERS FROM VARIOUS MIGRATION AREAS[a]

District[b]		Males				Bill/wing ratio[c]		Females			
		$\bar{x}$[d]	N	(S^2)	CV	Males	Females	$\bar{x}$	N	(S^2)	CV
Bill length											
A. Alberta	spring[e]	17.39	8	1.03	5.84	.1826	.2052	19.90	4	1.15	5.40
	autumn[e]	17.47	3	0.14	2.17	.1865	—	—	—	—	—
B. Saskatchewan/ Manitoba	spring	18.12	5	2.38	8.51	.1895	.2014	19.80[e]	3	2.17	7.44
C. Central US[f]	spring	18.21	10	0.61	4.29	.1945	.2065	19.77	7	0.85	4.66
D. Maryland to Georgia	spring	19.59	14	1.13	5.44	.2029	.2188	21.40	26	1.38	5.49
	autumn	18.15	12	1.69	7.17	.1924	.2088	20.33	6	1.47	5.96
E. New York to Maine	spring	20.00	9	1.41	5.94	.2044	.2207	21.81	23	1.49	5.60
	autumn	19.50	13	1.92	7.10	.2044	.2068	20.13	12	4.10	10.06
F. Southern Ontario[g]	spring[e]	19.32	34	1.20	5.66	.2020	.2136	20.79	32	0.92	4.62
	autumn[c]	17.68	4	0.62	4.44	.1927	.2059	19.64	5	0.27	2.64
G. Kamouraska, St. Lawrence R., Quebec	spring	19.83	13	0.70	4.23	.2056	.2224	21.57	3	0.21	2.14
	autumn	18.78	16	0.71	4.48	.1954	.2014	19.81	8	1.45	6.08
H. Magdalen Is., Quebec	autumn	19.03	10	0.91	5.01	.2005	.2108	20.43	12	1.79	6.54
Wing length											
A. Alberta	spring[e]	95.25	8	16.79	4.30			97.00	4	3.33	1.88
	autumn[e]	93.67	3	6.33	2.69			—	—	—	—
B. Saskatchewan/ Manitoba	spring	93.60	5	1.30	1.22			98.33[e]	3	2.33	1.55
C. Central US[f]	spring	91.64	10	11.2	3.66			93.74	7	5.24	2.44
D. Maryland to Georgia	spring	94.56	14	1.57	1.33			95.79	25	5.40	2.43
	autumn	92.33	12	6.12	2.68			95.37	6	1.51	1.29
E. New York to Maine	spring	95.86	9	4.06	2.10			96.82	23	3.36	1.89
	autumn	93.41	12	4.81	2.35			95.33	12	14.24	3.96
F. Southern Ontario[g]	spring[e]	95.62	34	6.67	2.70			97.31	32	3.71	1.98
	autumn[e]	91.75	4	8.25	3.13			95.40	5	2.30	1.59
G. Kamouraska, St. Lawrence R., Quebec	spring	94.46	13	4.27	2.19			95.00	3	7.00	2.79
	autumn	94.11	18	2.34	1.63			96.38	8	3.41	1.92
H. Magdalen Is., Quebec	autumn	92.90	10	2.32	1.64			94.92	12	7.90	2.96

[a] Measurements by BAH, except where noted.
[b] Letters refer to collection areas illustrated in Figure 1.
[c] 2 mm added to wing measurements by BAH, to enable comparison with values in Table 2.
[d] $\bar{x}$ = mean, N = sample size, S^2 = variance, CV = coefficient of variation.
[e] Measured by RIGM; subtract 2 mm from wings to compare with measurements by BAH.
[f] Includes areas between the Mississippi River and Rocky Mountains.
[g] Includes areas between Toronto and Long Point.

autumn migration. Few comparisons can be made with museum specimens owing to the small number of autumn specimens from central and western migration areas. However, for samples of live, unsexed birds trapped during autumn banding, mean bill lengths in Kansas are significantly ($P < 0.01$) shorter than at eastern

