MIGRATION STOPOVERS AND THE CONSERVATION OF ARCTIC-BREEDING CALIDRIDINE SANDPIPERS

OVERVIEW

MIGRATION STOPOVERS AND THE CONSERVATION OF ARCTIC-BREEDING CALIDRIDINE SANDPIPERS

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Long-distance migration, one of the most physically demanding events in the animal kingdom, is well developed in many species of Charadriidae and Scolopacidae. Some shorebirds renowned for their extraordinary long-distance migrations, notably American Golden-Plover (*Pluvialis dominica*), Red Knot (*Calidris canutus rufa*), and White-rumped Sandpiper (*C. fuscicollis*), travel as many as 15,000 km between southern South American wintering grounds and Canadian Arctic breeding areas. Migration strategies of shorebirds vary in many aspects. There are remarkable accounts of shorebirds, such as northbound Red Knots, that stage in a few key sites for 2–3 weeks and lay on extensive body stores, then fly nonstop for distances of ≤2,500 km (Harrington 2001, Piersma et al. 2005). Less well known are the examples of populations that refuel only briefly at stopover sites, disperse broadly on the landscape, and fly shorter distances between sites (Skagen 1997, Haig et al. 1998, Warnock et al. 1998). This latter pattern applies to many long-distance migrant shorebirds that cross the interior plains of North America during spring and fall migrations. For them, interior wetland complexes provide critical refueling resources along the direct routes between summering and wintering grounds (Skagen et al. 1999). In this issue of *The Auk*, Krapu et al. (2006) describe patterns and implications of fat deposition by Semipalmated Sandpipers (*C. pusilla*), White-rumped Sandpipers, and Baird's Sandpipers (*C. bairdii*) refueling during northward migration across the prairies of mid-continental North America.

En route, migrants face myriad ecological and physiological challenges during long-distance migrations. In addition to the energetic cost of transport, birds must find periodic stopovers to rest and refuel and, while there, cope with unfavorable weather, uncertainties of resource abundance and availability, intra- and interspecific competition, and predation pressures, all within the context of unfamiliar environments (Moore et al. 1995, 2005). These challenges, in concert with broadscale anthropogenic changes in habitats and landscapes along historical migratory pathways, suggest that intercontinental migration poses formidable hardships to many birds. Nearly half of 72 North American shorebird species and subspecies are believed to be declining, despite the limited information available to assess the population status of most taxa (Brown et al. 2001, Morrison et al. 2001). Collectively, significant threats to survival and fitness of shorebirds have been documented in all phases of their annual cycles—during breeding, migration, and winter.

Effective shorebird conservation requires an understanding of the biology of the birds and of the concept of limiting factors, as well as determination of when and how populations are limited and regulated. Identifying the effects and timing of limiting factors for migratory species is extremely difficult, however, not only because of the transitory nature of migration but also because events and conditions throughout the annual cycle are interconnected (Sillett and Holmes 2002, Piersma and Lindström 2004). Although there has been considerable effort to determine whether population limitation occurs on breeding and wintering grounds, there is emerging evidence that population limitation is also possible during migration. A recent study on seasonal variation in survival

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of Black-throated Blue Warblers (*Dendroica caerulenscens*), a long-distance passerine migrant, found dramatically lower survival during migration than during either breeding or overwintering periods (Sillett and Holmes 2002). In addition to the physiological demands of long-distance flights, the vicissitudes of stopover environments can exert a strong influence on the body condition or survival of birds during migration. Passerines can stay 5–7 times longer at stopover sites than in flight during migration (Mettke-Hofmann and Greenberg 2005). Baker et al. (2004) and Morrison (2006) demonstrated cases where Red Knots that failed to gain adequate mass on migration, or that were faced with severe weather, suffered reduced survival.

