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ABSTRACT.—We color-marked Sanderlings (*Calidris alba* Pallas) at 19 locations in 6 countries in the New World and coordinated a network of volunteers to locate banded individuals in migration over a five-year period. The observers reported 252 independent sightings of birds in countries different from the country of banding.

Sanderlings that migrate north to the Arctic from Chile and Peru travel principally through the central corridor (Texas and northward) of the United States and Canada; smaller numbers follow the Pacific coast. A few migrate north from the Pacific coast of South America along the Atlantic coast of the United States. Southbound from the Arctic to coastal Chile and Peru, many individuals switch eastward to stopovers on the Atlantic coast, including birds that migrated north along the U.S. Pacific coast. Sanderlings banded in Brazil during the nonbreeding period appear only on the U.S. Atlantic coast in migration.

Our results emphasize the individual nature of migration. We found considerable heterogeneity in migratory behavior among individuals that spend the nonbreeding season together on the same beaches. Individuals from widely separated nonbreeding sites often shared similar pathways. In this species and perhaps in others, no simple single migratory route connects breeding with nonbreeding regions. *Received 5 December 1988, accepted 21 August 1989.*

NEARCTIC shorebirds that migrate to South America for the nonbreeding season reach their "wintering" sites by several routes (Morrison 1984). For a few species with restricted distributions, general characteristics of their pathways can be predicted on the basis of armchair geography: Wandering Tattlers (*Heteroscelus incanus*) and Surfbirds (*Aphriza virgata*) virtually never appear anywhere but along the eastern rim of the Pacific Ocean. Their migration from Alaska to western South America would be unlikely to deviate far from the Pacific coast. The majority of Red Knots (*Calidris canutus rufa*) move along on the Atlantic between the Arctic and Tierra del Fuego (Harrington 1986).

Additional routes have been surmised from the seasonal appearance of large numbers of birds along elliptical routes. Hence, Cooke (1910) and others inferred that Lesser Golden-Plovers (*Pluvialis dominica dominica*) and White-rumped Sandpipers (*Calidris fuscicollis*), among others, travel south to Argentina via the Atlantic coast and north via coastal Texas and the Plains states.

Beyond these cases, deducing even the general nature of migration patterns becomes problematic. For some species, it is difficult to compile adequate records to substantiate the basic pattern. Baird's Sandpipers (*Calidris bairdii*; Jehl 1979) and Hudsonian Godwits (*Limosa haemastica*; Morrison 1984) are examples. Other species with broad breeding or wintering ranges, and with large numbers that move along more than

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one migratory pathway, provide few clues as to how a given population gets to its destination. In these cases, some progress has been made using morphometric cues to determine the breeding origins of birds in migration (e.g. Semipalmated Sandpipers, *Calidris pusilla*; Harrington and Morrison 1979). Rarely, however, are the morphometric differences sufficient to provide adequate resolution.

Sanderling (*Calidris alba*) migratory pathways in the New World cannot be inferred from either distributional studies or morphometric analyses because this species is broadly distributed in migration, and it lacks clear geographic differentiation. Most New World Sanderlings nest on dry arctic tundra north of 72°, principally on islands in the Canadian arctic archipelago and especially on Prince of Wales Island (Manning and MacPherson 1961). During the Northern Hemisphere winter, their range spans some 110° latitude, which encompasses most temperate and tropical beaches in the Americas. While broadly distributed, in fact most Sanderlings at this time of year occur in a few discrete concentration centers in the U.S. Northwest, southeastern Brazil, and especially on the coasts of Peru and northern Chile (Myers et al. 1985a, Morrison and Ross 1989). In migration, they occur commonly along all three U.S. coastlines, especially at staging sites in coastal Washington, coastal Texas, and Delaware Bay (New Jersey).

We began an investigation in 1982 to ascertain the migration route used by Sanderlings wintering in western South America. The shortest pathway from Chile and Peru would take birds north through Panama and thence up the U.S. Atlantic coast. Large numbers of Sanderlings observed during migration in Delaware Bay (Dunne et al. 1982) added credence to our initial prediction that many birds would use this pathway. We identified two alternative migration routes: the Gulf coast of Texas and the central corridor, or the Pacific coast through California, Oregon, and Washington. The null hypothesis, that Sanderlings do not migrate, seemed unlikely.