TABLE 4
BILL LENGTH STATISTICS FOR SEMIPALMATED SANDPIPERS CAUGHT DURING SPRING AND AUTUMN MIGRATION

Sampling site	Spring migration				Autumn migration			
	N[g]	$\bar{x}$	SD	CV	N	$\bar{x}$	SD	CV
Quebec: Magdalen Is.[a]	—	—	—	—	169	21.00	—	—
Mass.: Plymouth[b]	204	21.1	1.39	6.58	1929	20.19	1.50	7.43
Ontario: James Bay, North Point[b]	81	20.6	1.29	6.25	6809	19.43	1.36	6.99
Virginia[c]	32	19.8	1.36	6.87	13	19.90	1.21	6.66
Ontario: Ottawa[d]	—	—	—	—	286	19.63	1.31	6.67
Ontario: Long Point[e]	—	—	—	—	22	18.85	1.06	5.60
Kansas: Cheyenne Bottoms[f]	77	18.6	1.18	6.32	201	18.16	1.21	6.08

[a] Data from Burton 1974.
[b] Data from this study.
[c] Spring data from Wallops Island, courtesy of Charles R. Vaughn; autumn data from Cedar Island, courtesy of John S. Weske.
[d] Data courtesy of Richard M. Poulin.
[e] Data courtesy of Michael S. W. Bradstreet.
[f] Data courtesy of E. F. Martinez.
[g] N = sample size, $\bar{x}$ = mean, SD = standard deviation, CV = coefficient of variation.

sites (Table 4), and means in Massachusetts are significantly longer than at Ottawa or James Bay ($P < 0.01$, Table 4).

Another striking feature of the autumn migration is that mean bill lengths of birds in a given area are consistently shorter than in the same area in spring, for both banding samples and museum specimens. For banding samples, autumn means were significantly shorter ($P < 0.05$) at all sites, except in Virginia where only small samples were available (Table 4). For museum specimens, mean bill lengths of both males and females in eastern areas were up to 1.5 mm shorter in autumn than in spring, and comparison of samples over 10 birds showed the differences were statistically significant ($P < 0.01$). Similar trends were found with wing lengths (Table 3). The consistent decrease at all eastern sites, involving both sexes, indicates that many birds from western and central arctic breeding areas migrate southwards via the Atlantic coast in the autumn.

Means for both bill length and wing length decrease during the course of autumn migration in Semipalmated Sandpipers trapped in James Bay, 1975–76 (N = 8986), and at Plymouth, Mass., 1973–1977 (N = 1929) (Fig. 2). The large difference in wing measurements between sites is accounted for almost entirely by differences in measuring technique (see Methods). Bill lengths are consistently lower in James Bay than in Massachusetts, indicating that fewer eastern arctic birds are present in James Bay. Seasonal decreases in wing and bill length could be caused at least partly by an earlier migration of larger female birds, as would be anticipated from consideration of the species' breeding biology (Pitelka et al. 1974). However, other evidence presented below indicates that an increasing proportion of small birds from more westerly breeding areas also contributes to the decline as the migration proceeds.

Bill/wing ratios of adults

Breeding grounds.—The mean bill/mean wing ratio increases for both males (from approx. 0.185 to 0.210) and females (from approx. 0.195 to 0.220) from western to eastern breeding areas (Table 2, Fig. 3). Males from the Alaskan and

