

The staging paradigm and wetland conservation in arid environments: shorebirds and wetlands of the North American Great Basin

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North American efforts to protect shorebird populations have focused on the guidelines of the Western Hemisphere Shorebird Reserve Network, WHSRN. These guidelines are based upon numbers of migrant shorebirds congregating in an area relative to global and flyway population estimates. We discuss the assumptions underlying these guidelines by examining scale-dependence in shorebird habitat use, breeding behavior, and migration behavior. The "staging paradigm" used by WHSRN (the view of large, predictable stopover sites, identifiable by shorebird numbers at a global scale) is built primarily from long-distance migration patterns of *Calidris* sandpipers, and applied to all species. We suggest examples of migration pattern and wetland availability that might make this paradigm insufficient for protecting shorebird populations. Species that migrate in short hops or in a diffuse pattern may not form large congregations, and critical habitat could be missed under the WHSRN guidelines. In addition, when there is dramatic temporal variability in wetland availability, as in interior regions, sites may be critical for shorebird populations only in some years. Conserving sites important for large numbers of shorebirds during migration is not sufficient to protect all species of shorebirds, particularly those that have limited or declining breeding or wintering habitat. These points are illustrated for the case of wetlands of the North American Great Basin physiogeographic province, an area characterized by cold temperate desert and unpredictable wetland availability.

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Introduction

Wetlands are among habitats most vulnerable to anthropogenic degradation and disturbance (Howe 1987). Since 1780, more than 50% of all wetlands in the continental United States have been lost, an estimated 119 million ha (Dahl 1990). Approximately 80% of these wetlands were inland sites (Frayer *et al.* 1983). The impact of such dramatic losses on waterfowl and shorebird populations (*e.g.*, Page & Gill 1994) makes it imperative to identify and protect remaining critical wetland habitat.

Multiple organizations have established specific priorities for protecting wetlands. Some of these stated priorities include 1) identifying and preserving areas regularly used by the largest numbers of migrant birds, (*e.g.*, Western Hemisphere Shorebird Reserve Network, WHSRN, Myers *et al.* 1987), 2) protecting continental migration areas by controlling losses to development, disease, and contaminants (*e.g.*, North American Waterfowl Management Plan, Ratti & Kadlec 1992), 3) considering local wetland functions and values

(wildlife, fisheries, water supply, water quality, flood control, and recreation) when identifying wetlands to acquire (*e.g.*, National Wetlands Priority Conservation Plan, U.S. Fish and Wildlife Service 1989), and 4) developing water-quality standards for heavy metals, pesticides and other contaminants (*e.g.*, Catallo 1993) to be applied to individual wetlands. Some international efforts combine several of these objectives. For example, guidelines of the Ramsar Convention consider unique wetland types, rare species, ecological diversity, waterfowl numbers and socioeconomic values (Boyd & Piro 1989; Crockford & Piersma 1987).

The perceived importance of a wetland site for shorebirds relies, in part, on the temporal and spatial scales at which that importance is measured (see Appendix 1). Counts of shorebirds can be translated into importance in a number of ways. Temporally, importance could be measured based on the timing and frequency of counts, for example on a daily basis (bird-days), seasonal basis (numbers breeding, migrating, wintering), annual basis (total numbers), or longer-term basis (*e.g.*, peak numbers over 10

years). Depending on the way that count data are grouped spatially, importance also can be measured on a local (e.g., relative to numbers in a valley, county, etc.), regional (e.g., relative to numbers on the Atlantic Coast, Great Plains, or Great Basin, etc.), or global basis (relative to the total numbers of a species, Figure 1).

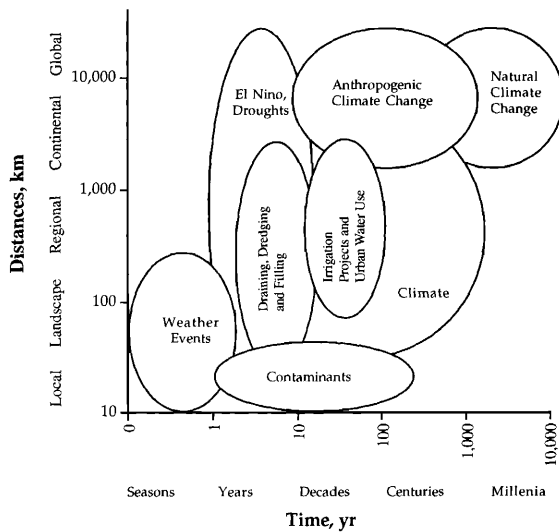


Figure 1. Spatial and temporal variability in factors that impact wetland birds. The factors affect some combination of wetland availability, array, suitability, and quality. Scales shown are for the processes themselves, not for their effects on shorebirds.

