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Shorebird migration and staging at a large prairie lake and wetland complex: the Quill Lakes, Saskatchewan

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Cover photo: Semipalmated Sandpiper
(C.L. Gratto-Trevor)

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Abstract

We examined the use of an extensive prairie lake and wetland complex at the Quill Lakes, Saskatchewan, by migrant shorebirds. The most common species observed there during northbound spring migration were (in order of abundance) Red-necked Phalarope *Phalaropus lobatus*, Semipalmated Sandpiper *Calidris pusilla*, Stilt Sandpiper *C. himantopus*, White-rumped Sandpiper *C. fuscicollis*, Least Sandpiper *C. minutilla*, and Sanderling *C. alba*. The most numerous species during southbound autumn migration were Red-necked Phalarope, dowitchers (primarily Long-billed Dowitcher *Limnodromus scolopaceus*), Stilt Sandpiper, Semipalmated Sandpiper, Lesser Yellowlegs *Tringa flavipes*, and Hudsonian Godwit *Limosa haemastica*. The most significant species in terms of relative population numbers and conservation concerns were Stilt Sandpiper (spring and autumn) and Hudsonian Godwit (autumn).

Birds migrated rapidly through the area in spring (the peak period was from the second week of May to the first week of June), and there was no evidence of mass gain. At least some members of species for which conservative flight range estimates could be made (Least Sandpiper, Lesser Yellowlegs, Semipalmated Sandpiper, Stilt Sandpiper) apparently had more than enough stored fat to fly nonstop to breeding areas. Some yearling Semipalmated, Least, and Stilt sandpipers and Lesser Yellowlegs migrated north in spring.

Autumn migration was more protracted than spring migration (the peak period was from the third week of July to the third week of August; average length-of-stay estimates ranged from seven to 16 days), and there was some evidence of birds gaining mass at the Quill Lakes (Hudsonian Godwits, Lesser Yellowlegs, Semipalmated Sandpipers, Stilt Sandpipers). Estimated flight ranges indicated that at least some individuals of each of these and other species could fly nonstop from Saskatchewan to the southern coasts of the United States or northern South America, with the exception of Long-billed Dowitchers. Only Long-billed Dowitchers and some Short-billed Dowitchers *Limnodromus griseus* were in active flight feather moult at Little Quill Lake.

Juveniles were common among locally breeding species during July and August. Among northern-nesting migrants, juveniles migrated later than adults. For Least and Semipalmated sandpipers, most southbound migrants were juveniles, which suggests that either adults and juveniles migrated along different routes or adults had sufficient energy reserves to overfly the Quill Lakes. For Hudsonian Godwits, Stilt Sandpipers, and Long-billed Dowitchers, juveniles were rarely, if ever, seen, which again suggests different routes or a much later migration for juveniles.

Shorebird species assemblages differed among habitats at the Quill Lakes, which suggests that species diversity was related to habitat diversity. Numbers and foraging locations of the most common species migrating through the area were related to the availability of suitable habitat. Shorebirds used the shoreline of Little Quill Lake more and the nearby marsh basins less as water levels in the area increased. In addition, species that forage mostly by probing substrates used deeper water and selected marsh habitats, whereas species that mostly peck selected lakeshore habitats. As a complex of large and small, permanent and temporary wetlands, the Quill Lakes area usually has some habitat suitable for foraging shorebirds each year and might function as a "refuge" for migrants during prairie droughts.

Résumé

Nous avons étudié comment les oiseaux de rivages migrateurs utilisaient un vaste complexe de lacs et de terres humides des prairies, aux Lacs Quill, en Saskatchewan. Les espèces les plus communes que nous y avons observées pendant la migration printanière vers le nord (par ordre d'abondance) sont le Phalarope hyperboréen (*Phalaropus lobatus*), le Bécasseau semipalmé (*Calidris pusilla*), le Bécasseau à échasses (*C. himantopus*), le Bécasseau à croupion blanc (*C. fuscicollis*), le Bécasseau minuscule (*C. minutilla*) et le Bécasseau sanderling (*C. alba*). Les espèces les plus nombreuses, lors de la migration d'automne vers le sud, étaient le Phalarope hyperboréen, les *Limnodromi,* surtout le Bécasseau à long bec (*Limnodromus scolopaceus*), le Bécasseau à échasses, le Bécasseau semipalmé, le Petit Chevalier (*Tringa flavipes*) et la Barge hudsonienne (*Limosa haemastica*). Les espèces les plus significatives quant à l'importance relative de leur population et la question de la conservation furent le Bécasseau à échasses (printemps et automne) et la Barge hudsonienne (automne).

La migration du printemps est passée rapidement à cet endroit (la période la plus forte a commencé à la deuxième semaine de mai et s'est terminée à la première semaine de juin) et il n'y avait aucun signe de gain de masse. Au moins quelques individus d'espèces dont il a été possible de faire une estimation conservatrice de leur distance d'envolée (le Bécasseau minuscule, le Petit Chevalier, le Bécasseau semipalmé et le Bécasseau à échasses) avaient apparemment emmagasiné assez de gras pour continuer leur envol sans escale jusqu'à leur aire de nidification. Certains petits d'une année parmi les Bécasseaux semipalmés, minuscules et à échasses, ainsi que les Petits Chevaliers, ont migré vers le nord au printemps.

La migration d'automne a été plus longue que celle du printemps (la période forte allant de la troisième semaine de juillet à la troisième semaine d'août); on a estimé la durée du séjour à entre sept et seize jours et on a pu observer que des individus avaient pris de la masse aux Lacs Quill (la Barge hudsonienne, le Petit Chevalier, le Bécasseau semipalmé, le Bécasseau à échasses). Des estimations de distances d'envolées indiquaient qu'au moins quelques individus de ces espèces et d'autres pouvaient, sans escale, se rendre de la Saskatchewan à la côte sud des États-Unis, ou au nord de l'Amérique du sud, sauf le Bécasseau à long bec. Seuls les Bécasseaux à long bec et certains Bécasseau roux (*Limnodromus griseus*) étaient en pleine mue de rémiges au Petit Lac Quill.

Il y avait des juvéniles partout parmi les nicheurs locaux aux mois de juillet et août. Parmi les migrateurs nicheurs du nord, les juvéniles ont migré plus tard que les adultes. En ce qui concerne les Bécasseaux minuscules et semipalmés, la plupart des migrateurs qui allaient au sud étaient des juvéniles, ce qui suggère que les adultes et les juvéniles empruntent des voies de migration différentes ou que les adultes avaient assez de réserves d'énergie pour continuer sans halte leur envolée au-dessus des Lacs Quill. Pour les Barges hudsoniennes, les Bécasseaux à échasses et Bécasseaux à long bec, on n'a vu qu'à peine, ou pas du tout, de juvéniles, ce qui laisse entendre encore qu'ils ont emprunté des voies différentes, ou que les juvéniles ont migré beaucoup plus tard.

Les assemblages d'oiseaux de rivage différaient selon les habitats aux Lacs Quill, ce qui suggère que la diversité des espèces va de pair avec la diversité des habitats. Les nombres et les lieux fourragers, pour les espèces migratrices les plus communes de l'endroit, dépendaient de la disponibilité d'habitats appropriés. Les oiseaux de rivage utilisaient plutôt le rivage du Petit Lac Quill, et les marais voisins, mais en diminuant à mesure que le niveau de l'eau augmentait. Les espèces qui se nourrissent surtout des substrats de fond fréquentaient des eaux plus profondes et choisissaient des habitats marécageux, alors que les espèces qui picorent choisissaient plutôt des habitats de rivage. Comme complexe de terres humides grandes et petites, permanentes et temporaires, la région des Lacs Quill offre habituellement, à chaque année, de bons habitats pour le fourrage des oiseaux de rivage et pourrait servir de « refuge » aux migrateurs durant les sécheresses des prairies.

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1. Introduction

Many species of shorebirds migrate to and from their breeding grounds along traditional routes, stopping in large numbers to replenish fat or to moult at the same places each year. The dependence of shorebirds on specific staging grounds (stopovers) makes them particularly vulnerable to environmental change (e.g., Lester and Myers 1991), which has led to concern among conservationists for the identification and preservation of critical areas (Senner and Howe 1984; Myers et al. 1987; Morrison 1991; Morrison et al. 1995).

Most critical shorebird staging grounds that have been recognized throughout the world are in coastal marine habitats, which normally have predictable patterns of water availability on a daily, seasonal, and annual basis (e.g., Morrison and Harrington 1979; Senner 1979; Hicklin 1987; Morrison and Ross 1989; Gill and Handel 1990; Zwarts and Piersma 1990). A number of these important coastal sites are known to have a super-abundance of prey when shorebirds are present, allowing birds to deposit large amounts of fat before undertaking long nonstop flights. The importance of inland habitats — often saline lakes and wetlands where water levels can vary dramatically and unpredictably among days, seasons, and years — is much less well understood and has been examined only rarely (Skagen and Knopf 1993). In the northern prairies, studies have been conducted at various small wetlands around Saskatoon, Saskatchewan (Lewis 1983), and at Last Mountain Lake, Saskatchewan (Colwell 1987, 1991; Colwell and Oring 1988; Colwell et al. 1988). In this publication, we provide information on shorebird migration and habitat use at a major inland stopover in the Canadian prairies.

Thirty-one species of shorebirds occur regularly as breeders (10 species) or migrants in the Northern Plains of North America (summarized by Helmers 1992). Among the migrants, some species use different routes for northbound and southbound migrations (e.g., Morrison 1984; Harrington et al. 1991; Gratto-Trevor and Dickson 1994). In addition, species might use a stopover for different reasons, including breeding, resting, acquiring energy reserves, or moulting. A knowledge of species composition, timing of occurrence, and purpose of stopover is needed for the development of site-specific wetland management strategies for shorebirds, including both simple preservation and more complex manipulation of shorebird habitat.

In 1986, the Canadian Wildlife Service initiated its Prairie Shorebird Program in response to the increasing interest in shorebird conservation throughout the western hemisphere (Dickson and Smith 1988). The first undertaking was a series of aerial surveys in the southern halves of Manitoba, Saskatchewan, and Alberta to identify potential concentration areas for shorebirds during migration (Smith and Dickson 1989). The Quill Lakes, a complex of saline lakes and marshes in the northern prairies of Saskatchewan, had particularly large numbers of shorebirds (see Appendix 1 for a list of species).

Sites with significant numbers of staging shorebirds have now been identified for both Canada (Morrison et al. 1995) and the United States (Harrington and Perry 1995) and given potential (or actual) Western Hemisphere Shorebird Reserve Network (WHSRN) designations. Official designation of an area as a WHSRN site provides it with international recognition and, indirectly, protection. WHSRN sites are categorized in importance by the absolute numbers of birds or percentages of flyway populations using the areas. The highest designation is a "Hemispheric Site," with more than 500 000 shorebirds per year or 30% of a flyway population. Next are "International Sites," with more than 100 000 shorebirds or 15% of a flyway population. Finally, "Regional Sites" must have at least 20 000 shorebirds or 5% of a flyway population. Throughout Canada and the United States, there are only 12 potential or actual Hemispheric Sites, including areas such as Shepody Bay and the Minas Basin of the Bay of Fundy, the Fraser River delta in British Columbia, the Copper River delta in Alaska, and Delaware Bay in New Jersey. There are a further 13 potential or actual International Sites, including the Quill Lakes in Saskatchewan. In the Canadian prairies, only the Old Wives/Chaplin/Reed lakes complex of wetlands and a suite of 12 lakes at the Alberta/Saskatchewan border have comparable numbers of shorebirds (Morrison et al. 1995). In Region 8 of the United States (Prairies), there are only Regional Sites listed (Harrington and Perry 1995).

As a result of the large numbers of shorebirds staging at the Quill Lakes (almost unique to the prairies) and because the area was slated to be the first major habitat project of the Prairie Habitat Joint Venture of the North American Waterfowl Management Plan (to be managed for the benefit of waterfowl), a series of studies was initiated there in 1988 to document the nature of the shorebird migration and to provide information that could be used to develop management strategies for shorebird habitat at the Quill Lakes and in the prairies in general. The results of the studies on prey availability, food habits, and body composition of select shorebird species are presented in Alexander (1994) and Alexander et al. (1996), whereas an analysis of the migration routes of Semipalmated Sandpipers (see Appendix 1 for scientific names of shorebirds) that use the Quill Lakes has been given by Gratto-Trevor and Dickson (1994).

This publication provides an overview of the use of the Quill Lakes by shorebirds during both spring and autumn migrations, particularly Little Quill Lake and its surrounding marsh basins. Where pertinent, inter- and intraseasonal variability are emphasized, as characteristic of interior versus coastal wetlands. This publication is split into two major sections. The first deals with shorebird migration at the Quill Lakes in terms of 1) species identification, 2) species composition and abundance, 3) age composition, 4) interrelationships between the stopover and other areas via resightings and recoveries of marked birds elsewhere, 5) chronology of migration and length of stay, 6) presence of active flight feather moult, 7) rates of mass gain, and 8) potential flight ranges of birds from the area. The second section discusses habitat selection by shorebirds at the Quill Lakes 1) by location, 2) in relation to habitat availability (water level fluctuations), 3) in relation to wading depth, and 4) in relation to feeding method. All field methods are presented in one location to avoid repetition of methods common to both major sections.

2. Study area

2.1 Geography and water chemistry

The Quill Lakes (approx. 52°N, 104°W) comprise three large, variably saline and alkaline bodies of water (Big, Middle, and Little Quill lakes; Fig. 1). They lie within the topographically level to gentle-rolling plains and lowlands of Saskatchewan at the southern edge of the aspen parklands (Richards and Fung 1969; see Hammer and Haynes [1978] for a discussion of saline lakes in relation to geographic factors throughout the Canadian prairies). The surrounding area is extensively cultivated. Much of the land immediately adjacent to the lakes is used for pasture. Climate fluctuates between humid and dry subhumid continental conditions.

The Quill Lakes lie within an area of saline soils; because evaporation often exceeds water input, the lakes can be highly saline, especially Big Quill Lake. In 1991 and 1992, water salinities (Wetzel 1983:179) at the Quill Lakes were as follows (Alexander 1994): 1521–6004 mg/L (pH = 6.7–8.8, mostly >8.0) at Little Quill Restriction, Milligan Creek Project, Jesmer Project, and Campbell Project Segments 6 and 7; 7242–10 258 mg/L (pH = 8.5–9.2) at Little Quill Lake; 4266–17 054 mg/L (pH = 8.0) at Middle Quill Lake; and 103 871–111 009 mg/L (pH = 8.1–8.7) at Big Quill Lake. Sulphate was the dominant ion. Salinity affects the composition and densities of both invertebrate prey and vegetation in and around wetlands (Hammer and Heseltine 1988; Kantrud et al. 1989; Hammer et al. 1990).

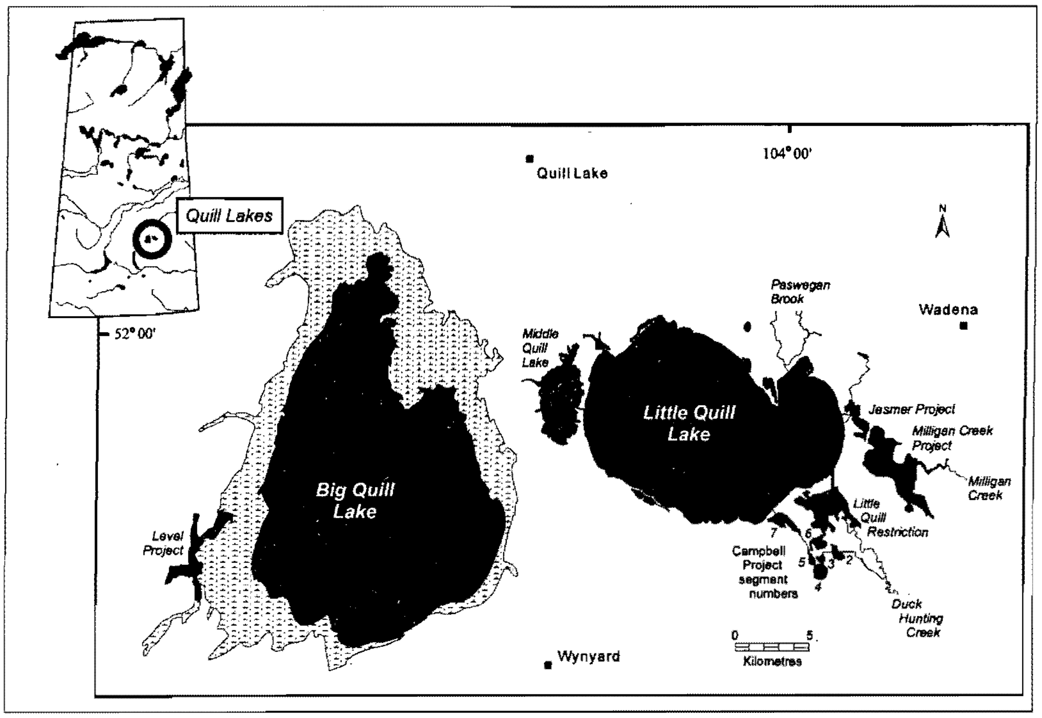
In Big Quill Lake and probably also Little Quill Lake, precipitation (direct and indirect through runoff and groundwater) accounts for approximately 50–70% of the changes in lake levels (Whiting 1977). Consequently, water levels, salinity, and pH fluctuate considerably within and among years. During the 20th century, water levels have generally decreased and salinity has increased at Big Quill Lake, although apparently not at Little Quill Lake (Alexander 1994). The high salinity at Big Quill Lake at the end of this study was likely the result of drought in the late 1980s and early 1990s. Water levels at Big Quill Lake were lower during this study (1989–1993) than at any other time in historical record (since the late 1800s, the highest levels were approximately 519.5 m above sea level [asl] in 1880 and 1920 and 516.8 m asl in 1958, whereas the lowest were approximately 515.7 m asl in the late 1940s and 513.6 m asl in 1993; summarized in Whiting 1977 and in Appendix 2).

In the past, there was flow from east to west between lakes, with Big Quill Lake as the terminal and most saline basin. Creeks flowing into and between the lakes are now mostly controlled. In 1936, the stream between Little Quill and Big Quill lakes was dammed (Hammer 1978), which effectively split the Quill Lakes drainage basin into two independent drainage basins (Whiting 1977). Since then, diversions and dams have been constructed on other streams (e.g., Milligan Creek in 1961 and Duck Hunting Creek, which feeds Little Quill Restriction, in 1963). In this permanent wetland complex, the amount of water in specific lakes, basins, and marshes is dependent primarily on environmental conditions, although water levels in certain areas can be controlled to some extent.

2.2 Lake and wetland substrates

Substrates range from mud at the southwest end of Little Quill Restriction to sandy mud at Little Quill Restriction's north end and Little Quill Lake's east shore to muddy sand along Little Quill Lake's southeast shore (Alexander 1994). The sandy mud substrates of Little Quill Lake's east shore lay between two stream mouths, both of which are now dammed. Middle Quill Lake substrates are dominated by clay, with increasing amounts of gravel and coarse sand at greater depths in the substrate. The west shore of Little Quill Lake is sandy in its central parts and increasingly muddy in the southern and northern stretches. Substrates in openings in the vegetation at Little Quill Restriction and in the recently flooded Jesmer Project are dominated by plant litter. Substrate softness increases with increasing mud content, decreases with increasing sand content, and decreases with increasing exposure of the substrate to the atmosphere (i.e., as the waterline recedes, unflooded substrates become harder) (Alexander 1994). Substrate type and penetrability can affect the ability of shorebirds to probe and detect prey (Myers et al. 1980; Quammen 1982; Kelsey and Hassall 1989; Mouritsen and Jensen 1992). Invertebrate species composition and distribution are also dependent on substrate type (Green 1968).

Figure 1
Saskatchewan (inset) and the Quill Lakes. Stippled areas indicate alkali flats. Projects are Ducks Unlimited (Canada) waterfowl management projects.



2.3 Lake and wetland vegetation

The vegetation in and around Little Quill Lake and surrounding marshes is typical of North American saline wetlands (Millar 1976; Hammer and Heseltine 1988; Kantrud et al. 1989). Sago Pondweed *Potamogeton pectinatus* was the most abundant submergent in the deeper open-water marshes and offshore in Little Quill Lake. Sago Pondweed also occurred in sparse and stunted stands in the shallows along the shore of Little Quill Lake. Horned Pondweed *Zanichellia palustris* and *Chara* sp. were also present in most marsh areas. The typical emergents in the open-water marshes (e.g., Little Quill Restriction, shoreline of Middle Quill Lake, Milligan Creek Project, Jesmer Project, Campbell Project Segment 7) were Alkali (Prairie) Bulrush *Scirpus maritimus* var. *paludosus*, Hardstem Bulrush *S. acutus*, other bulrushes (*S. validus*, *S. americanus*), spike-rushes (*Eleocharis palustris*, *E. acicularis*, *E. parvula* var. *anachaeta*), Wire Rush *Juncus balticus*, Whitetop Grass *Scolochloa festucacea*, and Common Cattail *Typha latifolia*.