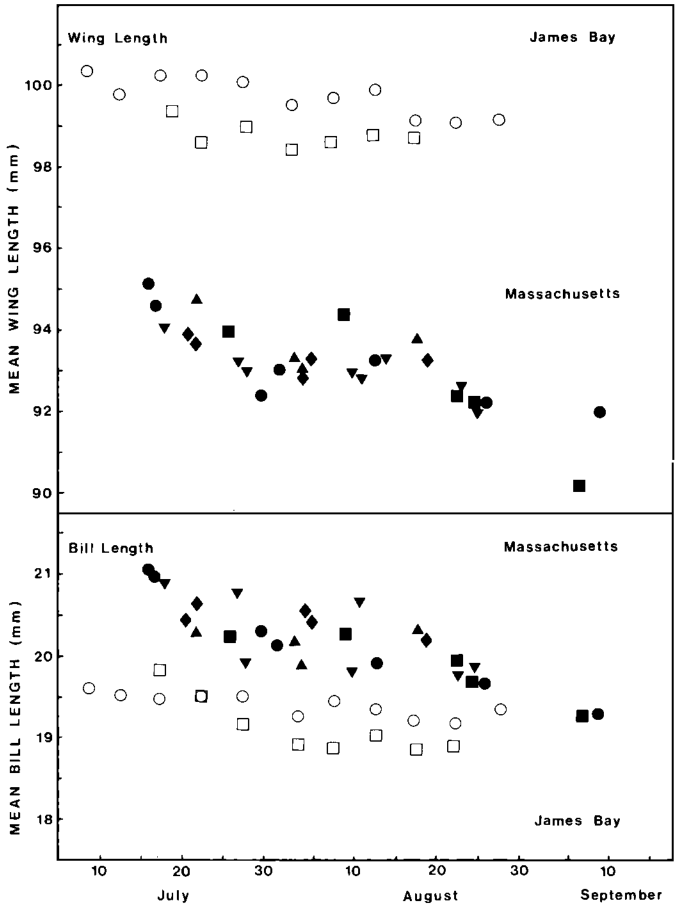

FIGURE 2. Mean wing lengths and mean bill lengths of Semipalmated Sandpipers captured at North Point, James Bay (□—1975, $N = 2177$; ○—1976, $N = 6809$), and Plymouth, Mass. (▼—1973, $N = 520$; ●—1974, $N = 492$; ▲—1975, $N = 214$; ◆—1976, $N = 366$; ■—1977, $N = 377$), during autumn migration. Points for Plymouth represent single catches, whereas those for James Bay represent means of 5-day periods. Note that means of both wing and bill fall during the passage. The large difference in wing length between sites is accounted for almost entirely by difference in measuring techniques. Bill lengths are, however, comparable and are consistently lower in James Bay than in Massachusetts, indicating the latter site probably receives a higher proportion of birds from eastern breeding areas.

central populations form a group with bill/wing ratios of ca. 0.185 to 0.190 at mean bill lengths of ca. 17.3 to 18.2 mm, whereas males from the eastern populations are grouped with bill/wing ratios between 0.20 and 0.21 and mean bills between 19.3 and 20.0 mm, respectively. Western and central area females broadly overlap the eastern male group (ratios 0.196 to 0.207 at bill lengths of 18.9 to 19.7 mm), but are themselves separated from females from eastern areas (ratios 0.209 to 0.221 at bill lengths of 21.0 to 21.5 mm). The separation of Alaskan/central and eastern (Baffin Island and northern Quebec) populations into two distinct groups (where the sex is known) is consistent with the suggestion of Manning et al. (1956) that there is possibly a discontinuity or step in the cline in the vicinity of

