05-025 W

ILLINOIS
DEPARTMENT OF
NATURAL
RESOURCES

ILLINOIS
NATURAL
HISTORY
SURVEY

Tim Kelley
Illinois Department of Natural Resources
700 S. 10th Street
Havana, IL 62644

9 March 2005

Dear Tim,

As per our recent messages, I am sending copies of three manuscripts written by Gabe Hamer (et al.) that resulted from research supported in part by a grant for $1000 from the Illinois Wildlife Preservation Fund. Please consider the manuscripts as our final report on the project titled "Shorebird predation on benthic invertebrates."

Gabe completed all the proposed research on schedule and finished his MS degree in December. He has moved on to a PhD program in Michigan. The three manuscripts are excerpted from his MS thesis, and all recognize the support from the Wildlife Preservation Fund and IDNR in the acknowledgements. If these manuscripts get published in professional journals, as we hope, we will send reprints to IDNR for your records as well.

Thank you for your support of this project. Although the amount in dollars was modest, such support helps graduate students immensely and I hope you will be pleased with the work accomplished. We hope the study has provided some data that will be useful for management and conservation as well as ecologically interesting.

Sincerely,

Edward J Heske

Dr. Edward J. Heske
Director, Center for Wildlife
and Plant Ecology

RECEIVED
MAR 24 2005
FEDERAL AID

607 East Peabody Drive, Champaign, Illinois 61820-6970 USA
(217) 333-6880 Fax (217) 333-4949
http://www.inhs.uiuc.edu

8 February 2004

Corresponding Author: Gabriel L. Hamer, Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources, East Lansing, Michigan 48824, USA Phone: (517) 355-6463 ext. 1596; E-mail: ghamer@msu.edu

Shorebird use of a wetland complex – Hamer et al.

Migrant shorebird use of a wetland complex in the Illinois River valley

Gabriel L. Hamer, Edward J. Heske, Jeffrey D. Brawn, and Patrick W. Brown

Address for Gabriel L. Hamer: Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, USA; Present address: Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Bldg., East Lansing, MI 48824; e-mail: ghamer@msu.edu

Address for Edward J. Heske: Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, USA.

Address for Jeffrey D. Brawn: Department of Natural Resources and Environmental Sciences, and Department of Animal Biology, University of Illinois, Shelford Vivarium, 606 E Healey, Champaign, Illinois 61820, USA.

Address for Patrick W. Brown: Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, USA; Present address: Michigan Natural Features Inventory, Michigan State University Extension, P.O. Box 30444 Lansing, MI 48909, USA.

Abstract

We assessed shorebird use of a wetland complex along the Illinois River during the spring and summer/fall migrations of 2003 and spring migration of 2004. Twenty four species of shorebirds and over 150,000 shorebird use-days were recorded. The spring migration in both years peaked in early-May and the fall migration peaked in early-August, however the migration chronology at each site was variable. Differing levels of river connectivity and management decisions played a role in the variable hydrology regimes at the 4 study sites. Wetland impoundments with greater connectivity to the Illinois river were vulnerable to flood events, resulting in sporadic shorebird use. Management at impoundments with more protection from flood events produced more consistent habitat for shorebirds. Management of stopover sites for shorebirds should aim to provide diverse habitat with available alternative sites in the case that traditional habitat is lost to floods or droughts. These results will aid wetland management and restoration efforts in the Mississippi Alluvial Valley to improve conservation efforts of interior migrating shorebirds.

Key words: connectivity, Illinois River, habitat use, shorebirds, wetland complex

Introduction

Many species of North American shorebirds (*Charadriiformes*) rely on mid-continental wetlands for replenishing fuel to complete their transcontinental migration. Unlike the predictable coastal stopover locations, the unpredictable nature of freshwater wetlands forces shorebirds migrating through the interior flyway to adopt flexible and opportunistic migration strategies (Skagen 1997). Migration surveys suggest many populations of Nearctic-breeding shorebirds are declining (Brown et al. 2001, Morrison et al. 2001), and migration stopover habitat may be limiting these populations (Harrington et al., 2002).

The Western Hemisphere Shorebird Reserve Network (WHSRN) was founded in 1986 to protect migratory shorebirds through conservation of key habitats (Harrington and Perry 1995). WHSRN and partner organizations have protected over 8 million hectares of the most critical shorebird habitat across the Americas (Harrington et al. 2002). This organization has made great contributions to shorebird conservation on a hemispheric scale. However, the designation of critical habitat used by WHSRN gives priority to single sites that receive heavy migratory and wintering use (Haig et al. 1998). Shorebirds migrating through the interior flyway are dispersed across a shifting mosaic of wetland complexes (Skagen and Knopf 1994), and a more comprehensive multi-site habitat designation may be warranted to identify wetland complexes that have significant conservation value (Farmer and Parent 1997).

Migrating shorebirds in the Illinois River valley exploit a highly degraded watershed. The establishment of drainage and levee districts in the early 1900's reduced the space for flow and increased flood stages (Havera and Bellrose 1985). The conversion of the Illinois River watershed from prairie to agriculture has increased runoff and sedimentation in the river (Havera 1999). The historic Illinois landscape dominated by wet-prairie has been displaced, and shorebird conservation efforts rely on appropriate management and wetland restoration to meet the needs of migratory shorebirds. Data is needed on how wetland connectivity to a river and management practices such as water level manipulations affect the quality of these sites as stopover areas for migrating shorebirds. Accordingly, we initiated an observational study at a wetland complex in the Illinois River valley to assess shorebird habitat use in relation to: (*i*) differing levels of wetland connectivity and (*ii*) differing management strategies.

Methods

The study was conducted on 4 field sites that are part of a large wetland complex along the Illinois River in west-central Illinois (Fig. 1). The floodplain wetlands include backwater lakes, sloughs, and marshes that are federally- or state-managed. Two field sites managed by the U.S. Fish and Wildlife Service (USFWS) include Chautauqua National Wildlife Refuge (NWR) (40°38'N, 89°99'W) and Emiquon NWR (40°32'N, 90°09'W). Chautauqua NWR was established in 1936 and contains 1,816 ha of large backwater lakes and bottomland and upland forest, and is located about 5 miles NNE of Havana, Illinois. Chautauqua has been designated as a stopover of international importance by the WHSRN (Harrington and Perry 1995). The management strategy of a late draw-down in July and August creates extensive shallow water mudflats that attract an estimated 100,000 to 250,000 shorebirds each fall (Bailey 2003). Comparatively little shorebird habitat is available at Chautauqua in the spring. During the spring, water levels are managed to remain elevated to prevent encroachment from the invasive species black willow (*Salix nigra*) and cocklebur (*Xanthium strumarium*) which interfere with moist soil plant production. Efforts to manage for shorebirds are also challenged by occasional floodwaters from the Illinois River that breach the levees of the refuge, and the threat of avian botulism from stagnant pools of water left after the draw-down.

Emiquon NWR is a 856 ha refuge comprised of backwater lakes, sloughs, forested wetlands, and a variety of other terrestrial habitats. Due to the recent acquisition of Emiquon NWR by the USFWS in 1993, much of the refuge is newly-established wetland and portions will remain in agriculture until leases with private landowners cease. The refuge is divided into two main units: the South Globe and the Wilder Tract. The Wilder Tract was taken out of agriculture production in 1998 and remains in moist-soil management (a practice which encourages native wetland plant germination). The South Globe unit was taken out of agricultural production for the first time in 2004, at which time the corn and bean stubble was flooded to create extensive shallow water habitat.

Two additional field sites include Rice Lake State Fish and Wildlife Area (SFWA) (40°48'N, 89°90'W) and Banner Marsh SFWA (40°53'N, 89°85'W), managed by the Illinois Department of Natural Resources. The initial 959 ha land purchase of Rice Lake SFWA occurred in 1945, and included a large bottomland lake just up river from Chautauqua. More recent land acquisitions increased the total land area to 2,290 ha. Most shorebird use of Rice Lake during 2003 and 2004 occurred at impoundments managed for waterfowl, and these impoundments have little protection from floodwaters. Banner Marsh SFWA is a 1,766 ha site that was acquired during the 1980s. The land was stripped for coal between 1956 and 1973, creating many lakes and marshes of various sizes and depth that exist today.

We censused shorebirds during the spring and summer/fall migration in 2003 (17 March to 14 November) and the spring migration in 2004 (28 February to 25 June). During the main portion (2 months) of the migrations, we censused twice per week; we censused once per week outside of this time period. We counted shorebirds along survey routes by vehicle or foot using 8x42 binoculars and a 15-45x scope. Only portions of the sites with suitable shorebird habitat, determined by the presence of shallow water and mudflats, were censused. As the location of the habitat changed with fluctuating hydrology, the survey route changed. When difficult access prevented the identification of some species, the small *Calidris* sandpipers were grouped as "peeps" and Long-billed and Short-billed Dowitchers were grouped as "dowitchers". Shorebird use-days were calculated by multiplying the mean number of individuals of a species observed on two consecutive censuses by the number of days between those counts (Rundle and Fredrickson 1981). We calculated the density of shorebirds per 100 ha, to account for the changes in amount of habitat between migrations. We delineated available shorebird habitat at each site during each season on a Digital Orthophoto Quadrangle to estimate total shorebird habitat. We then used the editor toolbar in ArcGIS 8.1 to create a polygon to estimate total area of shorebird habitat.

Results

Twenty-four shorebird species were observed during the study. The wetland complex provided over 150,000 shorebird use-days during the study, with individual species of shorebirds ranging from 10 to 38,171 use-days. Spring migration peaked in early-May in 2003 (109 shorebird use-days/100ha) and 2004 (688 shorebird use-days/100ha) and in early-August in 2003 (1014 shorebird use-days/100ha) (Fig. 2). The most frequently observed species (>26,500 use-days) were Lesser Yellowlegs, Pectoral Sandpipers, Killdeer, and ‘peeps’; together, these species comprised greater than 80% of the total shorebirds censused. The migration chronology for all the shorebirds showed high variation among sites and between years (Fig. 3 and 4).

Emiquon NWR had the most variation between years. In 2003, the Wilder Tract had very little water and shorebird use during early-spring, and the first flood of the Illinois River in May quickly elevated the water level into emergent vegetation, principally native smartweed species (Polygonaceae). Water levels remained stable for most of the summer/fall migration and quickly evaporated by late September. During the first year of the study, the South Globe remained in agricultural production and Killdeer were the only shorebird species observed using the unit. The availability of shorebird habitat at Emiquon changed dramatically from the spring of 2003 to 2004. The Illinois River flooded in March in 2004, two months earlier than the previous year, and allowed USFWS staff to elevate water levels in the Wilder Tract by opening water control structures. Because staff had mowed the entire unit in February 2004, the flood water that entered Wilder Tract provided shorebirds access to mudflats with less than 25% vegetation cover, an amount recommended by Helmers (1992). The South Globe was taken out of agricultural production for the first time in 2004. Instead of planting crops, the corn stubble was flooded in spring and instead of pumping water out of the unit as in previous years, FWS staff pumped water in. Shorebird use-days at Emiquon during the spring migration increased from 2,458 in 2003 to 16,691 in 2004.

There was relatively little variation in shorebird use-days between years at Chautauqua. Management in the South Pool is constrained by invasive vegetation (black willow, *Salix nigra* and cocklebur, *Xanthium strumarium*) and water levels are managed to remain elevated throughout the spring. Unfortunately, this provided very little shorebird habitat. In mid-summer when river levels receded, refuge staff opened water control structures and slowly lowered water levels. The gradual drawdown (5 to 7 cm/week) provided continuous availability of food resources, and allowed Chautauqua to receive over 100,000 shorebird use-days during the summer/fall migration in 2003.

Rice Lake SFWA is the site with the highest level of river connectivity and was the most vulnerable to the flood waters of the Illinois River. During both years of the study, water levels on the main body of water at Rice Lake remained elevated and the area received little shorebird use. Most of the shorebirds observed at Rice Lake occurred in the impoundments managed for walk-in duck hunting. When the river flooded, water levels in the impoundments rose quickly and offered shallow water habitat, but for only a short time. Likewise, when floodwaters that submerged impoundments began to recede, shorebird habitat was available, but only for a week or two. In 2004, the main impoundment at Rice Lake began to recede from flood waters in early May, and 1,384 shorebirds of 9 species were observed using the impoundment in one day; the window of opportunity for shorebird habitat in early May was about 10 days.

The site with the most protection from the river is Banner Marsh SFWA. The deep strip mine lakes at Banner Marsh have stable water levels throughout the year and offer little habitat to shorebirds. Site employees drained one pond during the construction of impoundments in 2003 and 2004; the resulting receding water was the location for most of the limited shorebird use occurring at the site.

Discussion

Shorebird use of this wetland complex revealed the contribution of river connectivity and water level regimes. Wetlands in the Mississippi Alluvial Valley (MAV) provide unpredictable wetland habitat, yielding spatially and temporally variable shorebird use of this stopover habitat. As the distance between wetlands decreases and the proportion of the landscape composed of wetlands increases, shorebirds make more inter-wetland movements (Farmer and Parent 1997). The close proximity of our 4 study sites suggests that shorebirds had the opportunity to sample all of the sites. Thus, differences in shorebird use of these sites likely reflect the amount and quality of stopover habitat. The availability of foraging microhabitat at each study site was a function of topography, river connectivity, precipitation, and management practices by site personnel.

The shorebird migration chronology of a site unprotected from the river, such as Rice Lake SFWA, shows short peaks of shorebird use followed by periods of very little use. The opportunistic shorebirds have the remarkable ability to exploit newly exposed invertebrate resources. However, sites with more protection (i.e. higher levees) from the river provided more consistent shorebird use and greater overall shorebird use-days per unit area.

Although wetland management is challenged by river flood events, unpredictable precipitation, and invasive species; management decisions play one of the largest factors in the availability of shorebird habitat. Changes in management decisions at Emiquon NWR resulted in shorebird use during the spring of 2004 to be over 6 times that of the previous year.

Because of the dynamic and unpredictable nature of interior wetlands such as this MAV wetland complex, migrant shorebirds in the interior flyway show site fidelity to larger wetland complexes rather than to particular wetlands (Skagen and Knopf 1994). Thus, interpreting shorebird counts at single stopover locations alone can bias the conclusions about migration chronology and provide misleading directions for management efforts. The abundance of habitat and shorebirds at Chautauqua NWR during the summer/fall migration creates a migration chronology with a summer/fall peak about 11 times the magnitude of the spring migration. As Chautauqua NWR is a representative of Illinois stopover locations, this disproportion might be misinterpreted by scientists studying shorebird migration systems in concluding that shorebirds bypass Illinois in the spring. This view would not consider that present management can detract from habitat availability in the spring.

Management recommendations

Many factors must be considered for management of interior wetlands, and management strategies are not universally effective across time and space. Recent emphasis has been placed on providing resources for a broad group of wildlife with an integrated approach to wetland management (Laubhan and Fredrickson 1993, Erwin 2002). This approach emphasizes wetland management at the landscape scale. Management should not rely on meeting all wildlife needs at individual wetlands, but should integrate and exploit the diverse characteristics provided by an entire wetland complex. Thus, managers of different areas need to cooperate to assure the needs of diverse flora and fauna are met.

One objective for shorebird management in the MAV is to provide sufficient stopover habitat for rest and refueling during the spring and summer/fall migration. Foraging microhabitat for 10 species representing 3 shorebird guilds had an average water depth of 2.3 cm, slope of 1.5 °, distance to the nearest woody vegetation of 54 meters, and percent vegetation of 20% (Hamer 2004). However, shorebird species vary in their foraging microhabitat, migration chronology, and diurnal activity. Species-specific management for high priority species, such as the Greater Yellowlegs and Short-billed Dowitcher in the Upper Mississippi Valley/Great Lakes Region, should attempt to assure specific microhabitats used for foraging by these species (Brown et al. 2001).

Most shorebirds migrate through the MAV during the spring from mid-April to late-May and during the summer/fall in late-July to early-September. Each impoundment does not need to meet shorebird habitat requirements during each migration. Instead, using coordinated strategies across multiple sites will increase the availability of appropriate habitat to migrating shorebirds. Many factors influence what strategies can be implemented for shorebird management: financial and staff support, water control abilities, invasive vegetation, and conflict with other interest groups. We suggest three management strategies to meet the needs of shorebirds during the spring and summer/fall migrations in the MAV as follows.

The first strategy involves impoundments flooded in the fall for waterfowl, which should remain flooded through the winter to insure survival of invertebrates during the winter (Helmers 1993). During the spring migratory period, units should be drawn down slowly (2-3 cm/week) to allow continual new exposure of shorebird prey (Rundle and Fredrickson 1981). Water fluctuations may also reduce the potential of invertebrate depletion from shorebird predation (Hamer 2004). If pumping capabilities exist, the sites which dry out in mid-summer should be reflooded about two to three weeks before the summer/fall migration to allow invertebrates to re-populate (Helmers 1991). Shallow discing or mowing of the vegetation before reflooding will provide better substrates for invertebrates and reduce the vegetation structure to amounts acceptable by shorebirds (Hands 1988).

A second strategy can be implemented at sites with out the ability to retain water throughout the winter. In these cases, units should be allowed to flood with spring precipitation and river flooding events. Chironomids (Chironomidae), a common prey item, rapidly exploit rising water (Pinder 1986). When flood waters recede or precipitation slows, water levels should slowly be drawn down during the remainder of the spring migration. If flood events occur late in the spring, draw down in these units can be timed to overlap the summer/fall migrations.

A third strategy is used to combat invasive vegetation by maintaining winter water levels through the spring to prevent early germination. Vegetation encroachment often interferes with moist-soil management for waterfowl and shorebirds. Invasive cattails (*Typha* spp.) have steadily encroached on large areas once suitable for shorebird habitat at Cheyenne Bottoms Wildlife Management Area in Kansas (Skagen 1997). Similar invasive species in the MAV include black willow (*Salix nigra*) and cocklebur (*Xanthium strumarium*), which interfere with moist soil plant production. If germination occurs in July and August, cocklebur, unlike moist-soil plants, do not have enough time to produce seed because of their longer maturation period. Maintaining high water levels through spring offers little shorebird habitat, but provides nesting and feeding habitat for many other waterbirds. A drawdown in July and August will then provide shorebird habitat during the summer/fall migration.