There is little shoreline marsh at Little Quill and Big Quill lakes. Nearshore gradients in both lakes are slight, resulting in rapid and frequent changes in the location and extent of shallow water in response to wind, precipitation, and evaporation. In 1990, there was a band of predominantly Alkali (Prairie) Bulrush (with smaller amounts of the other bulrushes and spike-rushes listed above) along Little Quill Lake's east shore. From 1990 to 1992, water levels dropped in Little Quill Lake, expanding its east and southeast shores by several hundred metres. These shoreline flats were invaded by such species as Perennial Sow Thistle *Sonchus arvensis*, Foxtail Barley *Hordeum jubatum*, Goosefoot (*Chenopodium* spp.), Biennial Sagewort *Artemisia biennis*, Samphire *Salicornia rubra*, and Alkali Grass *Puccinellia nuttalliana* (possibly also *Dystichlis stricta*; Hammer and Heseltine 1988).

3. Methods

3.1 Surveys

In order to identify and count shorebirds, ground surveys were conducted during northbound spring migration (May and early June) in 1989, 1990, 1992, and 1993 and during southbound autumn migration (July, August, and early September) in 1989–1992, inclusive. The surveys in spring 1989 were preliminary and limited in coverage; they are therefore excluded from most analyses. The subsequent surveys were conducted mostly at Little Quill Lake's west, east, and southeast shores, Middle Quill Lake's east shore, Little Quill Restriction, Milligan Creek Project, Jesmer Project, and Campbell Project Segments 2, 3, 5, 6, and 7 (Fig. 1). Survey coverage was similar in 1989 (autumn migration), 1991, 1992, and 1993. In 1990, most smaller basins surrounding Little Quill Lake were not surveyed. Milligan Creek Project was surveyed only in 1989, because water levels were too high for shorebirds in all other years. Big Quill Lake and Level Project were surveyed only during spring 1993. Some years and areas are excluded from analyses when inconsistencies in survey coverage cause biases.

Surveys were conducted every three or four days (usually between 09:00 and 17:00 Central Standard Time). The study area was divided into several sections (e.g., isolated small basins, stretches of shoreline), and data were tallied for each section separately. Most surveys within a season were conducted by the same two observers, but there was usually one new primary observer each year. Observers drove small all-terrain vehicles or walked along shorelines and recorded all shorebirds seen (aided by binoculars and a 15–60× spotting scope). Behaviour (feeding or not feeding) and substrate moisture or wading depth (dry, wet, water depth < tarsus length, water depth > tarsus length, swimming on water) were also recorded. Unidentifiable shorebirds were classified as small (SHSM, SHLS), medium (SHME), small–medium (SHOT), or large (SHLA) in size (see Appendix 1). Observers rarely differentiated between Long- and Short-billed dowitchers (*Limnodromus* spp.), both of which occurred in the area; therefore, all sightings of dowitchers were combined.

3.2 Banding and shorebird morphometrics

We captured shorebirds at Little Quill Lake from 1988 to 1992. As sample sizes were largest and measurements were standardized in 1990, 1991, and 1992, we present data only from those years. Spring migrants were caught in 1990 (26 May to 1 June) and 1992 (16 May to 3 June). Autumn migrants were sampled in 1990 (16 July to 23 August) and 1991 (11 July to 26 August).

All birds were captured in mist nets, primarily at night. We placed nets in groups of 2–10 along the shore of Little Quill Lake and/or in adjacent marshes. No more than 15 nets were in use at a time. The maximum number of shorebirds captured in one night was 345 (average number per night was 74).

Each bird was marked with a metal band (usually stainless steel), one or two white plastic (darvic) leg flags, and one colour band: red (adults) or green (juveniles). We measured wing length (±1 mm, maximum chord: flattened and straightened), bill length (±0.1 mm, exposed culmen: feathering to tip), and mass (±0.1 g, electronic balance). Dowitchers in the hand were identified to species according to plumage characteristics described by Prater et al. (1977). Several dowitchers could not be identified because of missing tail feathers and are not included in the analyses.

We aged all birds by plumage characteristics (Prater et al. 1977) and examined them for flight feather moult. Yearlings were identified in some species by the presence of partial postjuvenile wing (PPW) moult (Gratto and Morrison 1981). PPW moult is identified by differential wear of primaries and secondaries, with outer primaries and inner secondaries being the least worn, having been replaced in the bird's first winter (on the wintering grounds), whereas other flight feathers have not been replaced (Prater et al. 1977; Spaans 1979). Finally, the birds were dyed with a pattern of picric acid (yellow–orange) on their underparts and released 0.5–6 hours (usually <2 hours) after capture.

Individuals were weighed as soon as possible after capture. As temperatures at night were never above 30°C, loss of mass before release should have been less than 2% (Castro et al. 1991). Eighteen Semipalmated Sandpipers captured in the spring of 1990 were reweighed 2–3 hours after the initial weight was taken. Their mass decreased an average of 0.4 g (SD = 0.2, range 0–0.8), or 1% of initial mass. Mass gain in shorebirds at Little Quill Lake was measured in two ways. In some species, individual birds were retrapped some days after being first captured and actual change in mass was measured. Otherwise, correlations between date and mass of birds captured provided an indication of mass gain of the population.

CLGT measured nearly all birds in 1990 and 1992, and HLD (H.L. Dickson), GB (G. Beyersbergen), and CLGT almost all birds in 1991. Several series of birds were measured by these three researchers in 1991. Wing lengths measured by HLD and GB were consistently slightly shorter than those measured by CLGT. Therefore, all wing lengths were converted to those of CLGT by adding average differences of HLD or GB measurements to those of CLGT. The few wing measurements made by others were not used. Measurements of 1990 and 1991 autumn migrants were combined for each species, as were measurements of 1990 and 1992 spring migrants.

Several individuals of some common species were collected for other studies (food habits, isotope studies, toxics, DNA analysis). The birds were aged and measured as noted above, with the addition of tarsus length (±0.1 mm). Sex was determined by internal examination.

3.3 Length-of-stay estimates

In years when we colour-dyed shorebirds, a consistent part of the Quill Lakes area was censused every three days (28 May to 3 June in 1990 and 17 May to 4 June in 1992 during spring migration; 14 July to 28 August in 1990 and 17 July to 6 September in 1991 during autumn migration, with the exception of 25 August 1990, 29 July 1991, and 3 September 1991). For each three-day period (ending the morning before a census), all birds were given a specific dye pattern. We divided the underparts of a bird into four regions: 1, upper breast; 2, lower breast before legs; 3, belly including legs; and 4, under tail. Dye patterns included any number of these areas: for example, 1--4 meant that the bird was dyed on the upper breast and under-tail areas only.

During the consistent area censuses, dye patterns of all banded birds were noted. The percentage of resighted birds of a species and dye pattern per total number marked with that pattern was plotted against date. Length of stay for each dye pattern cohort was estimated from these graphs as the number of days since the middle of the dye period to the day when less than half of the originally resighted birds were present. Average length of stay was calculated as the mean of the length-of-stay estimates for that species. Only dye periods with more than 30 birds of a species marked were used in these estimates. These estimates are likely to be biased low because we do not know how long birds were present in the area before capture.

3.4 Flight range estimates

Alexander (1994) discussed in detail methods for calculating flight ranges of shorebirds and compared a number of equations based on theoretical and empirical approaches. He concluded that there is no definitive model for estimating flight ranges because of weak or untested assumptions about model parameters. Overall, most estimates tend to be conservative when compared with observed migratory flights.

Theoretical approaches estimate energy requirements from aerodynamic theory and the mechanics of flight (e.g., Pennycuick 1989; Rayner 1990). These models require as input an energy conversion factor that converts metabolic power to mechanical power for flight. The value of the factor and whether or not it scales with body size have a significant impact on estimated flight ranges (Alexander 1994). When energy conversion factors scale with body size, flight range estimates increase with increasing body size. Unfortunately, energy conversion factors for different types and sizes of birds are not well established (Walsberg 1990). Another weakness of the theoretical approaches is that their predicted flight speeds do not match speeds of migrating birds observed in the field. Both Biebach (1992) and Alexander (1994) (for passerines and shorebirds, respectively) concluded that Rayner's (1990) predictions of flight speed should probably be corrected by a factor of 1.5 to match observed flight speeds. Pennycuick's (1989) flight speed estimates were generally higher than Rayner's (1990) but still lower than field estimates. In addition, the theoretically derived models, especially those of Pennycuick (1989), include parameters for extrinsic factors such as flight altitude, air density, and wind speed, which are difficult to measure. These differences and difficulties need to be reconciled before researchers can place much confidence in theoretically derived equations.

Empirically derived models of flight range are based on cost-of-flight equations, which are fitted from observed relations between body dimensions and energy consumption. The earliest models considered only body mass (reviewed by Castro and Myers 1988), whereas more recent versions also include wing area and span (Rayner 1990) or wing length (Castro and Myers 1989). Empirically derived models have fewer initial assumptions (i.e., fewer parameters), making them easier to apply and more common in practice. These models, however, assume implicitly that factors such as altitude and air density are not important. Recently, for example, they have been justifiably criticized for excluding wind speed as a key factor affecting flight range, especially for long-distance migrants (Butler et al. 1997). In addition, current cost-of-flight equations are based mostly on passerines and are likely to overestimate flight costs and underestimate flight ranges of shorebirds, because shorebird metabolism is probably lower than passerine metabolism (Kersten and Piersma 1987) and because shorebirds, with their long, pointed wings, are probably more efficient in flight than most other birds, particularly passerines, which have relatively broader wings. Therefore, although empirically derived equations have been easier to apply, they are not necessarily more or less accurate than the theoretically derived models.

In this paper, we provide flight range estimates for shorebirds captured at the Quill Lakes based on an existing empirically derived equation. As we measured wing length and not area or span, we have used Castro and Myers' (1989) equation, which is the most recently published equation that uses wing length:

$$R = 26.88*C*S*L^{1.614}*(M_1^{-0.464} - M_2^{-0.464})$$

where R = flight range (km), C = a correction factor explained in the next paragraph, S = flight speed (km/h), L = wing length (cm), M_1 = mass at end of flight (g), and M_2 = mass at start of flight (g). Wing length used was the mean of each species/season/age group from Table 8 (e.g., Semipalmated Sandpiper/autumn/adult). As the sex of mist-netted birds could not be determined, sex differences in flight ranges were not examined. For each species or group, M_1 was the mass of the lightest bird captured whose wing length was at least average. This value was used to represent potential minimum mass at the end of flight. Two different versions of M_2 were used: mass of the heaviest bird in a species or group (resulting in a relatively high estimate of flight range), and mean mass (resulting in a more conservative estimate of flight range). Average mass at the initiation of flight should fall within these two values.

Alexander (1994) compared the Castro and Myers (1989) equation used in this study with others that were based on wing area and span (Pennycuick 1989; Rayner 1990) and with observed flight ranges. Average flight speed was Zwarts et al.'s (1990) estimate of 55 km/h (±8 [SD]). The Castro and Myers (1989) equation generated predictions that were overly conservative, especially for larger species such as godwits. (Most equations predict that larger species have greater flight ranges than smaller species for a given relative fat load, including theoretically derived models when energy conversion scales with body size. In contrast, the Castro and Myers [1989] equation and theoretically derived equations with non-scaling energy conversion predict only slightly higher flight ranges for larger species.) To compensate, we have used a flight speed of 55 km/h (Zwarts et al. 1990) and a correction factor of 1.36, which is equivalent to using a flight speed of 75 km/h and coincidentally similar to what has commonly been used in other shorebird studies (McNeil and Cadieux 1972; Summers and Waltner 1978; Jehl 1979; Mercier 1985; Castro and Myers 1989; Harrington et al. 1991). This generates estimates for larger shorebirds that are similar to estimates from the other equations in Alexander (1994) with flight speeds of 55 km/h or with flight speeds predicted from body size. For smaller shorebirds, estimates of flight range using the Castro and Myers (1989) equation with the 75 km/h flight speed equivalent tend to be 15–20% higher than estimates from the other equations in Alexander (1994). Given that all equations appear to be conservative (Alexander 1994), we consider our corrected estimates also to be conservative. Actual flight ranges would, of course, be modified greatly by wind (Butler et al. 1997).

3.5 Water levels

Ducks Unlimited (Canada) recorded water levels (m asl) at most of the waterfowl habitat management projects (Fig. 1) periodically throughout this study. In addition, field crews took qualitative notes on shorebird habitat availability in relation to water levels while conducting other fieldwork.

4. Shorebird migration at the Quill Lakes

4.1 Introduction

In order to develop appropriate management strategies for shorebird staging sites on the prairies (many of which have some water control capabilities but are often managed primarily for the benefit of other species), we must have knowledge of species composition, chronology of migration, and what use each species makes of the area in terms of breeding, resting, energy acquisition, and moulting.

In this section, we document which species and ages of shorebirds use the Quill Lakes area during migration. We also examine the evidence for seasonal differences in the populations (within species) that use the Quill Lakes and differences in the migration routes followed by adults and juveniles. In addition, this section provides information on the chronology of northbound spring and southbound autumn migrations, including the timing of migration of adults compared with that of juveniles and estimates of the duration of migratory stopover by individuals in the Quill Lakes area. Lastly, we examine the incidence of moult and mass gain and estimate flight ranges to provide evidence of how shorebirds are using the Quill Lakes during migration.

4.2 Results

4.2.1 Species identification during surveys

In most years, observers identified 91–96% of all shorebirds seen during surveys (excluding unidentified phalaropes, which were probably Red-necked Phalaropes, and unidentified plovers, which were Black-bellied Plovers or Lesser Golden-Plovers). In spring 1992 and at Big Quill Lake in spring 1993, observers identified only 70% and 56%, respectively, of the shorebirds seen (more unidentified phalaropes and plovers were recorded in 1992 as well). Most of the unidentified shorebirds were small and medium in size (most likely White-rumped, Baird's, Least, Semipalmated, and Stilt sandpipers). Potential bias related to poor identification is noted when it applies.

4.2.2 Species composition and abundance

For each species, the peak count within a season (i.e., spring or autumn migration) is interpreted as the minimum population estimate. Peak counts underestimate the actual number of birds using the area because they do not take into account turnover of individuals (e.g., a peak count of 1500 Stilt Sandpipers might be seen in spring; however, if each bird stays an average of only four days, the actual number migrating through the site might be as many as 7500 in a 20-day period).

Peak counts were approximately three times higher in spring than in autumn (based on the average among years of the sums of each species' seasonal peak; Table 1). Red-necked Phalaropes were the most common shorebirds in both seasons during most years. Six species were among the 10 most common species during both spring and autumn migrations: Red-necked Phalaropes, Semipalmated Sandpipers, Stilt Sandpipers, Least Sandpipers, American Avocets, and Baird's Sandpipers (Tables 1 and 2). In spring, White-rumped Sandpipers, Sanderlings, Black-bellied Plovers, and Red Knots were also among the top 10 species. In July and August, the top 10 included dowitchers, Lesser Yellowlegs, Hudsonian Godwits, and Semipalmated Plovers. These patterns were apparent whether using means across years of peak counts (Table 1) or total counts (i.e., the sum of counts from all surveys within a season; Table 2).

4.2.3 Age composition

We noted partial postjuvenile wing (PPW) moult (i.e., evidence of yearlings) only in Semipalmated Sandpipers, Least Sandpipers, Stilt Sandpipers, and Lesser Yellowlegs (Table 3). We suspect that many of the older Lesser Yellowlegs had migrated north prior to the onset of banding. Semipalmated Sandpiper yearlings were more abundant than adults later during spring migration and earlier during autumn migration. Stilt Sandpiper yearlings did not appear to migrate southward earlier than older birds.

Among species captured in large numbers (>100) during autumn migration, Least Sandpiper, Semipalmated Sandpiper, and Wilson's Phalarope juveniles were considerably more common than adults (i.e., >90% of birds captured were juveniles; Table 4). Roughly half of the Lesser Yellowlegs captured in July and August were juveniles. Few juveniles of other species, including local breeders, were captured.

Table 1
Peak numbers of shorebirds observed during spring and autumn migrations at the Quill Lakes,[a] Saskatchewan, 1989–1993

	Spring							Autumn				
Species[b]	1989	1990	1992	1993	1993[c]	Mean[a]	Species[b]	1989	1990	1991	1992	Mean
RNPH	9 230	45 188	4 662	3 892	43 448	15 743	RNPH	6 759	9 522	4 372	4 522	6 294
SESA	19 457	12 257	3 635	12 970	23 637	12 080	STSA	8 125	3 257	2 334	2 075	3 948
STSA	5 880	13 484	1 990	14 488	14 932	8 961	DOWI	3 204	3 454	2 915	2 454	3 007
WRSA	11 985	17 126	1 064	5 002	6 695	8 794	SESA	3 260	3 615	2 307	339	2 380
LESA	230	2 747	2 773	7 149	7 150	3 225	HUGO	1 541	950	2 934	373	1 450
SAND	2 962	620	949	4 246	15 640	2 194	LEYE	2 254	1 571	594	980	1 350
BASA	555	4 150	110	2 333	3 739	1 787	AMAV	1 149	1 037	543	376	776
BBPL	1 169	1 284	1 884	771	2 063	1 277	LESA	573	354	952	1 158	759
REKN	1 146	430	557	1 699	8 967	958	SEPL	328	304	411	797	460
AMAV	401	631	568	826	920	607	BASA	691	86	324	405	377
PESA	36	450	249	118	137	213	PESA	188	351	385	212	284
SEPL	117	138	267	324	324	212	SAND	464	507	112	27	278
LEGP[d]	99	23	422	262	965	202	WIPH	58	725	62	105	238
DOWI	170	37	294	211	363	178	MAGO	261	238	249	124	218
WILL	168	46	124	74	105	103	WILL	74	195	86	107	116
LEYE	2	78	237	90	92	102	BBPL	172	48	102	84	102
MAGO	112	50	88	130	155	95	KILL	42	83	46	86	64
WIPH	23	39	248	36	86	87	GRYE	95	29	31	57	53
DUNL	49	78	158	26	29	78	BBSA	48	10	93	28	45
RUTU	31	54	144	79	276	77	PIPL	31	21	42	11	26
KILL	23	30	40	26	66	30	WRSA	92	1	0	0	23
PIPL	34	8	14	21	66	19	REKN	21	6	3	3	8
HUGO	15	7	3	38	38	16	RUTU	4	10	7	2	6
BBSA	0	1	4	7	7	3	SPSA	5	2	5	10	6
GRYE	0	0	11	0	1	3	LEGP	8	6	1	3	5
SPSA	0	2	5	2	7	2	COSN	0	5	0	3	2
SOSA	0	0	0	1	1	0	SOSA	2	1	4	1	2
UPSA	0	0	1	0	0	0	UPSA	2	1	0	1	1
WHIM	0	1	0	0	12	0	DUNL	0	1	0	0	0
COSN	0	0	0	0	1	0	REPH	0	1	0	0	0
REPH	0	0	0	0	0	0	WHIM	1	0	0	0	0
Total	53 894	98 959	20 501	54 821	129 922		Total	29 452	26 391	18 914	14 343	

[a] Includes Little Quill Lake, Middle Quill Lake, and smaller basins around these two lakes, depending on survey coverage each year.
[b] See Appendix 1 for key to four-letter species codes.
[c] The second column for 1993 also includes Big Quill Lake and Level Project (excluded from the mean).
[d] Twelve hundred seen at Little Quill Lake in late May 1991 (G.W. Beyersbergen, pers. commun.).

4.2.4 Resightings and recoveries of shorebirds banded at Little Quill Lake

Observations and recoveries of shorebirds banded at Little Quill Lake are summarized in Table 5. As noted above, additional observations for Semipalmated Sandpipers may be found in Gratto-Trevor and Dickson (1994).

There were 12 observations of Least Sandpipers banded at Little Quill Lake and resighted at Ensley Bottoms, Tennessee (Table 5). All of the known-age birds seen there that had been banded in early spring 1992 were adults. As only 26 adults had been marked with the band combination observed on the birds in Tennessee, it is possible that the late August sightings in 1994 and 1995 were of the same bird, and the early September sightings of an adult in 1993, 1994, and 1995 may have been another. In contrast, all of the known-age Least Sandpipers seen in Tennessee that had been banded during autumn migration were juveniles, although there were only four sightings (probably two different individuals) of the 363 juveniles marked. It is also interesting that only one Least Sandpiper was seen in the year of banding, when the banded birds would have been most obvious as a result of the orange dye on their underparts. These observations suggest either that the spring and autumn migrants are primarily from different breeding populations and follow different migratory routes or that adults and juveniles follow different routes.