Materials and Methods

We color-marked as many Sanderlings as possible and organized search efforts to encounter them during migration. We carried out these activities under the aegis of the Pan American Shorebird Program (PASP), a collaborative venture coordinating various shorebird research and conservation efforts in the New World (Myers 1983).

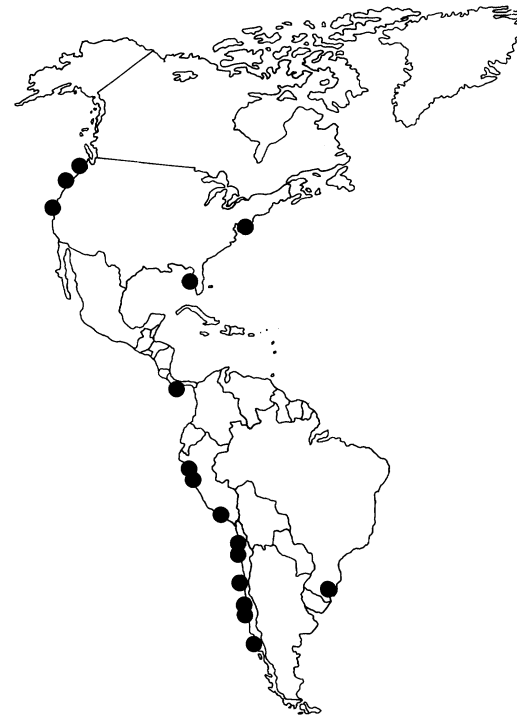

Fig. 1. Location of banding sites.

On the Pacific coast, netting sites extended from southern Chile through Panama to northwestern Oregon (Fig. 1). On the Atlantic Ocean and the Gulf of Mexico, we worked in New Jersey, Texas, and Brazil, with collaborators also banding in Florida and Argentina.

We netted Sanderlings in night roosts using mist nets placed over the surf zone. Each captured bird received a USFWS band plus some combination of color bands and flags. All plastic bands used UV-stable dyes to ensure the colors would not fade. In most cases, the combinations were unique and permitted identification of individual birds. Birds banded but not marked individually could be identified as members of a particular cohort, with known banding dates and locations. The coordinated marking scheme for the hemisphere used colored flags fashioned out of strips of PVC plastic. The marking scheme designates a combination of one or two leg flags for each country in the Western Hemisphere (see Appendices 1, 2).

The authors and assistants made repeated and extensive surveys of Sanderling habitats in Peru, Chile, Brazil, Argentina, Panama, and the United States (e.g. Myers et al. 1984b; Myers et al. 1985a, b; Tabilo 1985). From the literature and from knowledgeable birders,

TABLE 1. Number of Sanderlings banded in different New World countries (1983–1987).

Country	No. of locations	No. of birds
Brazil	2	246
Chile	6	1,273
Colombia	1	2
Panama	1	14
Peru	4	2,551
United States	5	1,673
Total	19	5,759

we identified a series of locations around the U.S. likely to be major passage points for Sanderlings in migration. Coastal Texas, western Washington/Oregon, and Delaware Bay received special attention. We surveyed these sites for flagged birds repeatedly over periods of weeks during the peak of migration. To supplement our own field efforts, we built a network of volunteers to survey likely Sanderling migration stopovers by soliciting for collaborators in popular articles, semiregular newsletters, and widely distributed posters, in both English and Spanish. We alerted the professional community working with migratory shorebirds by publishing updates in relevant outlets (e.g. Myers et al. 1984a, Myers and Sallaberry 1984, Myers et al. 1985b) and through extensive correspondence. Both positive and negative data were solicited and received.

When the volunteer network identified local concentration areas, we visited and personally surveyed Sanderlings for marked birds. This iterative process proved useful in allowing our geographic coverage to evolve as data accumulated.