Shorebird management strategies on big river ecosystems are often hindered by unpredictable flood events. The establishment of drainage and levee districts on the Illinois River in the early 1900's reduced the space for flow and increased flood stages (Havara and Bellrose 1985). Large flood events at the wrong time could greatly reduce available habitat. Flood waters breached the levee on the South Pool of Chautauqua in mid-June 2004. A flood event occurring in early-August would devastate the habitat relied upon by the large concentration of shorebirds that traditionally use this site during the summer/fall migration. Conservation of interior migrating shorebirds demands availability of nearby alternate sites when traditional sites are lost (Smith et al. 1991, Skagen and Knopf 1994), underlining the need for diverse complexes.

Acknowledgments. This research, conducted as part of a master's thesis, was funded by the Illinois Natural History Survey, the IDNR Wildlife Preservation Fund, The Nature Conservancy, and the Champaign County Audubon Society. We thank the staff at the Forbes Biological Field Station for their assistance during the project; J. Dassow, B. O'Neal, A. Bartlett, B. Kapusta, S. Yaremych for their assistance in the field; and the staff at the Illinois River National Wildlife and Fish Refuge and Rice Lake State Fish and Wildlife Area.

Literature Cited

Bailey, S.D. 2003. Lake Chautauqua and counting shorebirds. Meadowlark: A Journal for Illinois Birds 12: 54.

Brown, S., C. Hickey, B. Harrigton, and R. Gill. 2001. The U.S. Shorebird Conservation Plan 2nd ed. Manomet Center for Conservation Sciences, Manomet, MA.

Erwin, R. M. 2002. Integrated management of waterbirds: beyond the conventional. Waterbirds 25: 5–12.

Farmer, A. H., and A. H. Parent. 1997. Effects of the landscape on shorebird movements at spring migration stopovers. Condor 99: 698–707.

Haig, S. M., D. W. Mehlman and L. W. Oring. 1998. Avian movements and wetland connectivity in landscape conservation. Conservation Biology 12: 749–758.

Hamer, G. L. 2004. Migrant shorebird ecology in the Illinois River valley. Thesis, University of Illinois, Urbana-Champaign, Illinois, USA.

Hands, H. M. 1988. Ecology of migrant shorebirds in northeastern Missouri. Thesis, University of Missouri, Columbia, Missouri, USA.

Harrington, B. A., S. C. Brown, J. Corven, and J. Bart. 2002. Collaborative approaches to the evolution of migration and the development of science-based conservation in shorebirds. Auk 199: 914–921.

Harrington, B. and E. Perry. 1995. Important shorebird staging sites meeting western hemisphere shorebird reserve network criteria in the United States. United States Fish and Wildlife Service, Washington, D.C. USA.

Havera, S. P. 1999. Waterfowl of Illinois: status and management. Illinois Natural History Survey Special Publication, 21, Champaign, Illinois, USA.

Havera, S. P., and F. C. Bellrose. 1985. The Illinois River: a lesson to be learned. Wetlands 4: 29–41.

Helmers, D. L. 1991. Habitat use by migrant shorebirds and invertebrate availability in a managed wetland complex. Thesis, University of Missouri, Columbia, Missouri, USA.

Helmers, D. L. 1992. Shorebird Management Manual. Western Hemisphere Shorebird Reserve Network. Manomet, MA.

Helmers, D. L. 1993. Enhancing the management of wetlands for migrant shorebirds. Transactions of the 58th N.A. Wildlife & Natural Resources Conference 335–344.

Laubhan, M. K., and L. H. Fredrickson. 1993. Integrated wetland management: concepts and opportunities. Transactions of the 58th N.A. Wildlife & Natural Resources Conference 323–333.

Morrison, R.G., R.E. Gill, B.A. Harrington, S. Skagen, G.W. Page, C.L. Gratto-Trevor, S.M. Haig. 2001. Estimates of shorebird populations in North America. Occasional Paper Number 104. Canadian Wildlife Service.

Pfister, C., B. A. Harrington, and M. Lavine. 1992. The impact of human disturbance on shorebirds at a migration staging area. Biological Conservation 60: 115–126.

Pinder, L. C. V. 1986. Biology of freshwater chironomidae. Annual Review Entomology 31: 1–23.

Rundle, W. D., and L. H. Fredrickson. 1981. Managing seasonally flooded impoundments for migrant rails and shorebirds. Wildlife Society Bulletin 9: 80–87.

Skagen S. K. 1997. Stopover ecology of transitory populations: the case of migrant shorebirds. Ecological Studies 125: 244–269.

Skagen, S. K. and F. L. Knopf. 1994. Migrating shorebirds and habitat dynamics at a prairie wetland complex. Wilson Bulletin 106: 91–105.

Skagen, S. K. and H. D. Oman. 1996. Dietary flexibility of shorebirds in the western Hemisphere. Canadian Field-Naturalist 110: 419–444.

Smith, K. G., J. C. Neal, and M. A. Mlodinow. 1991. Shorebird migration at artificial fish ponds in the prairie-forest ecotone of northwestern Arkansas. Southwestern Naturalist 36: 107–113.

Figure 1. Location of 4 study sites in west-central Illinois (Chautauqua and Emiquon NWR, Rice Lake and Banner Marsh SFWA) along the Illinois River.

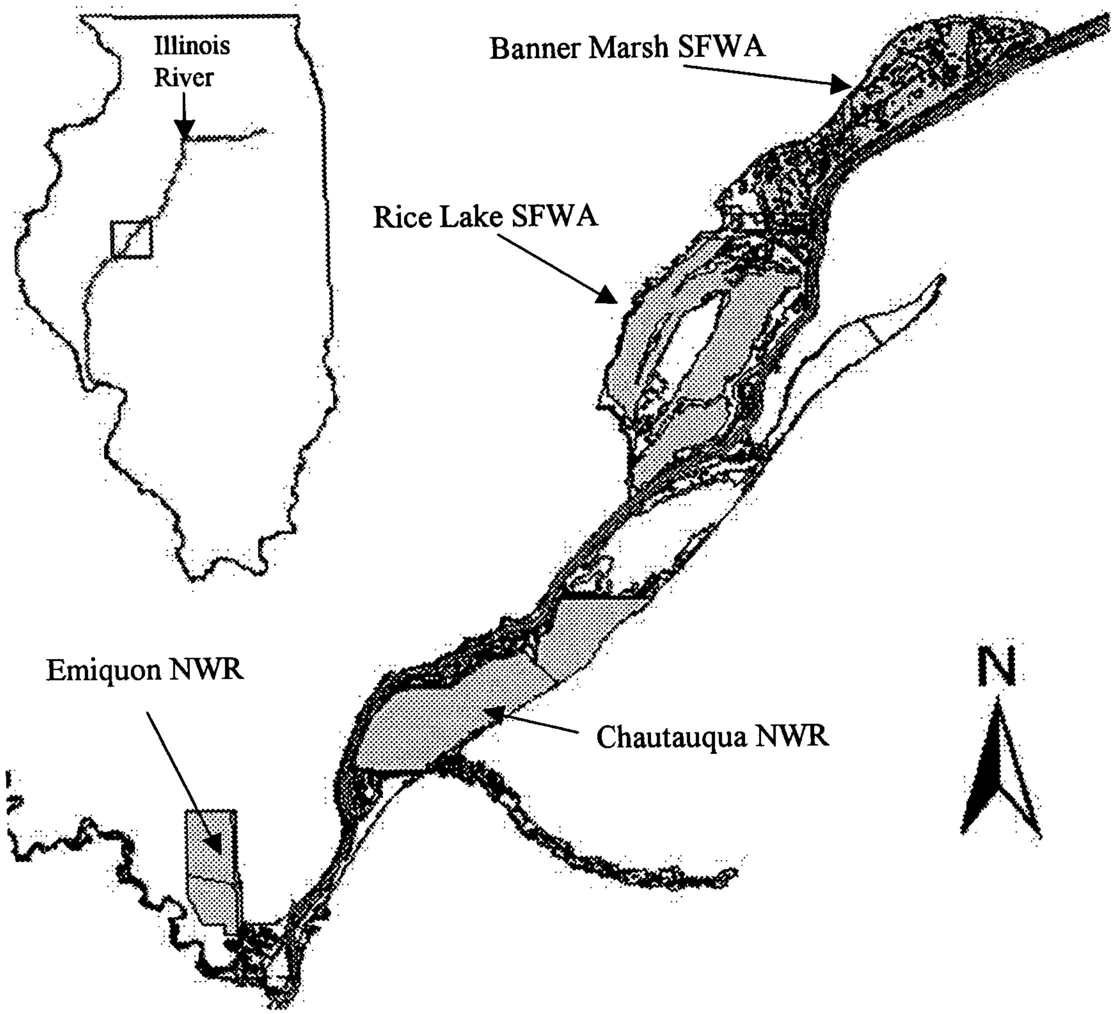


Figure 2. Extrapolated shorebird use-days / 100 ha at a wetland complex along the Illinois River during the spring migration and summer/fall migration of 2003 and spring migration of 2004. Spring 2003-2004 comparisons are not possible because of the addition of new habitat created at Emiquon NWR in 2004. Note difference in scale between 2003 and 2004

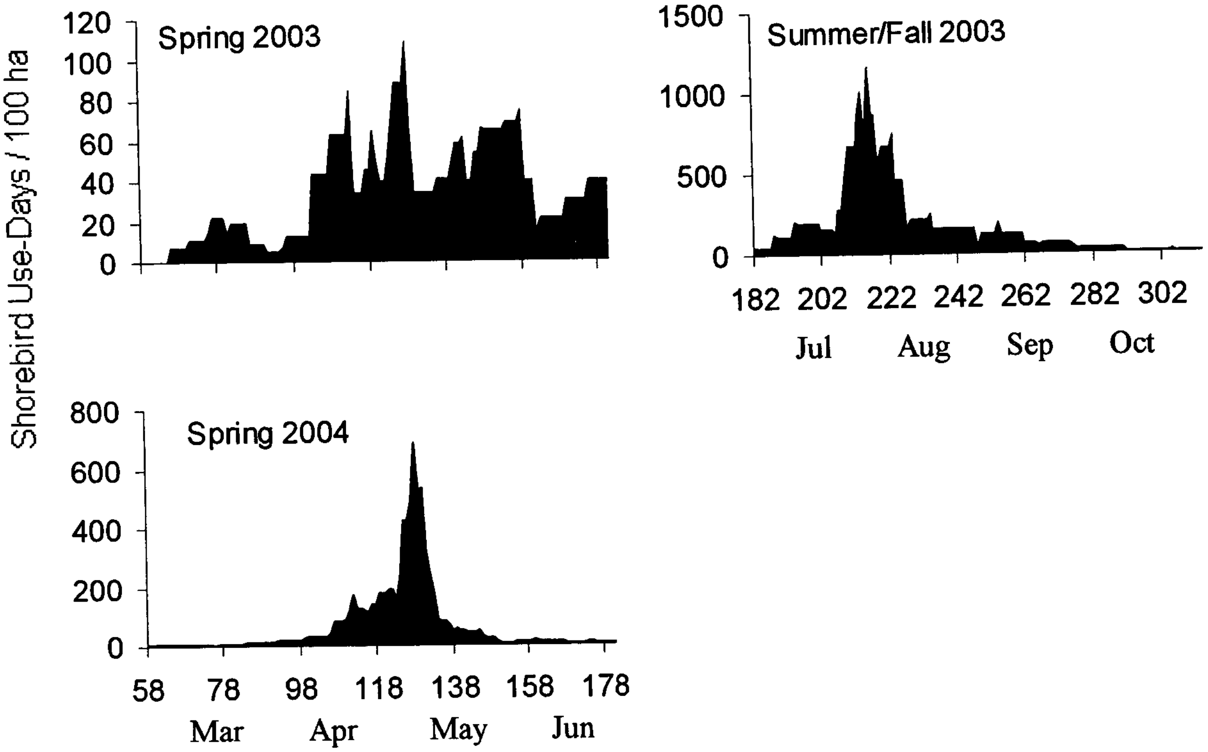


Figure 3. Extrapolated shorebird use-days at Rice Lake SFWA, Emiquon NWR, Chautauqua NWR, and Banner Marsh SFWA, Illinois, during the spring migration and summer/fall migration of 2003. The right y-axis is the Illinois River water level at the Havana, Illinois gage. River connectivity refers to the increasing level of influence from the Illinois River flood events. Study sites vary in size so note differences in scale

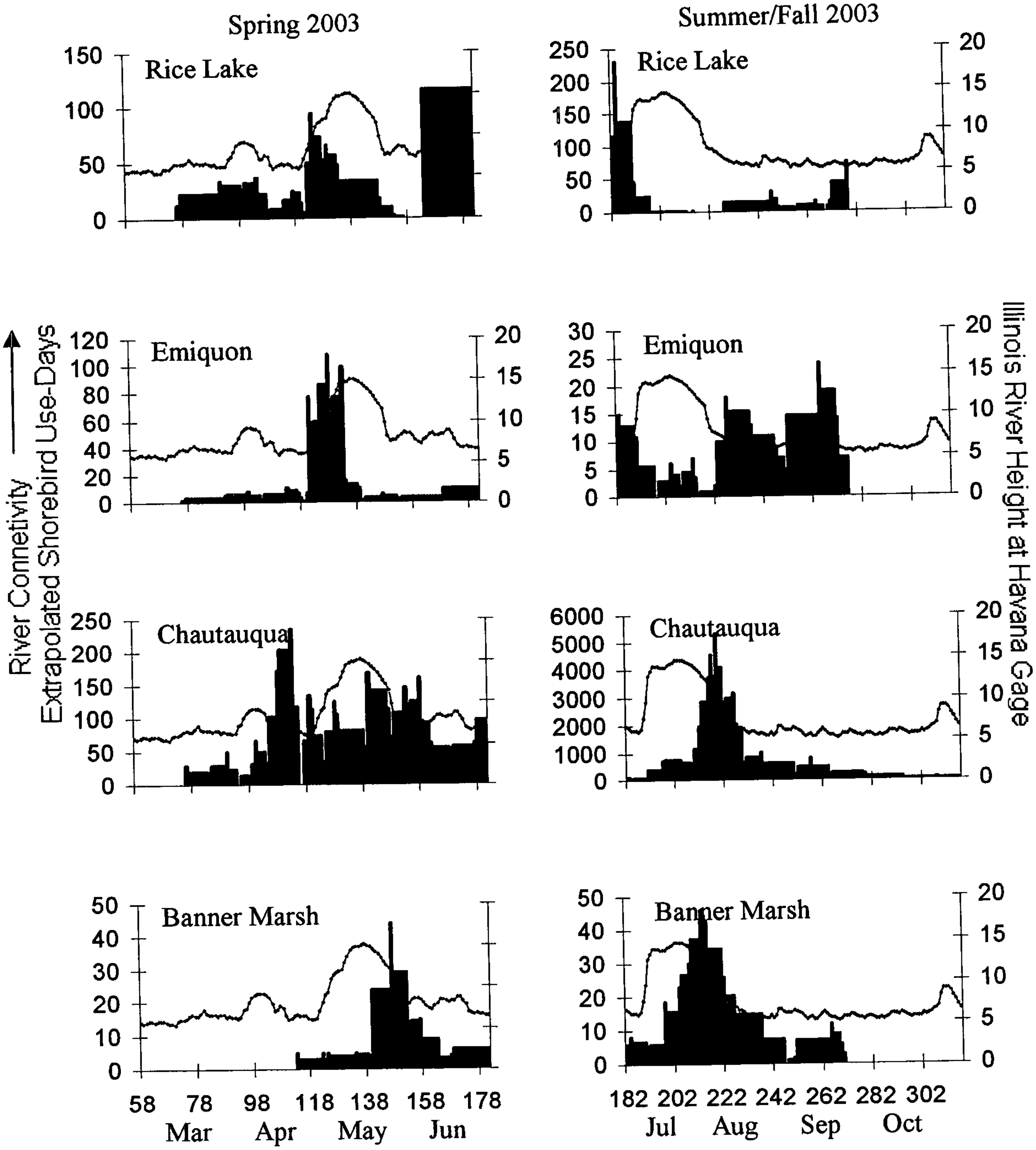
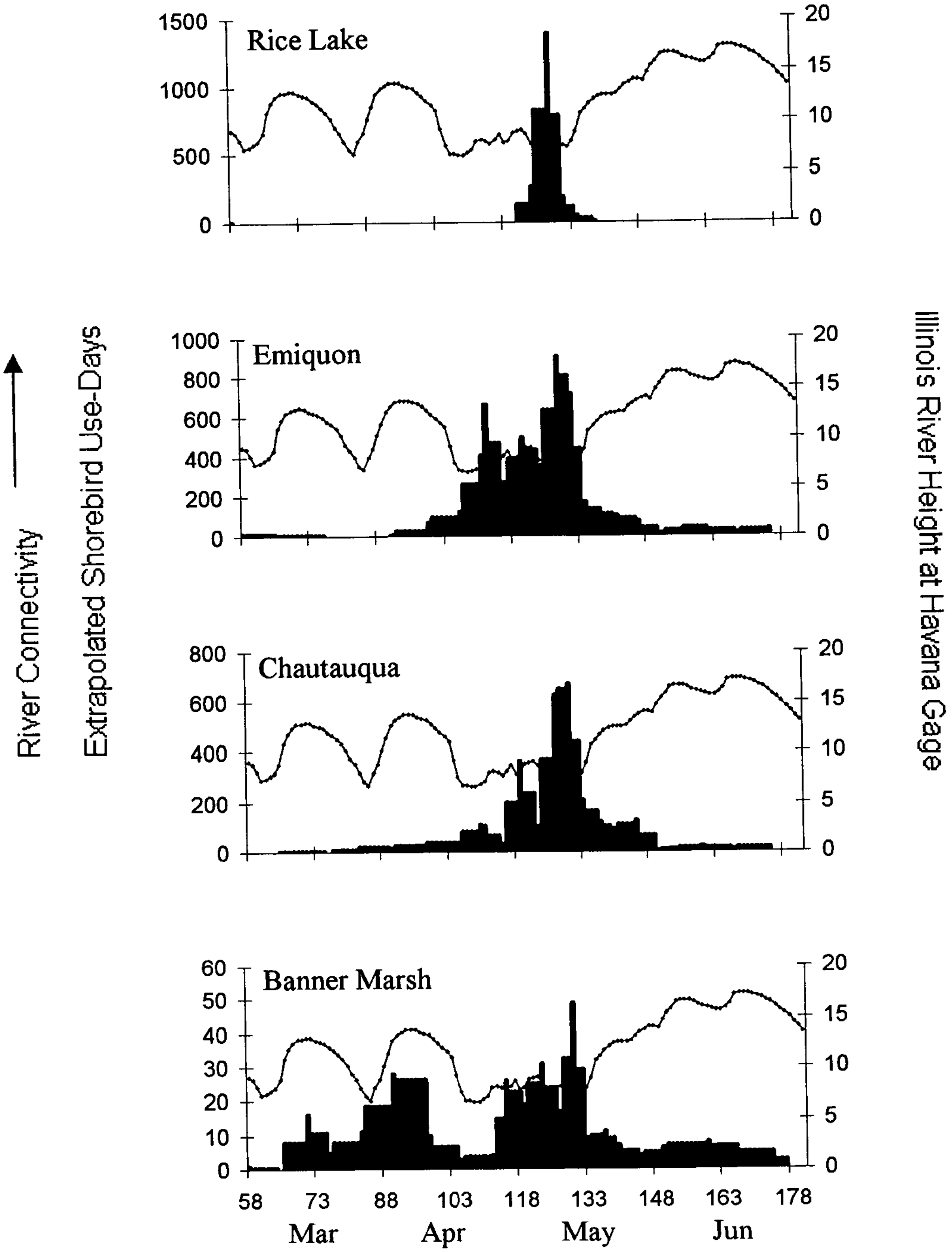


Figure 4. Extrapolated shorebird use-days at Rice Lake SFWA, Emiquon NWR, Chautauqua NWR, and Banner Marsh SFWA, Illinois, during the spring migration of 2003. The right y-axis is the Illinois River water level at the Havana, Illinois gage. River connectivity refers to the increasing level of influence from the Illinois River flood events. Study sites vary in size so note differences in scale

Spring 2004



Send proof to: Gabriel L. Hamer, Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources, East Lansing, Michigan 48824, USA Phone: (517) 355-6463 ext. 1596; E-mail: ghamer@msu.edu

Migration chronology and foraging microhabitat of 10 migrant shorebird species in Illinois, USA

GABRIEL L. HAMER,[1,2,5,6] EDWARD J. HESKE,[1,2] JEFFREY D. BRAWN,[2,3] AND PATRICK W. BROWN[1,4]

[1]Center for Wildlife and Plant Ecology, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL 61820, USA.