Over 100 adult Hudsonian Godwits were colour-marked at Little Quill Lake in 1988, but none has been observed out of Saskatchewan. The only two birds banded in autumn 1990 were seen back at Little Quill Lake in autumn 1991. The lack of recoveries from elsewhere is not surprising, as these birds stage, breed, and winter in areas where observers are rare. One adult male Semipalmated Plover that was banded at Little Quill Lake during autumn migration in 1991 was found on a nest in July 1992 in the outer Mackenzie Delta, Northwest Territories (by CLGT). Stilt Sandpipers banded during autumn migration were resighted in Montana (found dead during a botulism outbreak), New Jersey, Texas, and Venezuela.

Although no Sanderlings were marked at the Quill Lakes, two colour-marked adults were observed there. Birds seen on 24 May 1990 and 26 May 1992 had both been banded by T. Below on Marco Island, on the west coast of Florida.

4.2.5 Chronology and length of stay

4.2.5.1 Spring migration

Species that bred in the Quill Lakes area (i.e., American Avocets, Marbled Godwits, Willets, Wilson's

Table 2
Relative abundance of shorebirds (mean percentages across years of total counts) observed during spring and autumn migrations at the Quill Lakes, Saskatchewan, 1989–1993

	Spring 1990, 1992, 1993				Autumn 1989–1992			
	Species[a]	Mean	Max.	Min.	Species[a]	Mean	Max.	Min.
1	RNPH	24.47	48.82	7.31	RNPH	25.28	31.70	21.21
2	SESA	21.30	27.08	14.03	DOWI	16.88	25.82	9.63
3	STSA	14.20	25.33	7.82	STSA	16.32	24.44	11.76
4	WRSA	9.96	17.31	4.19	SESA	10.43	15.26	2.85
5	LESA	7.97	11.83	3.28	LEYE	8.47	11.40	6.55
6	SAND	6.04	11.10	0.76	HUGO	6.63	11.62	2.99
7	BBPL	3.55	8.22	1.19	AMAV	4.51	6.47	3.74
8	AMAV	3.01	5.65	1.01	LESA	2.76	5.35	0.88
9	BASA	2.27	4.10	0.53	SEPL	1.93	3.63	1.26
10	REKN	1.90	2.96	0.73	BASA	1.47	2.31	0.26
11	PESA	0.88	2.26	0.08	MAGO	1.00	1.44	0.82
12	LEGP	0.80	2.03	0.04	SAND	0.89	1.57	0.11
13	SEPL	0.58	1.17	0.20	PESA	0.77	0.94	0.52
14	WIPH	0.52	1.42	0.06	WIPH	0.71	1.73	0.11
15	MAGO	0.46	0.81	0.12	WILL	0.62	1.19	0.15
16	WILL	0.46	1.02	0.09	KILL	0.49	0.92	0.18
17	DOWI	0.43	1.03	0.05	BBPL	0.32	0.40	0.15
18	LEYE	0.34	0.76	0.10	GRYE	0.25	0.55	0.12
19	DUNL	0.29	0.69	0.07	PIPL	0.09	0.11	0.05
20	RUTU	0.27	0.65	0.07	BBSA	0.07	0.12	0.01
21	KILL	0.20	0.45	0.07	SPSA	0.02	0.04	0.01
22	PIPL	0.05	0.11	0.01	RUTU	0.02	0.04	0.01
23	HUGO	0.02	0.03	0.01	REKN	0.02	0.03	0.00
24	GRYE	0.01	0.04	0.00	WRSA	0.01	0.05	0.00
25	SPSA	0.01	0.02	0.00	LEGP	0.01	0.02	0.00
26	BBSA	<0.01	0.01	0.00	COSN	0.01	0.01	0.00
27	SOSA	0.00	0.00	0.00	SOSA	<0.01	0.01	0.00
28	COSN	0.00	0.00	0.00	DUNL	0.00	0.00	0.00

[a] See Appendix 1 for key to four-letter species codes.

Table 3
Incidence of partial postjuvenile wing (PPW) moult (i.e., evidence of yearlings) in shorebirds captured at Little Quill Lake, Saskatchewan, during spring and autumn migrations, 1990–1992

	Spring		Autumn	
Species	Year	% with PPW moult	Year	% with PPW moult
Least Sandpiper	1992	3 (2/69)	1990	5 (1/21)
Lesser Yellowlegs	1992	44 (7/16)	1990	13 (3/23)
			1991	15 (14/95)
Semipalmated Sandpiper	1990	2 (9/400)	1990	10 (3/31)
	1992	2 (6/325)	1991	14 (7/50)
Stilt Sandpiper	1992	4 (3/78)	1990	8 (24/317)
			1991	3 (14/470)

Table 4
Numbers of juveniles and adults among shorebirds captured at Little Quill Lake, Saskatchewan, during autumn migration, 1990–1991

Species	No. of juveniles	No. of adults	% juveniles
Common Snipe	12	0	100
Killdeer	12	0	100
Semipalmated Sandpiper	1861	91	95
Least Sandpiper	377	27	93
Willet	25	2	93
Marbled Godwit	10	1	91
Wilson's Phalarope	110	12	90
Lesser Yellowlegs	127	146	47
Short-billed Dowitcher	34	58	37
Semipalmated Plover	4	11	23
Pectoral Sandpiper	12	79	13
Red-necked Phalarope	2	31	6
Stilt Sandpiper	46	1186	4
Long-billed Dowitcher	2	87	2
Hudsonian Godwit	0	8	0

Phalaropes, and Killdeers) arrived earlier than northern breeders (Fig. 2). Daily counts of local breeders were less variable than those of northern breeders throughout the spring migration period.

Patterns of timing of migration were more distinct for northern breeders than for local breeders (Fig. 2). Early migrants peaked during the second and third weeks of May (Pectoral Sandpiper, Semipalmated Plover, dowitchers, Lesser Yellowlegs). Middle migrants peaked during the third and fourth weeks of May (Red-necked Phalarope, Stilt Sandpiper, Least Sandpiper, Baird's Sandpiper, Red Knot, Lesser Golden-Plover, Dunlin). Late migrants peaked in the fourth week of May and first week of June (Semipalmated Sandpiper, White-rumped Sandpiper, Sanderling, Black-bellied Plover, Ruddy Turnstone). Peaks occurred latest in 1993 in 13 of the 15 species with the most discernible peaks.

Few spring migrants that were dyed with picric acid were seen during subsequent censuses. The minimum length-of-stay estimates for spring migrant Semipalmated and Least sandpipers averaged 4–6 days (Table 6). Of seven adult White-rumped Sandpipers captured in spring 1990, two were resighted four days after banding. These data concur with the census results in suggesting that spring migration was rapid.

Table 5
Resightings of shorebirds banded at Little Quill Lake, Saskatchewan, during spring and autumn migrations, 1988–1995

Species[a]	Age	Banded[b]	Resighted Date	Location	Observer
SESA	Adult	Spring 1990	18 May 1993	South Is., 24 km S of Georgetown, South Carolina, USA	J. Lyons
SESA	Adult	26 May 1992	22 Sept. 1992	Captured near Itamaraca, Brazil	M.A. Severin, Jr.
SESA	Adult	Spring 1992	24 July 1994	Rock Pt. Prov. Park, 50 km W of Buffalo, Ontario, Canada	P. Yoerg
LESA	Adult	Spring 1992	Autumn 1992	Cranberry Marsh, near Whitby, Ontario, Canada	
LESA	Adult	Spring 1992	12 Sept. 1993	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Adult	Spring 1992	8 Aug. 1994	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Adult	Spring 1992	24 Aug. 1994	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Adult	Spring 1992	11 Sept. 1994	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Adult	Spring 1992	26 Aug. 1995	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Adult	Spring 1992	10 Sept. 1995	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Unknown	Autumn 1988	19–21 July 1991	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Unknown	Autumn 1990	19 Sept. 1990	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Juvenile	Autumn 1991	17–18 July 1993	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Juvenile	Autumn 1991	12 Sept. 1993	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Juvenile	Autumn 1991	13–23 July 1994	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
LESA	Juvenile	Autumn 1991	16 Sept. 1995	Ensley Bottoms, near Memphis, Tennessee, USA	J.R. Wilson
HUGO	Adult	Autumn 1990	Autumn 1991	Little Quill Lake, Saskatchewan, Canada	This study
HUGO	Adult	Autumn 1990	Autumn 1991	Little Quill Lake, Saskatchewan, Canada	This study
LEYE	Adult	Aug. 1990	6 Sept. 1990	Shot in Barbados, West Indies	G. Farm
LEYE	Adult	Autumn 1990	Autumn 1991	Little Quill Lake, Saskatchewan, Canada	This study
SEPL	Adult	Autumn 1991	July 1992	Male on nest, outer Mackenzie Delta, Northwest Territories, Canada	CLGT
STSA	Unknown	Autumn 1988	30 Aug. 1988	Aransas National Wildlife Refuge, 10 km SE of Austwell, Texas, USA	B. Jones
STSA	Adult	Autumn 1988	Several months later	Venezuela	S. Temple
STSA	Adult	Autumn 1991	Several months later	Venezuela	S. Temple
STSA	Unknown	Autumn 1991	28 July 1995	Cape May, New Jersey, USA	J.R. Wilson
STSA	Adult	6 Aug. 1991	5 Aug. 1996	Medicine Lake, Montana, USA	M. Ravenberg
WILL	Juvenile	8 Aug. 1990	26 Aug. 1990	San Luis Pass, SW tip of Galveston Is., Texas, USA	T. Ubanks

[a] See Appendix 1 for key to four-letter species codes.
[b] In most cases, banding date could not be determined because band numbers could not be seen by observers.

4.2.5.2 Autumn migration

Four of the five local breeders decreased steadily in number from early July to September (Fig. 3). The exception was Wilson's Phalarope, which in two of the three years peaked in numbers in the last week of July and first two weeks of August. Marbled Godwit juveniles dyed with picric acid remained in the area an average of 14 days after banding. Two Willet juveniles were resighted four days, one nine days, one 13 days, and two 14 days after capture. One Wilson's Phalarope juvenile was resighted 13 days after banding, but no others more than seven days after capture.

The autumn migration period for northern migrants was longer than the spring migration period, and peaks were less discernible (Figs. 2 and 3). There were three general patterns in the chronology of autumn migration: single peak (dowitchers, Lesser Yellowlegs, Hudsonian Godwit, Semipalmated Plover, Black-bellied Plover); multiple peaks (Red-necked Phalarope, Stilt Sandpiper, Semipalmated Sandpiper, Least Sandpiper, Baird's Sandpiper, Sanderling); and no clear pattern (Pectoral Sandpiper, Greater Yellowlegs). The multiple-peak group included most of the small and medium-sized Calidrids.

Multiple peaks were likely due to differential timing of migration between sexes and ages. Among commonly captured northern migrants, juveniles migrated later than adults (Fig. 4). Juveniles outnumbered adults by the first week in August for Least and Semipalmated sandpipers and by the second or third week in August for Lesser Yellowlegs and Stilt Sandpipers. The first juvenile Pectoral Sandpipers, Red-necked Phalaropes, and Semipalmated Plovers were captured usually by mid-August. Juveniles of local breeders (Wilson's Phalaropes, Willets, and Marbled Godwits) were present in the area from the first surveys in July.

Length-of-stay estimates indicated that individual shorebirds remained at the Quill Lakes longer during southbound than during northbound migration. The mean period between marking and resighting of dye pattern "cohorts" was seven days for Stilt Sandpipers, eight and nine days for juvenile Semipalmated Sandpipers, and seven and 10 days for juvenile Least Sandpipers (Table 6). Length of stay for adult and juvenile Lesser Yellowlegs ranged from 10 to 22 days, averaging 16 days (74 marked, 74 total resightings). One adult Hudsonian Godwit banded in 1990 was still in the area 30 days later. In 1991, one remained at least 12 days and another remained 11 days. Dyed dowitchers were observed as long as 30 days after banding, but more commonly 6–12 days after banding. In contrast, few adult Pectoral Sandpipers were resighted after banding, and none remained more than four days. No adult Semipalmated Plovers were resighted more than eight days after banding; most were resighted less than four days later.

The earliest northern migrants were Red-necked Phalaropes, Stilt Sandpipers, Lesser Yellowlegs, and Greater Yellowlegs (Fig. 3). For these species and many others, the peak period started in the third or fourth week of July. The clearest exception was the Black-bellied Plover, which peaked in mid- to late August. Least Sandpipers (mostly juveniles) were also late migrants, peaking in the third week of August. Sanderlings and Lesser Yellowlegs decreased in number by the fourth week of July or first week of August, which was earlier than most other species (except Sanderlings in 1991; Fig. 3). In most species, numbers declined during the second (dowitchers, Stilt Sandpipers, Semipalmated Plovers) or third (Red-

Figure 2
Abundance of shorebirds in relation to survey date during spring migration at the Quill Lakes, 1990–1993. Species are arranged top left to bottom right in order of decreasing average abundance. Numbers within graph panes indicate percentages greater than 50.

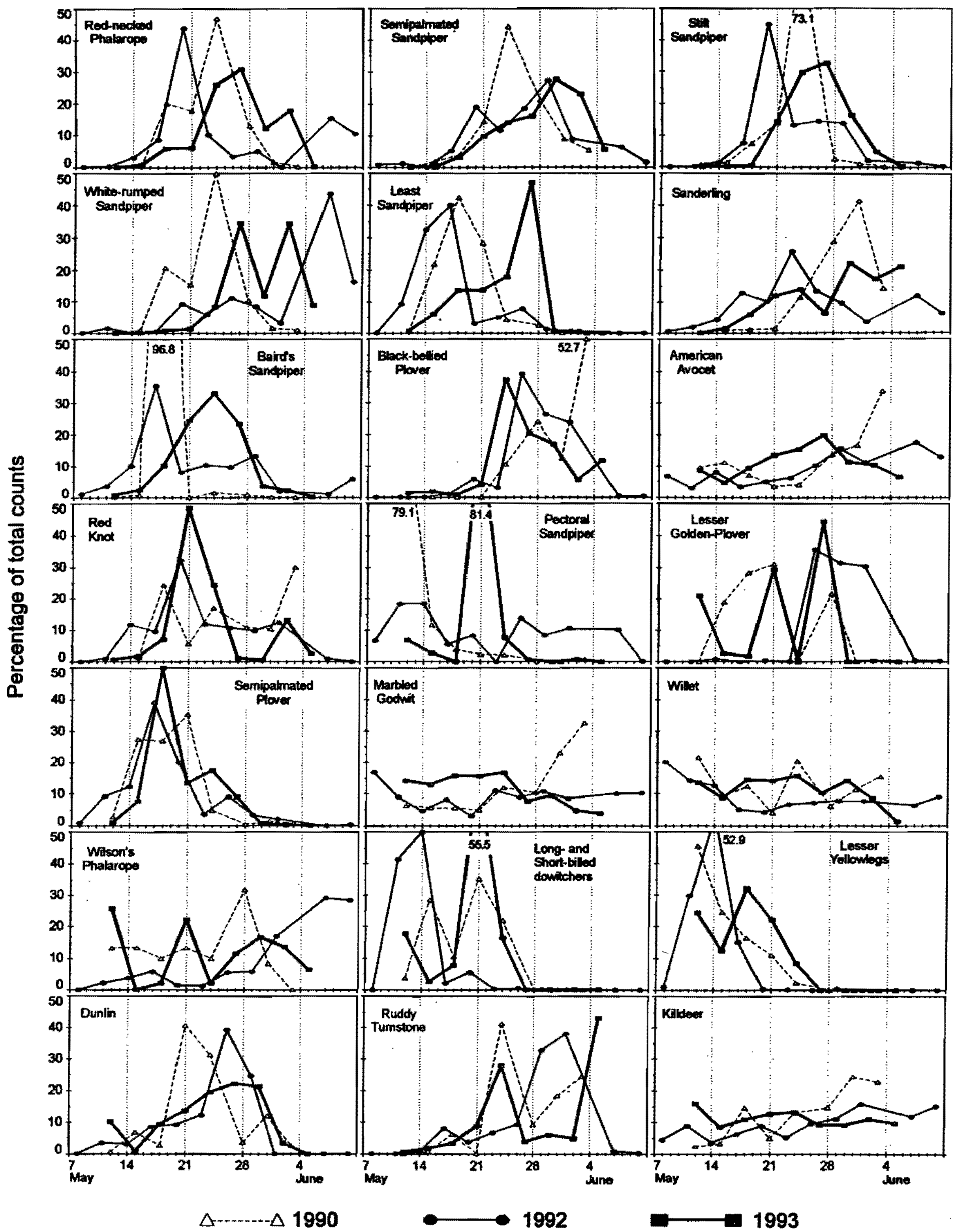


Table 6
Length-of-stay estimates for spring and autumn migrants at Little Quill Lake, Saskatchewan, 1990–1992

Species[a]	Season	Year	No. of birds	No. of dye pattern cohorts	Length of stay (days) Mean	SD	Range
SESA	Spring	1990	380	2	4	0.0	–
	Spring	1992	286	3	6	1.4	4–7
	Autumn	1990	684	5	8	1.3	7–10
	Autumn	1991	511	4	9	1.5	7–10
LESA	Spring	1992	49	1	4	–	–
	Autumn	1990	115	3	10	3.0	7–13
	Autumn	1991	111	2	7	4.2	4–10
STSA	Autumn	1990	307	4	7	2.4	4–10
	Autumn	1991	719	6	7	3.3	4–13

Note: See Methods for description of how length of stay was calculated. Only dye pattern "cohorts" with more than 30 birds are included in this table.

[a] See Appendix 1 for key to four-letter species codes.

necked Phalaropes, Semipalmated Sandpipers, Hudsonian Godwits, Least Sandpipers, Black-bellied Plovers) week of August. Baird's and Pectoral sandpipers appeared to have the most protracted migration period (third week of July to third and fourth weeks of August). The low length-of-stay estimate for Pectoral Sandpipers and the protracted migration period suggest that there was considerable turnover.

4.2.6 Active flight feather moult

Very few shorebirds moult flight feathers during migration in Canada (CLGT, unpubl. data). At the Quill Lakes, dowitchers were the only shorebirds found with active flight feather moult (i.e., wing and tail feathers were being replaced). In 1990, none of the six Short-billed Dowitchers examined was in active moult, whereas 43% (9/21) of the Long-billed Dowitchers examined were moulting. Birds captured as early as 19 July were moulting primaries, and some had initiated secondary moult by 25 July. In 1991, 42% (8/19) of the Short-billed Dowitchers examined were in moult, compared with 88% (15/17) of the Long-billed Dowitchers. Tail moult in dowitchers was first noted in early August; by 8 August, a few birds were missing all tail feathers. Wing moult progressed regularly from the first to outer primary, and secondary moult from the first to inner secondary. Secondary moult was initiated approximately at the time the sixth primary was moulted.

Moult might have been observed more commonly in Long-billed Dowitchers because they remained in the area throughout August, whereas few Short-billed Dowitchers were present after the first week. However, even some Short-billed Dowitchers present in mid-August were not moulting flight feathers, whereas all Long-billed Dowitchers were in active moult at that time.

4.2.7 Mass gain

4.2.7.1 Semipalmated Sandpipers

Semipalmated Sandpipers did not appear to gain mass during spring migration. One bird captured twice during spring migration gained only 0.1 g in six days. Another gained 1.7 g in seven days (0.2 g/day). Overall, mean mass was correlated negatively with date in 1990 and only slightly positively with date in 1992 (Table 7).

Most of the evidence indicates that Semipalmated Sandpipers gained mass at Little Quill Lake during autumn migration. In 1990, of 34 birds recaptured 2–15 days apart, 26 gained and eight lost mass (Fig. 5). Juveniles gained up to 2.4 g/day, averaging 0.5 g/day (SD = 0.5) for the 26 birds that had gained mass. Fewer juveniles were retrapped in 1991, but, of seven birds recaptured 2–5 days apart, six gained mass and one did not change. Gains ranged from 0.5 to 2.8 g/day, averaging 1.5 g/day (SD = 0.8). Overall, adults in 1990 and juveniles in 1991 showed significant positive correlations between mass and date, but adults in 1991 and juveniles in 1990 did not (Table 7). The data are not sufficient to indicate whether differences in rates of mass gain exist between years.