RESULTS

BANDING

From September 1983 through December 1987, we banded 5,759 Sanderlings at 19 locations in 6 countries (Table 1, Fig. 1). Most were netted along the Pacific coast of South America. Of these, 4,628 received individual combinations, while 1,131 were identified only to banding date and location.

SIGHTINGS

Only those sightings that were clearly attributable to country are included. Most of the time, attribution was straightforward because of the flagging system. On occasion, flags were not reported. In these cases, we were often able to identify the country of origin because of complicated and unique color-band combination schemes used at several sites. Observers failed to report a flag in some cases because they did not distinguish it or because they were unaware of the flag's significance. In other cases, we confirmed that the flag had fallen off. The frequency of sightings without flag information decreased through the course of the program.

From February 1984 through December 1987, we recorded 252 independent reports of color-marked Sanderlings in countries different from the country of banding (Table 2). Birds often stayed for variable periods ($\leq$3 weeks) at a given site (see below). Volunteer collaborators reported 55% of these sightings, particularly those away from our initial target search areas (see Methods). Of the reports from collaborators, 59% came from people actively involved in shorebird research (e.g. Manomet Bird Observatory personnel); the remainder came from non-professional volunteers.

Almost all the reported sightings in the United States of birds banded in South America were of Peruvian- or Chilean-marked birds (Table 2). This preponderance undoubtedly stemmed from the small number of Sanderlings marked in eastern South America (Table 1). The ratio of Peruvian to Chilean sightings did not differ significantly from that expected from the relative numbers of birds banded in each country (Tables 1, 2).

Northbound migration.—We recorded most northbound (February–June) Sanderlings banded on the Pacific coast of South America in the central corridor (Table 3, Fig. 2). Birds from this region also appeared regularly on the U.S. Pacific coast. During each of the first 3 yr of observation, we recorded one Pacific coast Sanderling in the Atlantic corridor at Delaware Bay. This comparatively small number of sightings in Delaware Bay was not due to lack of effort. During each Spring migration of the study, we carried out an intensive sighting campaign in Delaware Bay and obtained hundreds of sightings of Sanderlings banded in Delaware Bay during migration as well as a few birds marked in Florida and in Brazil.

Sightings of Chilean vs. Peruvian birds did not differ in their relative occurrence on these different pathways (Northbound: $\chi^2 = 1.5$, df = 2, $P > 0.47$; Southbound: $\chi^2 = 0.2$, df = 1, $P > 0.63$).

Most sightings of northbound Sanderlings in the central corridor were made in Texas (Fig.

TABLE 2. Total number of independent sightings of Sanderlings in countries different from country of banding. Multiple observations of the same bird over a period of days at one location were counted as one sighting.

Country of sighting	Country of banding					
	Argentina	Brazil	Chile	Panama	Peru	U.S.
Argentina	—	0	0	0	0	0
Brazil	0	—	0	0	0	5
Chile	0	0	—	0	9	2
Panama	0	0	0	—	0	0
Peru	0	0	3	0	—	3
United States						
Northbound	0	4	19	0	87	—
Southbound	0	1	32	0	83	—
Canada						
Northbound	0	0	1	0	1	0
Southbound	0	0	1	0	1	0
Total	0	5	56	0	181	10

2). Sightings were distributed along the Gulf coastline from North Padre Island to the Louisiana border, with a concentration near Galveston. This concentration may have been an artifact of the distribution of observers. If this were the only cause, however, we would have expected more observations near Corpus Christi because of daily census work by A. Amos (pers. comm.) on Mustang Island. Sightings in the central corridor extended northward as far as the Northwest Territories.

The second largest accumulation of sightings came from beaches in northwestern Oregon and southwestern Washington. This region is the major staging site for Sanderlings moving north from the U.S. Pacific coast (Myers et al. 1984b). Sightings of Pacific coast South American migrants were intermingled with observations of color-banded birds that had wintered repeatedly in central coastal California. Banded birds were rarely seen together. Birds from a given country were no more likely to be seen with marked birds from their own country than with marked birds elsewhere.

The earliest sighting of a northbound Sanderling was reported in February as a single 2-year-old, cohort-banded Chilean bird in Corpus Christi Bay, Texas. Otherwise, sightings clustered in Texas in April and early May, and later farther north (Fig. 3).