[2]Dept. of Natural Resources and Environmental Sciences, Univ. of Illinois, W-503 Turner Hall, 1102 South Goodwin Avenue, Urbana IL 61801, USA; and

[3]Dept. of Animal Biology, Univ. of Illinois, Shelford Vivarium, 606 E Healey, Champaign, IL 61820, USA

---

[4]Present address: Michigan Natural Features Inventory, Michigan State Univ. Extension, P.O. Box 30444 Lansing, MI 48909, USA.

[5]Present Address: Dept. of Fisheries and Wildlife, Michigan State Univ., 13 Natural Resources, East Lansing, MI 48824, USA.

[6]Corresponding Author: Gabriel L. Hamer e-mail: ghamer@msu.edu

Abstract.—Migrating shorebirds have specialized foraging niches that may reduce competition in the unpredictable habitat of the interior flyway. We studied migration chronology and foraging habitat segregation of 10 shorebird species common to the Upper Mississippi Alluvial Valley at a wetland complex along the Illinois River. High overlap occurred in migration chronologies, though the peak of migration varied among species. Most shorebirds at this wetland complex differed in foraging microhabitat with the first function of the discriminant analysis explaining 77% of the total dispersion between the species, where water depth was the most useful variable. Managing stopover habitat to provide diverse water depths could promote successful transcontinental migration by dispersing the foraging activity of different species over wider areas.

Key Words.—discriminant analysis, chronology, foraging microhabitat, Illinois, migration, shorebirds.

SHOREBIRD CHRONOLOGY AND MICROHABITAT

INTRODUCTION

Natural selection in coexisting shorebird (Charadriiformes) populations favors morphological and behavioral differences among species (Baker and Baker 1973, Eldridge 1987, Barbosa and Moreno 1999). The degree of niche overlap among shorebirds depends on several factors, including the amount of available food resources. For example, abundant food resources in the arctic decrease competition among breeding shorebirds and result in high dietary overlap and low foraging microhabitat diversity among species (Holmes and Pitelka 1968, Baker 1979), whereas a lack of abundant food resources in wintering habitat causes increased separation in foraging habitat among species (Baker and Baker 1973). Separation in foraging habitat of non-breeding shorebirds is primarily based on water depth (Brooks 1967, Helmers 1991, Isola et al. 2000), which is correlated with tarsus length (Eldridge 1987). Competition also is alleviated during the non-breeding season by the diverse feeding apparatuses and behaviors of shorebirds, accompanied by specializations in diet (Burton 1972, Lifjeld 1984, Senner et al. 1989, De Leon and Smith 1999, Davis and Smith 2001).

Most studies of niche segregation have occurred on breeding or wintering grounds, while the topic has received less attention at migratory stopovers, particularly in the interior flyway. Freshwater wetlands in the U.S. continue to be converted to agriculture and development (Dahl 2000), which might be a limiting factor explaining the population decline of many species of Nearctic-breeding shorebirds (Myers et al. 1987, Brown *et al.* 2001, Morrison *et al.* 2001, Harrington *et al.* 2002). The continued loss of stopover habitat may result in higher bird densities with increased competition, higher rates of prey depletion, and increased interference (Sutherland and Goss-Custard 1991). Habitat used by migrating shorebirds in the interior flyway need evaluation to help managers identify temporal and spatial characteristics of shorebird habitat that will attract and support a diverse shorebird assemblage.

In addition, most studies of shorebird niche segregation focus on single niche dimensions, which may be misleading (Weins 1989). Studies investigating niche relationships among coexisting shorebirds have focused on few species, and may miss the relationships present at a larger scale within a shorebird community.

Management decisions to benefit migrating shorebirds in the Upper Mississippi Alluvial Valley (UMAV) should be based on knowledge of community structure of the shorebirds migrating through the region. We initiated a study of shorebirds in the UMAV to better understand how species of shorebirds use foraging microhabitats during migration and the timing of those migrations. Our objectives included an assessment of 10 regionally common migrant shorebird species regarding their *i*) migration chronology, (*ii*) diurnal activity budgets, and (*iii*) foraging microhabitat.

METHODS

Study Area

The study was conducted on 4 field sites that are a part of a large wetland complex along the Illinois River in west-central Illinois (Figure 1). The floodplain wetlands include backwater lakes, sloughs, and marshes, that are federally- or state-managed.

Chautauqua National Wildlife Refuge (NWR) (40°38'N, 89°99'W) and Emiquon NWR (40°32'N, 90°09'W) are managed by the U.S. Fish and Wildlife Service (USFWS). Chautauqua NWR was established in 1936 and contains 1,816 ha of large backwater lakes and bottomland and upland forest, and is located about 5 miles NNE of Havana, Illinois. Chautauqua has been designated as a stopover of international importance by the Western Hemisphere Shorebird Reserve Network (Harrington and Perry 1995). The late draw-down in July and August creates extensive shallow water mudflats attracting an estimated 100,000 to 250,000 shorebirds each fall (Bailey 2003). Comparatively little shorebird habitat is available at Chautauqua in the spring. During the spring, water levels are managed to remain elevated to prevent encroachment from the invasive species black willow (*Salix nigra*) and cocklebur (*Xanthium strumarium*), which interfere with moist soil plant production. Efforts at management for shorebirds are also challenged by occasional floodwaters from the Mississippi River that breach the levees of the refuge, and the threat of avian botulism from stagnant pools left after the draw-down.

Emiquon NWR is a 856 ha refuge comprised of backwater lakes, sloughs, forested wetlands, and a variety of other terrestrial habitats. Due to the recent acquisition of Emiquon by USFWS in 1993, much of the refuge is newly-established wetland and portions will remain in agriculture until leases with private landowners cease. The refuge is divided into two main units: the South Globe and the Wilder Tract. The Wilder Tract was taken out of agricultural production in 1998 and remains in moist-soil management. The South Globe unit was taken out of production for the first time in 2004, at which time the corn and bean stubble was flooded to create extensive shallow water habitat.

Two additional field sites include Rice Lake State Fish and Wildlife Area (SFWA) (40°48'N, 89°90'W) and Banner Marsh SFWA (40°53'N, 89°85'W), managed by the Illinois Department of Natural Resources. The initial 959 ha land purchase of Rice Lake occurred in 1945, and included a large bottomland lake just up river from Chautauqua. More recent land acquisitions increased the total land area to 2,290 ha. Most shorebird use of Rice Lake during 2003 and 2004 occurred at impoundments managed for waterfowl, and these impoundments have little protection from flood waters. Banner Marsh SFWA is a 1,766 ha site that was acquired during the 1980s. The land was stripped for coal between 1956 and 1973 and now contains many lakes and marshes of various sizes and depth.

Surveys

We censused shorebirds during the spring and summer/fall migration in 2003 (17 March to 14 November) and the spring migration in 2004 (28 February to 25 June). During the main portion of each spring and summer/fall migration (late-April to late-May and late-July to late-September, respectively), each site was censused twice per week. Outside of the main portion of the migrations, censuses were conducted once per week. Shorebirds were counted while traveling survey routes by vehicle or on foot using 8x42 binoculars and a 15-45x scope. Only portions of the sites with suitable shorebird habitat, determined by the presence of shallow water and mudflats, were censused. As the location of the habitat changed with fluctuating hydrology, the survey route changed. Shorebird use-days were calculated by multiplying the mean number of individuals of a species observed on two consecutive censuses by the number of days between those counts (Rundle and Fredrickson 1981). The 10 species most common to the UMAV chosen for this study include: Killdeer, Semipalmated Plover, Greater Yellowlegs, Lesser Yellowlegs, Solitary Sandpiper, Pectoral Sandpiper, Semipalmated Sandpiper, Least Sandpiper, Short-billed Dowitcher, and Wilson's Snipe (scientific names in Figure 2).

Foraging Microhabitat

On designated census days, we used focal individual sampling (Altmann 1974) of all flocks greater than 5 individuals. One bird per flock was chosen for observation by directing a spotting scope on the flock and selecting the individual in the center of the field. After birds were observed feeding, the foraging location was approached on foot, with the exact location identified by tracks. Five measurements were recorded: water depth, distance to nearest soil/water interface, slope (of the land 1 m perpendicular to soil/water interface), distance to nearest woody vegetation > 2m in height, and percent mud in a 0.5 m radius of the foraging location (visual estimate, non-mud substrate consisted of live or dead vegetation).

We used discriminant analysis to determine if the feeding sites of the 10 species differed based on the 5 microhabitat variables. The scores from the first canonical function were tested in a one-way ANOVA and Fisher's LSD was used to determine which species differed significantly. To meet assumptions of normality, the percent vegetation variable was arcsine-transformed and all other variables were $\log_{10}(x + 1)$-transformed. Statistical significance was accepted at $p<0.05$ and all means are reported with 95% confidence intervals. All statistical procedures were performed using SYSTAT 10.2 (Systat 2000).

Diurnal Activity Budget

We selected individual shorebirds for behavioral assessment in the same manner used in assessment of foraging microhabitats. Observations were stratified by time of day into three diurnal periods: early (sunrise-11.00), midday (11.01-15.00), and late (15.01-sunset). Observations of each individual were recorded for 5 minutes, and in the case that an observed bird took flight, only observations greater than 2 minutes were analyzed. Behavior was recorded every 30 seconds using a digital stopwatch and was classified into seven categories (DeLeon and Smith 1999): feeding (actively feeding by pecking, probing, or scything), sleeping (motionless with bill tucked under wing, head and neck held stationary, or eyes closed), alert (stationary with bird visually scanning surroundings), body maintenance (bathing, preening, or wing and neck stretching), aggression-interspecific (chasing, pecking, or threatening another individual of different species), aggression-intraspecific (chasing, pecking, or threatening another individual of the same species), and locomotion (wading, walking, running, swimming, or flying).

Because of small sample sizes, the 10 species observed over the 2 years of the study were grouped into shorebird guilds based on Skagen and Oman (1996): *plover gleaner* (KILL, SEPL), *small gleaner/prober* (LESA, SESA), and *medium gleaner/prober* (PESA, SOSA, WISN, SBDO, LEYE, GRYE). We used a non-parametric test (Kruskal-Wallis) to assess differences in behavior among time periods (early, midday, late) among the 3 guilds.

RESULTS

Chronology

Migration chronologies of the 10 shorebirds species showed a high degree of overlap (Figures 2 and 3). Six of the 10 species had consistent migration peaks between the springs of 2003 and 2004: Wilson's Snipe (mid-April), Solitary Sandpiper and Lesser Yellowlegs (early-May), Short-billed Dowitcher (mid-May), and Semipalmated Sandpiper and Semipalmated Plover (late-May). Three species showed slight variation in the timing of spring migration between 2003 and 2004: Least Sandpiper (late-May, early-May respectively), Pectoral Sandpiper (late-April, early-May), and Greater Yellowlegs (early-May, late-April). Of the ten species chosen for this study, Killdeer are the only locally-breeding species, which explains why their migration chronology was much different. In 2003, Killdeer use-days were stable in the spring with a rise in mid-June from hatch-year birds and a peak in mid-August during the summer/fall migration. The summer/fall migration peaked in late-July for Semipalmated Sandpiper and

Solitary Sandpiper, in early-August for Least Sandpiper and Pectoral Sandpiper, in mid-August for Lesser and Greater Yellowlegs, Short-billed Dowitcher, and Semipalmated Plover, and in late-September for Wilson's Snipe.

Foraging Microhabitat

The first canonical function produced by discriminant analysis of the 5 microhabitat variables accounted for 77% of the total dispersion of the species with an eigenvalue of 2.297 ($F = 7.619$; $df = 45$; $P < 0.0001$). Water depth was most useful in discriminating among the species (weights of the first canonical discriminant function for water depth = 2.26, slope = 0.27, distance to soil/water interface = -0.13, percent mud = -0.15, and distance to woody vegetation = -0.29). Species differed in their along the first canonical function ($F = 40.067$, $df = 9$, $P < 0.0001$; Figure 4). Killdeer foraged in the shallowest microhabitat ($x = 0.2$; $SD = 0.6$) and Greater Yellowlegs foraged in the deepest water ($x = 7.5$ cm; $SD = 3.3$). Shorebirds occupying a similar microhabitat with water depths about 1 cm deep included Semipalmated, Least, and Pectoral Sandpipers and Wilson's Snipe. Overlap in foraging microhabitat also occurred in Short-billed Dowitcher, Solitary Sandpiper and Lesser Yellowlegs where the water depth ranged from 2 to 5 cm. The relationships between foraging microhabitat and peak spring migration time for the 9 non-resident species are shown in Figure 5.

Diurnal Activity Budget

About 82% of shorebird diurnal activity was devoted to foraging, and the remainder of the diurnal time was spent in an alert posture (7.5%), body maintenance (7.0%), locomotion (2.7%), and intraspecific aggression (0.3%). No focal shorebirds were observed sleeping or displaying interspecific aggression, although these activities were seen incidentally once or twice during the study in shorebirds not selected for observation. The activity of all shorebirds was significantly different among the 3 time periods (early, midday, late) for only the feeding ($p = 0.001$) and body maintenance ($p = 0.009$) activities, where less time was spent foraging during the midday time period. The percent of time spent foraging during the 3 time periods was different for the *medium* shorebird guild ($p < 0.001$), but not for the *plover* ($p = 0.814$) or *small* ($p = 0.898$) shorebird guilds. The *medium* shorebird guild spent significantly less time foraging during the middle portion of the day (Figure 6).

DISCUSSION

Shorebird species may partition resources during migration in at least 3 ways: (1) migration chronology, (2) foraging microhabitat, and (3) diurnal activity budget. The spring shorebird migration at our study sites peaked in May and the summer/fall migration peaked in August, which is consistent with other studies in the region (Hands 1988, Elliott-Smith 2003). Although there was considerable overlap, the peak migration dates varied among species.

Habitat is considered the most important dimension in niche partitioning by shorebirds (Davis and Smith 2001). As in previous studies (Brooks 1967, Helmers 1991, Isola et al. 2000), we found that water depth explained most of the variation in foraging microhabitat among species. Some pairs of species with similar migration chronologies, such as Greater and Lesser Yellowlegs, Least and Solitary Sandpiper, and Semipalmated Plover and Short-billed Dowitcher may reduce competition by foraging in different microhabitats. Other species that forage in similar microhabitats such as Wilson's Snipe and Pectoral Sandpiper, and Least Sandpiper and Semipalmated Plover, used our stopover sites at slightly different times. However, a few pairs of species such as Least and Pectoral Sandpipers where similar in both migration chronology and microhabitat use.

Resource partitioning by shorebirds through different diurnal activities was unlikely at our study site because shorebirds spent 82% of their diurnal activity feeding. The *medium* foraging guild spent less time foraging during the middle portion of the day, possibly allowing the *plover* and *small* shorebird guilds to continue to feed during mid-day with less interference from the *medium* shorebirds. However, other studies have shown that the higher metabolic rates of smaller shorebirds requires them to spend more time each day to meet food requirements than large shorebirds (DeLeon and Smith 1999, Pienkowski and Evans 1984). The availability of invertebrates in the wet substrate where most members of the *plover* and *small* shorebird guilds forage also could remain constant during the day. In contrast, many members of the medium shorebird guild forage visually in deeper water on invertebrates in the water column that may become inactive during the middle portion of the day and force these shorebirds to switch foraging tactics or spend less time feeding.

We did not investigate differences in diet selection, which also might affect resource use by species with similar migration chronology and foraging microhabitat, such as Short-billed Dowitcher and Lesser Yellowlegs. The shorebird feeding apparatus is highly specialized to exploit different food items. The foraging method and long bill of the Short-billed Dowitcher allows deep probing (Baker and Baker 1973, Hamer unpubl. data), and size of beak has a positive correlation with size of prey (Holmes and Pitelka 1968). Edridge (1987) also reported that larger shorebirds consume larger invertebrates. Senner et al. (1989) described another example of segregation along the food-type dimension where Western Sandpiper (*Calidris* *mauri*) diets were diverse and Dunlins (*Calidris alpina*) fed primarily on a single species of clam, *Macoma balthica*.