4.2.7.2 Stilt Sandpipers

There was no evidence of mass gain in Stilt Sandpipers at the stopover in the spring (Table 7). The mean mass of adults captured in autumn was significantly greater than that of juveniles (n = 1164 [adults], 42 [juveniles], $P < 0.0001$, t-test; Table 8). The only adult captured twice during autumn migration in 1990 gained 1.0 g in three days (0.3 g/day). In 1991, 16 adults were captured twice, 2–15 days apart. Eleven gained and five lost mass (Fig. 6). Mass gain was as much as 2.4 g/day and averaged 1.2 g/day (SD = 0.9) in the 11 birds that gained mass. In both 1990 and 1991, correlations between date and mass of all Stilt Sandpipers were significant (Table 7), although positive only in 1991. Stilt Sandpipers gained mass rapidly at the stopover in 1991 (up to 27 g in 15 days). The mean mass of adult Stilt Sandpipers was also significantly greater in 1991 (n = 816, mean = 70.7 g, SD = 12.0) than in 1990 (n = 348, mean = 63.7 g, SD = 4.1; $P < 0.0001$, t-test), which suggests possible differences in food availability between years.

4.2.7.3 Other species

No Hudsonian Godwits were recaptured within one season, but there is evidence for mass gain at the stopover, as the mass of 10 birds collected after 11 August 1992 averaged 365.7 g (SD = 37.9), significantly greater ($P = 0.008$, t-test) than that of 11 birds collected before 11 August 1992, which averaged 301.8 g (SD = 58.2). There were no significant differences between these two groups of birds in wing or bill length ($P > 0.05$, t-test).

One Lesser Yellowlegs adult caught twice in 12 days during autumn migration in 1991 gained 24.7 g (2.1 g/day). There were significant positive correlations between mass and date for juveniles in 1990 and 1991, suggesting that juveniles were acquiring fat at the stopover (Table 7). Similar correlations for adults captured in autumn were significant in 1991 but not in 1990, although there were periods during 1990 when mean mass increased. This may indicate that a group of adults arrived at the stopover, gained mass, left, and was replaced by another arriving flock of lighter birds, as suggested for Semipalmated Sandpipers elsewhere (Lank 1983). The average mass of adults in autumn was significantly higher

Figure 3
Abundance of shorebirds in relation to survey date during autumn migration at the Quill Lakes, 1990–1992. Species are arranged top left to bottom right in order of decreasing average abundance. Numbers within graph panes indicate percentages greater than 30.

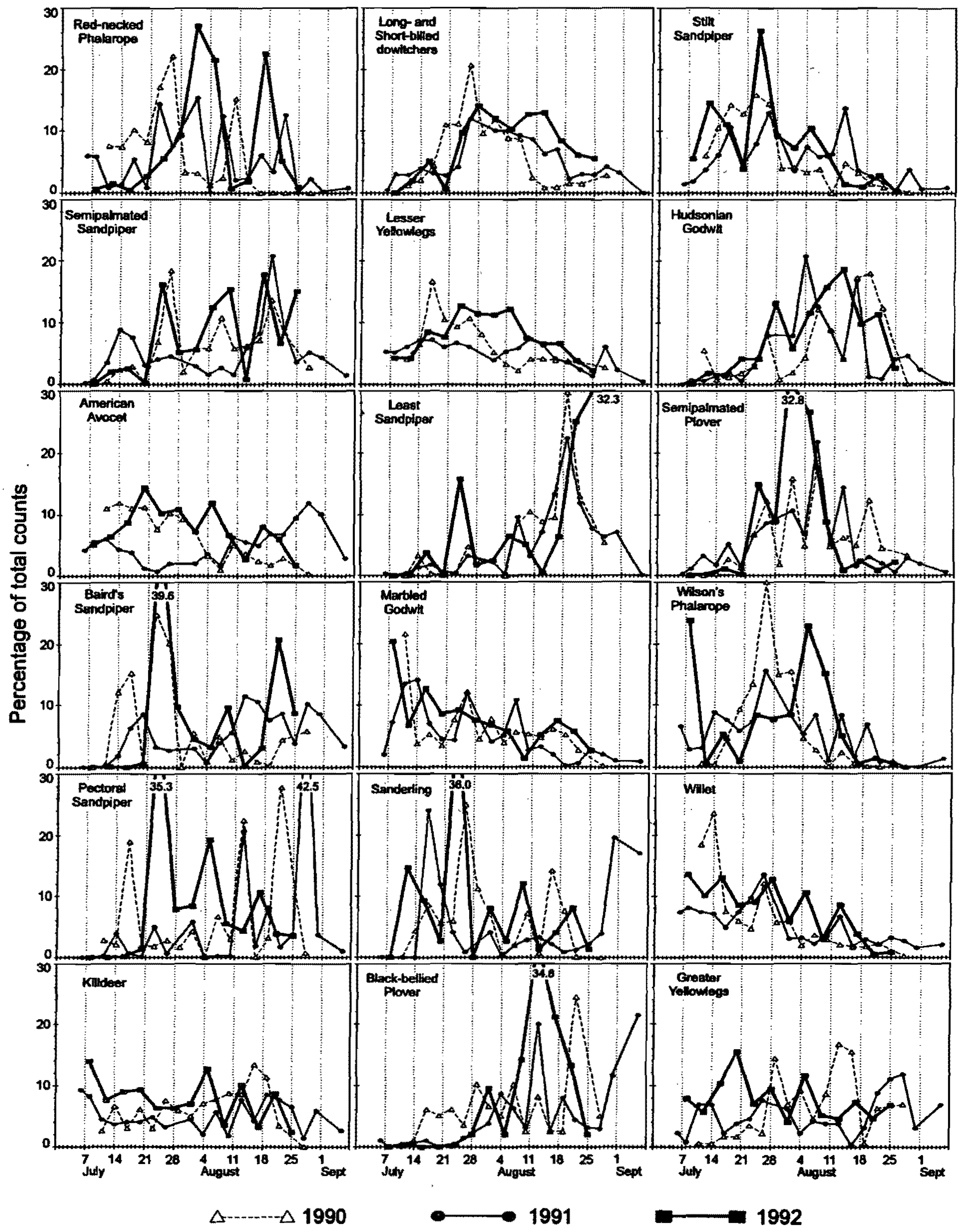
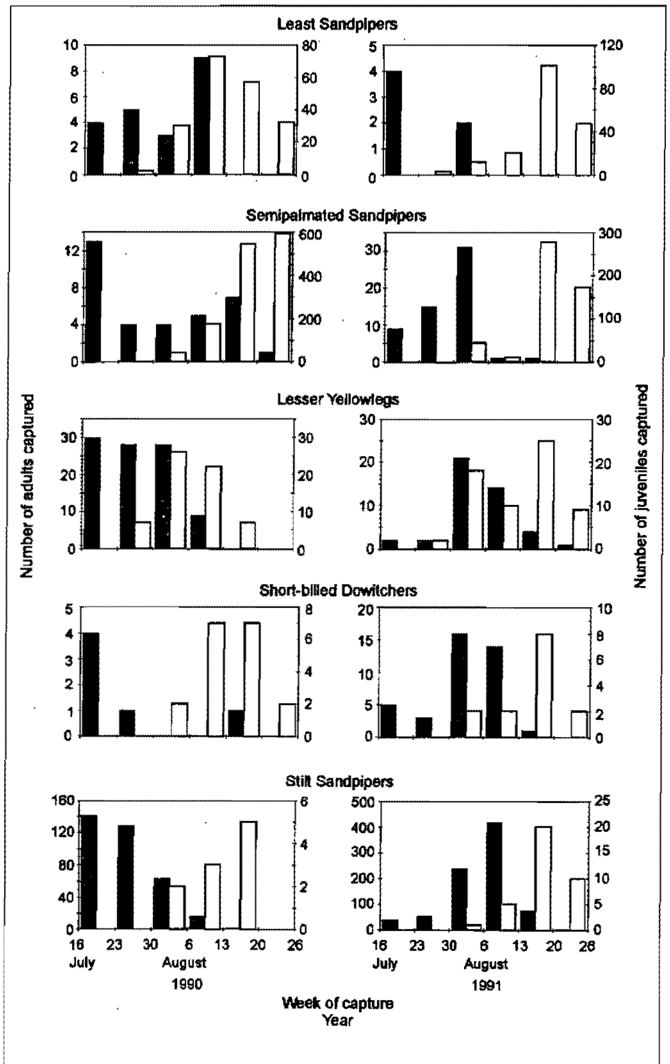


Figure 4
Abundance of mist-netted adult (black bars) versus juvenile (white bars) shorebirds in relation to capture date during autumn migration at Little Quill Lake, 1990 and 1991



than that of juveniles (n = 143 [adults], 127 [juveniles], P < 0.0001, t-test; Table 8).

Seven juvenile Least Sandpipers were captured twice during autumn migration, 3–10 days apart. Five gained mass (0.03–0.23 g/day), and two lost mass (−0.21 and −0.62 g/day). There was no evidence of a significant increase in mass during either spring or autumn migration (Table 7). One juvenile Short-billed Dowitcher, captured three times in 1990, gained 6.7 g in three days and a further 7.2 g in the next two days (average of 2.8 g/day). A Wilson's Phalarope that was captured twice in seven days gained only 0.6 g. There was no significant correlation between mass and date in either 1990 or 1991 for Wilson's Phalarope (Table 7).

4.2.8 Flight range

Wing lengths, the mean and maximum starting masses, and the minimum (final) masses used to estimate flight ranges are given in Tables 8 and 9. As sample sizes of banded Hudsonian Godwits were low, flight range estimates are based on both banded and collected birds.

Table 7
Pearson correlations (r) between mass (g) and date of capture

Species[a]	Age	Season	Year	n	P	r	Slope[b]
LESA	Adult	Spring	1992	69	0.19	–	–
	Juvenile	Autumn	1990	194	0.74	–	–
	Juvenile	Autumn	1991	184	0.10	–	–
LEYE	Adult	Autumn	1990	95	0.87	–	–
	Adult	Autumn	1991	51	0.05	0.28	0.53
	Juvenile	Autumn	1990	62	0.02	0.29	0.58
	Juvenile	Autumn	1991	65	0.0006	0.42	0.80
SESA	Adult	Spring	1990	400	0.0001	−0.28	−0.34
	Adult	Spring	1992	324	0.02	0.40	0.08
	Adult	Autumn	1990	34	0.0001	0.66	0.24
	Adult	Autumn	1991	57	0.22	–	–
	Juvenile	Autumn	1990	1355	0.78	–	–
	Juvenile	Autumn	1991	507	0.0001	0.25	0.18
STSA	Adult	Spring	1992	75	0.94	–	–
	Adult	Autumn	1990	349	0.0007	−0.18	−0.29
	Adult	Autumn	1991	837	0.0001	0.40	0.69
WIPH	Juvenile	Autumn	1990	78	0.06	–	–
	Juvenile	Autumn	1991	32	0.09	–	–

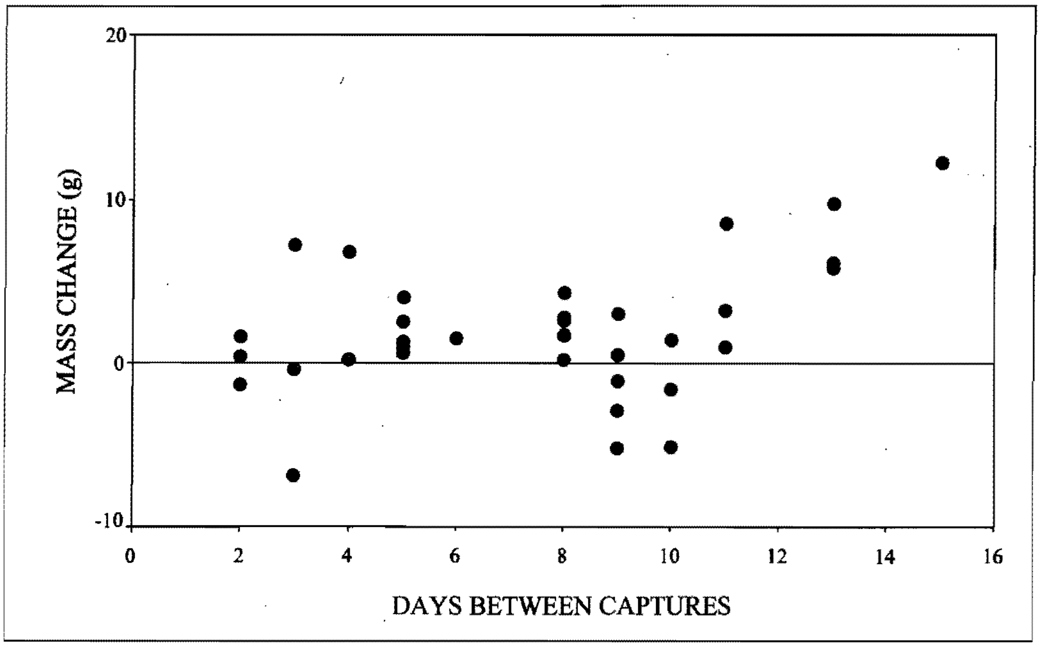
[a] See Appendix 1 for key to four-letter species codes.
[b] Slope obtained from linear regression on significant correlations, to indicate degree of average loss or gain (g/day).

Based on the conservative estimates of flight range, most birds at the Quill Lakes in spring would have been able to fly directly to at least the southern parts of their breeding ranges (Table 9). The maximum estimates suggest that most birds would have had excess reserves even without wind assistance. During autumn migration, at least some birds of all species, except perhaps Long-billed Dowitchers, would have been able to fly directly from the Quill Lakes to the southern United States. At least some individuals in species with maximum ranges exceeding 6000 km would have been able to fly nonstop to northern South America.

4.3 Discussion

The Quill Lakes area of Saskatchewan is an important interior staging site for shorebirds during both spring and autumn migrations in terms of total numbers of birds using the area and broad species composition. In total, 32 species of shorebirds were documented at the Quill Lakes (Table 1). To better focus conservation efforts, it is important to consider not only absolute numbers of a species in an area, but also how abundant the species is in relation to its world, subspecies, or flyway population size. There are no accurate population estimates for most North American shorebirds. Morrison et al. (1994a) made an attempt to estimate, very roughly (within an order of magnitude), the numbers of shorebirds breeding in or migrating through Canada. B.A. Harrington (unpubl. data, February 1997), with comments from other shorebird researchers, ranked all North American shorebirds in "conservation risk." Species ranked highest if their total population size was low, their breeding and wintering areas were limited, their populations were known to be decreasing, their breeding and/or wintering areas were likely to be lost or degraded, and the birds concentrated for migration at a few staging areas. Using the Morrison et

Figure 5
Change in mass of juvenile Semipalmated Sandpipers captured twice, 2–15 days apart, at Little Quill Lake during autumn migration, 1990



al. (1994a) estimates, the three most numerous shorebird species at the Quill Lakes relative to their Canadian population numbers were Stilt Sandpiper (spring and autumn), White-rumped Sandpiper (spring), and Sanderling (spring). Other species that were common relative to these population estimates were Baird's Sandpiper (spring), Hudsonian Godwit (autumn), Black-bellied Plover (spring), and Red Knot (spring). Red-necked Phalaropes and Semipalmated Sandpipers were as abundant as Stilt Sandpipers at the Quill Lakes, but much less common in relation to Morrison et al.'s (1994a) population estimates. Stilt Sandpipers and Hudsonian Godwits were ranked fourth and 10th highest, respectively (of 51 species), in Harrington's February 1997 conservation scores for North American shorebirds. The highest rankings refer to species considered most at risk of extinction.

Until recently, Hudsonian Godwits were thought to stage only at James Bay during autumn migration (Godfrey 1986). This species appears to have a disjunct breeding distribution, with an eastern population around the Hudson Bay area and a western population in the Mackenzie Delta, NWT–Alaska region. DNA analysis indicates that Hudsonian Godwits staging in the autumn at the Quill Lakes are from the western Arctic population (Haig et al. 1997). Specifically, birds analyzed were closest to Alaskan, rather than to Mackenzie Delta, breeders. Hudsonian Godwits at the Quill Lakes apparently represent a significant percentage of the western Arctic breeders.

In all cases, shorebird numbers varied considerably among years, likely in response to variation in habitat availability (see Section 5). In prairie wetlands, small differences in water levels can have profound effects on habitat structure, prey availability, and the overall suitability of an area to shorebirds (Colwell and Oring 1988; Alexander 1994; Skagen and Knopf 1994a, 1994b). The often unpredictable variations in prairie wetland conditions, and consequently in the numerical patterns of shorebirds staging at any given prairie stopover, make most prairie staging areas unsuitable for monitoring population trends of Arctic shorebirds, as has been done at some coastal sites (Howe et al. 1989; Morrison et al. 1994b).

Shorebird species composition and relative numbers were similar at Little Quill Lake and Last Mountain Lake, Saskatchewan (Colwell 1987), the only other location in the northern prairies where there have been similar surveys. The most striking difference was that Wilson's Phalaropes were relatively more abundant at Last Mountain Lake. Migration chronology was also similar at the Quill Lakes and Last Mountain Lake (Colwell et al. 1988): 1) peak numbers occurred from the second week of May to the first week of June and again from the third week of July to the third week of August; 2) autumn migration was more protracted than spring migration; and 3) some species migrated southward in several waves depending on sex and age (Figs. 3 and 4, Section 4.2.5.2). At the Quill Lakes, there was some evidence that local breeders arrived earlier in spring than northern breeders and that Wilson's Phalaropes and Willets congregated there prior to breeding. The banding data from Little Quill Lake indicate that, as in other areas (Marchant et al. 1986), Short-billed Dowitchers migrate south earlier than Long-billed Dowitchers (adult Short-billed Dowitchers in late June/July and Long-billed Dowitchers in August/September; juvenile Short-billed Dowitchers starting in late July and Long-billed Dowitchers in mid-August to September).

Mass gain, presumably mostly fat, was substantial for some individuals. No comparative information exists for Stilt Sandpipers, which have not been studied in any detail elsewhere during migration (Klima and Jehl 1997). Mass gain in Semipalmated Sandpipers has been examined

Table 8
Measurements of shorebirds banded at Little Quill Lake, Saskatchewan, from 1990 to 1992[a]

			Wing length (mm)					Bill length (mm)					Mass (g)				
Species[b]	Season	Age[c]	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.
COSN	Autumn	JUV	12	137.8	3.4	133	144	12	66.0	3.0	60.6	71.2	12	101.1	9.6	90.8	126.4
DUNL	Spring	AD	7	123.9	1.7	122	126	7	38.1	2.2	35.8	41.1	7	58.9	5.2	49.2	66.2
HUGO	Autumn	AD	8	220.1	6.9	206	228	8	78.9	8.7	66.2	91.0	6	335.3	50.6	284.0	407.0
	Autumn[d]	AD	35	221.1	6.1	206	235	35	79.5	7.1	66.2	93.7	33	335.9	55.4	209.0	436.0
KILL	Autumn	JUV	11	169.9	3.8	163	174	11	19.8	1.2	18.0	21.7	11	88.3	3.3	84.1	94.5
LBDO[e]	Autumn	AD	85	150.1	4.0	140	159	85	68.0	6.1	43.5	79.9	85	110.2	7.9	92.3	128.6
LESA	Autumn	AD	27	89.7	2.8	83	95	27	18.6	1.1	16.8	20.9	27	21.7	2.2	18.2	25.5
	Autumn	JUV	363	92.4	2.4	83	100	361	18.7	1.1	15.8	21.7	363	21.5	2.4	16.9	30.5
	Spring	AD	69	91.3	2.3	87	97	69	18.5	1.0	15.6	21.1	69	25.0	2.4	18.1	30.3
LEYE	Autumn	AD	139	160.9	3.8	150	172	144	36.0	1.5	30.8	40.0	143	110.4	19.2	71.5	149.8
	Autumn	JUV	127	161.6	3.5	152	170	127	35.8	1.5	31.8	39.5	127	91.0	16.6	65.9	133.5
	Spring	AD	16	163.4	4.9	156	175	16	36.5	1.9	32.7	39.7	16	95.2	8.7	85.1	114.9
MAGO	Autumn	AD	1	241.0	–	–	–	1	98.5	–	–	–	1	430.0	–	–	–
	Autumn	JUV	10	232.4	10.2	216	249	10	90.5	13.5	73.4	113.0	10	310.5	46.9	243.8	365.0
PESA	Autumn	AD	77	134.9	5.2	128	152	78	28.0	1.5	23.7	32.6	79	62.2	9.1	45.8	86.8
	Autumn	JUV	12	134.7	4.9	129	148	12	28.0	1.7	24.5	30.7	12	55.0	8.4	45.3	72.8
	Spring	AD	44	134.5	3.8	127	146	44	28.3	1.2	25.9	30.5	44	64.0	8.7	52.9	87.9
RNPH	Autumn	AD	31	112.2	3.7	100	121	30	22.9	1.3	19.6	25.5	31	32.9	4.9	24.5	47.9
SBDO[e]	Autumn	AD	58	148.4	3.9	141	155	58	60.6	4.9	51.9	75.5	58	109.9	12.5	88.0	148.4
	Autumn	JUV	29	149.8	5.5	126	158	29	57.7	3.1	53.5	64.4	30	104.1	12.1	81.2	138.2
SEPL	Autumn	AD	11	126.7	3.1	122	131	11	12.5	0.6	11.5	13.2	11	46.7	5.6	37.6	57.3
SESA	Autumn	AD	87	98.0	2.6	92	105	88	18.6	1.4	16.2	21.8	90	26.3	3.9	20.3	37.5
	Autumn	JUV	1800	98.4	2.4	91	106	1660	18.6	1.2	15.0	22.5	1801	26.6	3.9	16.3	41.5
	Spring	AD	724	98.7	2.4	92	105	724	19.0	1.2	15.9	22.9	723	26.2	2.4	21.1	35.2
STSA	Autumn	AD	1132	133.9	3.5	122	144	1165	40.6	1.8	35.4	46.4	1164	68.6	11.7	41.8	103.5
	Autumn	JUV	42	134.5	3.1	128	139	42	38.3	2.4	31.2	41.8	42	52.5	6.8	41.8	75.5
	Spring	AD	78	135.0	3.5	125	142	78	40.0	2.4	28.7	44.4	78	57.6	5.9	46.3	77.4
WILL	Autumn	AD	2	220.5	13.4	211	230	2	64.9	4.1	62.0	67.8	2	319.5	27.6	300.0	339.0
	Autumn	JUV	23	204.0	13.8	156	220	23	53.8	4.6	41.2	62.5	23	237.3	22.6	202.6	306.0
WIPH	Autumn	AD	12	125.6	2.5	121	130	12	31.1	0.8	29.9	32.4	12	51.6	5.2	44.1	58.9
	Autumn	JUV	107	125.6	8.0	99	141	107	30.2	2.1	24.3	36.4	107	48.9	7.3	36.7	85.3
WRSA	Spring	AD	16	124.3	3.5	119	130	16	22.7	1.1	20.7	24.8	16	42.1	4.0	37.4	49.5