The significance of sites for shorebirds in the Western Hemisphere has been largely assessed using the recommendations of WHSRN (1992), which classify wetlands into four categories of importance: 1) Hemispheric sites that support at least 500,000 shorebirds annually or 30% of a species' flyway population, 2) International sites that support at least 100,000 shorebirds annually, or 15% of a species' flyway population, 3) Regional sites that support at least 20,000 shorebirds annually or 5% of a species' flyway population, and 4) Sites that are critical to the survival of an endangered species with no minimum number of birds.

The WHSRN criteria of importance are intuitive and easily documented, making them invaluable in identification of critical shorebird habitat for certain species. However, WHSRN guidelines focus on a single temporal scale (usually migration), and two spatial scales (numbers relative to total shorebirds in the world, and numbers relative to a single species flyway population). To be certain that conservation criteria are sufficient to protect all shorebird species, the choice of scale must be examined critically. The numeric criteria emphasized by WHSRN guidelines might lead one to overlook other important considerations such as the use of wetland areas at different spatial and temporal scales (Senner & Howe 1984; Skagen & Knopf 1993). In particular, habitat that is critical to breeding or wintering birds, habitat critical to species that do not migrate long distances, or habitat that is annually unpredictable might be missed under the WHSRN criteria.

In this paper, we consider the influence of scale on shorebird conservation in the Great Basin. We evaluate 1) assumptions underlying current shorebird management approaches (the "staging paradigm," see below), 2) spatial and temporal variability in wetlands of the Great Basin, and 3) whether applying current management practices will be sufficient to identify critical wetlands and conserve shorebirds in non-coastal habitats such as the fragmented wetlands of the Great Basin.

Migration and spatial scale: The staging paradigm

The global view of shorebird migration through North America was founded on a review of *Calidris* sandpiper migration (Morrison 1984). Morrison followed the geographical pattern of flyways identified for ducks (Lincoln 1935) and identified the specific *Calidris* sp. that predominated in each. Although few shorebird species migrate solely along one of the identified flyways, this model has become the generally cited pattern for all shorebirds (e.g., Morrison & Myers 1987, 1989; Helmers 1992).

Along the migration route shorebirds may stop at staging areas, where they rest and fatten before continuing migration, or at stopover sites, where they may rest for a few days but do not regain large amounts of body fat. In coastal areas of the Atlantic and Pacific Flyways, migrating shorebirds collect in massive numbers at a small number of staging areas (summarized by Morrison 1984). These sites typically have predictable and abundant food resources, and shorebird numbers may track the abundance of these resources (Schneider & Harrington 1981). Some widely cited examples of dramatic shorebird numbers occur in spring at the Copper River Delta, Alaska (Senner 1979), and at Delaware Bay [preying on horseshoe crab (*Limulus polyphemus*) eggs, Botton *et al.* 1994]. Skagen & Knopf (1993) termed this view of large, predictable staging areas, identifiable by shorebird numbers of global importance (Myers 1983; Harrington *et al.* 1989) as the "coastal paradigm". However, given that there are equally good examples for some species at sites in interior North America (e.g., Mono Lake, California; Great Salt Lake, Utah; and Cheyenne Bottoms, Kansas; Morrison & Myers 1987), this term is misleading. Identifying the numeric importance of sites through counts on fixed dates includes an implicit assumption that birds use the site for a time interval longer than the count period. Thus, we feel it is more appropriate to refer to the identification of numerically important migration sites as the "staging paradigm."

Although typically viewed only as a large-scale process, migration is really a complex set of movements that occur at scales from local to global (e.g., Wilson 1993). There has been a growing awareness among conservation biologists that scale-dependent use of habitat by wetland birds needs to be incorporated into management approaches (Helmers 1992). Skagen & Knopf (1993) analyzed patterns of shorebird migration across

midcontinental wetlands and noted that inland migrants were more broadly dispersed spatially, and used habitats that were less temporally predictable than shorebirds that migrate along the coast. They concluded that "protection of habitat for species that use disjunct patches of habitat opportunistically or irregularly during migration is a difficult challenge that has received little attention" (Skagen & Knopf 1993:538). This sort of patch-use includes greater spatial and temporal variability than that in coastal habitats. In particular, importance of a target habitat may be realized only in years when habitat is relatively limited. Varying patterns of habitat use may disallow arbitrary use of numerical criteria in ranking wetlands by importance.