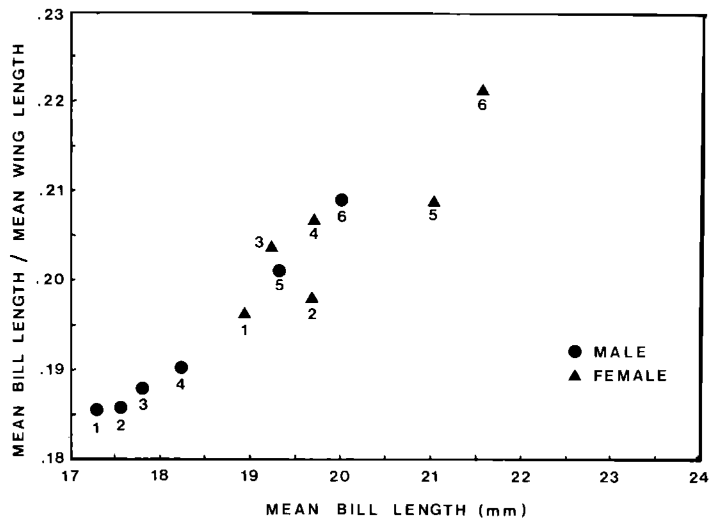

FIGURE 3. Mean bill length/mean wing length ratio vs. mean bill length for Semipalmated Sandpipers from different parts of the breeding range. Circles = males, triangles = females; numbers refer to areas illustrated in Figure 1. Birds from Alaskan (area 1)/central (2–4) and eastern (5, 6) parts of the breeding range form two groups for males and females, respectively, with eastern males and Alaskan/central females generally overlapping.

Southampton Island. Examination of the bill/wing ratio vs. mean bill length may thus be of value in establishing the possible breeding origin of migrants in museum collections where sexed samples are available.

Spring migration.—Plots of bill/wing ratio vs. mean bill length for males and females collected during spring migration from various areas are illustrated in Figure 4. Males collected during the spring in Alberta fell at the lower end of the Alaskan/central group, indicating most birds were probably from Alaskan or western arctic breeding areas. Males from the central U.S., comprising areas between the Mississippi River and the Rocky Mountains, and from southern Saskatchewan/Manitoba fell nearer the upper end of the Alaskan/central group, suggesting that most of them were from central parts of the breeding range. Males collected from areas along the eastern U.S. seaboard (New York, New England and Maryland to Georgia), the St. Lawrence River (Kamouraska, Quebec) and in southern Ontario all fell well within the range of values of males from eastern breeding areas.

Females collected in the central U.S., Alberta and Saskatchewan/Manitoba fall near the group from Alaskan and central breeding areas, whereas migrant females from the eastern coast of the U.S. and the St. Lawrence River fall well toward the upper end of the group from the eastern arctic, with southern Ontario migrants nearer the lower end of the group (Fig. 4).

These results demonstrate that birds passing through eastern areas of North America in spring are principally from breeding areas in the eastern arctic, and that those from central and western areas of the breeding grounds use interior migration routes through the central U.S. and Canada.

Autumn migration.—For areas in eastern North America, bill/wing ratios of migrant Semipalmated Sandpipers are generally lower in the autumn than in the