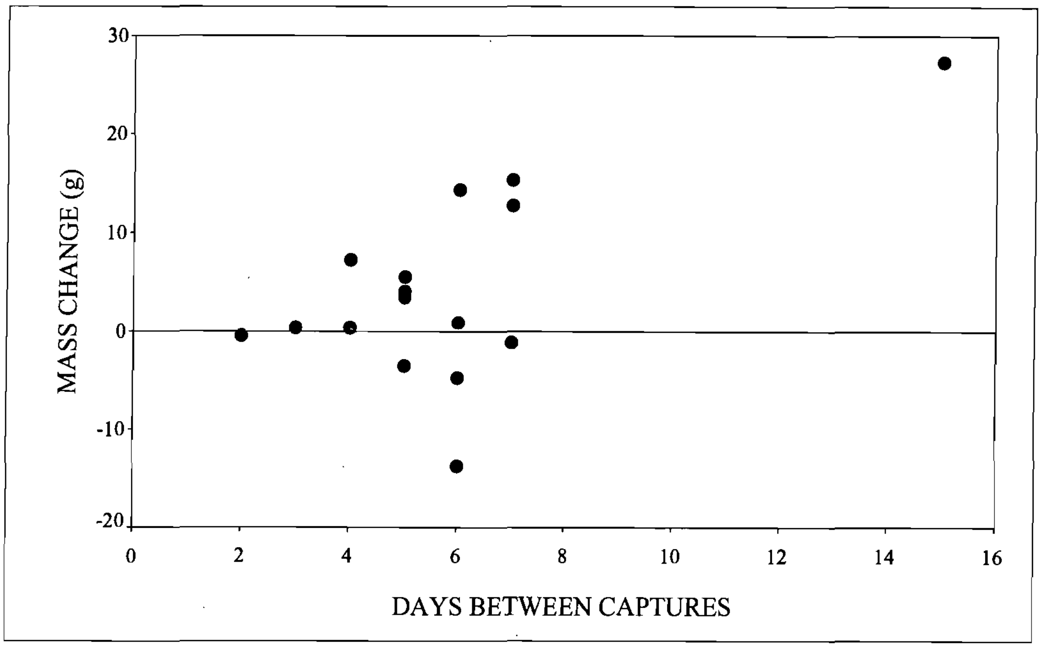
Note: See Appendix 3 for sex-related differences in morphometrics.

[a] Some species with very low sample sizes were omitted (AMAV, BASA, GRYE, REKN, SOSA, SPSA, WESA).
[b] See Appendix 1 for key to four-letter species codes.
[c] AD = adult, bird at least one year old. JUV = juvenile. In species that bred locally, measurements of juveniles might include individuals that had not completed growing.
[d] Includes the eight captured birds plus 27 collected birds.
[e] Differences between LBDO and SBDO agree with published measurements (Marchant et al. 1986), although bill lengths of a few SBDO were high and possibly were misidentifications.

at many locations in North America. Average mass gain at autumn staging sites ranged from 0.4 g/day at North Point, southern James Bay (Gratto 1983; Morrison 1984), to over 1.0 g/day at Dorchester Cape, Bay of Fundy (P. Hicklin, unpubl. data). Maximum rates reported were 1.1–1.3 g/day (Lank 1983; White 1985). Butler et al. (1997) reviewed estimates of maximum daily mass gain.

According to Lindström (1991), maximum fat deposition rates should be 2.6–4.3% of lean mass per day, whereas Zwarts et al. (1990) suggested that daily maximum rates are 4–5% of "winter" mass. For Stilt Sandpipers, this would be 1.4–2.3 g/day by Lindström's (1991) model (lean mass averaged 54 g; Alexander 1994), which is near the maximum reported here (2.4 g/day). The maximum rate in Semipalmated Sandpipers, however, according to these formulas, would be 1.2 g/day (lean mass 23 g, winter mass 24 g; Gratto-Trevor 1992). At Little Quill Lake, juvenile Semipalmated Sandpipers in 1991 averaged mass gains greater than this maximum (1.5 g/day), and some individuals gained over 2 g/day in both 1990 and 1991. Although it is possible that some of these measurements are in error, it is unlikely that many are, as birds were weighed with an electronic, digital readout scale under controlled conditions (not on a spring balance

Figure 6
Change in mass of adult Stilt Sandpipers captured twice, 2–15 days apart, at Little Quill Lake during autumn migration, 1991



in the wind). Furthermore, any abnormally high or low readings were verified. However, some juvenile Semipalmated Sandpipers were extremely light when captured (as low as 16.3 g, verified measurement; Table 8). Therefore, mass gains may have included unknown components of water and protein, or even structural mass, in addition to fat.

Skagen and Knopf (1994a) suggested that northbound Semipalmated and Western sandpipers staging in Kansas departed with inadequate fat reserves to enable a nonstop flight to their breeding grounds. They concluded that additional staging areas would be needed and that, in general, shorebirds migrating through interior North America required multiple staging sites. Skagen and Knopf's (1994a) flight range estimates were based on Castro and Myers' (1989) equations with a flight speed of 40–65 km/h. Even at the flight speed at the top end of this range, these estimates are likely to be conservative (Alexander 1994). Therefore, additional staging sites in central North America may not be as necessary as Skagen and Knopf (1994a) suggest, especially for individuals breeding at the southern limits of their range. At the Quill Lakes, northern-nesting species moved quickly through the area during spring migration and consequently gained little additional mass (Table 7). Some species appeared to have more than enough stored fat to fuel direct flights to northern breeding areas (Table 9), which suggests that some species acquired sufficient reserves south of the Quill Lakes. For those species, rest and maintenance of mass might be their dominant needs while in the Quill Lakes area as they move to breeding grounds as quickly as weather conditions allow. Suitable shallow-water habitat is likely abundant throughout the interior plains of North America during spring migration because of ephemeral sloughs fed by spring snowmelt (Millar 1976; Woo et al. 1993). This would reduce the dependence of shorebirds on any given staging site such as the Quill Lakes. The northern prairies and aspen parklands of Canada possibly provide the last major opportunity for shorebirds to acquire energy reserves prior to arrival on the breeding grounds.

The opposite is likely the case for southbound migrants, in that the prairies provide the first major stopover areas after departing from the breeding grounds. This could explain why individuals remained in the Quill Lakes area longer in autumn than in spring (Section 4.2.5.2) and gained mass in July and August (e.g., Hudsonian Godwits, Short-billed Dowitchers, Lesser Yellowlegs, Semipalmated Sandpipers, Stilt Sandpipers; Table 7). Also in contrast to spring, appropriate staging sites are likely to be less common during autumn migration, because many of the ephemeral sloughs present in spring have evaporated. This would concentrate birds at fewer sites and force birds to stay longer and acquire more reserves at any given staging area in order to ensure adequate stored energy for flying to the next stopover.

Presumably, the species that gained mass were depositing fat (Alexander 1994) in preparation for continued southbound migration. From estimated flight ranges, at least some Hudsonian Godwits, Lesser Yellowlegs, Red-necked Phalaropes, Semipalmated Sandpipers, and Stilt Sandpipers could fly nonstop from Saskatchewan to northern South America (Table 9). With the exception of Long-billed Dowitchers, some individuals of all other species could fly directly to the southern coasts of the United States. Long-billed Dowitchers are late migrants, and most adults captured were undergoing energetically costly flight feather moult at the Quill Lakes, as were a few Short-billed Dowitchers (no other species was in active flight feather moult).

Many species of shorebirds were observed in different numbers during spring and autumn migration (Tables 1 and 2). For some species (e.g., Semipalmated, Least, and White-rumped sandpipers, Red Knot, Sander-

Table 9
Flight range estimates of shorebirds at Little Quill Lake, Saskatchewan, calculated by the formula of Castro and Myers (1989)[a]

Species[b]	Season	Age	Final mass (g)[c]	Minimum range (km)[d]	Maximum range (km)[e]
DUNL	Spring	Adult	49.2	1541	2421
HUGO	Autumn	Adult	209.0	4886	6599
LBDO	Autumn	Adult	98.3	980	2224
LESA	Autumn	Adult	18.2	1426	2636
	Autumn	Juvenile	16.9	2062	4676
	Spring	Adult	18.1	2584	3949
LEYE	Autumn	Adult	75.1	3945	6606
	Autumn	Juvenile	72.8	2429	6056
	Spring	Adult	85.1	1176	3017
PESA	Autumn	Adult	53.8	1378	4214
	Autumn	Juvenile	51.1	728	3284
	Spring	Adult	54.0	1583	4226
RNPH	Autumn	Adult	24.5	2884	6032
SBDO	Autumn	Adult	90.2	1692	3986
	Autumn	Juvenile	81.5	2222	4498
SEPL	Autumn	Adult	42.9	823	2678
SESA	Autumn	Adult	21.5	1725	4396
	Autumn	Juvenile	16.8	4160	7425
	Spring	Adult	21.1	1894	4188
STSA	Autumn	Adult	46.4	3718	6964
	Autumn	Juvenile	44.7	1639	4922
	Spring	Adult	46.7	2097	4725
WRSA	Spring	Adult	38.3	928	2425

Note: Approximate distances from Little Quill Lake, Saskatchewan, to:
- northern South America: 6000 km
- southern coasts of the United States: 2500 km
- Mackenzie Delta coast, Northwest Territories: 2500 km
- Churchill, Manitoba: 1500 km

[a] See Methods for description of formula and discussion of flight speed.
[b] See Appendix 1 for key to four-letter species codes.
[c] Final mass = minimum mass (g) in each group with a wing length greater than or equal to the mean (M_1).
[d] Minimum range = minimum flight estimate (km), using mean mass (g) of the group as M_2. Mean mass is given in Table 8.
[e] Maximum range = maximum flight estimate (km), using maximum mass (g) of the group as M_2. Maximum mass is given in Table 8.

ling), the differences indicate that there are separate routes for northbound and southbound migrations (Morrison 1984; Harrington et al. 1991; Gratto-Trevor and Dickson 1994). This has been determined most clearly for Semipalmated Sandpipers (Gratto-Trevor and Dickson 1994). In brief, it had been hypothesized that central and western Arctic breeders migrate north through the interior of North America, whereas eastern Arctic breeders follow an Atlantic route (primarily Delaware Bay, New Jersey, and south of the Bay of Fundy). Western birds were thought to migrate back south through the interior, whereas most central and all eastern breeders presumably returned south through the Atlantic, primarily the Bay of Fundy, where sufficient shorebird prey is available only during autumn migration (Peer et al. 1986; Wilson 1989; P.W. Hicklin, pers. commun.). This would mean that migration routes of central and eastern breeders follow somewhat of an elliptical pattern, being farther east during autumn migration (Harrington and Morrison 1979; Lank 1983; Morrison 1984; Hicklin 1987). These proposed routes, including the elliptical migration of central breeders, were supported by sightings and measurements of Semipalmated Sandpipers banded at Little Quill Lake (Gratto-Trevor and Dickson 1994). Spring migrants from the Quill Lakes were seen throughout eastern Canada in the autumn, including the Bay of Fundy. Other birds captured at Little Quill Lake in the spring migrated south back through the interior, including the Quill Lakes. Southbound Semipalmated Sandpipers captured at Little Quill Lake were seen primarily in the southeastern United States during autumn migration in the same or subsequent years. Both spring and autumn migrants wintered in northern South America.

Similarly, for species in which juveniles were more common than adults at the Quill Lakes in July and August (i.e., Least and Semipalmated sandpipers), adults either migrated southwards along different routes or acquired greater energy reserves than juveniles north of the Quill Lakes, enabling them to overfly the area (Morrison 1984; Gratto-Trevor and Dickson 1994) or pause for shorter periods. The patterns of resightings of banded adult and juvenile Least Sandpipers in Tennessee (Table 5) provide strong support for the hypothesis that adults and juveniles use different routes. In some species (e.g., Hudsonian Godwits, Stilt Sandpipers, Long-billed Dowitchers), adults were much more common than juveniles, which again suggests different migration routes for adults and juveniles, although it is possible that juveniles passed through the Quill Lakes area in late September or October after the field program ended. Some yearling Least, Semipalmated, and Stilt sandpipers and Lesser Yellowlegs (i.e., birds with PPW moult) migrated north with the adults. PPW moult does not occur in most other species, so yearlings could not have been identified if they had migrated north.

5. Habitat selection by shorebirds at the Quill Lakes

5.1 Introduction

The Quill Lakes area is used by a diverse assemblage of migrating and breeding shorebirds. This diversity is likely attributable to the variety of habitats available (e.g., Colwell and Oring 1988), including temporarily flooded fields and meadows, ephemeral sloughs, open and vegetated marshes, lake shorelines with expansive dry and saturated beaches and flooded flats, and a variety of substrates dominated by sand, mud, or litter. The diversity of habitats reflects the underlying long- and short-term variations in water levels, which, along with salinity and human interventions, are among the primary factors affecting the development of vegetation (Millar 1976; Kantrud et al. 1989) and the productivity of shorebird prey in prairie wetlands (Murkin and Kadlec 1986; Neckles et al. 1990). As water depth greatly influences the accessibility of habitats to most shorebirds, the fluctuation of water levels is also a primary factor affecting the availability of shorebird habitats in prairie wetlands.

In this section, we examine the distribution of shorebirds among habitats at the Quill Lakes. First, we use similarity indices and cluster techniques to compare shorebird communities among habitats. If habitat diversity influences shorebird diversity, then shorebird species assemblages should differ among habitats. Next, we look for relations between shorebird distributions and habitat availability as influenced by water levels. Habitat availability was determined only qualitatively; therefore, we focus on broad variations in the use of lake shoreline versus marsh habitats. In one season, habitat availability could be indexed quantitatively in some lake and marsh habitats. A more rigorous use–availability analysis is presented for that season. Lastly, we examine the distribution of shorebirds in relation to wading depth and feeding methods.

5.2 Results

5.2.1 Variation of shorebird communities with location

Shorebird communities were compared among locations using cluster techniques. First, Morisita's index of similarity (Krebs 1989:305) was calculated for all location-by-year pairs (based on total counts, the sum of counts from all surveys within a season). This index is influenced by the relative abundances among species within habitats and the differences in those relative abundances between habitats, but not by absolute numbers. Total counts were used instead of peak counts because they give relatively more weight to species that have slower turnover rates and smooth out variation resulting from short-term redistributions of shorebirds among closely situated habitats. Groups of locations-by-year with greatest similarity were then chosen using average linkage clustering (Krebs 1989:316; Wilkinson et al. 1992). The following species were excluded from these analyses because they were rare: Common Snipe, Red Phalarope, Solitary Sandpiper, Spotted Sandpiper, Upland Sandpiper, and Whimbrel. Data for dowitcher species were combined. Otherwise, unidentified species of shorebirds were excluded. Red-necked Phalaropes were excluded from analyses in this section because they swam rather than waded in aquatic habitats at the Quill Lakes, making them very different from all other species examined and not necessarily subject to the same habitat constraints. Preliminary cluster analysis indicated that shorebird communities on Little Quill Lake's east and southeast shores were similar to each other but different from communities on the west shore. Therefore, Little Quill Lake's east and southeast shores were combined within years in both seasons.

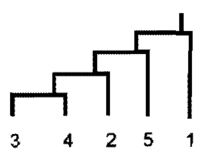
5.2.1.1 Spring migration

In general, shorebird species composition differed between the shoreline habitat of the larger lakes (Little Quill and Big Quill) and the smaller marsh habitats (Groups 2 and 4 versus Groups 1, 3, and 5; Table 10). Small northern-nesting migrants were more common on the large lake shorelines, whereas locally breeding species (American Avocet, Wilson's Phalarope, Willet, Marbled Godwit) were more common among the top 10 species in the smaller marsh habitats (e.g., Group 5). In 1993, however, Stilt, Semipalmated, and White-rumped sandpipers were the three most common species in both Group 3 (marsh basins) and Group 4 (shoreline areas of Little Quill Lake).

Little Quill Lake's west shore and Big Quill Lake (Group 2) were unique in their abundance of Sanderlings

Table 10
Relative abundance of shorebirds during spring migration at the Quill Lakes, Saskatchewan, 1990–1993. Data are percentages of total counts averaged within groups identified by cluster analysis of similarity indices (structure indicated below).

	Group 1		Group 2		Group 3		Group 4		Group 5	
	REST-92		LQW-92, 93 BQ-93		MQ, REST, JES, CAM3, 5, 6, 7-93		LQE-90, 92, 93 LQW-90 LEV-93		MQ-90, 92 JES, CAM5, 6-92	
1	PESA	46.14	SAND	39.18	STSA	44.03	SESA	32.57	AMAV	48.33
2	LEYE	11.82	SESA	26.64	SESA	23.01	STSA	17.08	WIPH	12.25
3	REKN	11.36	WRSA	7.98	WRSA	7.78	WRSA	15.04	STSA	11.85
4	DOWI	6.74	STSA	5.99	AMAV	7.56	LESA	9.17	SESA	4.82
5	WIPH	5.91	PIPL	4.89	LESA	6.70	SAND	7.74	WRSA	4.74
6	BBPL	4.55	BASA	3.44	MAGO	2.20	BBPL	3.82	LEYE	4.34
7	WILL	4.09	BBPL	2.75	BASA	1.84	BASA	2.84	MAGO	3.48
8	MAGO	3.94	REKN	2.54	WILL	1.32	AMAV	2.38	WILL	3.30
9	KILL	1.67	LESA	1.09	LEGP	1.13	REKN	1.81	PESA	1.62
10	LESA	1.14	AMAV	1.04	BBPL	1.06	PIPL	1.78	DOWI	1.20
11	SESA	0.76	MAGO	0.94	REKN	0.89	KILL	1.02	KILL	1.14
12	GRYE	0.53	LEYE	0.92	DOWI	0.71	LEGP	0.96	LESA	1.08
13	STSA	0.45	WILL	0.76	LEYE	0.55	DOWI	0.65	SAND	0.55
14	WRSA	0.45	RUTU	0.64	KILL	0.41	SEPL	0.61	BBPL	0.36
15	LEGP	0.38	SEPL	0.30	WIPH	0.41	PESA	0.45	BASA	0.29
16	DUNL	0.08	LEGP	0.28	SAND	0.14	WILL	0.40	GRYE	0.25
17	AMAV	0.00	PESA	0.20	SEPL	0.11	DUNL	0.37	REKN	0.19
18	BASA	0.00	KILL	0.12	PESA	0.05	RUTU	0.31	LEGP	0.09
19	BBSA	0.00	DOWI	0.12	DUNL	0.03	MAGO	0.30	DUNL	0.04
20	HUGO	0.00	DUNL	0.10	HUGO	0.03	LEYE	0.28	HUGO	0.04
21	PIPL	0.00	HUGO	0.07	RUTU	0.02	WIPH	0.26	RUTU	0.03
22	RUTU	0.00	WIPH	0.02	PIPL	0.01	HUGO	0.13	PIPL	0.00
23	SAND	0.00	BBSA	0.00	BBSA	0.00	BBSA	0.00	SEPL	0.00
24	SEPL	0.00	GRYE	0.00	GRYE	0.00	GRYE	0.00	BBSA	0.00



Locations: BQ = Big Quill Lake; CAM = Campbell Segment; JES = Jesmer; LEV = Level Project; LQE = Little Quill Lake's east and southeast shores; LQW = Little Quill Lake's west shore; MQ = Middle Quill Lake; REST = Little Quill Restriction.