Wetlands of the Great Basin

Spatial and temporal variability

Relative to coastal wetlands, Great Basin wetlands have a greater degree of temporal and spatial variability. Spatial variability in Great Basin wetlands comes from their naturally fragmented state. Over the last 15,000 years, they have been declining from their pluvial high points, becoming smaller and more isolated (Grayson 1993). In addition to these climatic changes, the Great Basin also experiences dramatic annual variation in precipitation, which leads to extraordinary annual variation in wetland area and quality. Wetland invertebrates and plants in the Great Basin are adapted to the cycles of inundation and drying that typify playa basins (Merickel & Wangberg 1981). Therefore, migratory birds ought to be more opportunistic and less committed to local sites in the Great Basin than in non-Great Basin sites.

The natural levels of spatial and temporal variability have been increased by human activities. In the arid Great Basin, water availability is the prime factor that determines whether a wetland is usable by shorebirds. Wetlands in the Great Basin have suffered continuing habitat loss and degradation due to urban water diversion and irrigated agriculture.

Increased urban use of riverine waters decreases the amount and quality of water available for terminal wetlands. Effects of such a decrease are twofold: first, some wetlands dry up, and second, remaining wetlands become more shallow, more saline, and/or more contaminated through evaporative concentration (e.g., Hoffman *et al.* 1990; Rubega & Robinson, this volume). For example, water diversions of eastern Sierra Nevada snow melt by the city of Los Angeles have, over the last century, dried Owens Lake completely (39,000 ha in area), and caused Mono Lake to drop more than 40 vertical feet, decrease in area from 50,000 ha to 24,000 ha, and triple in salinity (Patten *et al.* 1987).

Irrigated agriculture in closed basins also decreases quality and quantity of water in wetlands. For example, before manipulation by humans, 34,800 ha of wetlands of the Lahontan Valley, Nevada (Stillwater, Carson Lake, and Carson Sink) were maintained at the terminus of the Carson River (Hoffman *et al.* 1990; Neel & Henry, this volume).

After the Newlands [Irrigation] Project (U.S. Bureau of Reclamation, 1905) was completed, water from the Carson and Truckee rivers was used for irrigation, with spills and return flows released to much smaller (6150 ha) terminal wetlands (Hoffman *et al.* 1990). The irrigation accumulated salts and contaminants and concentrated them in the wetlands. In 1990, Federal legislation designed to end water disputes over the project (Public Law 101-618, 1990) mandated more efficient water use by the irrigation district. However, without other sources of fresh water, spillage reduction associated with more efficient irrigation operations further reduced wetland size and water quality (Hoffman 1994). The only way to offset dramatic reductions in wetland water quality was to purchase water rights for direct release into the wetlands (U.S. Fish and Wildlife Service 1992).

Shorebird use

Migrants. Shorebird migration through the Great Basin is not well understood. The Great Basin lies on the eastern edge of the Pacific Flyway (Page *et al.* 1992). The number of stopover sites is limited in years of low precipitation, while in the wettest years the Great Basin consists of thousands of small ephemeral wetlands. Between-year variability in wetland quality and use is much more extreme for Great Basin wetlands than for coastal wetlands (Page *et al.* 1992), and, thus, the role of small sites could be underrated.

Shorebirds that migrate through Great Basin wetlands differ from those using other interior biogeographic regions. Skagen & Knopf (1993) noted that the predominant species of spring migrants in the Great Basin and the Colorado Plateau tended to move shorter distances and to be of larger body sizes than species migrating through the Great Plains. Areas of unpredictable resource availability, such as are found in the central and western USA, receive large numbers of shorebirds during migration (Skagen & Knopf 1993). In some areas, passage of shorebirds through these wetlands appears to be gradual rather than the dramatic influx seen over the short term in coastal estuary systems (Skagen & Knopf 1994).

The variability in spatial and temporal scales that is integral to Great Basin wetlands could influence whether we designate a site important for migrants under current WHSRN criteria. An evaluation of the following three cases of scale-dependent migratory behavior exposes the potential for wetland areas inhabited by certain species groups to be overlooked.