Whether invertebrate resources at stopover locations are limiting to the point that they result in competition and affect fitness of shorebirds is not known. However, if current trends in loss of wetlands are not reversed, competition for resources is likely to increase in the remaining areas. Such competition could particularly affect individuals of species that specialize in foraging microhabitats (Durell 2000). Management for diversity of water levels and shifting location of soil/water interface would likely increase foraging habitat and would continue to expose new invertebrate prey during the course of spring or fall migration, allowing shorebirds to replenish energy and nutrient reserves.

ACKNOWLEDGEMENTS

This research, conducted as part of a master's thesis, was funded by the Illinois Natural History Survey, the IDNR Wildlife Preservation Fund, The Nature Conservancy, and the Champaign County Audubon Society. We thank the staff at the Forbes Biological Field Station for their assistance during the project; J. Dassow, B. O'Neal, A. Bartlett, and B. Kapusta for their assistance in the field; and the staff at the Illinois River National Wildlife and Fish Refuge and Rice Lake State Fish and Wildlife Area.

LITERATURE CITED

Altmann, J. 1973. Observational study of behavior: sampling methods. University of Chicago. Rec. 15:227-265.

Bailey, S.D. 2003. Lake Chautauqua and counting shorebirds. Meadowlark: A Journal for Illinois Birds 12:54.

Baker, M. C. 1979. Morphological correlates of habitat selection in a community of shorebirds (Charadriiformes). Oikos 33:121-126.

Baker, M. C. and A. E. Miller-Baker. 1973. Niche relationship among six species of shorebirds on their wintering and breeding ranges. Ecolological Monographs 43:193-212.

Barbosa, A. and E. Moreno. 1999. Evolution of foraging strategies in shorebirds: an ecomorphological approach. Auk 116:712-725.

Brooks, W.S. 1967. Food and feeding habits of autumn migrant shorebirds at a small midwestern pond. Wilson Bulletin 79:307-315.

Brown, S., C. Hickey, B. Harrington, and R. Gill. 2001. The U.S. Shorebird Conservation Plan 2nd ed. Manomet Center for Conservation Sciences, Manomet, MA.

Burton, P. K. 1972. The feeding techniques of stilt sandpipers and dowitchers. San Diego Society of Natural History Transactions 17:63-68.

Dahl, T.E. 2000. Status and trends of wetlands in the conterminous United States 1886 to 1997. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Davis, C. A. and L. M. Smith. 2001. Foraging strategies and niche dynamics of coexisting shorebirds at stopover sites in the southern great planes. Auk 118:484-495.

De Leon, M. T., and L. M. Smith. 1999. Behavior of migrating shorebirds at North Dakota prairie potholes. Condor 101:645-654.

Durell, S. 2000. Individual feeding specialization in shorebirds: population consequences and conservation implications. Biological Review 75:503-518.

Eldridge, J.L. 1987. Ecology of migrant sandpipers in mixed-species foraging flocks. Dissertation, University of Minnesota, Minneapolis, USA.

Elliott-Smith, E. S. 2003. Mudflat subsidence in a man-made reservoir: the importance of topography to migrant shorebirds. Thesis, Southern Illinois University, Carbondale, USA.

Hands, H. M. 1988. Ecology of migrant shorebirds in northeastern Missouri. Thesis, University of Missouri, Columbia, USA

Harrington, B. and E. Perry. 1995. Important shorebird staging sites meeting western hemisphere shorebird reserve network criteria in the United States. United States Fish and Wildlife Service, Washington, D.C., USA.

Harrington, B. A., S. C. Brown, J. Corven, and J. Bart. 2002. Collaborative approaches to the evolution of migration and the development of science-based conservation in shorebirds. Auk 199:914-921.

Helmers, D. L. 1991. Habitat use by migrant shorebirds and invertebrate availability in a managed wetland complex. Thesis, University of Missouri, Columbia, USA.

Helmers, D. L. 1992. Shorebird Management Manual. Western Hemisphere Shorebird Reserve Network. Manomet, MA, USA.

Holmes, R.T. and F.A. Pitelka. Food overlap among coexisting sandpipers on northern Alaska tundra. Systematic Zoology 17:305-318.

Isola, C. R., et al. 2000. Interspecific differences in habitat use of shorebirds and waterfowl foraging in managed wetlands of California's San Joaquin Valley. Waterbirds 23:196-203.

Lifjeld, J. T. 1984. Prey selection in relation to body size and bill length of five waders feeding in the same habitat. Ornis Scandinavia 15:217-226.

Morrison, R.G., R.E. Gill, B.A. Harrington, S. Skagen, G.W. Page, C.L. Gratto-Trevor, S.M. Haig. 2001. Estimates of shorebird populations in North America. Occasional Paper Number 104. Canadian Wildlife Service.

Myers, J. P., R. G. Morrison, P. Z. Antas, B. A. Harrington, T. E. Lovejoy, M. Sallaberry, S. E. Senner, and A. Tarak. 1987. Conservation strategy for migratory species. American Scientist 75:19-27.

Pienkowski, M. W., and Evans, P. R. 1984. Migratory behavior of shorebirds in the Western Paleartic. Pages 73-123 *in* J. Burger and B.L. Olla, editors. Shorebirds: migration and foraging behavior. Vol 6, Plenum Press, New York and London.

Rundle, W. D., and L. H. Fredrickson. 1981. Managing seasonally flooded impoundments for migrant rails and shorebirds. Wildlife Society Bulletin 9:80-87.

Schoener, T. W. 1974. Resource portioning in ecological communities. Science 185: 27-39.

Senner, S. E., D. W. Norton and G. C. West. 1989. Feeding ecology of western sandpipers, *Calidris mauri*, and dunlins, *C. alpina*, during spring migration at Hartney Bay, Alaska. Canadian Field-Naturalist 103:372-379.

Skagen, S. K. and F. L. Knopf. 1994. Residency patterns of migrating sandpipers at a midcontinental stopover. The Condor 96:949-958.

Skagen, S. K. and H. D. Oman. 1996. Dietary flexibility of shorebirds in the western Hemisphere. The Canadian Field-Naturalist 110:419-444.

Sutherland, W.J., and J.D. Goss-Custard. 1991. Predicting the consequence of habitat loss on shorebird populations. Proceedings International Ornithological Congress 20:2199-2207.

Systat (Version 10.2). 2000. Computer Software. Richmond, Ca. Systat Software Inc., http://www.systat.com/products/systat/.

White, D. H., and C. A. Mitchell. 1990. Body mass and lipid content of shorebirds overwintering on the south Texas coast. Journal Field Ornithology 61:445-452.

Weins, J.A. 1989. The Ecology of Bird Communities, vol. 1: Foundations and Patterns. Cambridge University Press, Cambridge, United Kingdom.

Figure 1. Location of 4 study sites in west-central Illinois (Chautauqua and Emiquon NWR, Rice Lake and Banner Marsh SFWA) along the Illinois River.

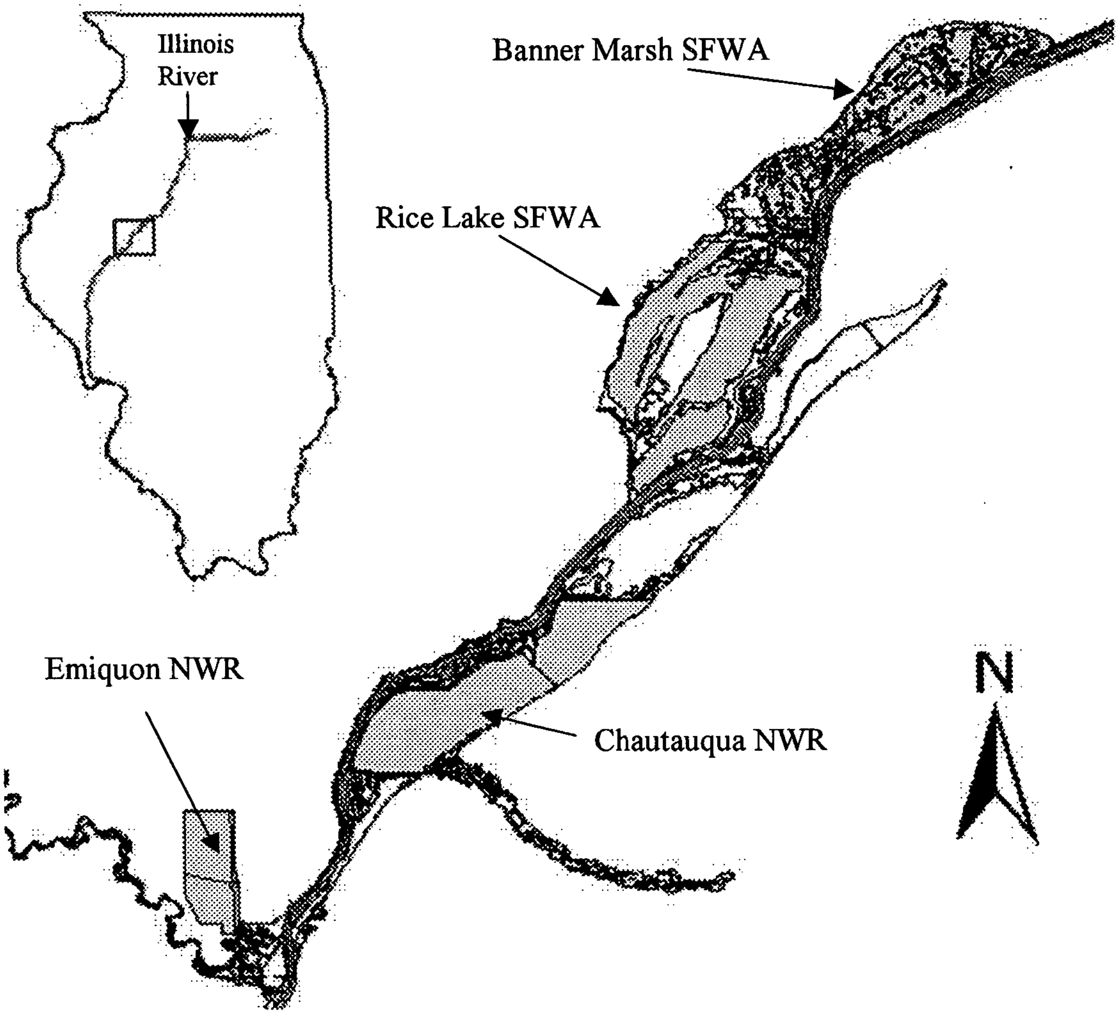
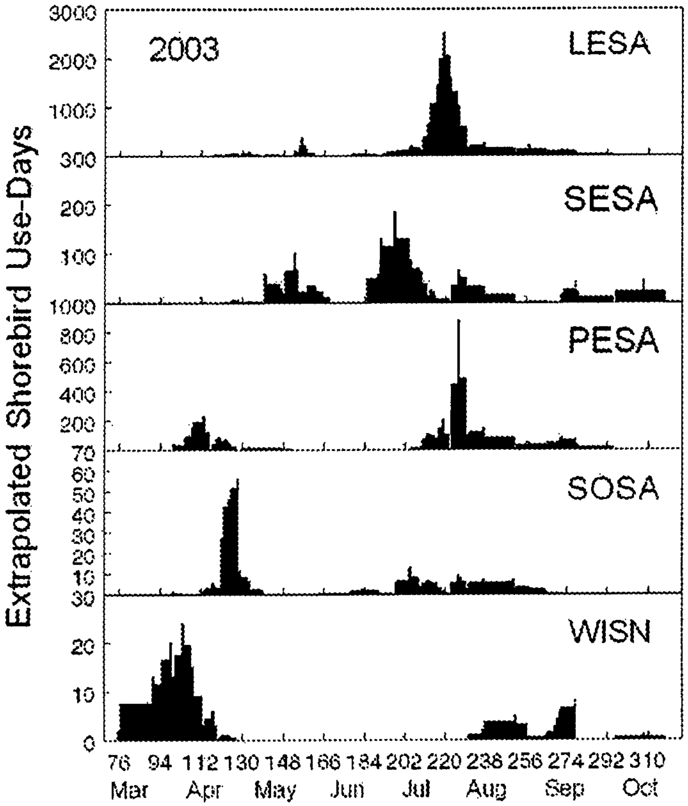
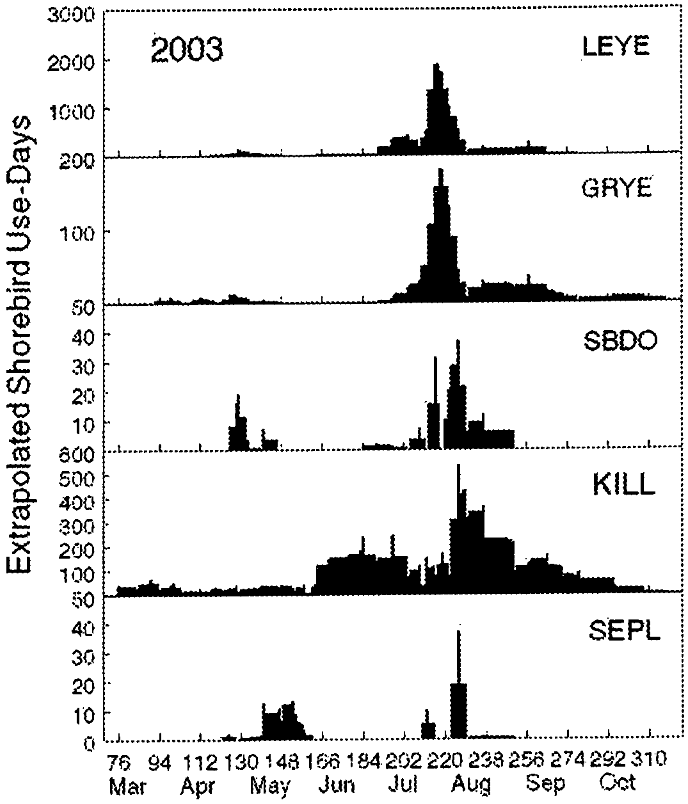

Illinois River
Banner Marsh SFWA
Rice Lake SFWA
Emiquon NWR
Chautauqua NWR
N

Figure 2. Extrapolated shorebird use-days for 10 common migrant shorebirds during the spring and summer/fall migration along the Illinois River in 2003. Species: Killdeer (KILL) *Charadrius vociferous*, Semipalmated Plover (SEPL) *Charadrius semipalmatus*, Greater Yellowlegs (GRYE) *Tringa melanoleuca*, Lesser Yellowlegs (LEYE) *Tringa flavipes*, Solitary Sandpiper (SOSA) *Tringa solitaria*, Pectoral Sandpiper (PESA) *Calidris melanotos*, Semipalmated Sandpiper (SESA) *Calidris pusilla*, Least Sandpiper (LESA) *Calidris minutilla*, Short-billed Dowitcher (SBDO) *Limnodromus griseus*, and Wilson's Snipe (WISN) *Gallinago delicate*.

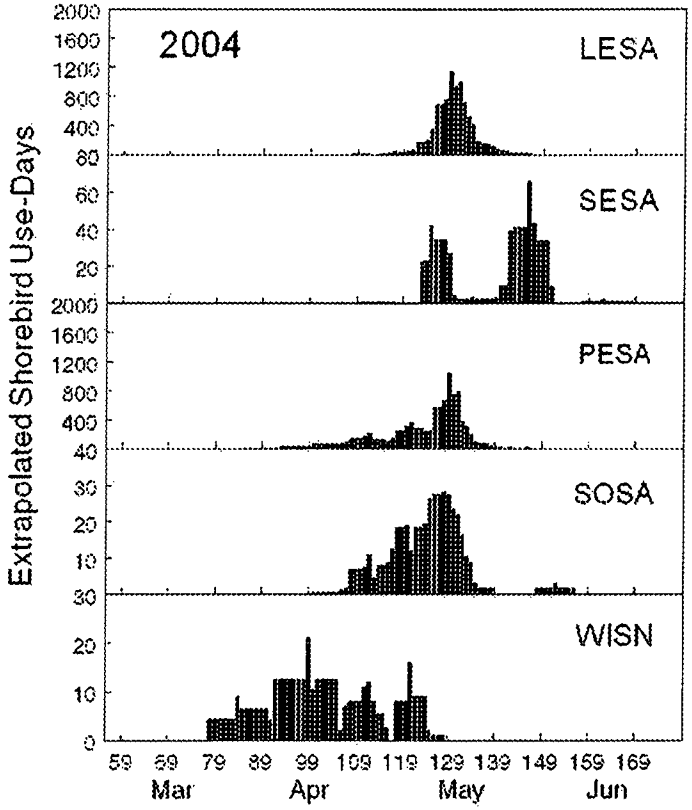


Extrapolated Shorebird Use-Days
2003
LESA
3000
2000
1000
300
SESA
200
100
1000
PESA
800
600
400
200
70
SOSA
60
50
40
30
20
10
30
WISN
20
10
0
76 94 112 130 148 166 184 202 220 238 256 274 292 310
Mar Apr May Jun Jul Aug Sep Oct



Extrapolated Shorebird Use-Days
2003
LEYE
3000
2000
1000
200
GRYE
100
50
SBDO
40
30
20
10
600
KILL
500
400
300
200
100
50
SEPL
40
30
20
10
0
76 94 112 130 148 166 184 202 220 238 256 274 292 310
Mar Apr May Jun Jul Aug Sep Oct

Figure 3. Extrapolated shorebird use-days for 10 common migrant shorebirds during the spring migration along the Illinois River in 2004.