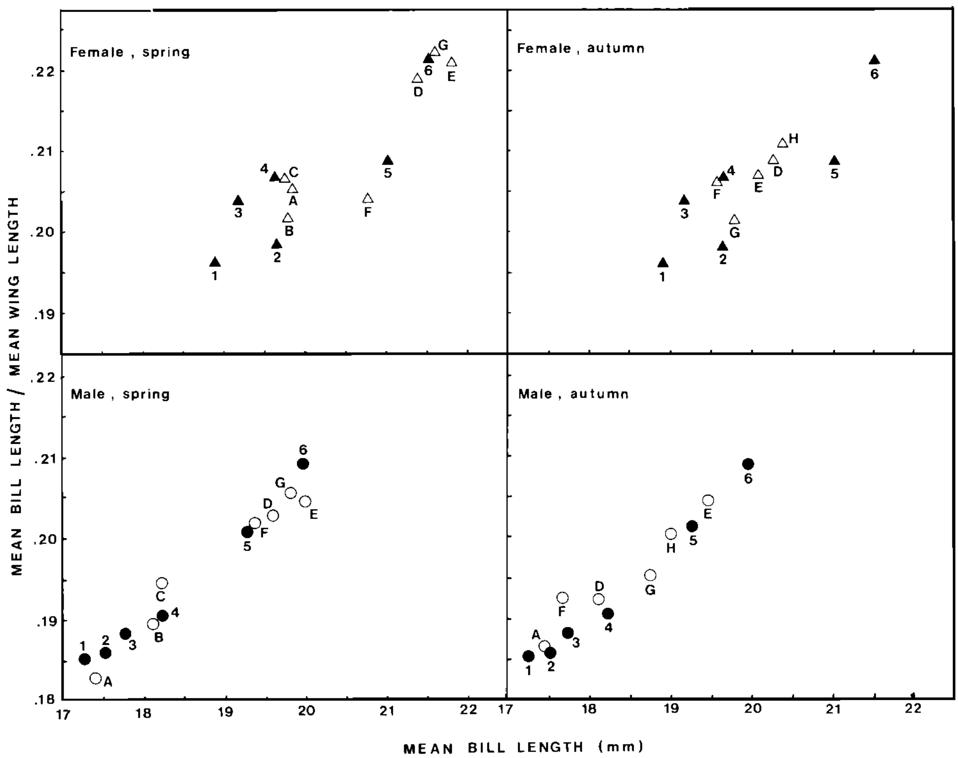

FIGURE 4. Mean bill length/mean wing length ratio vs. mean bill length for male and female Semipalmated Sandpipers collected in migration areas (open symbols, letters) during spring and autumn in North America. Reference points for samples from different parts of the breeding range (solid symbols, numbers, see Figure 3) are included. Numbers and letters refer to areas illustrated in Figure 1. Note that in spring, males and females using central migration routes (areas A, B, C) appear to derive principally from Alaskan/central populations, whereas those from the Atlantic seaboard and eastern Canada (areas D, E, F, G) are principally from eastern breeding areas. In the autumn, many western/central arctic birds would appear to use sites on the eastern seaboard (see text for details).

spring for both males and females (Table 3, Fig. 4), providing further evidence that many birds from central and possibly western breeding areas migrate to their wintering areas via the Atlantic seaboard. The effect appears to be least pronounced towards the edges of the migration corridor and most pronounced towards the middle, and may be partly seasonally dependent. Thus, bill/wing ratio vs. mean bill points for autumn males in Alberta fall well within the Alaskan/central group, indicating most birds are from western breeding areas, as in spring (Fig. 4). On the east coast, males collected in the Magdalen Islands (August) and NY/New England areas (July/August) fall closest to the eastern breeding group, with bill/wing vs. mean bills for females falling between the eastern and Alaskan/central groups, indicating a relatively high proportion of eastern birds on the north and eastern sections of the Atlantic seaboard.

Males collected during August between Maryland and Georgia have bill/wing vs. mean bill plots close to the group from Alaskan/central breeding areas, indicating a high proportion of birds from those areas, in contrast to the spring when the majority of birds appeared to be from eastern breeding areas. Measurements

TABLE 5

COEFFICIENTS OF VARIATION FOR BILL LENGTHS OF SEMIPALMATED SANDPIPERS COLLECTED IN ARCTIC BREEDING AREAS, AND FOR COMBINATIONS OF SAMPLES FROM DIFFERENT AREAS

	Males		Females		Males + Females	
Area[a]	CV	*N*	CV	*N*	CV	*N*
A	4.43%	53	3.02%	33	6.54%	86
B	3.98	33	3.70	14	5.46	47
C	4.84	42	4.30	18	6.08	60
A + B	4.59	86	3.43	47	5.90	133
B + C	6.22	75	5.96	32	7.25	107
A + C	7.70	95	6.63	51	8.21	146
A + B + C	7.00	128	6.14	65	7.70	193

Statistical comparison (*t*-test) of coefficient of variation for bill lengths of mixed sex samples from different breeding zones, and of combinations of samples from different breeding zones.