Shorebird species which migrate inland in large, conspicuous flocks are easily documented from annual counts. American Avocets (*Recurvirostra americana*), Long-billed Dowitchers (*Limnodromus scolopaceus*), Western Sandpipers (*Calidris mauri*) and Wilson's Phalaropes (*Phalaropus tricolor*) all exhibit a migration strategy that leads to large numbers in shorebird counts (e.g., right hand side in Figure 2), and are more likely to be protected under the staging paradigm, at least at the sites where they congregate. Three Great Basin sites have been proclaimed as Hemispheric Reserves: Mono Lake, the Lahontan Valley (Stillwater/Carson Lake), and Great Salt Lake.

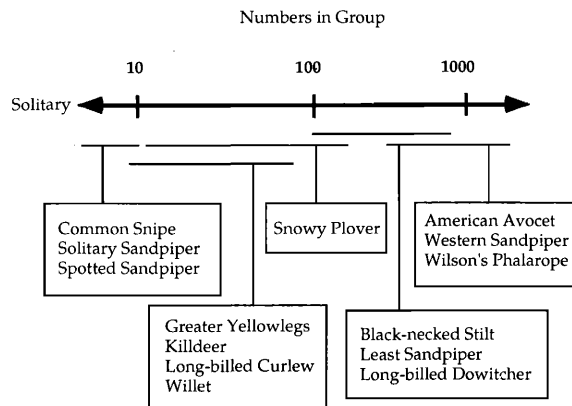


Figure 2. Clumping behavior of shorebirds at stopover sites during migration. Representative species along regions of the continuum are indicated. For scientific names, see text.

Other species tend to migrate in smaller flocks that rapidly turn over at large wetlands. In the Great Basin, Black-bellied Plovers (*Pluvialis squatarola*), Black-necked Stilts (*Himantopus mexicanus*), Dunlin (*Calidris alpina*), Semipalmated Plovers (*Charadrius semipalmatus*) and Willets (*Catoptrophorus semipalmatus*) might be migrating in smaller flocks (cf., Figure 2), but the sum of their numbers at sites that are not WHSRN Hemispheric Reserves (Page *et al.* 1992) suggests that the importance of Great Basin sites could be underestimated at a global scale.

Finally, a few species tend to migrate in small flocks that either use small wetlands as they are encountered, or use habitat that is not readily surveyed. Solitary Sandpipers (*Tringa solitaria*), and Greater and Lesser Yellowlegs (*T. melanoleuca* and *T. flavipes*) are usually seen in small numbers during migration (cf., Figure 2). In addition, at least four shorebird species use habitat in areas unlikely to be surveyed in organized counts, and thus are unlikely to be protected: Common Snipe (*Gallinago gallinago*), Killdeer (*Charadrius vociferus*), Long-billed Curlews (*Numenius americanus*), and Snowy Plovers (*Charadrius alexandrinus*).

Breeding birds. While little may be known regarding migration of shorebirds through the Great Basin, less is known about shorebirds that breed there. A few species of shorebirds (e.g., American Avocets and Black-necked Stilts, Alberico 1993) nest in conspicuous colonies. The importance of these breeding areas can be determined easily because they are readily counted. It is more difficult to determine the importance of sites for the larger number of species that breed in a more dispersed pattern (Pienkowski *et al.* 1987). The ephemeral nature of Great Basin wetlands means that breeding shorebirds face unpredictable habitats. Individual birds respond to wetland fragmentation by redistributing themselves among remaining wetlands (e.g., Robinson & Oring 1996). Individual redistribution, rather than an immediate loss of individuals (May 1981), has the propensity to conceal population declines. A few preliminary recommendations for managing interior wetlands for breeding shorebirds have been made (Eldridge 1992; Hand *et al.* 1991; Helmers 1992), but the field is in its infancy (Oring &

Elphick 1993). Alarming, temperate-breeding shorebirds such as those in the Great Basin recently were ranked as the shorebird species most vulnerable to environmental change (Page & Gill 1994).

Can the staging paradigm be applied to the Great Basin?

Identifying globally-important staging areas is an important first step in large-scale efforts to conserve shorebirds. A staging paradigm has been used to determine which sites are numerically most important by measuring shorebird numbers during migration relative to global and flyway population estimates. This approach, as applied by WHSRN, is a benchmark for other global conservation programs for migratory birds (Patterson 1994). Does the WHSRN approach identify enough critical wetlands to adequately conserve all species of shorebirds in the Great Basin?