2004
LESA
SESA
PESA
SOSA
WISN
Extrapolated Shorebird Use-Days
2000
1600
1200
800
400
80
60
40
20
2000
1600
1200
800
400
40
30
20
10
30
20
10
0
59
69
79
89
99
109
119
129
139
149
159
169
Mar
Apr
May
Jun

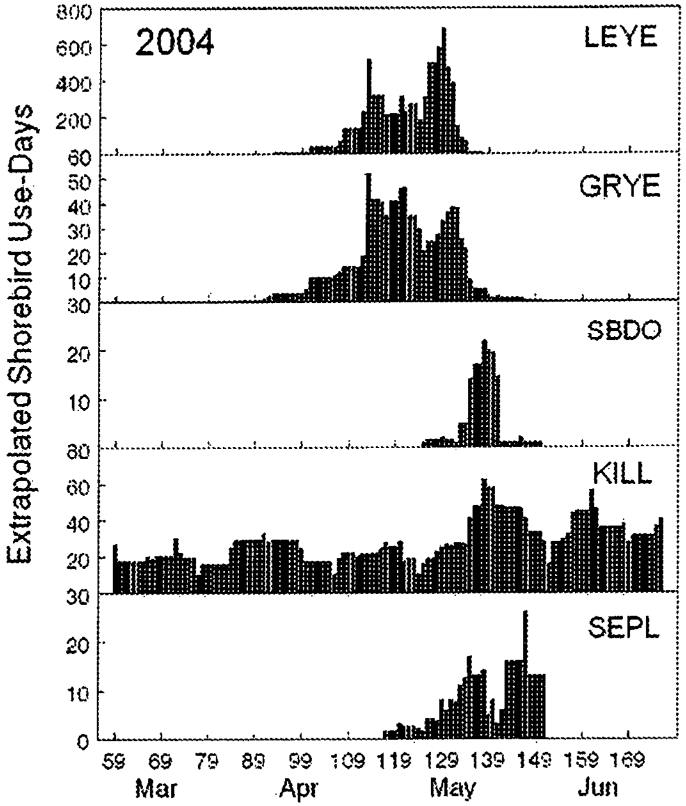

2004
LEYE
GRYE
SBDO
KILL
SEPL
Extrapolated Shorebird Use-Days
800
600
400
200
60
50
40
30
20
10
30
20
10
80
60
40
20
30
20
10
0
59
69
79
89
99
109
119
129
139
149
159
169
Mar
Apr
May
Jun

Figure 4. Canonical scores of the first function explaining 77% of the total dispersion of the species. The water depth variable is most helpful for discriminating among species. Species with the same letter are not different ($p < 0.05$) by Fisher's LSD test. Samples sizes: KILL (14), SEPL (9), SESA (17), LESA (25), WISN (12), PESA (20), SBDO (9), SOSA (20), LEYE (21), GRYE (23).

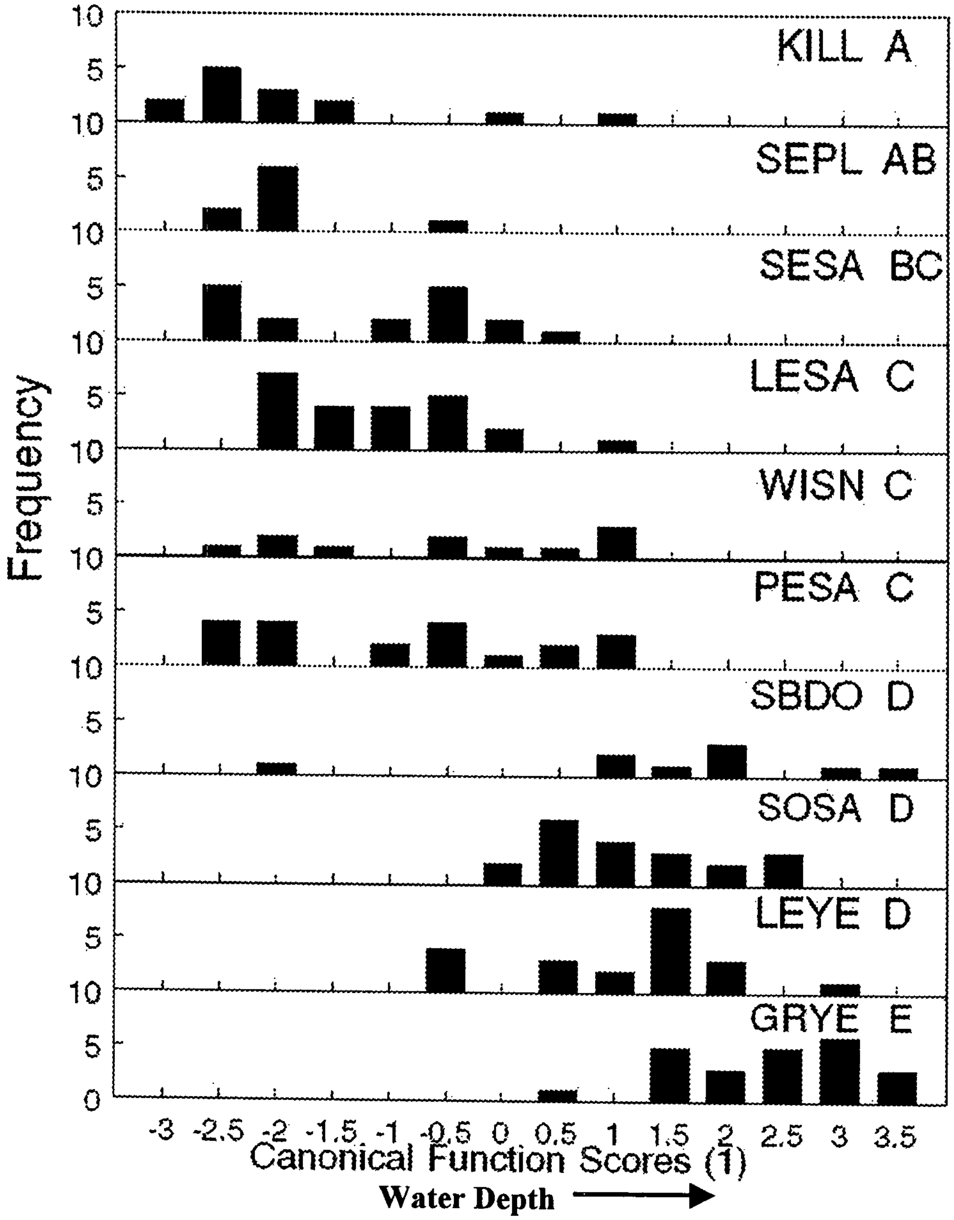

Frequency
10
5
0
KILL A
SEPL AB
SESA BC
LESA C
WISN C
PESA C
SBDO D
SOSA D
LEYE D
GRYE E
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
3.5
Canonical Function Scores (1)
Water Depth

Figure 5. Habitat and temporal segregation of 10 species of shorebirds occurring at a wetland complex along the Illinois River near Havana, Illinois during the spring of 2004.

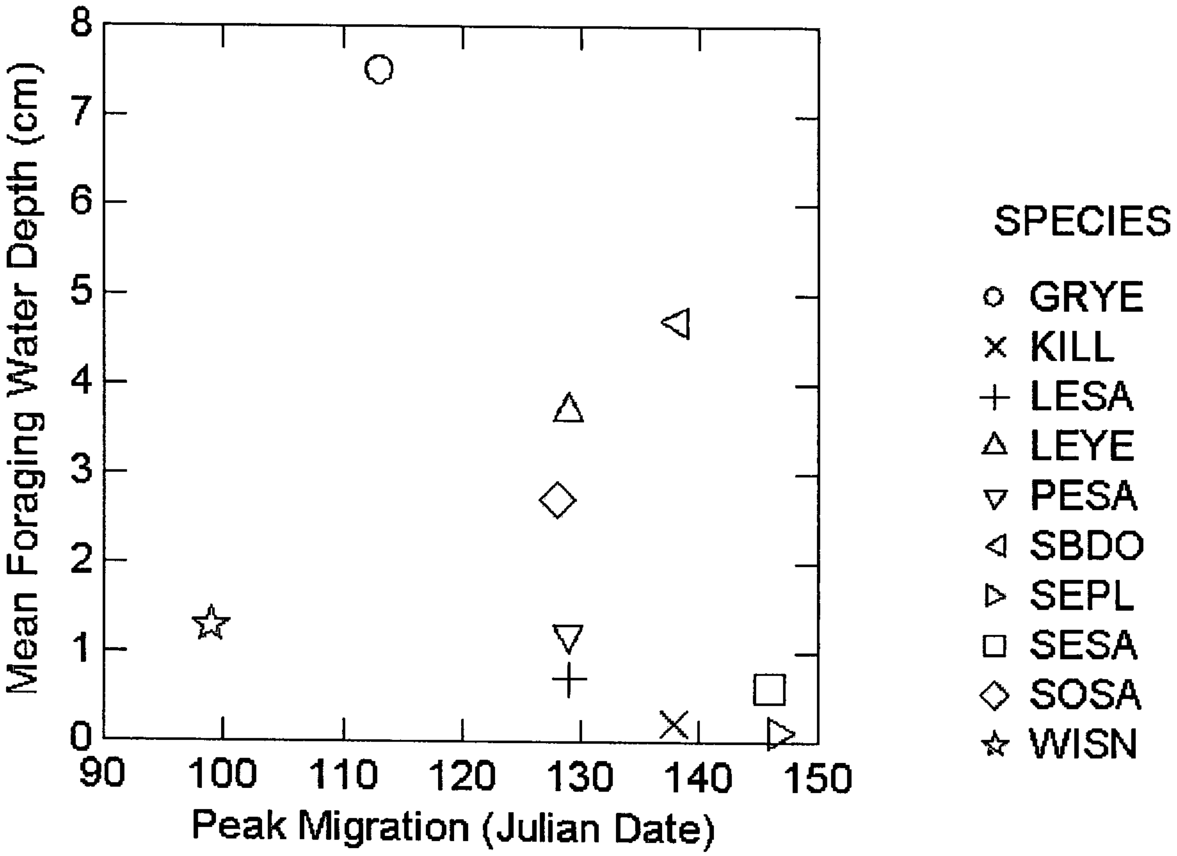
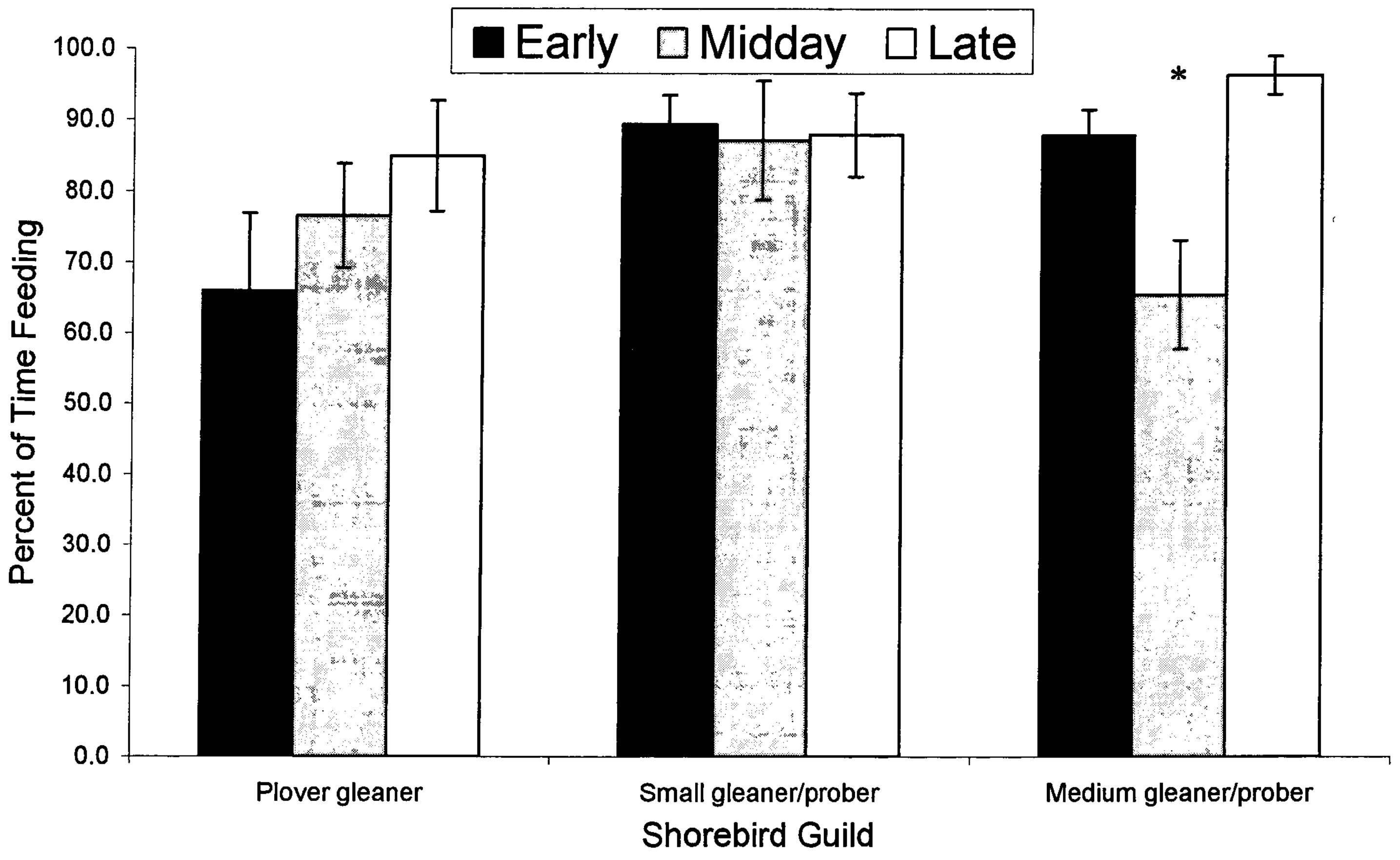

Mean Foraging Water Depth (cm)
0
1
2
3
4
5
6
7
8
90
100
110
120
130
140
150
Peak Migration (Julian Date)
SPECIES
○ GRYE
× KILL
+ LESA
△ LEYE
▽ PESA
◁ SBDO
▷ SEPL
□ SESA
◇ SOSA
☆ WISN

Figure 6. Percent of time spent foraging of the 3 foraging guilds (plover gleaner n = 20, small gleaner/prober n = 19, medium gleaner/prober n = 59) during the 3 time periods along the Illinois River during the spring and summer/fall migration in 2003 and spring migration in 2004. Non-parametric test (Kruskal-Wallis): * ($p<0.05$) represents a significant difference between time periods. Sample sizes: plover 10 (early), 7 (midday), 3 (late), small 11 (early), 5 (midday), 3 (late), medium 35 (early), 14 (midday), 10 (late).


Early
Midday
Late
100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
Percent of Time Feeding
*
Plover gleaner
Small gleaner/prober
Medium gleaner/prober
Shorebird Guild

MIGRANT SHOREBIRD PREDATION ON BENTHIC INVERTEBRATES ALONG THE ILLINOS RIVER

GABRIEL L. HAMER,[1,2,5,6] EDWARD J. HESKE,[1,2] JEFFREY D. BRAWN,[2,3] AND PATRICK W. BROWN[1,4]

[1]Center for Wildlife and Plant Ecology, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL 61820, USA.

[2]Dept. of Natural Resources and Environmental Sciences, Univ. of Illinois, W-503 Turner Hall, 1102 South Goodwin Avenue, Urbana IL 61801, USA.

[3]Dept. of Animal Biology, Univ. of Illinois, Shelford Vivarium, 606 E Healey, Champaign, IL 61820, USA.

[4]Current address: Michigan Natural Features Inventory, Michigan State Univ. Extension, P.O. Box 30444 Lansing, MI 48909, USA.

[5]Current Address: Dept. of Fisheries and Wildlife, Michigan State Univ., 13 Natural Resources, East Lansing, MI 48824, USA.

[6]Corresponding Author; e-mail: ghamer@msu.edu

Send page proofs to corresponding author at the above e-mail address.

ABSTRACT.---The interaction between migrating shorebirds (Charadriiformes) and benthic invertebrates was studied at a wetland complex along the Illinois River during the spring migration. The effect of shorebird predation on invertebrates was evaluated using a new exclosure experiment design adapted to the shifting nature of foraging microhabitat of interior wetlands. Shorebird predation did not significantly deplete total invertebrate density or total biomass in open treatments compared to exclosure treatments. Chironomids and oligochetes were the most common invertebrates occurring in substrate samples. The density of oligochaetes was lower in open treatments, though the degree of this difference varied both spatially and temporally. Shorebird density was positively correlated with the amount of invertebrate biomass removed from the substrate during the late-May sampling period. Results of this study suggest shorebirds use an opportunistic foraging strategy and consume the most abundant invertebrate prey. The dynamic hydrology characterized by the study site likely played a role in preventing invertebrate depletion by continually exposing new foraging areas and prey.

Migrating shorebirds (Charadriiformes) require stopover resources for rest and the rapid accumulation of energy to fuel their transcontinental migration (Myers et al. 1987). As freshwater wetlands in the United States continue to be converted to agriculture and development (Dahl 2000), the reduction in stopover areas is believed to negatively affect shorebird populations (Harrington et al. 2002, Sutherland and Goss-Custard 1991). In consequence, many North American shorebirds are listed as threatened, endangered, or species of special concern (Morrison et al. 2001, Brown et al. 2000), including Greater Yellowlegs, Short-billed Dowitcher, and Buff-breasted Sandpiper in the Mississippi Alluvial Valley and Great Lakes region.

While migrating through the interior United States, shorebirds are faced with an unpredictable habitat that is much different from coastal systems (Skagen and Knopf 1994a). The predictability of tidal cycles and blooms of food resources in intertidal zones in coastal systems supports large concentrations of shorebirds and high site fidelity in locations such as Delaware Bay and the Copper River Delta. In contrast, shorebirds using the interior flyway are more dispersed and occur at stopover habitats in smaller numbers than those along the coast (Skagen and Knopf 1993). Instead of the long non-stop flight characteristic of some shorebirds, many species do not depart with enough fuel to reach their destinations, and must make multiple stops to refuel during migration (White and Mitchell 1990, Skagen and Knopf 1994b, Farmer and Wiens 1999), a strategy that is less energetically challenging (Piersma 1987).

Shorebirds are opportunistic feeders and readily shift diets to exploit locally abundant invertebrate resources (Skagen and Oman 1996). Studies of shorebird diet in interior stopover habitats report chironomid larvae to be the dominant prey item (Helmers 1991, Mihue 1997). Much less is known about the importance of oligochaetes, which are often the most abundant invertebrate in freshwater mudflats in the Mississippi Alluvial Valley (Mitchell and Grubaugh in review, Elliott-Smith 2003, Hamer 2004), as prey (Safran et al. 1997). The importance of oligochaetes may be underestimated because they are small, fragile, sensitive to post-mortem digestion in esophageal, proventricular, and gizzard contents, and are thus often ignored in analysis (Rundle 1982, Safran et al. 1997). However, oligochaetes are comparable to chironomids in caloric value (5575 and 5424 calories/gram dry weight, respectively), crude protein, and gross energy (Cummins and Wuycheck 1971, Anderson and Smith 1998).