See Appendix 1 for key to four-letter codes.

Group numbers increase with decreasing internal similarity.

and Piping Plovers. The plovers were most common at Big Quill Lake. There, however, 44% of all sightings were unidentified small and medium-sized shorebirds, which were excluded from the analysis. This lake was difficult to survey because its broad and soft alkali flats were often impassable. Therefore, the lake's species composition might have been biased towards species that used the upper beach or were easier to identify, both of which would apply to Piping Plovers.

5.2.1.2 Autumn migration

In most cases, the species compositions on large lake shorelines and smaller marsh habitats differed (Table 11). The exceptions were Little Quill Lake's east and southeast shores in 1989 and 1990 (Groups 6 and 3, respectively). Group 3 contained only three marsh habitats and was most similar to Group 7, which contained only lake shoreline. Semipalmated and Stilt sandpipers were the most common species in Groups 3 and 7. Dowitchers, Stilt Sandpipers, and Lesser Yellowlegs were the three most common types of shorebirds in Groups 4 and 6, which included most of the smaller marsh habitats (14 out of 20). Unlike during spring migration, there was no evidence that locally breeding species were more prevalent among the top 10 species in marsh habitats.

Middle Quill Lake in 1989 and 1991 (Group 2) comprised the only group in which Hudsonian Godwits were the most common species, although they were among the top five species at Little Quill Lake's west shore in 1989 and 1990 (Group 5), Little Quill Restriction in 1989 and 1991, Milligan in 1989, Little Quill Lake's east and southeast shores in 1991, and Campbell Segment 7 in 1992 (apparent in the data prior to clustering). Hudsonian Godwits were considerably less common in Middle Quill Lake in 1992 (1.7% of total observations) than they were in 1989 and 1991.

5.2.2 Shorebird distribution and abundance in relation to habitat availability

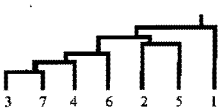
In this section, proportions of total counts rather than actual counts are used to compensate for differences in frequency and number of surveys conducted among years. Data for 1990 were excluded from this analysis because only Little Quill Lake was surveyed that year.

5.2.2.1 Water level fluctuations and habitat availability

Water levels fluctuated considerably in all basins over the course of this study (Fig. 7; Appendix 2). Most basins were below their full supply levels (FSL), except during spring 1990. Milligan Creek Project, Little Quill Restriction, and Jesmer Project were above or near their FSL more often than other basins. These areas have the

Table 11
Relative abundance of shorebirds during autumn migration at the Quill Lakes, Saskatchewan, 1989–1992. Data are percentages of total counts averaged within groups identified by cluster analysis of similarity indices (structure indicated below).

	Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Group 7	
	CAM6-91		MQ-89, 91		LQE-90 CAM2-89, 91 CAM6-89		MQ-92 REST-89, 90 MILL-89 CAM2-92		LQW-89, 90		LQE-89 REST-91, 92 JES-91, 92 CAM7-89, 91, 92 CAM5, 6-92		LQE-91, 92 LQW-91, 92	
1	AMAV	72.07	HUGO	46.08	SESA	29.39	STSA	46.21	SAND	32.57	DOWI	54.87	SESA	17.43
2	LEYE	6.55	LEYE	12.64	STSA	22.84	LEYE	16.15	SESA	22.47	STSA	14.09	STSA	14.60
3	DOWI	5.38	STSA	11.88	DOWI	19.65	DOWI	8.83	LEYE	11.07	LEYE	10.30	LEYE	12.69
4	BASA	5.07	SESA	10.78	AMAV	11.87	SESA	8.17	HUGO	8.39	AMAV	7.77	LESA	10.55
5	SESA	3.51	MAGO	4.61	LEYE	4.57	LESA	5.05	SEPL	4.76	SESA	3.39	SEPL	9.55
6	WILL	2.81	LESA	2.74	LESA	3.02	HUGO	3.37	STSA	4.29	HUGO	2.74	AMAV	8.55
7	WIPH	1.33	AMAV	2.73	HUGO	2.94	PESA	2.26	MAGO	2.72	LESA	1.47	HUGO	7.59
8	LESA	0.94	BASA	2.10	BASA	2.76	WIPH	2.04	WILL	2.61	PESA	1.20	BASA	6.22
9	HUGO	0.94	SAND	1.60	SEPL	0.74	SEPL	1.95	BBPL	2.20	WIPH	0.96	WILL	2.40
10	PESA	0.62	DOWI	1.55	WIPH	0.57	MAGO	1.34	BASA	1.83	BASA	0.89	SAND	2.13
11	GRYE	0.31	BBPL	1.14	MAGO	0.45	BASA	1.32	LESA	1.53	MAGO	0.79	DOWI	1.77
12	MAGO	0.23	SEPL	0.79	KILL	0.36	AMAV	1.24	PIPL	1.32	KILL	0.55	KILL	1.41
13	STSA	0.23	KILL	0.37	PESA	0.33	KILL	0.71	AMAV	1.20	GRYE	0.39	BBPL	1.28
14	LEGP	0.00	WRSA	0.32	WILL	0.26	GRYE	0.62	KILL	0.93	SEPL	0.27	MAGO	1.25
15	SEPL	0.00	WILL	0.27	BBPL	0.08	WILL	0.59	PESA	0.55	WILL	0.24	BBSA	0.69
16	KILL	0.00	GRYE	0.10	GRYE	0.07	BBPL	0.13	REKN	0.47	BBPL	0.05	GRYE	0.51
17	PIPL	0.00	WIPH	0.10	SAND	0.05	PIPL	0.01	GRYE	0.31	BBSA	0.01	PIPL	0.50
18	REKN	0.00	PESA	0.09	PIPL	0.01	LEGP	0.00	WIPH	0.27	SAND	0.01	PESA	0.40
19	WRSA	0.00	REKN	0.05	RUTU	0.01	BBSA	0.00	DOWI	0.23	LEGP	0.00	WIPH	0.30
20	BBSA	0.00	LEGP	0.03	BBSA	0.01	DUNL	0.00	RUTU	0.21	DUNL	0.00	RUTU	0.08
21	BBPL	0.00	PIPL	0.02	REKN	0.00	REKN	0.00	WRSA	0.04	PIPL	0.00	REKN	0.06
22	DUNL	0.00	BBSA	0.01	LEGP	0.00	RUTU	0.00	BBSA	0.03	REKN	0.00	LEGP	0.02
23	RUTU	0.00	DUNL	0.00	DUNL	0.00	SAND	0.00	LEGP	0.01	RUTU	0.00	DUNL	0.00
24	SAND	0.00	RUTU	0.00	WRSA	0.00	WRSA	0.00	DUNL	0.00	WRSA	0.00	WRSA	0.00



Locations: CAM = Campbell Segment; JES = Jesmer; LQE = Little Quill Lake's east and southeast shores; LQW = Little Quill Lake's west shore; MILL = Milligan; MQ = Middle Quill Lake; REST = Little Quill Restriction.

See Appendix 1 for key to four-letter species codes.

Group numbers increase with decreasing internal similarity.

highest input from precipitation throughout the Little Quill Lake watershed. Milligan Creek Project and Little Quill Restriction were shallowest in 1989 and had abundant shorebird habitat, although by mid-August they were dry. In all subsequent years, Milligan was too deep for shorebirds. Little Quill Restriction was too deep for shorebirds in spring 1990 and 1992, but it had some shallow water by August of those years, particularly among openings in the emergent vegetation along the south and west perimeter. Shallow-water habitat was abundant in Little Quill Restriction during July and August of 1991. Some shallow water was also available in spring 1991 and 1993. Jesmer, which receives water from Milligan, had little shorebird habitat when the water level was higher than 518.4 m asl.

Water levels declined at Little Quill Lake from May to September each year, except 1993 (Appendix 2). With Little Quill Lake's shallow gradient, the small drop in water level between 1990 and 1993 and the within-season decreases caused large horizontal changes in the shoreline. The waterline also shifted by as much as 100 m in response to the wind. In general, Little Quill Lake usually provided abundant shallow-water habitat and exposed, wet, unvegetated beach.

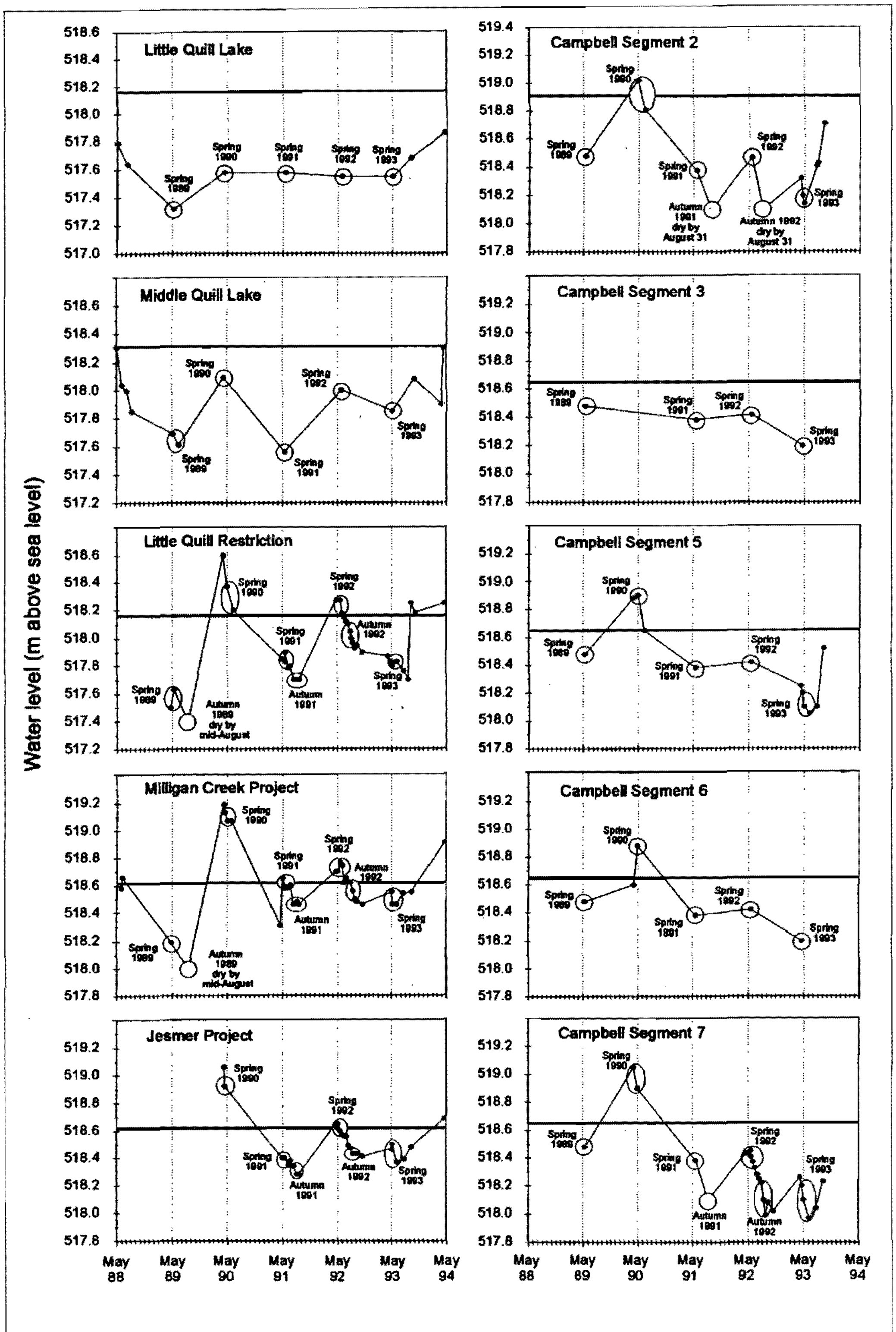
Middle Quill Lake's east shoreline has roughly three zones affecting the availability of shorebird habitat: a narrow (<100 m) beach; a narrower (<50 m) band of emergent vegetation (the north end has no beach, just emergent vegetation); and open water, which deepens to several decimetres close to the band of emergents. When the water is high, shallow pools occur on the beach and in openings among the emergent vegetation. As the water drops, there is a period when the beach dries while the open-water area remains too deep for shorebirds. This occurred in 1990, 1992, and 1993. In 1991, and probably also in 1989, there was shallow water available in the open-water zone.

Most of the Campbell Project basins were often too deep for wading shorebirds beyond the first couple of metres out from the shore and had little in the way of saturated substrates suitable for the smallest species. Segments 2 and 6 were most likely to have shallowly flooded or wet substrates, and a large part of the north end of Segment 7 was shallow during July and August of 1991 and 1992. Segment 4 had virtually no habitat suitable for shorebirds and was not surveyed during this study.

5.2.2.2 Spring migration

In 1992, 84% of all sightings of shorebirds were made on Little Quill Lake (Table 12). In 1993, only 69% of sightings were made on Little Quill Lake. Among other basins, the biggest increase in sightings from 1992 to 1993 occurred at the Campbell Project basins. The difference between years was greatest for small and medium-sized northern migrants, which were also more numerous in

Figure 7
Water levels at lakes and marshes around Little Quill Lake between 1988 and 1994. Circle with dot = actual reading; circle without dot = no reading, plotted for illustration only. Black horizontal line indicates full supply level.



1993 than in 1992 (Tables 1 and 12). Water levels were lower during spring in 1993 than in 1992 (Fig. 7). Therefore, shallow-water habitat was more available in the smaller basins in 1993. The abundance of local breeders changed little between years, but their distribution changed as they made greater use of Jesmer Project when water was lower in 1993.

Table 12
Distribution of shorebirds (percentages of total counts and mean number of birds per survey) at the Quill Lakes, Saskatchewan, during spring migration, 1992 and 1993

	Similar-looking northern migrants		Other northern migrants		Local breeders	
	1992	1993	1992	1993	1992	1993
	Baird's Sandpiper		Black-bellied Plover		American Avocet	
Little Quill Lake	95.5	87.3	97.7	81.9	20.4	11.8
Campbell Projects	3.8	8.3	0.1	1.7	31.3	23.3
Jesmer Project	0.0	1.0	0.0	0.0	8.5	44.4
Little Quill Restriction	0.0	1.2	1.3	9.4	0.0	1.2
Middle Quill Lake	0.7	2.1	0.9	7.0	39.8	19.2
No. of birds per survey	32	504	532	210	294	314
	Least Sandpiper		Dowitchers		Killdeer	
Little Quill Lake	98.7	79.0	57.5	25.3	50.2	16.5
Campbell Projects	0.4	4.5	7.3	12.9	12.4	24.5
Jesmer Project	0.0	6.8	0.0	33.8	1.0	18.7
Little Quill Restriction	0.2	0.6	14.8	26.7	9.6	5.8
Middle Quill Lake	0.7	9.1	20.4	1.3	26.8	34.5
No. of birds per survey	767	1 656	67	28	23	17
	Pectoral Sandpiper		Lesser Yellowlegs		Marbled Godwit	
Little Quill Lake	25.2	75.3	4.1	15.4	32.4	33.8
Campbell Projects	0.3	8.2	2.9	18.5	14.0	28.6
Jesmer Project	0.0	9.6	13.2	41.2	4.8	4.1
Little Quill Restriction	49.5	5.5	35.4	4.6	12.2	0.7
Middle Quill Lake	25.0	1.4	44.4	20.4	36.6	32.8
No. of birds per survey	137	9	49	33	37	76
	Sanderling		Lesser Golden-Plover		Piping Plover	
Little Quill Lake	98.2	99.7	97.7	57.6	100.0	91.2
Campbell Projects	0.9	0.1	0.3	39.7	0.0	0.0
Jesmer Project	0.0	0.0	0.0	0.0	0.0	0.0
Little Quill Restriction	0.0	0.2	0.4	0.0	0.0	0.0
Middle Quill Lake	0.9	0.0	1.6	2.7	0.0	8.8
No. of birds per survey	378	1 390	131	60	6	4
	Semipalmated Sandpiper		Red-necked Phalarope		Willet	
Little Quill Lake	96.0	75.7	58.5	51.4	30.8	14.2
Campbell Projects	1.8	15.1	21.9	44.9	6.1	18.0
Jesmer Project	0.0	0.8	0.0	1.8	3.1	11.6
Little Quill Restriction	0.1	4.2	0.1	0.6	12.2	4.6
Middle Quill Lake	2.1	4.2	19.4	1.2	47.9	51.6
No. of birds per survey	1 446	2 959	1 024	1 014	47	49
	Stilt Sandpiper		Red Knot		Wilson's Phalarope	
Little Quill Lake	80.3	49.6	89.2	86.9	5.1	11.0
Campbell Projects	3.1	27.3	0.6	0.0	24.2	41.3
Jesmer Project	0.0	8.8	0.0	0.0	8.4	23.9
Little Quill Restriction	0.1	6.4	8.7	0.1	8.6	13.8
Middle Quill Lake	16.6	7.8	1.5	13.0	53.7	10.1
No. of birds per survey	505	3 527	192	362	65	14
	White-rumped Sandpiper		Ruddy Turnstone			
Little Quill Lake	83.8	71.1	99.5	91.5		
Campbell Projects	5.8	24.8	0.5	0.0		
Jesmer Project	0.0	1.0	0.0	0.0		
Little Quill Restriction	0.3	1.8	0.0	4.9		
Middle Quill Lake	10.2	1.2	0.0	3.7		
No. of birds per survey	227	1 102	42	10		
	Dunlin		Semipalmated Plover			
Little Quill Lake	99.0	87.2	100.0	88.1		
Campbell Projects	0.7	4.3	0.0	4.0		
Jesmer Project	0.0	1.1	0.0	7.3		
Little Quill Restriction	0.2	2.1	0.0	0.3		
Middle Quill Lake	0.0	5.3	0.0	0.3		
No. of birds per survey	45	12	75	44		
	Sum of above plus unidentified small–medium-sized shorebirds		Sum of above plus PHAL, PLOV, and unlisted others		Sum of above	
Little Quill Lake	92.4	71.9	73.0	62.6	22.7	16.4
Campbell Projects	1.4	15.2	11.8	28.1	25.1	24.0
Jesmer Project	<0.1	4.1	0.3	2.5	7.2	32.7
Little Quill Restriction	1.7	3.4	3.0	2.0	3.8	2.0
Middle Quill Lake	4.5	5.4	11.9	4.7	41.1	25.0
No. of birds per survey	6 433	12 231	2 286	1 766	472	474
			All shorebirds			
Little Quill Lake			84.0	68.9		
Campbell Projects			5.2	17.1		
Jesmer Project			0.5	4.8		
Little Quill Restriction			2.1	3.2		
Middle Quill Lake			8.2	6.0		
No. of birds per survey			9 192	14 471		

5.2.2.3 Autumn migration

Of the 20 species considered in detail (Table 13), 11 were most abundant in 1989 and least abundant in either 1991 or 1992 (excluding 1990; Table 1). The overall trends from 1989 to 1992 were as follows: 1) a decrease in abundance; 2) an increase in use of Little Quill Lake shoreline; and 3) a corresponding decrease in use of the smaller basins. The overall trends occurred in each category of shorebird (i.e., subtotals in Table 13) and for each of the seven most abundant species except dowitchers, which used Little Quill Lake's shoreline less than other species. In general, there was decreasing availability of shallow-water habitat in the smaller basins from 1989 to 1992, especially in Milligan, Little Quill Restriction, and Middle Quill Lake (Fig. 7). Hudsonian Godwits appeared to be particularly responsive to water levels in Milligan, Little Quill Restriction, and Middle Quill Lake, because their numbers remained high as long as shallow-water habitat was available in one of these marshes.

Red-necked Phalaropes followed the overall pattern of increasing use of Little Quill Lake between 1989 and 1992. They were seen most often at Milligan in 1989 and Little Quill Restriction in 1991, which suggests that even this species, which swims rather than wades, derived some benefit from the shallow waters in the marsh basins.

Least Sandpipers, Semipalmated Plovers, Killdeers, and Willets increased in number from 1989 to 1992. These species were recorded most often on Little Quill Lake each year, which suggests that they were less influenced than other species by the availability of shallow-water habitat in the marshes.