Here, I address several general concepts regarding migration, but my primary focus is on refueling by long-distance migrant calidridine sandpipers traversing the interior of North America en route to Arctic and sub-Arctic breeding grounds. Shorebirds that follow a transcontinental migration route can be more vulnerable to population declines than coastal or oceanic migrants (Thomas et al. 2006). I also explore the role of interior migration stopover sites in the long-term conservation outlook for this group of species, which primarily includes Semipalmated Sandpiper, Least Sandpiper (*C. minutilla*), White-rumped Sandpiper, Baird's Sandpiper, Pectoral Sandpiper (*C. melanotos*), and Stilt Sandpiper (*C. himantopus*). I examine the importance of migration stopovers in interior North America for refueling and query whether these changing habitats can support migration needs of shorebirds in the future.

En-route Distribution of Calidridines during Northward Migration

Interior wetlands of North America appear to be especially important to calidridine sandpipers during northward migration. Recent population estimates suggest that >5 million northbound calidridines use wetlands in the north-central United States and compose >70% of the total northbound en-route shorebird populations (S. K. Skagen unpubl. data). Wintering range and migration distance appear to influence distributional patterns as migrants stop to refuel in the mid-continental region. Calidridine species that winter predominantly in South America (Semipalmated,

White-rumped, Baird's, Pectoral, and Stilt sandpipers) cross the mid-continental region of North America in a narrow band mainly between about 90°W and 100°W longitude, whereas calidridines with more northerly wintering ranges (e.g. Least Sandpipers) are more widespread in distribution during migration (Skagen et al. 1999). These species also occur earlier in the southern United States and arrive later, in a graduated fashion, in the more northerly latitudes. The occurrence of birds from south to north along the narrow band, coupled with the gradual arrival patterns, suggests that many individuals traversing North America make several feeding stops punctuated by short- or intermediate-distance flights ("hops" and "skips"; Piersma 1987) rather than long flights ("jumps") between stopover sites. An alternative explanation for the graduated timing patterns (with later arrivals in the north) is that later migrants may settle to refuel at more northerly sites than earlier arrivals. In support of the first explanation, that birds are taking shorter hops between refueling bouts, are flight-range estimates for Semipalmated Sandpipers departing the central plains in Kansas; these estimates suggest that most individuals need to refuel before reaching their breeding grounds (Skagen and Knopf 1994).

In contrast to the other calidridines, White-rumped Sandpipers do not appear gradually at more northerly latitudes, but rather they arrive at latitudes between 35°N and 55°N almost simultaneously and do so all along the south–north narrow band (Skagen et al. 1999). This pattern suggests the concurrent termination of longer flights. White-rumped Sandpipers employ both short-distance multiple-stop and long-distance nonstop flight patterns when crossing South America (Harrington et al. 1991, Parmelee 1992) and probably do so across North America as well. Flight-range estimates of White-rumped Sandpipers departing Kansas also suggest that some birds need to refuel before reaching their breeding grounds (Skagen and Knopf 1994).

Calidridine species that winter exclusively in coastal habitats are more likely than interior wintering birds to make long flights to specific regions of North America during spring migration. Red Knots, Sanderlings (*C. alba*), and Dunlin (*C. alpina*) overfly the central plains as they proceed northward. During migration, Red Knots occur in large numbers along the shores

of large lakes of Saskatchewan but are rare elsewhere in the interior. Red Knots that breed in the western North American Arctic (subspecies *roselaari*) winter along the southern Pacific, Atlantic, and Gulf coasts of North America. Red Knots that breed in the central Canadian Arctic (subspecies *rufa*) winter in the southern coastal regions of South America as far south as Tierra del Fuego (Piersma et al. 2005). The Red Knots in Saskatchewan may have been refueling after long flights from the Gulf and southern Atlantic coasts or from coastal regions of South America. In interior North America, Sanderlings occur in large numbers in the Great Salt Lake area and along shores of large lakes of Saskatchewan and Alberta, with only small flocks appearing elsewhere. Dunlin (subspecies *hudsonia*) wintering on the Gulf Coast appear to overfly the central plains, but occur regularly in large numbers in the prairie pothole landscapes of eastern North and South Dakota (Skagen et al. 1999).