	A + B	B + C	A + C	A	B	C
A	n.s.	$P < 0.05$	$P < 0.001$	—	—	—
B	n.s.	$P < 0.01$	$P < 0.001$	n.s.	—	—
C	n.s.	n.s.	$P < 0.01$	n.s.	n.s.	—

[a] The areas are combinations of samples from Table 2 grouped to represent: (A) Alaskan arctic (area 1 in Fig. 1); (B) central Canadian arctic (areas 2–4 in Fig. 1); and (C) eastern Canadian arctic (areas 5 and 6 in Fig. 1).

of females from the Maryland/Georgia coast, and of both males and females collected in southern Ontario (July/September) and Kamouraska on the St. Lawrence estuary (August), indicate the presence of many western/central birds in the latter areas during the autumn, particularly late in the season, consistent with the observations of Manning et al. (1956) who noted that the culmen/bill width ratios of 11 migrants collected at Tadoussac, Quebec (July/August) indicated the birds were from western breeding areas, an interpretation also suggested by Ouellet et al. (1973).

Bill/wing ratios of birds trapped in James Bay and Massachusetts fall during the period of autumn migration (not illustrated). Little seasonal information could be obtained from museum specimens owing to small sample sizes, though the available material from the New York area indicated a decline in bill/wing ratios vs. mean bill for both males and females between July and August. These results again suggest that seasonal decreases are not caused simply by changing sex ratios but by an increasing proportion of birds from central and western breeding areas.

Coefficient of variation

Breeding grounds.—The coefficients of variation (CV) for samples of breeding adult Semipalmated Sandpiper bill lengths are given in Table 5. The values are lowest within samples of one sex from one breeding zone (range 3.02–4.84% in Table 5), being higher (i) in samples of one sex from different breeding zones (3.43–7.70%), (ii) in samples of both sexes from one zone (5.46–6.54%), and (iii) most of all in samples of both sexes from different breeding areas (5.90–8.21%). The CV values from any one region in Table 5 are not significantly different from those of any other single region. Statistical differences occur only when a single region is tested against two or more regions combined, providing the combination includes birds from the eastern arctic (Table 5).

Spring migration.—The CVs from museum samples are directly comparable to values obtained from live birds, because they are based upon measures of relative rather than absolute variation.

The CV values found for bill lengths in samples of live sandpipers caught during spring are not significantly different between stopover sites (Table 4); each is within the range expected in a randomly selected, sexually mixed sample drawn from a relatively narrow portion of the breeding range (Table 5). For example, the highest spring value, 6.25% from James Bay, is not significantly different (t = 1.06, $P < 0.30$, 126 df) from the lowest value (5.46%) among the museum groups representing breeding areas (Table 5).

Autumn migration.—CV values were higher during autumn than during spring migration at each site where samples of 30 or more birds could be compared (Table 4), though the difference was statistically significant only in Massachusetts (t = 2.45, $P < 0.05$, 2131 df). At James Bay and in Massachusetts, two areas where autumn monthly sample sizes can be compared, the CVs were lower in July than in August. The James Bay CV during July 1976 was 6.81% (N = 3,370), close to the spring value and to the values found in mixed-sex samples from single portions of the breeding range (Table 5). In August, the James Bay CV was 7.14% (N = 3439), significantly higher (t = 2.76, $P < 0.01$) than in July, and similar to values found for mixed-sex groups combined from more than one part of the breeding range (cf. Table 5). At Plymouth, the July (N = 582) and August (N = 1337) CVs were 6.59% and 7.71% respectively (t = 4.59, $P < 0.001$). These changes in CVs at both sites suggest a larger geographic representation at autumn stopover areas in August than in July, or than found in spring.

DISCUSSION

Our results corroborate evidence that Semipalmated Sandpipers use different routes for north and south migration (Cooke 1910, Loftin 1962, McNeil et al. 1973, 1977). The migration strategy is more complex than previously understood because it is not the same for birds from different parts of the breeding range. We have divided the breeding range into three general areas, Alaskan arctic (area 1 in Fig. 1), central Canadian arctic (areas 2–4 in Fig. 1), and eastern Canadian arctic (areas 5–6 in Fig. 1).