5.2.2.4 Use–availability analysis: autumn migration 1991

From July to September 1991, the water level in Little Quill Restriction was low and shorebird habitat was distributed relatively linearly along the edge of the open-water zone. This was also the case along Little Quill Lake's shoreline, but not in other basins in 1991 or in other years. Therefore, shoreline length was used as an index of habitat availability for that season: 4.4 km on Little Quill Lake's west shore, 6.7 km on Little Quill Lake's east and southeast shores, and 3.8 km on Little Quill Restriction. Shorebird "selection and avoidance" of the three habitats were assessed using Bailey's continuity-corrected confidence intervals (Cherry 1996). "Selection" of a habitat is implied when the proportion of the total count of birds (± the simultaneous 99% confidence interval) exceeds what is expected based on the amount of habitat available. A high confidence interval was used to reduce the influence of lack of independence of individual sightings of birds arising from the tendency in some species to flock. Differences among locations in the breadth of suitable habitat would bias the habitat availability indices. Dry or saturated foreshore substrates were more extensive on Little Quill Lake than in Little Quill Restriction. Little Quill Lake will appear more selected than it actually was by species that forage in such habitats. Such differences were not as apparent with shallow-water habitat.

Eight of 20 species were more common than expected on Little Quill Restriction and less common than expected on Little Quill Lake (Table 14). The other 12 species were more common than expected on Little Quill Lake shoreline. In general, species that usually forage on beaches or at the waterline "selected" Little Quill Lake's shorelines and "avoided" Little Quill Restriction, whereas species that probed and fed in deeper water "selected" the marsh habitat over the lakeshore habitat (see also Sections 5.2.3 and 5.2.4).

5.2.3 Shorebird distribution in relation to wading depth

At the Quill Lakes, most Red-necked Phalaropes and some Wilson's Phalaropes swam while feeding (Fig. 8). American Avocets were the only other shorebirds observed swimming. Some species (e.g., dowitchers, Hudsonian Godwits, Stilt Sandpipers) fed mostly while wading, often in water above their tarsus. Other species (e.g., plovers, Ruddy Turnstones, Buff-breasted Sandpipers) fed rarely on flooded substrates. For most species, there were no discernible differences in water depths used between habitats (lake versus marsh) or seasons (spring versus autumn migration). The clearest exceptions were Pectoral and Semipalmated sandpipers, which fed in deeper water when in marsh habitats than when in lakeshore habitats, and dowitchers, which fed in deeper water during autumn migration.

5.2.4 Shorebird distribution in relation to feeding method

In general, shorebirds that fed mostly by pecking were observed more commonly on Little Quill Lake than were shorebirds that fed mostly by probing (Tables 15 and 16). The pattern occurred during both spring and autumn migrations and in all years, although both types of shorebirds were more common on Little Quill Lake in spring than in autumn. In addition, probers made greater use of deeper water, whereas peckers made greater use of shallow water or unflooded substrates.

5.3 Discussion

Complex wetlands with a mixture of lakes, marshes, sloughs, meadows, and fields provide greater habitat diversity and resilience under varying hydrological conditions (Skagen and Knopf 1994b). At Last Mountain Lake, complex wetlands were used by a greater number and variety of shorebirds than were simple basins (Colwell and Oring 1988; Colwell 1991). At the Quill Lakes, shorebird species composition differed among habitat types (i.e., among Little Quill Lake sandy versus muddy shorelines, Big Quill Lake, and the adjacent smaller marsh basins; Tables 10 and 11), reflecting the connection between shorebird species diversity and habitat diversity.

In general, the availability of shallow water within the smaller lakes and marshes affected both the amount and diversity of shorebird habitat, which in turn affected the number and distribution of shorebirds. Within seasons, fewer shorebirds overall used the Little Quill Lake area when water levels were high (i.e., during spring migration in 1992 and during autumn migration in 1991 and 1992; Tables 12 and 13). In addition, when water levels were high, proportionally fewer shorebirds used the marsh

Table 13
Distribution of shorebirds (percentages of total counts and mean number of birds per survey) at the Quill Lakes, Saskatchewan, during autumn migration, 1989–1992

	Similar-looking northern migrants			Other northern migrants			Local breeders		
	1989	1991	1992	1989	1991	1992	1989	1991	1992
	Baird's Sandpiper			Black-bellied Plover			American Avocet		
Little Quill Lake	52.8	50.1	75.1	67.5	78.4	84.6	7.7	25.8	82.2
Campbell Projects	13.1	22.3	18.5	1.1	0.4	0.0	59.1	29.6	14.9
Jesmer–Milligan Project	24.2	3.3	3.9	1.2	6.5	0.0	24.1	1.2	0.6
Little Quill Restriction	4.7	11.1	0.7	0.0	2.9	0.0	0.7	42.4	0.4
Middle Quill Lake	5.2	13.3	1.9	30.2	11.8	15.4	8.4	0.9	1.8
No. of birds per survey	208	141	79	46	24	19	455	228	201
	Least Sandpiper			Buff-breasted Sandpiper			Killdeer		
Little Quill Lake	67.9	41.0	75.1	97.8	98.6	96.3	41.5	75.3	57.3
Campbell Projects	9.0	26.3	20.7	0.0	0.0	3.8	7.9	5.5	14.1
Jesmer–Milligan Project	15.6	6.4	0.7	2.2	0.0	0.0	14.1	5.9	0.5
Little Quill Restriction	3.9	11.2	0.0	0.0	0.0	0.0	25.0	1.8	1.3
Middle Quill Lake	3.6	15.2	3.5	0.0	1.4	0.0	11.5	11.5	26.8
No. of birds per survey	156	213	276	6	7	6	21	25	47
	Pectoral Sandpiper			Dowitchers			Marbled Godwit		
Little Quill Lake	22.0	12.1	10.6	11.6	1.5	3.2	19.4	23.5	30.0
Campbell Projects	6.2	11.6	15.6	34.9	18.1	35.5	0.2	5.9	26.2
Jesmer–Milligan Project	66.8	57.2	18.1	52.9	24.7	30.0	36.6	1.9	7.9
Little Quill Restriction	3.8	17.8	14.8	0.4	54.1	27.6	3.0	39.5	4.1
Middle Quill Lake	1.0	1.3	40.8	0.3	1.5	3.8	40.8	29.2	31.8
No. of birds per survey	60	45	46	1 117	1 203	1 330	99	88	47
	Sanderling			Greater Yellowlegs			Piping Plover		
Little Quill Lake	88.0	88.2	98.7	31.7	56.9	28.2	88.6	100.0	100.0
Campbell Projects	0.0	0.0	1.3	4.5	10.0	14.6	0.0	0.0	0.0
Jesmer–Milligan Project	0.0	0.0	0.0	43.3	15.0	11.4	9.2	0.0	0.0
Little Quill Restriction	0.0	4.3	0.0	11.2	16.5	15.2	0.0	0.0	0.0
Middle Quill Lake	12.0	7.5	0.0	9.4	1.5	30.6	2.2	0.0	0.0
No. of birds per survey	183	23	6	14	13	28	12	7	3
	Semipalmated Sandpiper			Hudsonian Godwit			Willet		
Little Quill Lake	28.5	46.0	82.5	26.0	15.0	73.0	74.0	75.8	77.9
Campbell Projects	25.3	29.8	10.6	1.6	0.3	18.6	4.3	9.3	5.2
Jesmer–Milligan Project	33.6	2.9	0.2	33.5	0.1	0.3	3.6	1.7	0.3
Little Quill Restriction	7.9	8.6	0.4	6.4	35.0	3.2	6.0	7.5	1.0
Middle Quill Lake	4.7	12.7	6.4	32.5	49.7	5.0	12.1	5.7	15.7
No. of birds per survey	1 771	556	147	927	709	154	18	32	61
	Stilt Sandpiper			Lesser Yellowlegs			Wilson's Phalarope		
Little Quill Lake	3.1	14.5	37.5	17.5	28.0	42.3	11.0	9.6	15.9
Campbell Projects	10.0	24.2	29.4	5.1	13.8	19.9	30.0	18.1	32.4
Jesmer–Milligan Project	56.8	19.1	4.1	38.8	22.5	8.1	35.0	14.9	7.7
Little Quill Restriction	27.6	30.7	5.4	25.5	23.9	9.9	17.0	54.7	17.7
Middle Quill Lake	2.5	11.4	23.6	13.1	11.9	19.7	7.0	2.8	26.3
No. of birds per survey	2 836	848	606	1 039	400	587	13	20	34
				Red-necked Phalarope					
Little Quill Lake				3.4	37.0	62.6			
Campbell Projects				27.6	10.4	36.1			
Jesmer–Milligan Project				39.3	0.4	0.5			
Little Quill Restriction				20.6	47.9	0.3			
Middle Quill Lake				9.0	4.4	0.6			
No. of birds per survey				2 461	1 422	1 283			
				Semipalmated Plover					
Little Quill Lake				90.4	69.4	80.2			
Campbell Projects				0.1	5.1	4.1			
Jesmer–Milligan Project				7.4	13.3	0.0			
Little Quill Restriction				0.4	3.0	0.0			
Middle Quill Lake				1.6	9.2	15.6			
No. of birds per survey				151	94	187			
	Sum of above plus unidentified small–medium-sized shorebirds			Sum of above plus PHAL, PLOV, and unlisted others			Sum of above plus unlisted local breeders		
Little Quill Lake	17.4	31.3	55.0	13.3	22.3	38.6	14.2	32.8	66.3
Campbell Projects	16.6	25.4	24.1	18.5	11.1	30.3	44.7	20.3	16.2
Jesmer–Milligan Project	41.5	12.4	3.2	37.1	10.6	12.7	25.1	2.4	2.1
Little Quill Restriction	16.9	19.5	4.8	13.6	43.4	12.2	2.4	36.3	2.7
Middle Quill Lake	7.5	11.4	12.9	17.6	12.7	6.2	13.7	8.2	12.7
No. of birds per survey	6 152	2 027	1 679	6 173	3 873	3 599	618	401	396
				All shorebirds					
Little Quill Lake				15.3	25.9	44.9			
Campbell Projects				18.8	16.3	27.4			
Jesmer–Milligan Project				38.6	10.7	9.4			
Little Quill Restriction				14.6	35.2	9.6			
Middle Quill Lake				12.7	12.0	8.7			
No. of birds per survey				12 949	6 300	5 759			

Table 14
Shorebird habitat selection at Little Quill Restriction (REST) and Little Quill Lake (east and southeast shores LQE, west shore LQW) during autumn migration, 1991

	Species that selected Restriction					Species that avoided Restriction				
Location[a]	Species	N[b]	Exp.[c]	CI[d]	S/A[e]	Species	N	Exp.	CI	S/A
REST	Dowitcher	9378	2467	0.964–0.974	S	Black-bellied	11	98	0.009–0.062	A
LQE		275	4351	0.024–0.034	A	Plover	297	173	0.703–0.831	S
LQW		22	2857	0.001–0.004	A		76	113	0.141–0.262	A
REST	Hudsonian	3428	1313	0.646–0.685	S	Killdeer	8	39	0.012–0.124	A
LQE	Godwit	1533	2315	0.279–0.317	A		128	69	0.725–0.909	S
LQW		187	1520	0.029–0.045	A		17	45	0.047–0.200	A
REST	Lesser	1507	722	0.504–0.560	S	Least	434	541	0.179–0.231	A
LQE	Yellowlegs	993	1273	0.324–0.377	A	Sandpiper	1272	955	0.567–0.630	S
LQW		330	836	0.099–0.135	A		417	627	0.171–0.223	A
REST	Marbled	540	206	0.616–0.714	S	Red-necked	2005	2511	0.192–0.216	A
LQE	Godwit	252	364	0.264–0.360	A	Phalarope	5485	4427	0.542–0.572	S
LQW		17	239	0.009–0.040	A		2355	2907	0.227–0.252	A
REST	Wilson's	151	46	0.743–0.910	S	Semipalmated	863	1275	0.157–0.189	A
LQE	Phalarope	26	80	0.075–0.234	A	Sandpiper	2807	2249	0.540–0.582	S
LQW		2	53	0.000–0.054	A		1331	1477	0.248–0.285	A
REST	American	1136	466	0.587–0.654	S	Willet	26	95	0.036–0.116	A
LQE	Avocet	564	822	0.277–0.341	A		262	167	0.628–0.769	S
LQW		129	540	0.054–0.090	A		84	110	0.164–0.293	A
REST	Stilt	3472	1432	0.599–0.637	S	Greater	37	44	0.128–0.314	—
LQE	Sandpiper	1823	2525	0.306–0.343	A	Yellowlegs	119	78	0.571–0.782	S
LQW		321	1658	0.048–0.067	A		17	51	0.041–0.178	A
REST	Pectoral	150	64	0.504–0.689	S	Semipalmated	56	286	0.032–0.071	A
LQE	Sandpiper	83	112	0.246–0.424	A	Plover	552	505	0.447–0.535	—
LQW		16	74	0.026–0.121	A		515	332	0.414–0.502	S
REST						Baird's	300	390	0.167–0.227	A
LQE						Sandpiper	670	688	0.400–0.475	—
LQW							560	452	0.330–0.403	S
REST						Buff-breasted	0	32	0.000–0.044	A
LQE						Sandpiper	45	57	0.230–0.482	—
LQW							82	38	0.505–0.759	S
REST						Piping Plover	0	23	0.000–0.061	A
LQE							46	41	0.342–0.653	—
LQW							45	27	0.332–0.642	S
REST						Sanderling	20	110	0.021–0.083	A
LQE							69	193	0.111–0.217	A
LQW							341	127	0.728–0.845	S

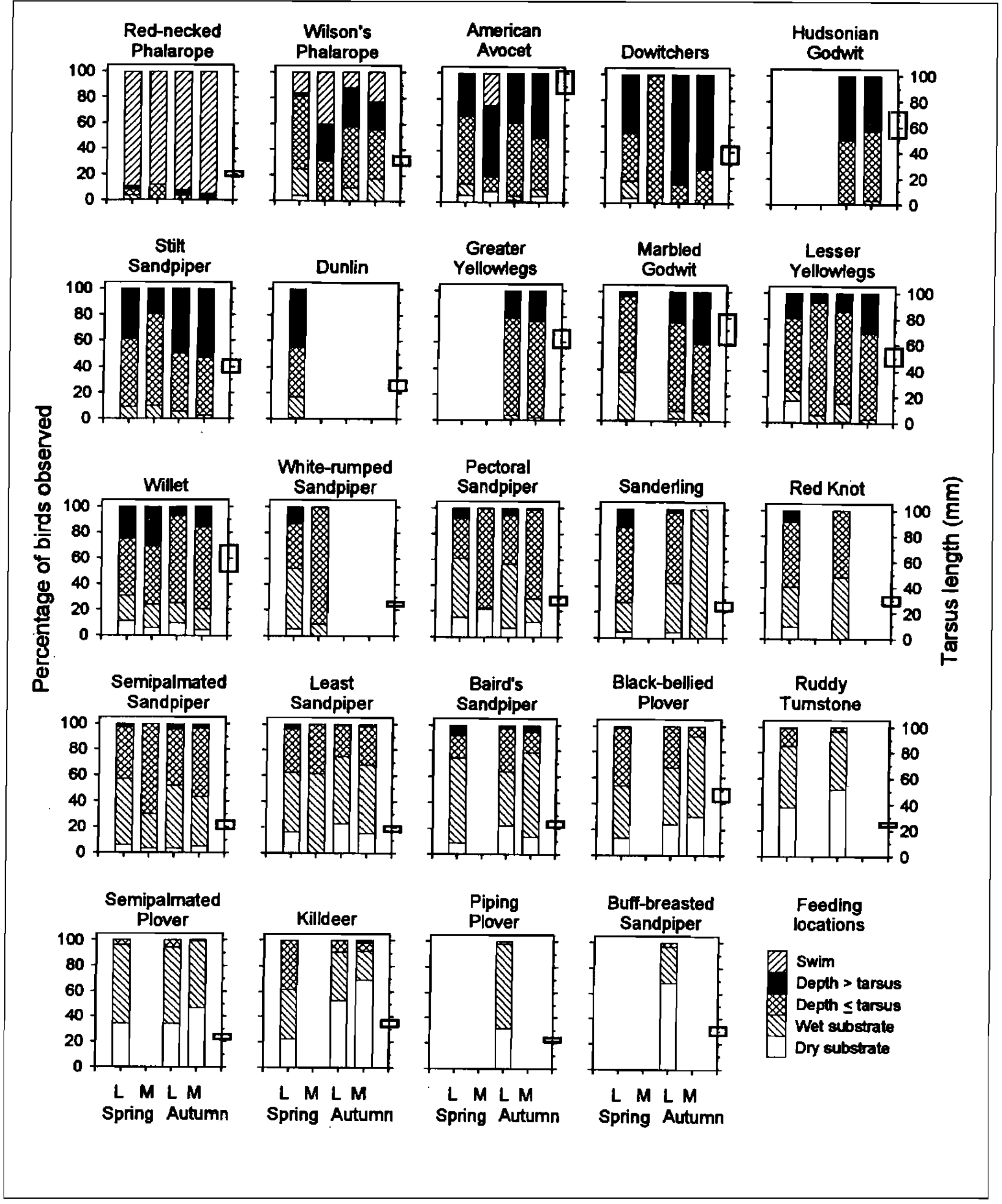
[a] Distance covered (km): REST 3.8; LQE 6.7; LQW 4.4.
[b] Total number observed during 18 surveys, 11 July to 6 September 1991.
[c] Expected number of birds based on habitat availability.
[d] Simultaneous 99% confidence intervals. All goodness-of-fit tests, $P < 0.001$.
[e] Expected relative distribution (P_i) is based on relative shoreline length: REST 0.255; LQE 0.450; LQW 0.295. Selection or avoidance was determined by comparing expected relative distribution to the corresponding simultaneous confidence intervals: P_i < CI indicates selection (S); P_i > CI indicates avoidance (A); P_i = CI indicates neither selection nor avoidance (—).

basins while more used Little Quill Lake's shoreline. In this respect, Little Quill Lake was used more than the marsh basins during spring migration (higher water) compared with autumn migration (lower water); during spring 1992 (higher water) compared with spring 1993 (lower water); and, in decreasing order, during autumn migration 1992 (highest water), 1991 (lower water), and 1989 (lowest water). Similar changes in diversity and abundance of shorebirds in response to changes in habitat availability were observed at Last Mountain Lake, although in an opposite situation, in which habitat became limited through wetland desiccation (Colwell 1991). The Quill Lakes and Last Mountain Lake studies demonstrate that migrant shorebirds select habitats that are neither excessively wet nor dry.

In spring, the locally breeding species were more prevalent in the shorebird communities at the smaller lakes and marshes than on Little Quill Lake (Table 10), although northern breeders were usually more abundant than local breeders at all locations. Colwell and Oring (1988) also found differences in habitat use between local breeders and northern migrants at Last Mountain Lake, but there the differences were related primarily to a greater use of upland habitats by local breeders for breeding activities. They also noted that, as reproductive activities subsided, local breeders used upland areas less and wetland areas more.

The abundance and distribution of probing and pecking shorebirds followed the general patterns outlined above. In all cases, however, probing shorebirds made less

Figure 8
Distribution of feeding shorebirds in relation to water depth and substrate moisture at Little Quill Lake (L) and surrounding marshes (M) during spring and autumn migrations. Boxes on right axes indicate range of tarsus lengths given by Marchant et al. (1986). Data are mean percentages across years: spring L = 1990, 1992; spring M = 1992; autumn L & M = 1990, 1991, 1992.



use of Little Quill Lake than did pecking shorebirds (Table 15). Stilt Sandpipers and Hudsonian Godwits, species for which there are serious conservation concerns, appeared to be particularly influenced by the availability of habitat in the marsh basins (Tables 12 and 13). Both species were most common and made more use of marsh basins when water levels were low. Dowitchers and Marbled Godwits were usually most common in the marsh basins regardless of water levels. Probers tended to wade more deeply (relative to their own size) than did peckers, which indicates greater tolerance of relatively deeper water (Table 16).

The apparent selection for marsh habitats shown by probing shorebirds was likely related to prey abundance and substrate penetrability. During July and August, prey biomass (i.e., chironomid larvae and Sago Pondweed tubers) was higher in the marshes (Little Quill Restriction, Middle Quill Lake) than in Little Quill Lake (Alexander 1994). Hudsonian Godwits, for example, ate mostly Sago Pondweed tubers, which grew in lusher, more productive stands in Little Quill Restriction and Middle Quill Lake than in the shallow, accessible parts of Little Quill Lake. Hudsonian Godwit numbers were lowest in the Little Quill Lake area when those marsh basins were too deep.