Agreeing with Skagen & Knopf (1993), we found that assumptions underlying numerical criteria used by WHSRN are not met at all inland wetlands. Fragmented ephemeral wetlands receive opportunistic use by migrant shorebirds, and thus the importance of a site may be missed by inconsistent surveys. Shorebirds use wetland habitat in arid areas in a more diffuse manner than habitat in coastal areas, making application of simple numeric criteria more difficult. A wetland site in the Great Basin might be used by few birds until a drought year when it becomes critical habitat for a species. Equivalently, a site that had been dry for several years could be flooded suddenly and be used by large numbers of shorebirds. These wetlands may form a critical link in the life histories of the individuals and species using them. If the importance of a site is based only on use by consistently large numbers of birds, then a significant portion of critical shorebird habitat may not be identified and preserved.

Effective conservation of shorebird habitat in the mid-continent region must reflect the need for intermediate stopping points between major staging sites and breeding areas (Skagen & Knopf 1994). In particular, we need to better understand the habitat needs and wetland spatial array required by the shorter-distance migrants typical of the Great Basin.

The importance of Great Basin wetlands cannot be judged solely on the numbers of birds using a site during migration, or even on whether birds use a site every year. Wetlands in the Great Basin could be important globally for some species (e.g., those that use habitat diffusely) without meeting the criteria of the WHSRN program. Until we have a better understanding of the way that individuals, populations and species depend on the natural patterns of variability in Great Basin wetlands, we should not unquestioningly adopt absolute numeric criteria. Knowing the number of shorebirds using an area is not in itself a sufficient basis for proscribing conservation measures (Wilson 1993).

We suggest that more flexible criteria be applied for identifying critical shorebird habitat for migrants at Great Basin and other inland wetlands. Several additional criteria of importance could be used. 1) Habitats needed by shorebirds in years when precipitation is above normal and habitats needed in years when precipitation is below normal must both be protected. Wetlands that serve as refugia for birds that are displaced in extremely dry years (*i.e.*, aperiodically achieve WHSRN numeric criteria) should be considered as WHSRN conservation sites even if they do not have the requisite numbers of shorebirds present every year. Equivalently, places that support large numbers of shorebirds when flooded in wet years should be eligible for protected status regardless of shorebird use when dry. 2) Wetlands that are small but of consistent availability and quality should be considered as International or Regional sites even if their shorebird use is inconsistent. The appropriate criteria for such sites may be specific to the region. 3) Reduced numeric criteria should be applied to species that do not congregate at a few large staging areas. In particular, numeric criteria should be applied carefully to species that are short-distance migrants and species that use habitats in an opportunistic manner.

Perhaps most importantly, the significance of a Great Basin wetland to breeding birds also must be considered. Great Basin habitats support temperate-breeding shorebirds that may be most vulnerable to continuing habitat loss. However, management approaches for the species and habitats in the Great Basin are undeveloped. We cannot assume that protecting the currently designated WHSRN Reserves is sufficient for protecting the integrity of wetland habitats and shorebird populations in the Great Basin.

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Appendix 1: Scale-dependent processes in shorebird conservation

Considerations of temporal and spatial scale are paramount for evaluating conservation approaches (Noss 1990; May 1994). The basic processes of avian biology, including habitat selection, breeding site fidelity, natal philopatry, and migration, are all scale-dependent. Scale-dependent patterns are those that "show a change in some measure of the pattern with a change in either the resolution or range of measurements" (Schneider 1994). Just as natural biological processes occur at varying scales, the factors that disrupt these processes and adversely affect birds also occur at different temporal and spatial scales (Figure 1). Of necessity, management activities designed to alleviate these impacts also occur at different scales.

A critical consideration in formulating management plans at one scale is whether that activity will have undesired effects at other scales. For example, reducing the number of sites at which a species is found (by protecting some sites and not others) might reduce total population densities (Dolman & Sutherland 1994; Goss-Custard 1979; Goss-Custard *et al.* 1994; Lawton *et al.* 1994). Second, reducing population densities within sites (by habitat degradation) might reduce the number of sites occupied by reducing the amount of movement between sites (Lawton *et al.* 1994). Thus, management activities that favor certain sites selected at a larger scale may lead to unforeseen declines at smaller scales. Furthermore, reduced quality of a few sites (a smaller scale process) might lead to declines at other sites (a larger scale process) even though the other sites are fully protected.