Fat Deposition and Use

Rates of fat deposition in northbound shorebirds in the prairie region are positively related to the conditions at stopover habitats, which in turn are related to precipitation patterns (Krapu et al. 2006). In the early 1990s, female Pectoral Sandpipers stopping to refuel in Missouri wetlands gained larger fat loads in wet years than in dry years (Farmer and Wiens 1999), and Least and Western sandpipers in the playa region of western Texas had 7–9% greater fat reserves in a wet than in a dry year (Davis et al. 2005). At times, migrants arrive on stopover sites while carrying fat reserves from prior refueling bouts. Some female White-rumped Sandpipers arriving on North Dakota wetlands and unsexed birds landing on Manitoba wetlands had substantial fat reserves acquired at prior, unknown stopping points (Krapu et al. 2006).

Krapu et al. (2006) also evaluated the contribution of stored fat toward energy requirements for migration to the Arctic breeding grounds and nutrient needs for reproduction. That calidridine sandpipers can arrive on breeding grounds carrying fat and protein accumulated at their last stopover sites has been deduced from flight-range calculations and direct measurement of fat of arriving birds in breeding areas (Davidson and Evans 1988, Farmer and Wiens 1999, Morrison and Hobson 2004, Morrison et al. 2005, Krapu et al. 2006, Morrison 2006). At least 25% of Semipalmated and White-rumped sandpipers departing North Dakota wetlands arrive at the nearest parts of their breeding ranges with 35–52% of stored fat remaining. Many White-rumped Sandpipers departing Manitoba wetlands are also likely to retain substantial portions of their stored fat upon arrival at the closest part of their breeding range (Krapu et al. 2006). Similarly, in an earlier study, interior-migrating female Pectoral Sandpipers arrived at their Arctic breeding grounds with extra energy reserves (Farmer and Wiens 1999).

Theoretically, the optimal fat load to carry to the next stopover site or to the breeding grounds is determined by balancing the benefits and costs of fat storage (Gudmundsson et al. 1991, Sandberg and Moore 1996). There are several costs in acquiring fat beyond what is needed to reach the next destination. Increased body mass may reduce a bird's agility and thereby increase its vulnerability to predation (Lank et al. 2003), increase the flight costs of migration, or delay arrival at the breeding grounds because of additional foraging time at a stopover.

Females of many calidridine sandpipers, including Baird's, Semipalmated, and White-rumped sandpipers, have tremendous nutritional needs because they lay clutches of eggs equal to 80–120% of female body mass (Gratto-Trevor 1992, Parmelee 1992, Moskoff and Montgomerie 2002). Sandpipers are considered "income" breeders, relying on nutritional resources acquired locally on the breeding grounds for reproduction, rather than "capital" breeders that mobilize body stores (Drent and Daan 1980). A recent and innovative technique, the analysis of stable isotopes in feathers and body tissues, has made it possible to test hypotheses regarding these strategies in shorebirds. Klaassen et al. (2001) evaluated stable-carbon isotopes in egg material and neonate feathers produced by Arctic-breeding shorebirds in Greenland and Arctic Canada. Because many of the focal species of this study fed in coastal estuaries during migration and winter and switched to a terrestrial system, the tundra, during breeding, Klaassen et al. (2001) searched for evidence of marine versus terrestrial isotopic signatures in the eggs and feathers of hatchlings; they found no evidence of marine signatures and concluded there was no support

for a capital breeding strategy. Morrison and Hobson (2004) also evaluated carbon-isotope signatures of eggs, as well as postarrival blood samples, of three shorebird species on Ellesmere Island. Although finding a small contribution of marine reserves to first-laid eggs, they also concluded that, in general, high-Arctic breeding shorebirds use income- rather than capital-breeding strategies (Morrison and Hobson 2004).