Alaskan Semipalmated Sandpipers apparently follow a north migration route through the Great Plains region of the United States and Canada, judging from the short average bill lengths in live samples caught in Kansas (Table 4) and the generally short bill lengths in museum specimens collected in the Great Plains (Table 3). The bill/wing ratios of Alaskan and central breeders are also similar to those specimens collected during spring in the Great Plains (Fig. 4).

In autumn many Alaskan Semipalmated Sandpipers retrace the North American portion of their spring route. An additional, unknown proportion may also use routes farther east, a possibility we cannot accurately resolve. Evidence for the first part of this conclusion comes partly from banding and morphometric studies in Kansas by E. F. Martinez. The average bill length in autumn at Cheyenne Bottoms is short (Table 4), and the CV is low, both results suggesting that Alaskan breeders are involved. One bird banded during spring in Kansas has been recovered on the Alaskan North Slope and two birds banded at Barrow, Alaska, were subsequently trapped at Cheyenne Bottoms (Martinez 1974). A number of Semipalmated Sandpipers banded during spring in Kansas have been recaptured at the same site in autumn (Parmelee et al. 1969, Martinez, pers. comm.).

Semipalmated Sandpipers that breed in eastern Canadian arctic regions apparently migrate north by an Atlantic route on the United States seaboard, probably turning cross-country in the northeastern United States and southeastern Canada. Evidence for this view includes the long average bill lengths found in samples caught for banding in Massachusetts (Table 4) as well as the long averages from specimens collected in New England and Quebec (Table 3). The low CV values in the Massachusetts banding samples indicate a mixed-sex sample from one geographic region which, because of the bill lengths, could only be the eastern region. Bill/wing ratios of migrants in eastern areas again indicate spring migrants are en route to eastern arctic breeding areas (Fig. 4). The western margin of the migration corridor for eastern birds is not clear. The spring bill/wing ratios (Table 3) from southeastern sites are similar to the values farther northeast, indicating that spring migrants there are from eastern breeding areas. However, the significantly ($P < 0.001$) lower average bill length of the spring sample in Virginia compared to Massachusetts makes this conclusion somewhat less clear. A sexual bias (more males) in the Virginia banding sample could account for the difference. The relatively low CV would be unlikely if the sample included both sexes from central and eastern breeding areas, reinforcing the possibility of a sexual sampling bias.

The point at which the autumn route of eastern Semipalmated Sandpipers crosses the North American Atlantic seaboard apparently is somewhat north and east of the spring route. The average bill lengths, CV values from banding samples (Table 4) and bill/wing ratios from museum collections (Fig. 4) indicate the presence of eastern breeders in a zone along the east coast between Chesapeake Bay and the Gulf of St. Lawrence, with highest proportions of eastern birds in samples from northern stations. These conclusions are supported by banding and other studies at the mouth of the St. Lawrence estuary (cf. McNeil and Burton 1973, 1977, McNeil and Cadieux 1972), which show that many of the sandpipers that visit the Magdalen Islands launch a transoceanic flight to Caribbean islands. An unknown proportion travel southwest from the Magdalen Islands in a coastwise movement to the Maritimes, but relatively few continue further south along the coast of the United States (McNeil and Burton 1973, 1977, Morrison 1977a). These results agree well with the morphometric studies described here. The bill length averages in Massachusetts (Table 4) are shorter in autumn than in spring, suggesting a lower proportion of long-billed, eastern birds. The high CV values in autumn (Table 4) indicate the presence of eastern breeders, as well as birds from other regions.

Taken together, evidence shows that the majority of eastern Semipalmated Sandpipers use an autumn migration route over eastern North America that passes to sea in a zone centered in southeastern Canada. International shorebird surveys organized jointly by the Canadian Wildlife Service and the Manomet Bird Observatory, Massachusetts, have shown that by far the highest numbers of Semipalmated Sandpipers on the Atlantic seaboard in autumn occur in this zone, particularly in the upper Bay of Fundy (Morrison 1977a). This route lies slightly north and eastward of the one used for spring migration.