Southbound migration.—During their southbound migration, Sanderlings from the South American Pacific coast shifted eastward (Table 3, Fig. 2). None was encountered southbound along the Pacific coast; most appeared on the Atlantic coast. This change in the distribution of sightings between migration directions was highly significant (χ^2 on the Total columns, Table 3; $\chi^2 = 168$, df = 2, $P < 0.0001$).

Birds were reported from Prince Edward Island south through Florida, but they were concentrated in coastal Massachusetts, especially Monomoy Island, and on the outer banks of the mid-Atlantic states of Maryland, Virginia, and North Carolina. The ratio of Chilean birds sighted north of Long Island, New York, to those south (14:14) appeared lower than the comparable ratio for Peruvian sightings (52:23). This would suggest birds headed for Chile use stopover sites farther south than those headed for Peru, but the difference was not significant at the 0.05 level ($\chi^2 = 3.3$, df = 1, $P > 0.069$).

Of 12 sightings in the central corridor, 8 were in Texas. The remainder were east of the spring sightings. One individual was observed 15 August 1985 in Presqu'ile Provincial Park, Ontario, and on 31 August at Surfside, Texas.

Two Sanderlings banded at a spring staging site at the Columbia River mouth in Oregon were observed on Cape Cod, Massachusetts, during southbound migration. One appeared the subsequent autumn, the other the next year.

We examined the sighting data for birds from Chile and Peru to determine if birds from one site travel together and if birds from different sites mix in migration (Table 4). First, birds from the same banding site were seen regularly in different migration corridors and at different

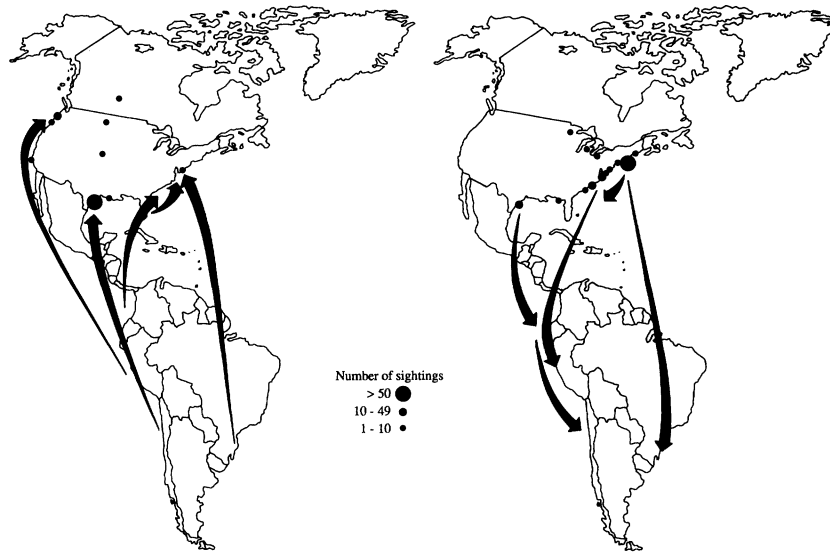

Fig. 2. Movements of Sanderlings banded in Peru, Chile, Brazil, and Florida to and from locations in the United States and Canada.

sites within the same corridor. Second, mixing was the rule not the exception. Banded birds were unlikely to be seen together; if they were, they often were closest to banded birds from other sites or even from other countries. The only exception involved the simultaneous appearance of at least six marked birds from central coastal Peru near Galveston, Texas, in early May 1985.

Our methods were not designed to yield quantifiable data on the passage times of marked birds through given areas. We depended on volunteers whose frequency of visits to appropriate habitat was usually insufficient to produce the data. Further, most often the authors' fieldwork involved broad sweeps across lengthy coastal sectors (e.g. the Texas coast) rather than repeated surveys of local sites. Nonetheless, in five locations we accumulated data on lengths of stay of both northbound and southbound birds (Table 5). No difference was apparent between lengths of stay in northbound vs. southbound directions (comparing rows of totals, Table 4: $\chi^2 = 2.0$, df = 3, $P > 0.56$).