The marshes also tended to have softer substrates than Little Quill Lake's shoreline, although there was considerable variability within locations (Alexander 1994). Substrate type and penetrability affect the ability of

Table 15
Distribution of shorebirds in relation to primary feeding method[a] (mean percentages of total counts and mean number of birds per survey) during spring and autumn migrations at the Quill Lakes, Saskatchewan, 1989–1993

	Spring		Autumn		
	1992	1993	1989	1991	1992
Probing shorebirds[b]					
Little Quill Lake	48.8	46.0	16.4	13.3	30.9
Campbell Projects	6.2	19.3	10.6	12.0	25.1
Jesmer–Milligan Project	1.2	14.1	49.3	20.6	12.1
Little Quill Restriction	19.2	9.8	8.3	35.4	11.0
Middle Quill Lake	24.6	10.8	15.4	18.6	21.0
No. of birds per survey	746	3639	5040	2893	2182
Pecking shorebirds[c]					
Little Quill Lake	82.7	69.6	62.2	67.3	74.8
Campbell Projects	2.4	10.9	5.9	10.2	9.4
Jesmer–Milligan Project	1.1	6.0	16.1	6.5	2.1
Little Quill Restriction	4.6	2.7	7.1	7.6	2.4
Middle Quill Lake	9.2	10.9	8.8	8.5	11.3
No. of birds per survey	3991	8411	3623	1533	1445

[a] Feeding methods are given in Table 16.
[b] Marbled and Hudsonian godwits, Pectoral and Stilt sandpipers, and dowitchers.
[c] Baird's, Least, Semipalmated, White-rumped, and Buff-breasted sandpipers, Sanderlings, Dunlins, Black-bellied, Semipalmated, and Piping plovers, Lesser Golden-Plovers, Lesser and Greater yellowlegs, Red Knots, Ruddy Turnstones, Killdeers, and Willets.

shorebirds to probe and detect prey (Myers et al. 1980; Quammen 1982; Kelsey and Hassall 1989; Mouritsen and Jensen 1992). Probe depth and the probability of detecting prey increase with increasing substrate softness. Soft substrates also reduce the energy required to probe down to (Grant 1984) and extract prey, although energy spent walking might increase if the substrates are too soft (Goss-Custard et al. 1992). Substrate penetrability might be particularly important to godwits, because their primary prey (tubers) are buried more deeply than other species' primary prey (chironomid larvae) (Alexander 1994). Therefore, the marsh basins, when shallow, probably provided better habitat (greater prey biomass, softer substrates) than Little Quill Lake for species that probe flooded substrates.

Most of the species that pecked while feeding (e.g., excluding yellowlegs) used either unflooded substrates or shallower water than the probers (Fig. 8). Little Quill Lake was used more by pecking shorebirds than were the other locations (Table 15), probably because it provided more unflooded or very shallowly flooded (i.e., <20 mm) substrates than did the marshes. In addition, substrate penetrability would have been less important in relation to prey capture for peckers than for probers. Prey availability within the shallow habitat that was available in the

Table 16
Summary of feeding locations and feeding methods of shorebirds observed at the Quill Lakes, Saskatchewan

		Feeding location[b]				Feeding method[c]			
Species	Lake vs. marsh[a]	Dry	Film	Shallow flood	Deep flood	Peck	Probe	Grab	Sweep
Local breeders									
Piping Plover	⊙	●	●			●		○	
Killdeer	○	●	●	○		●		○	
Willet	○	⊙	○	●	○	●	○		
Marbled Godwit	●		○	●	●	○	●	○	
Wilson's Phalarope	●		⊙	●	●	○		●	
American Avocet	●	⊙	⊙	●	●				●
Northern migrants									
Buff-breasted Sandpiper	⊙	●	○	⊙		●		○	
Semipalmated Plover	⊙	●	●	⊙		●		○	
Ruddy Turnstone	–	●	●	⊙		●	○	○	
Baird's Sandpiper	⊙	○	●	○	⊙	●	○		
Black-bellied Plover	○	○	●	●		●		○	
Lesser Golden-Plover	–	○	●	●		●		○	
Least Sandpiper	○	○	●	●	⊙	●			
Pectoral Sandpiper	●	○	●	●	⊙	●	●	○	
Red Knot	–	⊙	●	●	⊙	●	○		
Sanderling	⊙	⊙	●	●	⊙	●		○	
Semipalmated Sandpiper	○	⊙	●	●	⊙	●	○	○	
White-rumped Sandpiper	–	⊙	○	●	⊙	●	○		
Lesser Yellowlegs	●	⊙	⊙	●	○	●		○	
Greater Yellowlegs	○			●	○	●		○	
Dunlin	–		○	●	●	●	●		
Stilt Sandpiper	●		⊙	●	●	●	●	○	
Dowitchers	●		⊙	●	●	○	●		
Hudsonian Godwit	●			●	●	○	●	○	
Red-necked Phalarope	○			⊙	●	○		●	

[a] Lake vs. marsh = results of use–availability analysis (summarized from Table 14): "selected" = counts were higher than expected based on amount of habitat available; ⊙ = Little Quill Lake's west shore (muddy sand) "selected"; ○ = Little Quill Lake's east and southeast shores (sandy mud) "selected"; ● = Little Quill Restriction (marsh) "selected"; dash = insufficient data.
[b] Feeding locations (summarized from Fig. 8): Film = saturated substrate, ≈0–3 mm standing water; Shallow flood = depths less than tarsus; Deep flood = depths up to maximum leg length (≈1.3 max. tarsus length). ● = most used location; ○ = second-most used; ⊙ = least used.
[c] Feeding methods (Baker and Baker 1973; Lewis 1983; SAA, pers. obs.): Peck = insert bill <¼ length; Probe = insert bill >¼ length; Grab = pluck prey from substrate surface or water column; Sweep = lateral movement of bill through water. ● = primary method; ○ = secondary method.

marshes would, however, have been higher than on the lakeshore (Alexander 1994). In limited habitat, shorebird densities might increase to the point at which interference among individuals would decrease foraging rates, thus countering the advantages of higher prey densities (Goss-Custard 1980). Prey availability for species that foraged on exposed shoreline was not examined at the Quill Lakes. The impact on prey availability of wind-induced changes in location of shorelines, which were considerably more pronounced on the large lakes, was also not examined quantitatively, but patterns were discernible from casual observations: water movement upslope deposited prey on upper beaches (sometimes in great abundance) or created temporary shallow areas with current-transported prey, whereas water movement downslope exposed potentially productive areas that would otherwise have been inaccessible.

6. Conclusions

The Quill Lakes area is an important stopover for shorebirds that migrate through the interior of North America, in terms of both absolute numbers using the area and the availability of suitable foraging habitats under most climatic conditions, but particularly in drought years. As noted above, there appear to be only two other sites with comparable shorebird use in the Canadian prairies or northern prairies of the United States (Harrington and Perry 1995; Morrison et al. 1995). The Quill Lakes area provides habitat and resources for numerous species of shorebirds to rest, moult, or acquire energy for continued migration and possibly breeding. The collection of shorebirds present at the Quill Lakes differs between spring and autumn migrations in terms of species and age composition and, in some cases, geographic segments of a species' population.

The Quill Lakes area owes much of its value to its diversity of habitats and to the relative permanence of the lakes. The lakes provide a base of more consistently available habitat relative to the surrounding basins. It is difficult to assess the importance to shorebird populations of open-marsh habitat in the smaller basins relative to lakeshore habitat in the larger lakes. Therefore, it is difficult to predict the impact of the loss of shorebird habitat in the marshes through either excessive flooding or desiccation (natural or induced). It was beyond the scope of this study to determine where shorebirds went during years when water levels were high around Little Quill Lake. Furthermore, we did not assess the impact of differences in habitat availability on shorebird body condition or life history parameters. However, rates of mass gain, although variable, were sometimes extremely high, suggesting high food availability in some years and locations (see Sections 4.2.7 and 4.3).

Skagen and Knopf (1993) suggested that "shorebird movements across the [interior] plains [of North America] are characterized by dispersion and opportunism rather than by concentration and predictability." It is possible that little shorebird habitat would be available at Little Quill Lake or its marshes if water levels increased to the high levels encountered in the mid-1980s and late 1970s or earlier (Whiting 1977; Appendix 2). However, with drought conditions predicted to occur more often as a result of global warming (Woo 1992), low water conditions should be more common in the future. In wet years, there would likely be more shorebird habitat available throughout the prairies and so temporarily less dependence on large wetland complexes such as Little Quill Lake and its surrounding marshes. Smaller, reflooded sloughs usually have high rates of invertebrate production (Murkin and Kadlec 1986; Neckles et al. 1990) and therefore might be preferred shorebird habitat in wet years. In the interior plains of North America, where wetland conditions are so variable from year to year, large complexes presumably function most importantly as refuges during drought years, such as were encountered during this study. Then, shallow-water habitat would be most available in the marshes around Little Quill Lake, in the very years when they would be most important to shorebirds.

With continued destruction of small prairie wetlands and drier prairie conditions anticipated as a result of global warming, it will be increasingly important for wetland managers to ensure that the Quill Lakes area and other relatively large and potentially permanent prairie wetland complexes continue to provide habitat suitable for staging shorebirds. The Quill Lakes complex was designated as a Ramsar site in 1987, was designated an International Reserve in the WHSRN in 1994, and was listed in the WHSRN Piping Plover Registry in 1993 (Morrison et al. 1995), which provides some protection through international recognition.

The Quill Lakes area is also used for staging by tens to hundreds of thousands of migrating ducks, geese, and Sandhill Cranes *Grus canadensis*. Consequently, numerous impoundment and water diversion projects have been undertaken to benefit waterfowl. Management strategies sensitive to the needs of both shorebirds and waterfowl are needed for the Quill Lakes and other prairie wetlands. Recommendations specifically for the management of the Quill Lakes and associated marshes for the benefit of shorebirds have been prepared by Alexander (1995). He concludes that the Quill Lakes marshes are regulated more by existing climatic and hydrological conditions than by human water management activities, but some limited drawdown and flooding activities may be necessary to ensure appropriate water conditions and to control excess vegetative growth.

More general recommendations for the management of habitat for staging shorebirds in the Canadian prairies are as follows:

1. Wetland basins should provide shallow-water habitat (0.1–12 cm) during spring (mid-May to early June) and autumn (early July to early September) migration periods.

2. As most species prefer to feed in areas lacking standing vegetation, drawdowns and/or flooding may be necessary to reduce vegetation in the shallow-water zone.

3. Natural fluctuation in water levels should be maintained as much as possible. Most migrant shorebirds feed on small aquatic invertebrates or plant (Sago Pondweed) tubers, which are apparently most productive under variable water conditions.

4. If a series of wetland basins are maintained with variable water levels, some suitable habitat is likely to be available at all times, especially if human-made wetland basins are created with gradually sloping sides. As prairie-staging shorebirds have historically encountered variable habitat conditions within and between years and across areas, habitat can be managed on a regional basis (Skagen and Knopf 1993).

5. More shorebirds appear to stage in the prairies during spring compared with autumn migration, although autumn migrants spend more time in the prairies than do spring migrants. More shallow-water habitat is usually available in the spring, whereas ephemeral wetlands are generally dry by fall migration. Therefore, it may be most necessary to actively manage wetland basins for autumn migrants. Many shorebirds migrating through the prairies in the fall apparently breed in Alaska or the western Canadian Arctic (Gratto-Trevor and Dickson 1994; Haig et al. 1997; this study). Many spring migrants do not migrate south through the prairies but breed in the central Arctic and migrate through eastern Canada (including the Maritimes) in the fall.

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Appendices

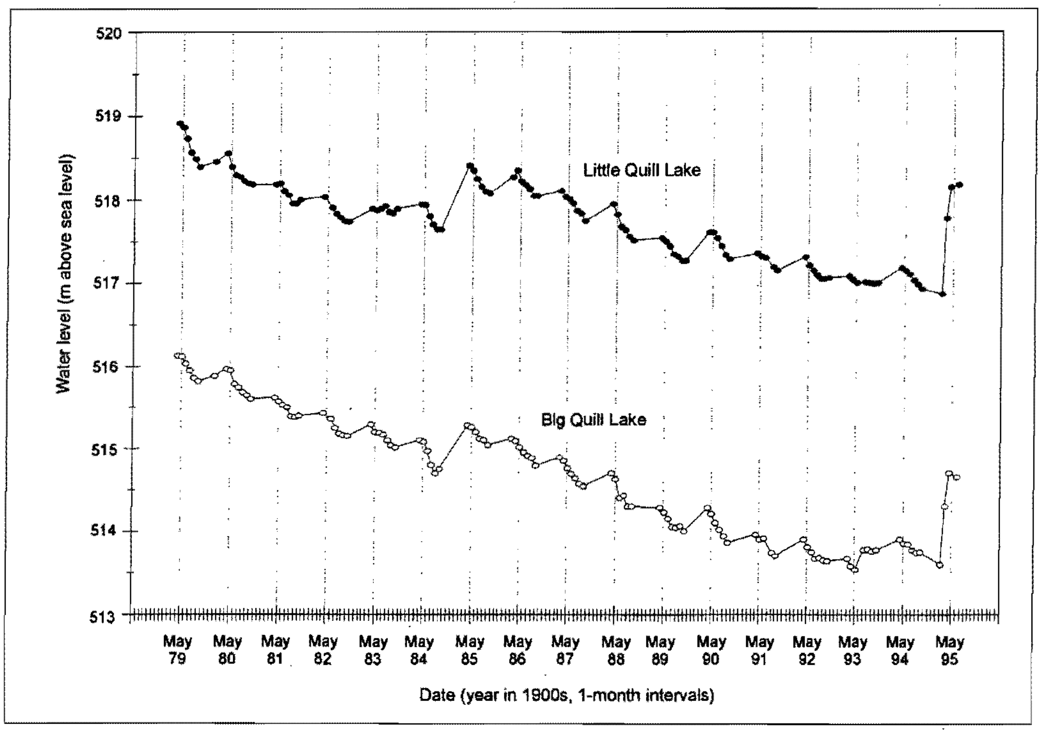
Appendix 1
Scientific names and four-letter codes for shorebirds observed at the Quill Lakes, Saskatchewan

Common name[a]	Scientific name	Four-letter code
Local breeders		
Piping Plover	*Charadrius melodus*	PIPL
Killdeer	*C. vociferus*	KILL
American Avocet	*Recurvirostra americana*	AMAV
Willet	*Catoptrophorus semipalmatus*	WILL
Spotted Sandpiper	*Actitis macularia*	SPSA
Upland Sandpiper	*Bartramia longicauda*	UPSA
Marbled Godwit	*Limosa fedoa*	MAGO
Common Snipe	*Gallinago gallinago*	COSN
Wilson's Phalarope	*Phalaropus tricolor*	WIPH
Migrants		
Black-bellied Plover	*Pluvialis squatarola*	BBPL
Lesser Golden-Plover	*P. dominica*	LEGP
Semipalmated Plover	*Charadrius semipalmatus*	SEPL
Greater Yellowlegs	*Tringa melanoleuca*	GRYE
Lesser Yellowlegs	*T. flavipes*	LEYE
Solitary Sandpiper	*T. solitaria*	SOSA
Whimbrel	*Numenius phaeopus*	WHIM
Hudsonian Godwit	*Limosa haemastica*	HUGO
Ruddy Turnstone	*Arenaria interpres*	RUTU
Red Knot	*Calidris canutus*	REKN
Sanderling	*C. alba*	SAND
Semipalmated Sandpiper	*C. pusilla*	SESA
Least Sandpiper	*C. minutilla*	LESA
White-rumped Sandpiper	*C. fuscicollis*	WRSA
Baird's Sandpiper	*C. bairdii*	BASA
Pectoral Sandpiper	*C. melanotos*	PESA
Dunlin	*C. alpina*	DUNL
Stilt Sandpiper	*C. himantopus*	STSA
Buff-breasted Sandpiper	*Tryngites subruficollis*	BBSA
Short-billed Dowitcher	*Limnodromus griseus*	SBDO
Long-billed Dowitcher	*L. scolopaceus*	LBDO
Red-necked Phalarope	*Phalaropus lobatus*	RNPH
Red Phalarope	*P. fulicaria*	REPH
Shorebird groups		
SBDO, LBDO		DOWI
HUGO, MAGO		GODW
RNPH, WIPH		PHAL
BBPL, LEGP		PLOV
BBPL, LEGP, AMAV, GRYE, WILL, WHIM, HUGO, MAGO		SHLA
SESA, LESA		SHLS
LEYE, RUTU, REKN, PESA, DUNL, STSA, BBSA, DOWI		SHME
SESA, LESA, WRSA, BASA		SHSM
SHME, SHSM		SHOT
GRYE, LEYE		YELL

[a] Nomenclature follows Godfrey (1986).

Appendix 2

Water level changes at Little Quill Lake and Big Quill Lake from 1979 to 1995 (data from Saskatchewan Water Corporation)



Appendix 3

Differences in morphometrics between males and females in seven species of shorebirds at the Quill Lakes, Saskatchewan

Differences in morphometrics of known males and females were determined in species that were collected for other studies (Table A). In all species examined (Hudsonian Godwits, Long and Short-billed dowitchers, Least Sandpipers, Marbled Godwits, Stilt Sandpipers, Semipalmated Sandpipers), female measurements averaged slightly larger than those of males. A greater proportion of these birds could be identified to sex correctly on the basis of bill length compared with wing or tarsus length (Table B).

Table A

Measurements of male and female shorebirds collected at Little Quill Lake, Saskatchewan, 1990–1992

			Wing length (mm)					Bill length (mm)					Tarsus length (mm)				
Species[a]	Season	Sex	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.
HUGO	Autumn	F	13	226.1	4.3	221	235	13	85.6	3.3	80.2	93.7	13	65.0	3.3	57.6	70.0
		M	14	216.9	3.0	212	222	14	74.2	3.5	67.7	78.8	14	59.6	2.0	56.5	64.4
LBDO	Autumn	F	17	153.8	2.2	150	158	17	72.3	3.5	63.1	77.4	17	43.9	2.0	38.8	46.3
		M	17	148.5	2.5	145	154	18	62.4	2.9	57.0	66.8	18	40.5	1.8	37.2	45.4
LESA	Autumn	F	4	91.5	2.1	89	94	4	19.2	0.8	18.3	20.1	3	20.8	0.8	20.2	21.7
		M	4	93.2	2.6	91	97	4	18.3	1.0	17.5	19.7	3	20.9	0.9	20.0	21.7
MAGO	Autumn	F	13	241.9	6.5	229	249	13	103.7	12.1	83.6	119.0	13	76.6	3.8	69.5	82.0
		M	12	235.1	7.7	225	251	12	88.8	11.4	73.9	110.9	12	74.2	2.9	67.8	78.2
SBDO	Autumn	F	1	153.0	–	–	–	1	67.6	–	–	–	1	42.2	–	–	–
		M	4	147.5	1.3	146	149	4	57.1	1.9	55.6	59.6	4	37.7	0.8	37.0	38.8
SESA	Autumn	F	12	97.8	2.2	93	102	12	18.9	1.0	18.1	21.2	11	22.8	0.9	21.5	24.1
		M	8	96.5	1.8	95	100	8	17.6	0.6	16.7	18.5	7	22.4	0.6	21.4	23.3
	Spring	F	5	100.0	2.3	97	102	5	20.0	0.6	19.0	20.6	5	23.1	1.2	21.4	24.6
		M	8	96.9	2.4	95	101	8	18.1	0.9	16.7	19.1	8	21.8	0.8	20.4	22.7
STSA	Autumn	F	13	137.3	3.1	132	142	13	41.5	1.5	38.1	44.4	12	45.0	2.3	40.6	48.7
		M	17	133.2	2.4	129	138	17	39.5	1.9	34.9	42.5	17	42.8	1.4	40.5	45.9

[a] See Appendix 1 for key to four-letter species codes.

(cont'd)

Appendix 3 (*cont'd*)

Table B

Relative accuracy of three body measurements in determining sex of birds previously sexed by examination of internal organs (SAS Linear Discriminant Analysis)

				% correctly sexed[b]			
Species[a]	Season	No. of females	No. of males	Wing length	Bill length	Tarsus length	Combined lengths
HUGO	Autumn	13	14	93	100	89	100
LBDO	Autumn	17	17	79	94	86	94
MAGO	Autumn	13	12	72	76	68	80
SESA	Autumn	12	8	67	75	56	79
	Spring	5	8	68	84	84	84
STSA	Autumn	13	17	72	81	75	80

[a] See Appendix 1 for key to four-letter species codes.

[b] Results are given as percentages of correctly sexed birds using only wing length, only bill length, only tarsus length, and wing, bill, and tarsus lengths combined. As the same individuals were used to generate and test the discriminant function, the percentages of correctly sexed birds are biased and valid only in comparison with each other.

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