The question then remains: if they are not used in egg production, what is the importance of energy stores at arrival? Shorebirds experience high energetic demands during the postarrival, prebreeding period that precedes egg formation. Body reserves on arrival at Arctic breeding grounds may provide a source of energy for survival, especially important in adverse weather conditions (Farmer and Wiens 1999, Morrison and Hobson 2004). Further, Morrison and Hobson (2004) postulated that body stores present on arrival contribute nutrients for the rapid physiological changes that must occur during the bird's transition from migratory to breeding activities. During migration, there is an increase in the size of the flight muscles and a decrease in the size of muscles and organs that are less needed during arduous flights, especially the digestive organs (Piersma and Gill 1998, Piersma et al. 1999). These organs must be restored to proper functioning upon arrival at breeding grounds. Morrison et al. (2005) found large stores of fat and muscle in Red Knots arriving on their high-Arctic breeding grounds. Prior to egg laying, the birds' fat and muscle stores diminished as organs such as digestive organs and gonads increased in size, which suggests that such stores play an integral role in enabling the birds to make the transition from migration to breeding condition.

Further, females must remain in good condition after the energetic demands of egg laying to make it through the time- and energy-consuming activities of incubation. Both male and female Baird's and Semipalmated sandpipers incubate and rear young, but only female White-rumped and Pectoral sandpipers are involved in these energetically costly functions. Interestingly, female Pectoral Sandpipers put on more fat at interior North American stopover sites than males (Farmer and Wiens 1999).

LINKAGES OF PERIODS IN THE ANNUAL CYCLE

Krapu et al. (2006) draw attention to the apparent connections between periods in the yearly cycles of calidridine sandpipers. Events in one phase of a bird's annual cycle clearly can influence survival or reproductive success in a subsequent phase (Sandberg and Moore 1996, Marra et al. 1998, Gill et al. 2001, Drent et al. 2003, Baker et al. 2004, Morrison 2006). Generally, only individuals in good condition can afford to arrive at breeding sites early and lay eggs early (Drent et al. 2003). Early arrival on breeding areas often confers reproductive advantages as birds compete for territories and choose mates, and early-laid clutches often fare better, or contribute more to lifetime reproductive fitness, than clutches laid later in the breeding season. The benefits of early arrival must also outweigh the survival and energetic costs of arriving too early, especially if conditions are bad or food is scarce.

Linkages between the quality of nonbreeding foraging sites, migration schedules, and body and plumage condition are illustrated by several recent studies. American Redstarts (*Setophaga ruticilla*) wintering in higher-quality habitats arrive on breeding grounds earlier and in better condition that conspecifics that winter in habitats of poorer quality (Marra et al. 1998). Similarly, Black-tailed Godwits (*Limosa limosa icelandica*) departing wintering sites where they experience high prey-intake rates in spring arrive on breeding grounds earlier than conspecifics that depart sites with lower prey-intake rates (Gill et al. 2001). Drent et al. (2003:274) highlighted the tight relationship between en-route body condition and subsequent breeding success in Pink-footed Geese (*Anser brachyrhynchus*) and emphasized the "critical role of the final take-off site." Further, quality of breeding plumage can serve as an information badge to potential mates. In Bar-tailed Godwits (*L. lapponica*), completeness of nuptial plumage during spring stopover correlates positively with body mass and local survival (Piersma and Lindström 2004).

The reproductive success and fitness of midcontinental migrant sandpipers may be inextricably linked with foraging conditions at the last few or penultimate stopover sites in the northern plains, as is the case with coastal shorebird migrants at their final spring stopover area. What do we know about the status and current

conditions of their wetland stopover habitats in the Great Plains of North America?

Interior Stopover Habitats: Present Conditions and Future Scenarios

Most long-distance migrant calidridines are wetland-dependent during winter and migration. The conditions and spatial juxtaposition of wetlands that serve as suitable refueling sites for shorebirds at a given time are determined by several ecological processes, including geomorphology and wetland basin topography, climate patterns, hydrology, depth to groundwater, vegetation history, and land-use changes. In the mid-continental region of North America, many wetlands are "geographically isolated" wetlands, or depressional wetlands surrounded by upland (Tiner 2003a). The millions of depressional wetlands in the Prairie Pothole Region (PPR) of central North America were formed by the melting of large ice blocks left by the receding ice of the Wisconsin glaciation during the late Pleistocene. These depressional wetlands eventually provided aquatic and benthic food resources to the avian communities expanding northward.