We achieved daily coverage only on Mustang Island, Texas. One individual reappeared there on multiple migrations (see below) and stayed in the area at least 24 days in spring 1985. It defended a territory while foraging on the beach, but was not present on the beach every day during that period.

Dispersion of Sanderlings at staging sites.—Sand-

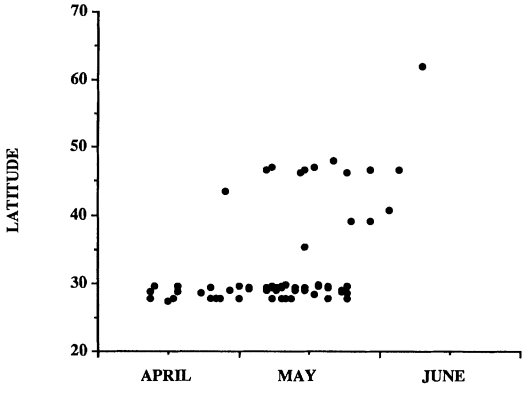

Fig. 3. Latitude of sightings of Sanderlings banded in Chile and Peru during northbound migration in the United States and Canada.

TABLE 3. Number of sightings of color-marked Sanderlings from Peru and Chile in migration corridors in North America.

Corridor	Northbound			Southbound		
	Peru	Chile	Total	Peru	Chile	Total
Pacific	11	4	15	0	0	0
Central	74	14	88	8	4	12
Atlantic	2	1	3	76	28	104

TABLE 4. Sightings at migration stopovers in North America of Sanderling[a] color-marked at nonbreeding locations in Peru and Chile.

Migration stopover	Peru			Chile		
	Villa	Pracas	Mejia	Hornitos & Mejillones	Coquimbo	Valdivia
Northbound						
SW Washington[b]	1	3	2	1	1	0
Clatsop Beach, Oregon	1	2	1	1	0	0
Galveston area, Texas[c]	3	18	4	2	3	1
Southbound						
Duxbury, Massachusetts	0	2	2	0	1	0
Monomoy, Massachusetts	2	4	7	4	2	0
Assateague, Maryland/Virginia	2	3	2	2	1	0
Outer Banks, North Carolina	2	1	4	2	2	1

[a] Multiple observations of the same individual at the same site are excluded. See Figure 1 for banding locations.
[b] Includes all birds observed from Long Beach, Washington, to Moclips, Washington.
[c] Includes all birds observed from Galveston Island, Texas, north to Crystal Beach, Texas.

erling dispersion differed markedly at the three principal staging sites. Along the Texas coast, individuals were widely dispersed and often defended linear territories along coastal beaches. In Washington, Sanderlings occurred in large feeding flocks with densities reaching 900 birds/km. In contrast, as many as 30,000 Sanderlings were observed on 1 km of Delaware Bay.

Multiple sightings of the same bird.—We saw only four individually marked birds on more than one migration. On Mustang Island, Texas, one female from Peru was reported on three successive migrations (northbound twice and southbound once). On each migration, this female defended the same small feeding territory on the outer beach. The position of her territory deviated at most by a few meters from one migration season to the next.

There were two other cases of same-location sightings on more than one northbound migration; both were in Texas and involved a bird sighted in two successive years. One occurred at the same place and within 6 calendar days between years; the other appearance was separated by 17 calendar days and ca. 20 km.

We accumulated only one such southbound record, a Peruvian-banded Sanderling seen in two successive years on Monomoy Island, Massachusetts. Many individuals were seen at Monomoy in successive years with the same cohort combination, although individual birds were not identifiable.

DISCUSSION

The geographic distribution of sightings reflects in part the distribution of volunteer observers and the authors' inability to cover all

TABLE 5. Lengths of stay of individually identified Sanderlings at migratory stopovers in North America.