To assess the interactions between shorebirds and their prey, observational studies, esophageal analysis, and exclosure experiments have been used. Food consumption has been measured using indirect visual methods in many studies of coastal and Palearctic shorebird foraging ecology (Evans et al. 1979, Moreira 1997). However, these indirect methods often challenging in an inland system where prey is small and successful foraging pecks and probes are not distinguishable. Collecting individual shorebirds for esophageal analysis supplies valuable information on shorebird diet but does not determine the effect of shorebird predation on the invertebrate community and may produce bias caused by missing soft-bodied invertebrates. A less invasive technique to investigate shorebird-prey relationships is the use of exclosure experiments. Exclosure experiments, also termed caging experiments, involve construction of an exclosure structure that prevents shorebirds from feeding on invertebrates within the enclosed substrate. The invertebrate community within the exclosure can be compared to the invertebrate community within equal substrate outside the exclosure for an indirect measure of shorebird predation of invertebrates.

Recent studies have implemented exclosure experiments at freshwater shorebird stopover sites (Mihue et al. 1997, Ashley 2000, Mitchell and Grubaugh in review), but the majority of exclosure experiments have been conducted in marine intertidal systems (Wilson 1991, Mercier and McNeil 1994, Weber and Haig 1997). Results of these exclosure experiments are varied; some studies report up to 90% reduction in prey densities by shorebirds (Schneider and Harrington 1981, Szekely and Bamberger 1992), whereas other studies document no measurable effect of shorebird predation (Raffaelli and Milne 1987, Mitchell and Grubaugh in review). Whether shorebirds deplete their invertebrate prey at stopover areas in the interior flyway during migration is not clear.

We conducted an exclosure experiment at a shorebird stopover location in the Upper Mississippi Alluvial Valley. Our primary objectives were to evaluate: (1) whether shorebird predation depletes invertebrate prey during migration along an interior flyway; (2) which invertebrates and size classes are removed from the substrate; (3) the chronology in abundance and biomass of benthic invertebrates; and (4) a new design of an exclosure experiment adapted to the unpredictable nature of the interior habitat.

METHODS

Study area.---The study was conducted at Chautauqua National Wildlife Refuge (NWR) (40° 38' N, 89° 99' W) and Emiquon NWR (40° 32' N, 90° 09' W), which are part of a large wetland complex along the Illinois River in west-central Illinois (Fig. 1). These refuges contain backwater lakes, sloughs, and marshes that are managed by the United States Fish & Wildlife Service.

The 4,488-acres contained in Chautauqua were established in 1936 and consist of large backwater lakes and bottomland and upland forest. Chautauqua also has been designated a stopover of international importance by the Western Hemisphere Shorebird Reserve Network (Harrington and Perry 1995). The late draw-down in July and August creates extensive shallow water mudflats attracting an estimated 100,000 to 250,000 shorebirds each fall (Bailey 2003). Comparatively little shorebird habitat is available at Chautauqua in the spring. During the spring, water levels are managed to remain elevated to prevent encroachment from the invasive exotic species black willow (*Salix nigra*) and cocklebur (*Xanthium strumarium*), which interfere with moist soil plant production.

Emiquon NWR is a 2,114-acre refuge comprised of backwater lakes, sloughs, forested wetlands, and a variety of other terrestrial habitats. Due to the recent acquisition of Emiquon in 1993, much of the refuge is newly established wetland and portions remain in agriculture until leases with private landowners cease. The refuge is divided into two main units: the Wilder Tract (486-acre) and the South Globe (712-acre). The Wilder Tract unit was taken out of agriculture production in 1998 and has remained in moist soil management. The South Globe unit was taken out of production for the first time in 2004 and the corn and bean stubble was flooded to create extensive shallow water habitat.

Field methods.---The exclosure experiment was conducted during the spring shorebird migration from March through June, 2004. Three open plots were established at each of the three field sites, for a total of nine plots. Each open plot was 1 ha in size (100 m x100 m designated by flags on the 4 corners) and contained two treatments: the exclosure and the open treatment (Fig. 2). The exclosure consisted of a 16 m x 1 m sheet of metal fencing (5 cm x 10 cm mesh) that was laid horizontally and supported at a height of 10 cm above the substrate by metal stakes at all 4 corners and at 5 m intervals along both sides. The long axis of the exclosure was perpendicular to the shoreline to allow the fluctuating soil/water interface to stay within the length of the exclosure (Fig. 3). Because the fence sagged between the metal stakes, small sections of black willow were used to prop up the fence to maintain the unit at a 10 cm height. Few predators of benthic invertebrates other than shorebirds, largely predatory invertebrates and crayfish, occur in this inland system. The lack of sides on the exclosure allowed access by other predators and only excluded avian predation. The open treatment consisted of flags marking the same dimensions as the exclosure, but lacked the fencing. Plots were not established at the same time due to the changing hydrology and changing locations of shorebird habitat. The first plot was established on 27 February and the last was on 29 April.

We determined shorebird use of the plots by censuses conducted twice per week at each plot during the peak of the migration (mid-April to the end of May) and once per week during the remainder of the spring migration. During each census, all shorebirds in the 1-ha plot were identified from a vehicle or on foot using 8x42 binoculars or a 15-45x spotting scope. Water levels were recorded during each census using a PVC pipe marked at 1-cm intervals placed at each plot vertically in the water at a location deeper than the exclosure. Change in water level was determined by measuring the water level between each 2 week sampling period at each plot. The absolute value of the change in water level was used in the analysis.

Benthic invertebrates were sampled in each treatment before establishment of the plot and then at 2-week intervals throughout the spring migration. Each treatment was sampled at the soil/water interface, which serves as the shorebird foraging zone. Only one sample was taken from each treatment to avoid potential re-sampling of the same area in subsequent sampling periods and to avoid sediment disturbance. Ashley et al. (2000) conducted a study in which two cores were sampled in each treatment, found no difference between the subsamples and recommended the elimination of subsampling in future exclosure studies. Core samplers, similar to those developed by Swanson (1978), were modified by using metal conduit piping with a sharpened edge. The sampler extracted a core sample 5 cm in diameter to a depth of 5 cm (Sherfy 2000). Once the core sampler was inserted into the substrate, a plumber's stopper plug was placed in the end of the core sampler to aid in removal of the core. Contents of the sampler were placed in a re-sealable plastic bag containing 95% ethyl-alcohol, stained with Rose Bengal, and kept cool until sorted.

Laboratory methods.--- Invertebrates were removed from the preserved sample using a number 30 mesh sieve and identified to order or family according to Pennak (1989) and Merrit and Cummins (1996). All samples were sorted by one observer to reduce bias. Chironomids and gastropods were sorted into two size classes: ≤5 mm and >5 mm. All of the invertebrates, excluding gastropods, were dried at 70°C for 24 hours on pre-dried and pre-weighed glass micro-fiber filters. Samples were then weighed to the nearest 0.0001 gram using a Mettler balance to determine biomass. Invertebrate densities and biomasses were computed per m^2 squared to compare to other studies reporting invertebrate values in the same units. However, density comparisons between studies can only be made if core samples were taken to the same depth.

Statistical analysis.--- Initial core samples taken before the establishment of plots were compared using a paired t-test to determine if differences in invertebrates existed between the two treatments prior to the experiment.

We analyzed invertebrate density and biomass using a repeated measures mixed model analysis of variance using PROC MIXED (Littell et al. 1998, Sherfy 2003) in SAS 8.0 (SAS 2000). Fixed factors in the model included sampling period, site, predation, and all 2-way and 3-way interactions. Predation (defined as the number of invertebrates removed) was determined by subtracting the values for invertebrates in the open treatment from values for invertebrates in the exclosure treatment, for each pair. Values above zero indicate higher values for invertebrates in the exclosures, suggesting shorebirds removed invertebrates from outside the exclosure treatment. The random factors of plot(site) were included as error terms in the model and site represents the main blocking factor. We also included $\log_{10}(x + 1)$-transformed shorebird density and change in water level variables as covariates in the model.

A separate analysis was performed for all eight invertebrate density (ind/m^2) variables (oligochaete, total chironomid, small chironomid, large chironomid, invertebrate, total gastropod, small gastropod, large gastropod) and for invertebrate biomass (g/m^2). Data on large chironomids and large gastropods included many zero values that resulted in an infinite likelihood error, and therefore are not reported. To meet assumptions of normality, we $\log_{10}(x + 1)$-transformed all invertebrate data prior to analysis.

PROC MIXED allows specification of the covariance structure of the R matrix (Littell et al. 2000). We used the compound-symmetry structure which has constant variance and covariance between repeated measures and assumes all repeated measures on a subject are equally correlated regardless of their temporal relationship. Correlations between shorebird density and invertebrate density and biomass removed were analyzed by linear regression. A separate analysis was performed for all 9 plots sampled in early May and late May to avoid repeated measures.

RESULTS

We found no difference in oligochaete density ($P = 0.807$; df = 15) and invertebrate biomass ($P = 0.984$; df = 15) between the exclosure and control treatments from the initial samples when the plots were established. Differences in chironomid density ($P = 0.048$; df = 15) and invertebrate density ($P = 0.043$; df = 15) were not considered meaningful due to the abundance of zero values in the data, and were not consistently higher in one treatment over the other. These results indicate that the treatment and control contained similar invertebrate communities at the onset of the experiment.

Shorebird density reached a peak across all plots in early May (12.3 ± 2.7 ind/ha) (Fig. 4). Oligochaetes reached a peak density in late May (32934.7 ± 28412.7 ind/m^2), and chironomid density peaked in early May (4753.5 ± 956.6 ind/m^2).

Density of chironomids and gastropods did not differ between treatments (Table 1). The only predation effect approaching significance occurred for oligochaete density ($P = 0.06$), and the significant predation*period*site interaction indicated the effect varied both spatially and temporally (Table 1). The grand mean for oligochaete density was 1.2x higher in the exclosure than the open treatments. Oligochaete and chironomid density varied between treatments at each site over time (Fig. 5 and 6). Total invertebrate density, which consisted mostly of oligochaetes, was nearly significant for the predation effect ($P = 0.08$). Using the total means of invertebrate density for all the plots, shorebirds removed about 18.9% of the total invertebrates from the substrate.

Mean shorebird densities censused inside each plot were highest in May, with a peak of 20.6 ind/ha occurring at Chautauqua. The change in water level recorded every two weeks at each plot had a total mean at all the sites of 8.9 cm (SD = 4.2). The change in water level only was related to oligochaete density and the shorebird density covariate was not related to any of the response variables (Table 1).

Shorebird density correlated positively with invertebrate biomass ($r^2 = 0.64$, $P = 0.010$) and invertebrate density ($r^2 = 0.39$, $P = 0.071$) in late May (Fig. 7). Chautauqua contributed the most to the positive correlation between shorebird density and invertebrate biomass removed.

DISCUSSION

Exclosure design.---A concern with exclosure experiments in soft sediments is the presence of artifacts produced by the exclosure structure (Virnstein 1978). However, many of these artifacts are associated with marine intertidal systems, where the influence of the exclosure structure appears greater than in non-intertidal systems. Hulberg and Oliver (1980) found that exclosures alter the level of sedimentation, which in turn influences populations of polychaetes. Their study was performed on a wave-exposed coastal beach which is a very different environment than our system, which lacks wave perturbations and a diurnal tide. Quammen (1981) established an exclosure design to separate the effects of multiple predators within a system. A floating exclosure without sides prevented access by shorebirds while allowing fish to enter the exclosure during high tide. This design is not as appropriate for a system without tides and with fewer predators of benthic invertebrates. Although common carp (*Cyprinus carpio*) were observed in our impoundments, no fish were observed foraging at the soil/water interface where samples were taken. Even if other predators of benthic invertebrates went unnoticed, the lack of sides on our exclosure should allow normal access. We also had no evidence that the exclosure provided shelter or obstruction for larger predators, such as crayfish.

A potential problem with exclosure experiments is the build-up of algae on the cage structure (Virnstein 1978). Algae grew on several of our exclosures, but only where the fence was immersed in deeper water (>10cm) and was not present at the location of sampling. If water levels had dropped quickly at an exclosure with algae growth, the physical nature of the soil/water interface could have been influenced. However, this did not occur in our study.

Exclosure structures are often used as avian roosts, which could influence the nutrient levels in the exclosure through the addition of feces. Weber and Haig (1997) reduced tern and gull roosting on wooden stakes by sharpening their ends. Our metal stakes were occasionally used as roosts by red-winged blackbirds (*Agelaius phoeniceus*), and feces at the base of some stakes were present in small amounts. Core samples were taken from the middle of the exclosure and open treatments, and thus avoided the base of stakes by at least 0.5 meters.

Interior freshwater wetlands are challenging environments for exclosure experiments because of their unpredictable hydrology. The zone of shorebird foraging habitat constantly shifts with the dynamic water levels. The commonly used exclosure design in marine intertidal systems consists of 1 m^2 treatments. This treatment is not appropriate in the interior system as the exclosure would not be large enough to capture the fluctuating shallow water foraging zone. Mitchell and Grubaugh (unpublished manuscript) used the traditional square exclosure design and established 113 plots in the Lower Mississippi Alluvial Valley. The plots were repeatedly sampled over the course of two summer/fall migrations, but only the plots representing shorebird foraging habitat (wet substrate or water depth less than 10 cm) were sampled. As a result, many plots were never sampled during their study. Our new design aimed to compensate for the dynamic hydrology by establishing each treatment as a linear transect perpendicular to the soil/water interface. This allowed repeated samples during changing water levels over the course of the spring. However, even with this modified design, only 9 of 16 plots originally established were used in the study because the water level changed so dramatically in 7 plots that the soil/water interface was no longer within the treatments.

When the height of the exclosure structures was maintained at 10 cm above the substrate, prevention of shorebird predation was accomplished. On two occasions, however, we found evidence that shorebirds were inside the exclosure (presence of tracks and feces). This occurred when the fence sagged below 5 cm (shorebirds walked over the fence), or was above 15 cm (shorebirds walked under fence).

We believe that the only major factor accounting for differences in the response variables (e.g. invertebrate density) between the two treatments was the exclusion of avian predators. Waterfowl that were observed inside the plots (mostly in March) foraged in deeper water and likely did not influence the benthic invertebrates at the soil/water interface. Therefore, differences between the treatments were attributed to shorebird predation.

Exclosure experiments continue to be a valuable tool to study predator-prey interactions. Future studies in non-intertidal soft sediments may benefit from implementation of an experimental design similar to the one used in this study. Researchers are well-aware of exclosure artifacts in marine systems, but little is known about the influence of the exclosure structure in interior wetlands. A third treatment (in addition to exclosure and open control) used in many marine studies includes the use of a “cage control,” containing a top and two sides, which is designed to identify the effects of the cage structure while allowing normal predation (fish or crabs could enter the cage from the two open sides). However, the presence of the top of the exclosure is likely to influence normal shorebird foraging. Weber (1994) accounted for this by establishing a cage control identical to the exclosure but lacking the cover, which evaluates the influence of the stakes but does not consider the potential artifacts of the exclosure cover.

Predator–prey interactions.---Our results indicate that migrating shorebirds did not locally deplete invertebrate populations at our study sites. Only oligochaete density was reduced by shorebird foraging. That access by shorebirds affected oligochaete densities but not chironomid densities is surprising. Chironomids are known to be important shorebird prey throughout interior stopover locations (Eldridge 1987, Skagen and Omen 1996, Mihue 1997, Helmers 1991). Our results suggest that shorebirds do not select chironomids over other prey. Oligochaetes are often the most abundant freshwater invertebrate in mudflats in the Mississippi Alluvial Valley (Mitchell and Grubaugh 2004, Elliott-Smith 2003) and were the most abundant prey at our study sites (Hamer 2004). Our results support the hypothesis of Skagen and Omen (1996) that dietary flexibility allows shorebirds to exploit variable resources. The effect of shorebird predation varied spatially, and at least four factors can be identified that influence shorebird predation pressure on benthic invertebrates.

First, the energy demands of shorebirds are highly variable. The different intensities of shorebird predation occurring seasonally on the coast of Venezuela are explained by the different energy demands of molt, fat deposition, and foraging habitat (Mercier and McNeil 1994). Wilson (1991) compared episodic shorebird predation in the Bay of Fundy, Nova Scotia, and Grays Harbor, Washington, and found a significant reduction of the major prey at the Bay of Fundy but no effects of predator exclusion at Grays Harbor. The difference in the intensity of predation was explained by the differing migration strategies at the two sites. Shorebirds at Grays Harbor tend to migrate in short hops (Warnock and Bishop 1998, Iverson et al. 1996) and do not need to accumulate the massive fat reserves required for a transoceanic migration strategy like that of the shorebirds departing from the Bay of Fundy. The short hop migration strategy of interior shorebirds (Farmer and Wiens 1999, Skagen and Knopf 1994b) may explain why other studies of shorebird predation in the interior U.S. also show little effect of predator exclusion on invertebrate prey (Ashley et al. 2000, Mihue et al. 1997, Mitchell and Grubaugh in review). Multiple stops reduces the need to accumulate large amounts of fuel at one location.

Second, shorebird territoriality may influence the degree of episodic predation on invertebrates. As the density of shorebirds increases, interference (fighting, kleptoparasitism, disturbance) between territorial birds limits the depletion of resources (Goss-Custard 1980). Duffy et al. (1981) studied shorebird competition for prey resources at a wintering ground in Peru and did not find invertebrate prey depletion; one factor reducing the importance of competition may have been territoriality of the wintering birds. Migrant shorebirds at our stopover location are mostly non-territorial (Hamer 2004) such that territorial interactions likely did not play a role in the shorebird/prey dynamics at our study sites.

Third, shorebird predation pressure is higher in locations with higher densities of foraging birds. The densities of shorebirds observed during our study averaged 5.5 shorebirds/ha with a peak of 20.6. Coastal flyways receive much greater concentrations of shorebirds where densities can approach 100 shorebirds/ha in coastal South Carolina and 4,500 shorebirds/ha in coastal Venezuela (Mercier and McNeil 1994, Weber and Haig 1997). The dispersed migration through the interior habitat results in lower shorebird densities and possibly reduces the predation pressure per unit area.