Strategies for migrating across the midcontinental region of North America thereafter evolved within the context of highly dynamic habitat conditions resulting from the extreme and variable climate of the Great Plains interacting with the geomorphology of the region. Before humans settled in the Great Plains, shorebirds crossing the North American interior experienced periodic severe droughts and prolonged intense rainy periods, or deluges, which no doubt strongly influenced the natural prairie ecosystem. Paleoclimatic data show that drought was more extensive and variable before the 20th century and that decade-long droughts of great magnitude occurred repeatedly during the past 2,000 years (Woodhouse and Overpeck 1998).

With human settlement and the advent of agriculture, land conversion and wetland loss began in earnest at unprecedented rates. In the 200-year history of wetland conversion in the United States, there has been substantial loss of wetland habitats and suitable migration stopover sites in the mid-continental region. Two decades ago, estimates of wetland losses in the Great Plains states since European settlement ranged from 35% to 89% (Dahl 1990), and

presently in the U.S. region of the PPR, nearly 70% of grasslands and >50% of wetlands have been converted to agriculture or lost (Euliss and Laubhan 2005). In addition, conversion of native prairie to cropland altered the runoff dynamics of the entire landscape. Surface runoff events, which were moderated by native vegetation during presettlement times, have now increased in intensity, and the time available for infiltration, and thus replenishment of groundwater and underlying aquifers, has decreased (Gleason and Euliss 1998). Agricultural runoff affects organisms at all trophic levels, and direct effects at one level of the aquatic food chain result in indirect effects at other levels. For example, sediments and contaminants negatively affect aquatic and benthic invertebrates (Euliss and Mushet 1999) that form the basis of migrant shorebirds' food resources.

Many of the remaining wetlands in the PPR and elsewhere in the plains have been severely altered by agricultural practices, including tillage of uplands and wetlands, sedimentation, and application of agricultural pesticides and fertilizers (Euliss and Mushet 1996). The geographically isolated wetlands used by shorebirds in the midcontinent are highly vulnerable to land conversion, agricultural policies and practices, hydrology alteration, and water pollution. Today, groundwater withdrawal and increasing rates of sedimentation pose far-reaching yet subtle threats (Tiner 2003b). Removal of native vegetation in the uplands surrounding wetlands exacerbates the effects of sedimentation and contaminants, resulting in runoff rates that are twice—to as high as 70×—the rates for native grassland landscapes (Martin and Hartman 1987, Gleason and Euliss 1998). At current rates of sedimentation in the Texas Southern High Plains region (9.7 and 4.8 mm year^{-1} in medium- and fine-texture soils, respectively), all cropland playas could be filled within 95 years (Luo et al. 1997); cropland playas in this region contain 8.5× more sediment than playas surrounded by rangeland, and many have lost all their original basin volume. This is in contrast to natural sedimentation rates of wetlands in undisturbed landscapes. For example, sedimentation rates are <3.0 mm year^{-1} in Alaska (van der Valk et al. 1983).

Future scenarios of drought severity recognize the susceptibility of the Great Plains to severe drought caused by human land-use

practices and enhanced likelihood of drought because of global warming (Woodhouse and Overpeck 1998). Wetlands that are the most vulnerable to climate changes are those that depend on precipitation for their source of water, such as playas and temporary wetlands, whereas wetlands that receive discharge from groundwater are less vulnerable to changes in climate because of the "substantial buffering capacity of the regional ground water flow systems" (Winter 2000:311). Extensive loss of temporary wetlands under scenarios of global warming with decreases in precipitation are projected to severely reduce suitable breeding habitat within the present-day range of waterfowl (Johnson et al. 2005); suitable shorebird foraging habitat, no doubt, would also be reduced under this scenario. Over the next 50 years, substantial environmental change will be driven by the demand for food of a 50% larger global human population. Models forecast expansions of cropland, increases in eutrophication, and unprecedented ecosystem simplification (Tilman et al. 2001). Such agriculturally driven changes are believed to rival climate change in their environmental effects.