Stopover	Length of stay			
	1 day	≤1 week	1–2 weeks	2–3 weeks
Northbound				
Galveston, Texas	21	7	4	2
Mustang Island, Texas	3	2	0	1
Washington-Oregon				
Mouth of Columbia River to Moclips	5	1	2	0
Total	29	10	6	3
Southbound				
Monomoy Island, Massachusetts	14	5	6	1
Duxbury Beach, Massachusetts	10	1	2	0
Total	28	6	8	1

relevant sites with equal intensity. This inherent bias prevents definitive calculations of the proportions of different populations that use specific pathways. The major patterns of movement are clear:

1. South American Pacific coast Sanderlings migrate northward along all three migration corridors, with emphasis on the Central route and, to a lesser extent, the Pacific routes. Southbound, the main pathways are farther east, largely on the U.S. Atlantic coast. Some individuals use the Pacific northbound and the Atlantic southbound; thus their migration patterns delineate a large, circumcontinental ellipse.
2. South American Atlantic coast Sanderlings move to and from breeding sites in the Arctic exclusively on the Atlantic coast.
3. Sanderlings wintering on the North American Pacific coast move north and south on the Pacific coast. Northbound, they mix with South American birds at staging sites in Oregon and Washington; southbound, they have that corridor to themselves.

Observations of the same color-marked individuals on both the Pacific (northbound) and the Atlantic (southbound) coasts of the U.S. were important to establish these patterns. The most parsimonious explanation of these bicoastal appearances is that they involved South American birds that had migrated via North America along the Pacific coast, where they were banded. After nesting in the Arctic, they returned to South America along the U.S. Atlantic coast, where they were again encountered. This is the most likely explanation because (1) they were caught in a nocturnal roosting flock that contained banded birds from Chile and Peru; (2) to produce the observed change in distribution of sightings (Table 3), many individuals must switch their migration corridor between spring and autumn; (3) none of the 1,200+ Sanderlings banded in coastal California since 1975 was ever detected on the U.S. Atlantic coast during migration or winter; and (4) nonbreeding Sanderlings from North and South America show high interyear site faithfulness to their wintering sites (Myers et al. 1988). We hedge our conclusion, nonetheless, because neither of the two individuals involved was ever seen in South America and because we also caught Sanderlings previously banded in Oregon and California from within the same nocturnal roost. We noted one exception to this general pattern. An individual banded in May at the Columbia River mouth in Oregon subsequently reappeared southbound in Oregon and then on the Galápagos Islands.

Even with this general overview, questions remain. A central one focuses on the discreteness of the major wintering sites. While our data demonstrate little if any movement among wintering sites for birds after their first nonbreeding season, we cannot resolve how the initial nonbreeding site is chosen in the first autumn migration. There may be a considerable genetic influence on this process in passerines (e.g. Berthold and Querner 1981, Berthold 1984). If there is significant genetic control in Sanderlings as well, then this would imply that Sanderlings wintering in different regions segregate on the breeding grounds.

We do not know where birds from the different wintering areas breed. There may be three breeding centers of Sanderlings in the Arctic: northwestern Greenland and Baffin Island, the central Canadian arctic islands, and the Taimyr Peninsula (Cramp and Simmons 1983). Birds from the first two areas winter in the Old World. Whether birds from all three major New World nonbreeding areas converge and mix in the central Canadian Arctic, or whether they segregate into distinct breeding populations, still remains an open question.

We can reject definitely only the null hypothesis—Sanderlings clearly migrate. We found that South American Pacific coast Sanderling use each of the major corridors, and migration occurs principally in large, clockwise ellipse patterns. Most individuals move northbound through the central corridor and southbound along the Atlantic. Few birds use the route we first regarded as most likely, north and south on the Atlantic.

More generally, we demonstrated considerable heterogeneity in migratory behavior within and among "nonbreeding populations" of birds that superficially might be expected to share breeding areas and migration routes. Birds from the same nonbreeding site may use markedly different pathways northbound and southbound. Conversely, birds from widely separated nonbreeding sites may share migratory pathways more than do some birds from the same nonbreeding site. Heterogeneity thus emerges as a central feature of Sanderling migration, and it means that no single, simple migratory route connects nonbreeding with breeding areas. Instead a web of sites are linked

by many different migratory pathways. We predict that comparable data from other species will reveal similar diversity.