Finally, the dynamic water levels recorded during our study may be an additional factor reducing the effect of shorebird predation on benthic invertebrates. Water levels fluctuated an average of 8.9 cm for each 2-week interval at all study sites. Gradual draw-down or flooding continuously shifts the location of foraging habitat and exposes new invertebrate prey (Rundle and Fredrickson 1981). Even though managers at Chautauqua's South Pool attempted to maintain a stable water level over the course of the spring, the average fluctuation over each two-week period was 7.6 cm. Much of this variation can be explained by wind-driven seiches (wind fetch). Wind-driven seiches in large shallow wetlands can expose new foraging habitat (Laubhan and Fredrickson 1993). Without this phenomenon, shorebird reduction of invertebrates at Chautauqua may have been greater.

Shorebirds are size-selective in their predation of invertebrates and can influence the invertebrate community structure in soft sediments (Peterson 1979, Wilson 1989, Kent and Day 1983). Predation of marine polychaetes often targets large individuals. The resulting predation of adult invertebrates leads to an increase in recruitment of juveniles, producing an increased density of invertebrates of smaller size classes. As a consequence, exclosure experiments measuring only prey densities can miss interactions of size-class predation and size-dependent competition. Our evidence does not suggest that episodic shorebird predation influenced the invertebrate community structure. However, the mixed model analysis did not run for the large chironomid and large gastropod variables due to an infinite likelihood from too many zero values. There was no evidence of size-selection of chironomids, but, the mean density of large gastropods was over 7 times greater in the exclosure than the open treatment (106.1 ind/m^2 and 14.1 ind/m^2 respectively). Thus, it seems likely that shorebirds selected large gastropods, which has been observed elsewhere in the Mississippi Alluvial Valley (Brooks 1967, Rundle 1982).

Competition for prey resources at migration stopover locations may result when early migrants deplete prey resources and reduce the successful foraging rate of later-arriving shorebirds, thus increasing the necessary length of stay (Wilson 1991). Although this occurs at some locations (Schneider and Harrington 1981), later migrants at our study site were not likely disadvantaged by reduction of prey density by early migrants because of the dynamic hydrology that constantly exposed new food resources.

In conclusion, migrating shorebirds at this stopover location may have reduced oligochaetes and larger gastropods. Flexible and opportunistic foraging strategies are beneficial to shorebirds facing the unpredictable nature of the interior flyway. The removal of oligochaetes, the most abundant invertebrate, suggests that shorebirds fed opportunistically on the most available prey. Dynamic hydrology and the continual availability of invertebrate prey likely offer sufficient invertebrate resources for migrating shorebirds in the Mississippi Alluvial Valley.

ACKNOWLEDGMENTS

This research, conducted as part of a master's thesis, was funded by the Illinois Natural History Survey, the IDNR Wildlife Preservation Fund, The Nature Conservancy, and the Champaign County Audubon Society. We thank the staff at the Forbes Biological Field Station, D. Soucek, and J. Levengood for their assistance with the project; M. Wetzel and E. Dewalt for aid in identification of invertebrates; J. Dassow, B. O'Neal, A. Bartlett, and B. Kapusta for their assistance in the field and lab; and the staff at the Illinois River National Wildlife and Fish Refuge and Rice Lake State Fish and Wildlife Area.

LITERATURE CITED

Anderson, J. T., and L. M. Smith. 1998. Protein and energy production in Playas: implications for migratory bird management. Wetlands 18:437-446.

Ashley, M. C., J. A. Robinson, L. W. Oring, and G. A. Vinyard. 2000. Dipterian standing stock biomass and effects of aquatic predation at a constructed wetland. Wetlands 20:84-90.

Bailey, S. D. 2003. Lake Chautauqua and counting shorebirds. Meadowlark: A Journal for Illinois Birds 12:54.

Brooks, W. S. 1967. Food and feeding habits of autumn migrant shorebirds at a small midwestern pond. The Wilson Bulletin 79:307-315.

Brown, S., C. Hickey, B. Harrington, and R. Gill. 2001. The U.S. Shorebird Conservation Plan 2nd ed. Manomet Center for Conservation Sciences, Manomet, MA.

Cummins, K. W. and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Komitee Fur Limnologische Methoden 18:1-159.

Dahl, T. E. 2000. Status and trends of wetlands in the conterminous United States 1886 to 1997. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. 82 pp.

Duffy, D. C., N. Atkins, and D. C. Schneider. 1981. Do shorebirds compete on their wintering grounds? Auk 98:215-229.

Elliott-Smith, E. S. 2003. Mudflat subsidence in a man made reservoir: The importance of topography to migrant shorebirds. M.S. Thesis, Southern Illinois University, Carbondale.

Evans, P. R., D. M. Knights, and M. W. Pienkowski. 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. Oecologia 41:183-206.

Farmer, A. H. and J. A. Wiens. 1999. Models and reality: time-energy trade-offs in pectoral sandpiper (*Calidris melanotos*) migration. Ecology 80:2566-2580.

Goss-Custard, J. D. 1980. Competition for food and interference among waders. Ardea 68:31-52.

Hamer, G. L. 2004. Migrant shorebird ecology in the Illinois River valley. M.S. Thesis, Univ. Illinois, Urbana-Champaign.

Harrington, B. A., S. C. Brown, J. Corven, and J. Bart. 2002. Collaborative approaches to the evolution of migration and the development of science-based conservation in shorebirds. Auk 199:914-921.

Harrington, B. and E. Perry. 1995. Important shorebird staging sites meeting western hemisphere shorebird reserve network criteria in the United States. U.S. Fish and Wildlife Service, Washington, D.C.

Helmers, D. L. 1991. Habitat use by migrant shorebirds and invertebrate availability in a managed wetland complex. M.S. Thesis, University of Missouri, Columbia.

Helmers, D. L. 1992. Shorebird Management Manual. Western Hemisphere Shorebird Reserve Network. Manomet, MA.

Hulberg, L. W. and J. S. Oliver. 1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. Canadian Journal Fisheries and Aquatic Sciences 37:1130-1139.

Iverson, G. C., et al. 1996. Spring migration of western sandpipers along the pacific coast of North America: a telemetry study. The Condor 98:10-21.

Kent, A. C. and R. W. Day. 1983. Population dynamics of an infaunal polychaete: the effect of predators and an adult-recruit interaction. Journal of Experimental Marine Biology and Ecology 73:185-203.

Laubhan, M. K., and L. H. Fredrickson. 1993. Integrated wetland management: concepts and opportunities. Trans. 58th N. A. Wildlife & Natural Resources Conference 323-333.

Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. Journal Animal Science 76:1216-1231.

Littell, R. C., J. Pendergast, R. Natarajan. 2000. Modelling covariance structure in the analysis of repeated measures data. Statistics in Medicine 19:1793-1819.

Mercier, F. and R. McNeil. 1994. Seasonal variations in intertidal density of invertebrate prey in tropical lagoon and effects of shorebird predation. Canadian Journal Zoology 72:1755-1763.

Merritt, R. W. and K. W. Cummins. 1996. An introduction to the aquatic insects of North America. 3rd ed. Kendall-Hunt, Dubuqe, Iowa.

Mihue, J. R., C. H. Trost and T. B. Mihue. 1997. Shorebird predation on bentic macroinvertebrates in an irrigation reservoir. Great Basin Naturalist 57:245-252.

Mitchell, D. W. and J. W. Grubaugh. 2004. Impacts of shorebirds on macroinvertebrates in the lower Mississippi Alluvial Valley. In Review.

Moreira, F. 1997. The importance of shorebirds to energy fluxes in a food web of a south European estuary. Estuarine, Coastal and Shelf Sciences 44:67-78.

Morrison, R. G., R. E. Gill, B. A. Harrington, S. Skagen, G. W. Page, C. L. Gratto-Trevor, S. M. Haig. 2001. Estimates of shorebird populations in North America. Occasional Paper Number 104. Canadian Wildlife Service.

Myers, J. P., I. G. Morrison, P. Z. Antas, B. A. Harrington, T. E. Lovejoy, M. S. Sallaberry, S. E. Seener, and A. Tarak. 1987. Conservation strategy for migratory species. American Scientist 75:19-26.

Pennak, R. W. 1989. Fresh-water invertebrates of the United States: protozoa to mollusca. 3rd ed. Wiley and Sons, New York.

Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. Pages 233-264 in Ecological Processes in Coastal and Marine Systems (R.J. Livingston Ed.), Plenum Press, NY.

Piersma, T. 1987. Hop, skip, or jump? Constraints on migration of artic waders by feeding, fattening, and flight speed. Limosa 60:185-194.

Quammen, M. L. 1981. Use of excolsures in studies of predation by shorebirds on intertidal mudflats. Auk 98:812-817.

Raffaelli, D., and H. Milne. 1987. An experimental investigation of effects of shorebird and flatfish predation on Estuarine invertebrates. Costal and Shelf Science 24:1-13.

Rundle, W. D. 1982. A case for esophageal analysis in shorebird food studies. Journal of Field Ornithology 53:249-257.

Rundle, W. D., and L. H. Fredrickson. 1981. Managing seasonally flooded impoundments for migrant rails and shorebirds. Wildlife Society Bulletin 9:80-87.

Safran, R. J., C. R. Isola, M. A. Colwell, and O. E. Williams. 1997. Benthic invertebrates at foraging locations of nine waterbird species in managed wetlands of the Northern San Joaquin Valley, California. Wetlands 17:407-415.

SAS Institute. 2000 SAS/STAT, version 8.0. SAS Institute, Cary, North Carolina, USA

Schneider. D. C., and B. A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. Auk 98:801-811.

Sherfy, M. H. and R. L. Kirkpatrick. 2003. Invertebrate response to snow goose herbivory on moist-soil vegetation. Wetlands 23:236-249

Sherfy, M. H., R. L. Kirkpatrick, and K. D. Richkus. 2000. Benthos core sampling and chironomid vertical distribution: implications for assessing shorebird food availability. Wildlife Society Bulletin 28:124-130.

Skagen, S. K., and F. L. Knopf. 1993. Toward conservation of midcontinental shorebird migrations. Conservation Biology 7:533-541.

Skagen, S. K., and F. L. Knopf. 1994a. Migrating shorebirds and habitat dynamics at a prairie wetland complex. Wilson Bull. 106:91-105.

Skagen, S. K., and F. L. Knopf. 1994b. Residency patterns of migrating sandpipers at a midcontinental stopover. The Condor 96:949-958.

Skagen, S. K., and H. D. Oman. 1996. Dietary flexibility of shorebirds in the western Hemisphere. The Canadian Field-Naturalist 110:419-444.

Sutherland, W.J. & Goss-Custard, J.D. 1991 Predicting the consequence of habitat loss on shorebird populations. Acta XX Congressus Internationalis Ornithologici, 2199-2207.

Swanson, G. A. 1978. A simple lightweight core sampler for quantifying waterfowl foods. Journal Wildlife Management 42:426-428.

Szekely, T. and Z. Bamberger. 1992. Predation of waders (Charadii) on prey populations: an exclosure experiment. Journal Animal Ecology 61:447-456.

Warnock, N. and M. A. Bishop. 1998. Spring stopover ecology of migrant western sandpipers. Condor 100:456-467.

Weber, L. M. and S. M. Haig. 1997. Shorebird diet and size selection of Nereid polycharetes in South Carolina coastal diked wetlands. Journal Field Ornithology 68(3):358-366.

White, D. H., and C. A. Mitchell. 1990. Body mass and lipid content of shorebirds overwintering on the south Texas coast. Journal Field Ornithology 61:445-452.

Wilson, W. H. Jr. 1989. Predation and the mediation of intraspecific competition in infaunal community in the Bay of Fundy. Journal Experimental Marine Biology and Ecology 132:221-245.

Wilson, W. H. Jr. 1991. The foraging ecology of migratory shorebirds in marine soft-sediment communities: the effects of episodic predation on prey populations. American Zoologist 31:840-848.

Virnstien, R. W. 1978. Predator caging experiments in soft sediments: caution advised. Pages 261-274 in Estuarine Interactions (M. L. Wiley, Ed.). New York, Academic Press Inc.

TABLE 1. Results of repeated measures mixed model analysis of variance for shorebird predation effects on invertebrate density (ind/m²) and biomass (g/m²) in mudlfats at Chautauqua and Emiquon NWR, Havana, Illinois during March to June 2004.

		Oligochaete Density		Chironomid Density		Small Chironomid Density		Gastropod Density		Small Gastropod Density		Invertebrate Density		Invertebrate Biomass	
Effect	df	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Site	6	0.14	0.875	0.53	0.614	0.44	0.665	0.01	0.992	0.33	0.734	4.00	0.079	1.46	0.304
Period	16	2.00	0.134	0.48	0.787	0.51	0.766	1.46	0.258	0.68	0.646	2.97	0.044	2.36	0.087
Period*Site	16	2.81	0.046	1.93	0.138	0.51	0.790	0.65	0.693	1.44	0.259	4.04	0.012	2.60	0.059
Predation	38	5.42	0.025	0.10	0.749	0.41	0.524	4.55	0.039	8.57	0.005	6.02	0.020	0.02	0.889
Predation*Site	38	3.81	0.032	2.11	0.136	0.08	0.922	2.69	0.108	4.21	0.046	2.63	0.086	0.40	0.676
Predation*Period	38	1.81	0.135	1.46	0.227	0.90	0.490	5.07	0.004	4.07	0.007	2.87	0.028	1.36	0.261
Predation*Period*Site	38	1.88	0.112	0.40	0.811	0.91	0.487	.	.	.	.	3.07	0.016	2.24	0.062
Shorebird Density	38	0.18	0.670	0.03	0.870	0.31	0.578	6.52	0.014	3.50	0.068	2.23	0.144	14.53	0.001
Change in Water Level	38	1.70	0.200	0.02	0.890	0.02	0.897	0.00	0.973	0.25	0.622	0.53	0.473	2.65	0.112

FIG. 1. Location of the three study sites in west-central Illinois (Chautauqua: South Pool, Emiquon: South Globe, Wilder Tract). White squares show approximate location of plots.

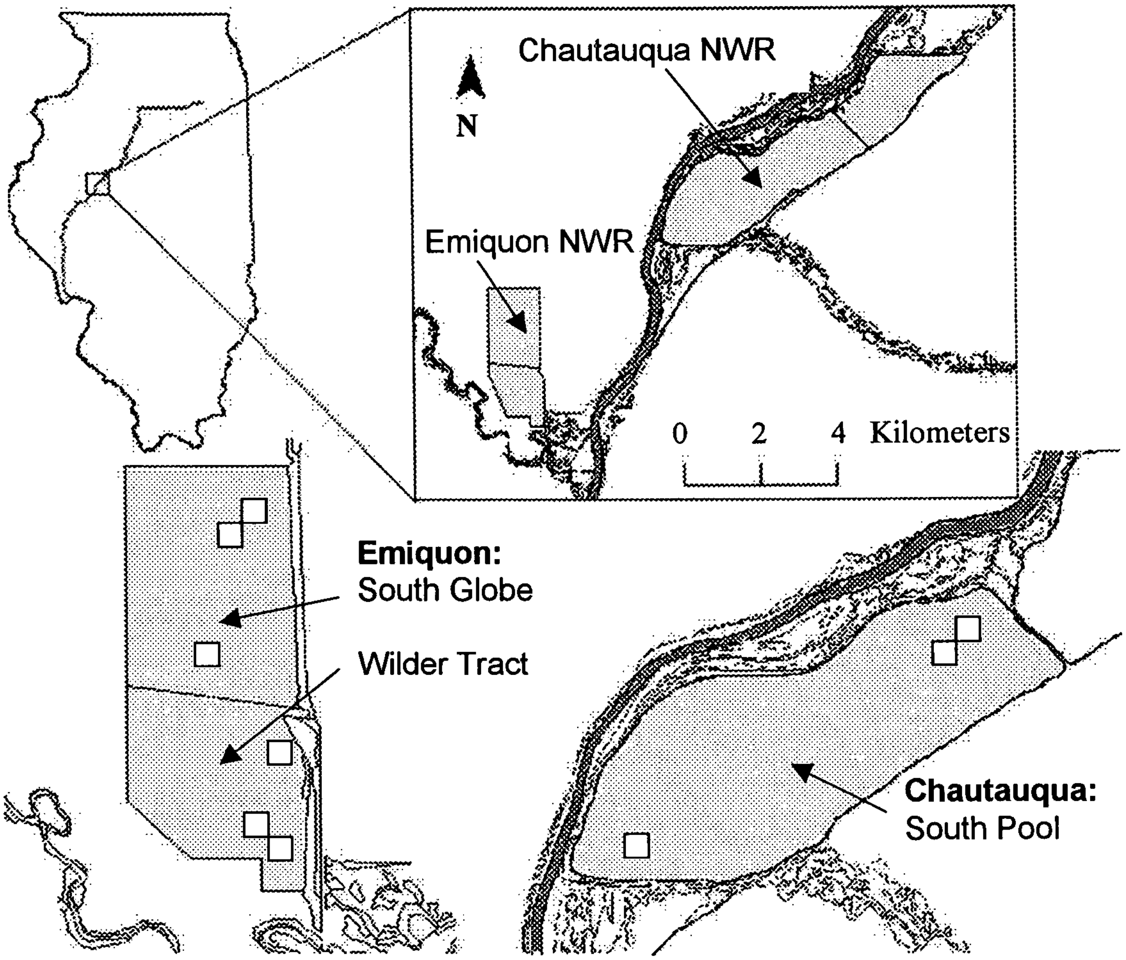
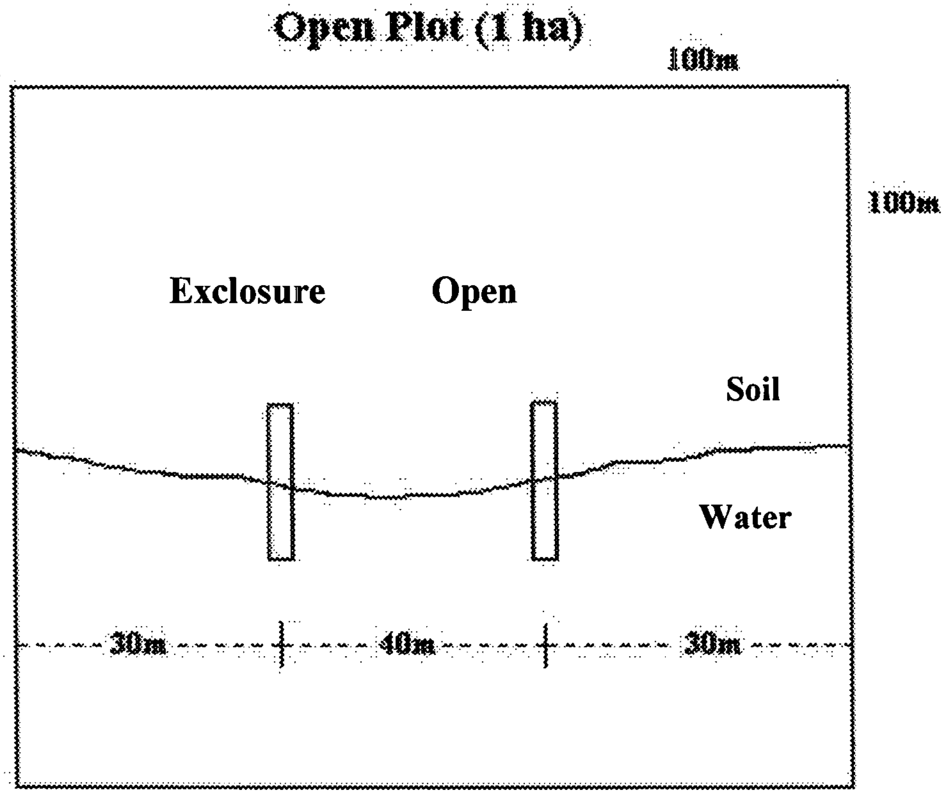

Chautauqua NWR
N
Emiquon NWR
0 2 4 Kilometers
Emiquon:
South Globe
Wilder Tract
Chautauqua:
South Pool

FIG. 2. Depiction of open plot (one hectare) containing one exclosure and one open treatment.