The migration routes used by Semipalmated Sandpipers from the central Canadian arctic come closest to conforming to the concept of an elliptical migration route involving a northerly passage through the central U.S. followed by an autumn migration across the Atlantic seaboard (see McNeil 1970, McNeil and Burton 1973, 1977). Morphometric and banding data indicate a spring passage across the Gulf of Mexico and north through central North America in a zone between the Rocky Mountains and the Appalachian mountains. In Kansas, the higher average bill length in spring than in autumn (Table 4) is probably caused by the mixing of central arctic with Alaskan birds in spring but not in autumn. Such mixing probably would not increase the CV significantly unless eastern Canadian birds were involved (Table 5).

Current information does not allow testing whether some central Canadian birds might also arrive on the southeast Atlantic coast in spring and then pass overland, possibly via Appalachian water gaps or other routes. If this does happen, few birds reach as far north as Massachusetts, judging from the high average bill length and the low CV value found there (Tables 3 and 4).

In autumn, central Canadian Semipalmated Sandpipers appear to migrate east of their spring routes, thus accounting for the lower average bill length than in spring in the banding samples at James Bay and Plymouth (Table 4) and in all the eastern groups of museum specimens (Table 3). The bill lengths found at James Bay (Figure 2) suggest that the majority of Semipalmated Sandpipers there are from central breeding regions, though the presence of some eastern birds is indicated by the high CV values (Table 4). The proportion of eastern birds must be low by comparison to Massachusetts where average autumn bill lengths are significantly longer (Fig. 2, Table 4). To summarize, the morphometric information indicates that central Canadian birds travel southwards in a corridor that intersects the Atlantic coast in a zone between the Gulf of St. Lawrence and Virginia, occurring in lower proportions from Massachusetts northwards, and in higher proportions south of Massachusetts.

Banding evidence shows that many Semipalmated Sandpipers travel north through the central United States and Kansas, and south via eastern corridors including the James Bay and Atlantic coasts (Anderson 1968, Parmelee et al. 1969, Martinez 1974 and pers. comm.), thus agreeing well with the morphometric data. In addition, color-marking work carried out at North Point, James Bay, has resulted in numerous sightings of Semipalmated Sandpipers in a coastal zone between the St. Lawrence estuary and Virginia. A much higher proportion of sightings occurred in the United States sector of this zone from work in James Bay than from similar studies on the Magdalen Islands (McNeil and Burton 1973, 1977; Morrison 1977a, b, 1978).

Our results indicate that different migration strategies are used by Semipalmated Sandpipers from the eastern and western parts of the breeding range. The somewhat earlier northward movement of Alaskan/central populations through the Great Plains appears to be influenced by climatic factors. Surface winds are generally southerly along the coast of the Gulf of Mexico and in the southern central parts of the U.S. between March and May (Bryson and Hare 1974, Court 1974), and western areas further north, including inland Alaska, generally warm up earlier than eastern areas at equivalent latitudes, leading to an earlier thaw (Hare and Hay 1974). In some years short-billed migrants have virtually completed their passage through midwestern areas and started arriving in Alaska in late May (Bailey 1948, Gabrielson and Lincoln 1959, Irving 1960), a time when peak passage of long-billed birds on the east coast is just beginning.

During July and August, marine invertebrate food resources are likely to be at their peak in east coast estuaries, and the prevailing airflow patterns are from the northwest (Bryson and Hare 1974). Many birds from eastern and central breeding areas thus appear to have adopted an autumn migration strategy involving a flight to staging areas on the Atlantic seaboard, followed by a transocean flight to wintering grounds in South America. Most Alaskan birds, on the other hand, appear to retrace their spring route, moving southward through the interior. It is not clear whether this overland section is accomplished in a series of relatively short flights or by long stages, nor where the principal wintering grounds may be, though areas in Central America and on the west coast of South America appear probable. It also seems possible that the molt strategy of the Alaskan birds may differ from those from eastern areas (E. F. Martinez, pers. comm.).

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