The maintenance of this heterogeneity in Sanderlings is perplexing. Its existence suggests that migratory route, at least the choice of routes as different as the Pacific and Central corridors, may not contribute importantly to reproductive fitness. Our data do not resolve this but instead raise questions about the interplay of environmental and genetic factors that control an individual's selection of its migratory route and wintering area.

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APPENDIX 1. The Pan American Shorebird Program Marking Scheme.

A plan to coordinate color-marking schemes employed in investigations of shorebird migration patterns was circulated within the shorebird banding community (Myers et al. 1983) and met wide acceptance. We describe it here to bring it to the attention of ornithologists generally who might observe one of the marked birds or might face similar problems with other migratory bird groups.

Each country in the New World has been assigned a unique one- or two-flag combination (Appendix 2). During sightings, this flag combination immediately identifies the country of banding. Further identification detail is then coded into standard color-band combinations. Whether this detail identifies only the bird's banding cohort (e.g. site, date, age) or whether it identifies the specific individual is left to the discretion of the bander. In either case, the system increases radically the likelihood that a sighting will yield useful information about the origins of a banded bird. Instead of having to interpret the entire combination, an observer can pinpoint the country of origin just by noting the flag color.

The flag system reduces the potential for "combination competition" to other banders of the same species in the same country. As a result, coordinating color-combinations becomes much easier. The U.S. Fish and Wildlife Service, which issues color-banding permits in the United States, has informally consulted with the Pan American Shorebird Program (PASP) to avoid combination overlap. At the same time, individual banders consult with one another directly, through the PASP, or with the research group taking the lead on a particular species (e.g. Harrington [1986] and the Red Knot).

In addition to dictating flag color, the original protocol (Myers et al. 1983) proposed tight control of flag placement (e.g. left leg for northbound, right leg for southbound). This proved too inflexible to meet the goals of individual research projects, and flag placement now varies according to individual research program needs. The approach has evolved to the point where some stations vary flag position as one element of individual color combinations. Others use flag position to help encode banding cohort. As these more precise identifications are coded with standard color bands, the critical point is to coordinate in-country. Once a flag is used, "combination competition" with other countries is no longer an issue.

Two additional efforts to coordinate banding methods merit description. Since 1983 the Pan American Shorebird Program has been distributing modest banding supply kits to South American collaborators. These include color bands, materials for making flags (sold by A. C. Hughes, Ltd. (London) as leg blanks), Pesola scales, mist nets, data forms, manuals, and lists of unique color-band combinations. The lists are generated using an IBM-compatible PC and copies remain in PASP files. Increasingly North American banders including Manomet Bird Observatory (Red Knots), the Canadian Wildife Service (many species), and others have also been using lists generated by PASP. This growing practice ensures hemisphere-wide coordination of unique color combinations used on migratory shorebirds.

Second, under the auspices of a grant from the J. N. Pew Charitable Trust, PASP is distributing a small number of microcomputers and database software to collaborating banding stations in Central America and South America. A principal requirement is that collaborators exchange banding data with others, which is made possible by the common software and data formats. This will enhance further the level of international cooperation in shorebird migration and conservation studies. Source code for the software (written in dBaseIII+) is available from the authors.

APPENDIX 2. Pan American Shorebird Program flag code for Western Hemisphere countries.

North America. White (Canada), green (United States).
Central America. **Red over** the following colors: yellow (Mexico), grey (Honduras), black (Costa Rica), orange (Guatemala), dark green (Nicaragua), light green (Belize), blue (El Salvador), white (Panama).
Caribbean. **Yellow over** the following colors: red (Haiti), dark green (Puerto Rico), white (Dominican Republic), orange (Cuba), black (Jamaica).
Northern South America. black (Venezuela), light green (Suriname). **Light green over** the following colors: yellow (Colombia), red (Ecuador), dark green (Guyana), blue (French Guiana).
Central South America. Yellow (Peru), blue (Brazil). **Orange over** the following colors: red (Bolivia), yellow (Paraguay), blue (Uruguay).
Southern South America. Red (Chile), orange (Argentina).