*Approximately to size

FIG. 3. A schematic drawing of the two treatments (exclosure and open) used in the experiment.

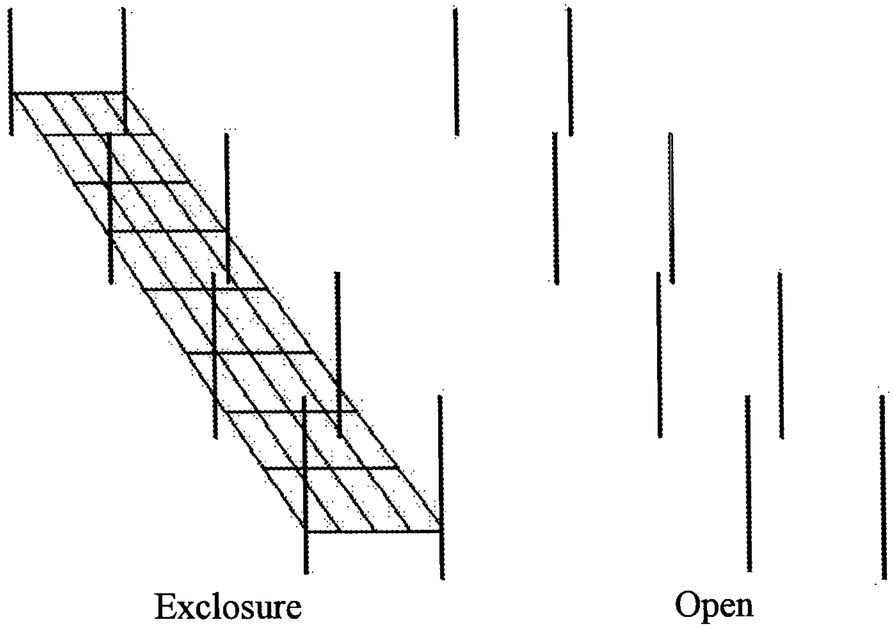
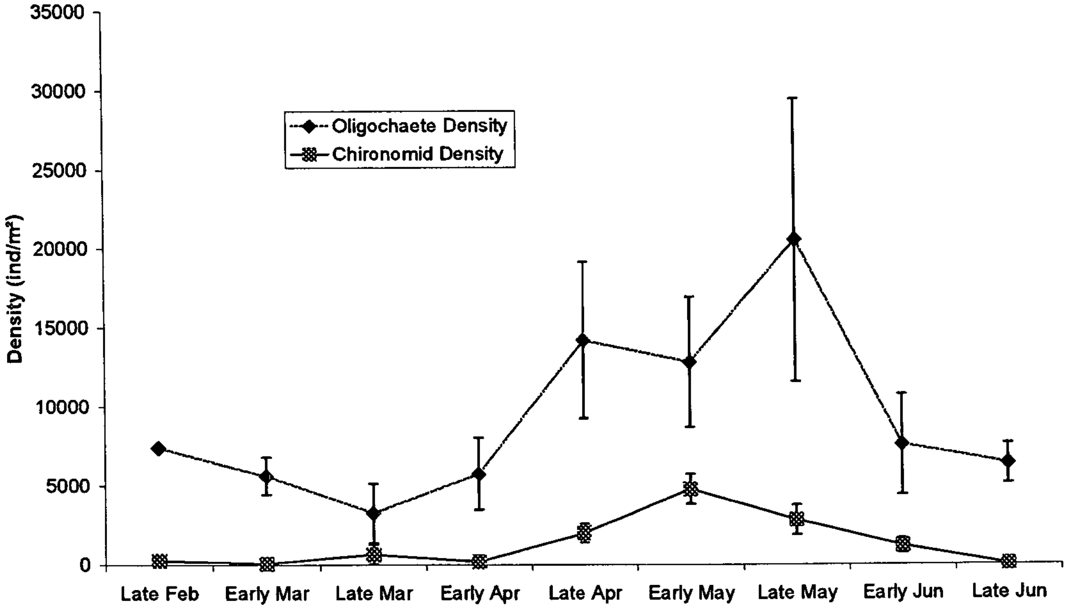

Exclosure
Open

FIG. 4. Mean oligochaete, chironomid, and shorebird density at the 3 field sites (Chautauqua South Pool, and Emiquon: Wilder Tract, and Emiquon: South Globe) in Havana, Illinois from Feb. – Jun. 2004. Error bars represent 95% confidence intervals.


35000
30000
25000
20000
15000
10000
5000
0
Density (ind/m²)
Oligochaete Density
Chironomid Density
Late Feb
Early Mar
Late Mar
Early Apr
Late Apr
Early May
Late May
Early Jun
Late Jun

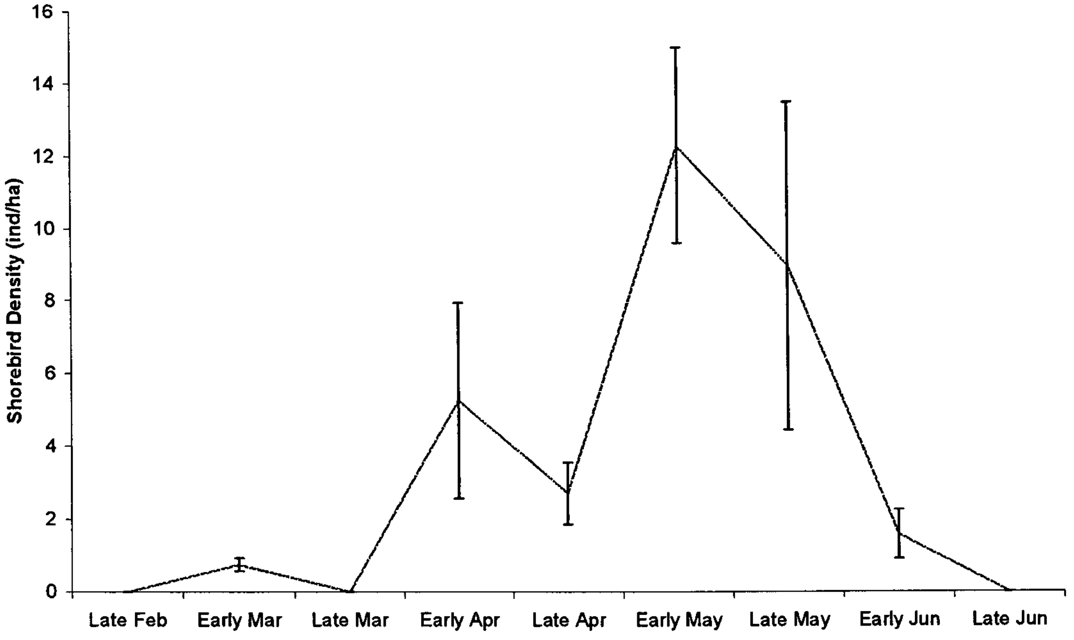
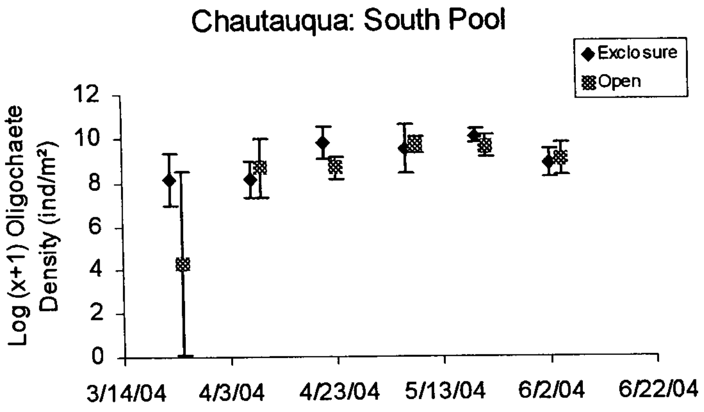
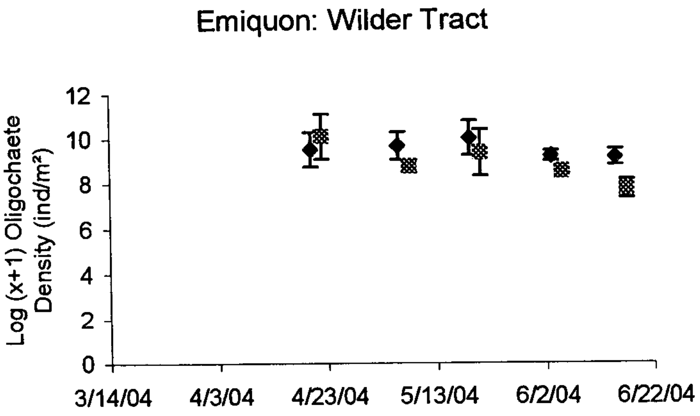

16
14
12
10
8
6
4
2
0
Shorebird Density (ind/ha)
Late Feb
Early Mar
Late Mar
Early Apr
Late Apr
Early May
Late May
Early Jun
Late Jun

FIG. 5. Mean density of oligochaetes in exclosure and control treatments at the 3 field sites (Chautauqua South Pool, and Emiquon Wilder Tract, and Emiquon South Globe) in Havana, Illinois from late-Mar. to early-Jun. 2004. Error bars represent 95% confidence intervals.


Chautauqua: South Pool
◆ Exclosure
▨ Open
Log (x+1) Oligochaete Density (ind/m²)
12
10
8
6
4
2
0
3/14/04
4/3/04
4/23/04
5/13/04
6/2/04
6/22/04


Emiquon: Wilder Tract
Log (x+1) Oligochaete Density (ind/m²)
12
10
8
6
4
2
0
3/14/04
4/3/04
4/23/04
5/13/04
6/2/04
6/22/04

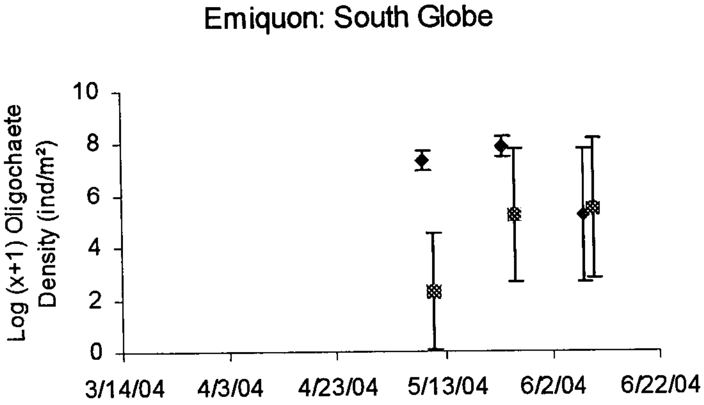
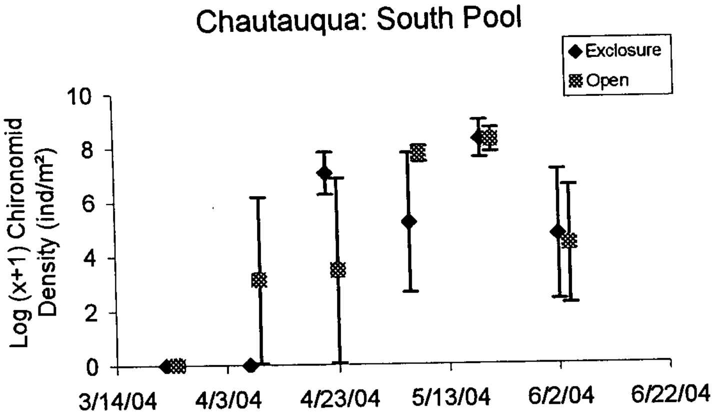
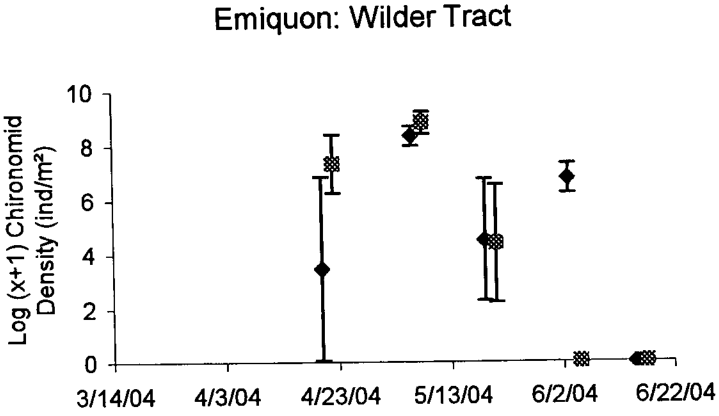

Emiquon: South Globe
Log (x+1) Oligochaete Density (ind/m²)
10
8
6
4
2
0
3/14/04
4/3/04
4/23/04
5/13/04
6/2/04
6/22/04

FIG. 6. Mean density of chironomids in exclosure and control treatments at the 3 field sites (Chautauqua South Pool, and Emiquon Wilder Tract, and Emiquon South Globe) in Havana, Illinois from late-Mar. to early-Jun. 2004. Error bars represent 95% confidence intervals.


Chautauqua: South Pool
◆ Exclosure
▨ Open
Log (x+1) Chironomid Density (ind/m²)
10
8
6
4
2
0
3/14/04
4/3/04
4/23/04
5/13/04
6/2/04
6/22/04


Emiquon: Wilder Tract
Log (x+1) Chironomid Density (ind/m²)
10
8
6
4
2
0
3/14/04
4/3/04
4/23/04
5/13/04
6/2/04
6/22/04

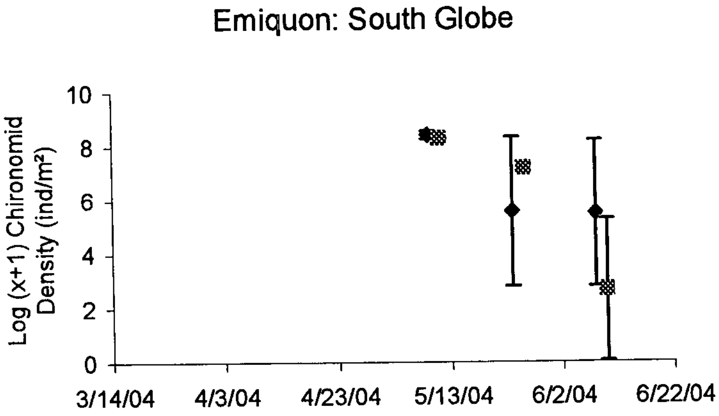
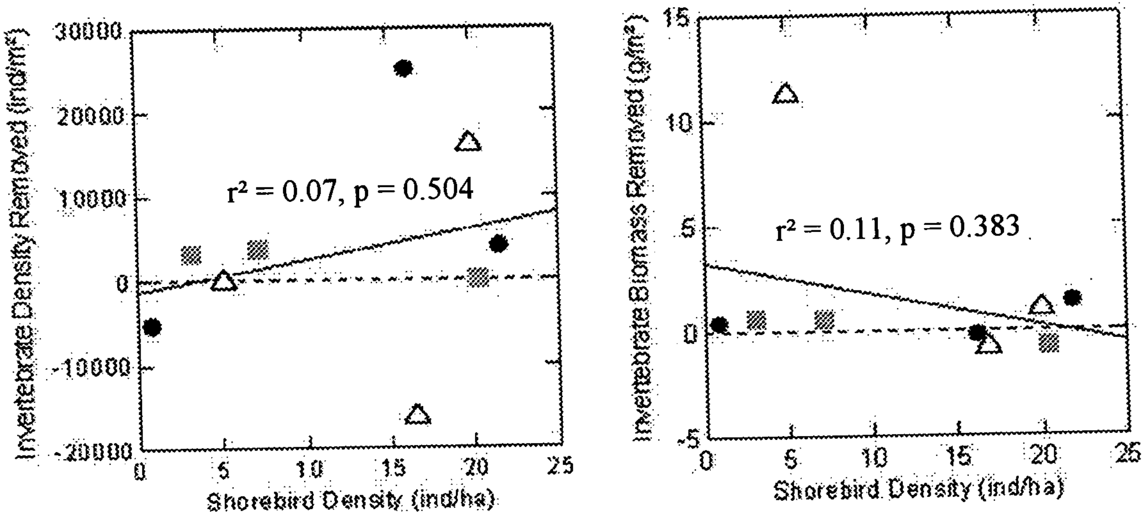

Emiquon: South Globe
Log (x+1) Chironomid Density (ind/m²)
10
8
6
4
2
0
3/14/04
4/3/04
4/23/04
5/13/04
6/2/04
6/22/04

FIG.7. Relationship between invertebrate biomass removed (g/m^2) (and invertebrate density removed ind/m^2) and shorebird densities (ind/ha) inside open plots at Chautauqua: South Globe and Emiquon: South Globe and Wilder Tract, Havana, Illinois in 2004. Removed values are calculated by subtracting open from exclosure values. A value of zero (dashed line) represents equal biomass (or density) in the exclosure and open treatments. Values above zero indicate higher biomass (or density) in the exclosure from predator exclusion.

● Chautauqua-SP ▨ Emiquon-SG △ Emiquon-WT

Early May



Late May