Here, we discuss the scale-dependent processes that should be considered in protecting shorebird populations. We have two purposes in listing these processes. First, we emphasize and distinguish scale considerations during migration from other times of the year. Ideal management approaches should incorporate such seasonal-scale differences, and are important considerations in whether a management scheme built on migratory biology is sufficient for conservation on an annual or greater temporal scale. Second, we underscore scale-specific assumptions that underly current approaches for conservation of migrant shorebirds. Making these assumptions explicit should allow more careful evaluation of the applicability of specific criteria (*e.g.*, the WHSRN criteria) to regions where the assumptions are not met.

Habitat use

Habitat use by shorebirds reflects underlying needs that change at different times in the annual cycle (*i.e.*,

Table 1. Scales of breeding site fidelity and natal philopatry for shorebirds that breed in the Great Basin. + and ++ indicate relative degrees to which fidelity and philopatry are predictable at the given scale. See text for discussion of scales.

Species (Reference)	Breeding site fidelity			Natal philopatry		
	micro.	local	regional	micro.	local	regional
American Avocet (Robinson & Oring, unpubl.)		++	+		+?	+?
Black-necked Stilt (Robinson & Oring, unpubl.)			+			+?
Killdeer (Oring, unpubl.)	++	+		+	++	?
Long-billed Curlew (Redmond & Jenni 1982)		+			+	+
Spotted Sandpiper (Reed & Oring 1993, & <i>op cit.</i>)	++	+			++	
Snowy Plover (Stenzel <i>et al.</i> 1994)		+	++			
Willet (Wilcox 1980)	++				++	
Wilson's Phalarope (Colwell <i>et al.</i> 1988)		+	+		+	++

at different temporal scales). For example, nesting habitat generally is used at a microhabitat scale, but brood-rearing habitat often is used at a local scale (Sedinger 1992). Pre-migratory birds use habitat at both local and regional scales, moving from breeding sites to congregate in nearby wetland areas before departing on migration (Connors *et al.* 1979; Gill & Handel 1990), or searching for new breeding sites for future use (Reed & Oring 1992). Habitat use while migrating also can be detected at the microhabitat (Burger *et al.* 1977), local, regional (Skagen & Knopf 1993), as well as global (Morrison & Myers 1987) scales. Wintering shorebirds also use habitat at local to regional scales; on a local scale, movements of hundreds to thousands of meters over a day may be made by shorebirds switching between foraging sites or from roosting to foraging sites (Kelly & Cogswell 1979; Connors *et al.* 1981, Warnock & Takekawa 1996). Within the wintering season, many species of shorebirds also undertake movements on a regional scale, traveling 10 - 100s of km in response to changes in weather patterns, prey distribution or predator density (Connors *et al.* 1981; Ruiz *et al.* 1989; Warnock *et al.* 1995).

(*e.g.*, territoriality) and habitat that is predictable year after year (Oring & Lank 1984). Tendency for regional movements also may depend on the spatial distribution of suitable habitat (Haig & Oring 1988b).

Breeding biology and spatial scale

Breeding site fidelity and natal philopatry occur at local to regional scales in most shorebirds (shown for shorebirds that breed in the Great Basin in Table 1). The scale at which these processes should be studied is the scale at which they are predictable, and this depends on the species in question. For example, Reed & Oring (1993) found their estimates of fidelity and philopatry for Spotted Sandpipers (*Actitis macularia*) differed when a small core study site was compared to a larger site that included less optimal habitat. At the core site, they found that natal philopatry was male-biased (see Oring & Lank 1984; Oring 1988). However, when patches of less-optimal habitat were included, philopatry was similar for both sexes. This effect was due to older territorial females preventing recruitment of young females to the core optimal habitat. Measuring philopatry at only the core site gave an inaccurate picture of recruitment into the population.

Breeding birds of some shorebird species typically show regional movements. Those that move regionally *within* breeding seasons usually move in response to nesting failure or for second nesting attempts (*e.g.*, Haig & Oring 1988a; Oring *et al.* 1994; Reed & Oring 1993). Stenzel *et al.* (1994) document within-breeding-season movements of up to 1140 km by Snowy Plovers, possibly to permit more nesting attempts per season or the exercise of female mate choice.

Regional movements *between* breeding seasons have been documented for other shorebird species. These movements are observed most often in species that rely on unpredictable nesting habitat, or possibly that select breeding habitat on the basis of social factors (as do most male ducks in the northern hemisphere, Anderson *et al.* 1992). Shorebirds that do not move regionally tend to have social behavior that restricts movements during the breeding season