Can Migrant Shorebirds Find Sufficient Resources in the Context of Pervasive Landscape Change?

To understand the current status and speculate about the future of migration stopover habitats in interior North America, we must seek perspectives from the evolutionary past and the influences of a strongly seasonal climate. Molecular studies of migratory birds have yielded insights into the evolution of migration and have revealed the profound effects that Pleistocene glaciations have had on the current genetic architecture of birds breeding in the northern hemisphere (Joseph 2005). During 1.8 million years of the Quaternary, 22 glacial–interglacial cycles provided strong stimuli for long-distance migration in birds (Steadman 2005). Although modern species of birds arose mainly in the late Pliocene and Pleistocene (0.08–5.3 mya; James 2005), the origin of current migratory paths of shorebirds across mid-continental North America probably coincided with the retraction of the last glacial ice sheets during the late Pleistocene, ~18,000 years ago, as is hypothesized for passerines

(Joseph 2005) and appears to be the case for Red Knots (Buehler and Baker 2005).

How did migrants cope with unfamiliar and highly unpredictable stopover environments? It is highly adaptive for birds facing such uncertainty to be flexible both in physiology and behavior. In fact, Alerstam et al. (2003) refer to the "great evolutionary flexibility" associated with long-distance migration in general, recognizing the continuing evolution of migration patterns in some species even during the past few thousand years. Physiological or phenotypic flexibility, such as modifications of digestive organs in response to migratory periods, has been explored in detail and appears to be common to most long-distance avian migrants (Piersma and Drent 2003). Ecological plasticity, or behavioral responses to variable resources (Mettke-Hofmann and Greenberg 2005), is exhibited by shorebirds crossing the midcontinent as they opportunistically colonize suitable sites in dynamic wetland landscapes. Dietary plasticity also allows for exploitation of the variable resources birds encounter throughout the year (Parrish 2000). Shorebirds are known to select as wide a variety of invertebrate taxa as availability allows throughout their annual cycles; Semipalmated Sandpiper diets span a minimum of 25 orders and 37 families of invertebrates (Skagen and Oman 1996).

The great flexibility associated with migration allows for evolution of new routes in response to environmental changes. Sutherland (1998) summarized 43 cases of changes in avian migration routes in historical times, including a recent shift in the migration route of the Blackcap (*Sylvia atricapilla*) in the past three decades (Berthold et al. 1992, Bearhop et al. 2005). Sutherland's (1998) review suggested that some species will adapt to global environmental change by adopting new migration routes if necessary, but that other species may continue to use existing routes even if they become suboptimal. Species with culturally determined migration routes (i.e. extended parental care and young that migrate with adults) may be able to evolve new routes more rapidly than species with genetically determined migration behavior (Sutherland 1998).

Before human settlement, en-route migrant shorebirds were exposed to, and ostensibly coped with, intensive and extensive perturbations such as glaciation and decade-long

droughts across the prairie wetland landscapes. Yet the rapidity of changes experienced by the interior North American wetland landscapes since human settlement is unparalleled. Current threats to the ability of prairie wetland landscapes to provide adequate stopover resources for shorebirds over the next several decades include intensification of agriculture, with concomitant increasing rates of sedimentation and contaminant exposure, and the possibility of climate change with the predicted broad-scale loss of interior wetlands. Ecological plasticity, a powerful defense against large-scale perturbations, has allowed some avian species to cope with environmental changes in many ways—behaviorally, physiologically, or through evolution of new migration routes. Before we can predict the future of calidridine shorebird migration across the North American interior, many questions remain. To what extent can shorebirds alter behavior and physiology to accommodate changing environments? Is there a threshold of environmental change beyond which shorebirds cannot adapt? Is it possible for western hemispheric populations of calidridine sandpipers to evolve new migration routes if suitable interior habitats are lost?

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