MIGRANT SHOREBIRD PREDATION ON BENTHIC INVERTEBRATES ALONG THE ILLINOIS RIVER, ILLINOIS

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ABSTRACT.—We evaluated the effect of shorebird predation on invertebrates at a wetland complex along the Illinois River, west-central Illinois, during spring migration. Using a new exclosure experiment design adapted to the shifting nature of foraging microhabitat of interior wetlands, we found that shorebird predation did not significantly deplete total invertebrate density or total biomass in open (no exclosure) versus exclosure treatments. Chironomids and oligochaetes were the most common invertebrates occurring in substrate samples. The density of oligochaetes was lower in open treatments, though the degree of 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. Our results suggest that shorebirds use an opportunistic foraging strategy and consume the most abundant invertebrate prey. The dynamic hydrology at our study site likely played a role in preventing invertebrate depletion by continually exposing new foraging areas and prey. *Received 16 February 2005, accepted 30 December 2005.*

Migrating shorebirds (Charadriiformes) require stopover resources for rest and 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 have negative effects on shorebird populations (Sutherland and Goss-Custard 1991, Harrington et al. 2002). Consequently, many North American shorebirds are listed as threatened, endangered, or species of special concern (Brown et al. 2001, Morrison et al. 2001), including Greater Yellowlegs (*Tringa melanoleuca*), Short-billed Dowitcher (*Limnodromus griseus*), and Buff-breasted Sandpiper (*Tryngites subruficollis*) in the Mississippi Alluvial Valley and Great Lakes region.

While migrating through the interior United States, shorebirds are faced with unpredictable habitats that are much different from coastal systems (Skagen and Knopf 1994a). The predictability of tidal cycles and blooms of food resources in the intertidal zones of coastal systems support large concentrations of shorebirds and high levels of site fidelity in locations such as Delaware Bay along the northeast Atlantic coast and the Copper River Delta in the Gulf of Alaska. In contrast, shorebirds using interior flyways are more dispersed and occur at stopover habitats in smaller numbers than those using coastal flyways (Skagen and Knopf 1993). Some shorebirds undertake long, nonstop flights; many other species do not depart with enough fuel to reach their final destinations and must make multiple stops to refuel during migration (White and Mitchell 1990, Skagen and Knopf 1994b, Farmer and Wiens 1999)—a less energetically challenging strategy (Piersma 1987).

Shorebirds are opportunistic feeders and readily shift their diet to exploit locally abundant invertebrate resources (Skagen and Oman 1996). Studies of shorebird diet among interior stopover habitats indicate that chironomid larvae are the dominant prey items (Helmers 1991, Mihue et al. 1997). Much less is known about the importance of oligochaetes—often the most abundant invertebrates in freshwater mudflats in the Mississippi Alluvial Valley (Elliott-Smith 2003, Hamer 2004, Mitchell and Grubaugh 2005)—as prey (Safran et al.

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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 (5,575 and 5,424 calories/g dry weight, respectively), crude protein, and gross energy (Cummins and Wuycheck 1971, Anderson and Smith 1998).

Observational studies, esophageal analyses, and exclosure experiments have been used to assess the interactions between shorebirds and their prey (Brooks 1967, Schneider 1978, Evans et al. 1979, Rundle 1982, Swennen 1990). Food consumption has been measured using indirect visual methods in many studies of the foraging ecology of Palearctic, coastal shorebirds (Evans et al. 1979, Moreira 1997). These indirect methods, however, are often challenging to use in inland systems where prey are small and successful and unsuccessful foraging pecks and probes are not distinguishable. Collecting individual shorebirds for esophageal analysis provides valuable information on diet, but it does not determine the effect of shorebird predation on the invertebrate community and may produce bias caused by missing soft-bodied invertebrates (Rundle 1982). A less invasive technique for investigating shorebird-prey relationships is to use exclosure experiments, also termed caging experiments, which entail structures that prevent shorebirds from feeding on invertebrates within the enclosed substrate. The invertebrate community within the exclosure can be compared with that in equivalent substrate outside the exclosure for an indirect measure of shorebird predation on invertebrates.

Recently, researchers have implemented exclosure experiments at freshwater shorebird stopover sites (Mihue et al. 1997, Ashley 2000, Mitchell and Grubaugh 2005), but previously the majority had 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 have revealed up to 90% reductions in prey densities due to shorebird predation (Schneider and Harrington 1981, Szekely and Bamberger 1992), whereas other studies document no measurable effect (Raf-

faelli and Milne 1987, Mitchell and Grubaugh 2005). During migration in the interior flyways, the extent of shorebird predation on different invertebrate taxa at stopover areas 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 exclosure-experiment design adapted to the unpredictable nature of interior shorebird foraging habitats.

METHODS

Study area.—Our 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 near Havana (Fig. 1A). The 1,816-ha refuge at Chautauqua NWR was established in 1936 and consists 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 drawdown in July and August at this refuge 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, when water levels are elevated to prevent encroachment of exotic invasives—black willow (*Salix nigra*) and cocklebur (*Xanthium strumarium*)—that interfere with moist-soil plant production.

Emiquon NWR is an 856-ha refuge composed of backwater lakes, sloughs, forested wetlands, and a variety of other terrestrial habitats. Because Emiquon was only just acquired in 1993, much of the refuge comprises newly established wetland, and portions will remain in agriculture until leases with private landowners expire. The refuge is divided into two main units: Wilder Tract (197 ha) and South Globe (288 ha). The Wilder Tract was taken out of agricultural production in 1998 and is
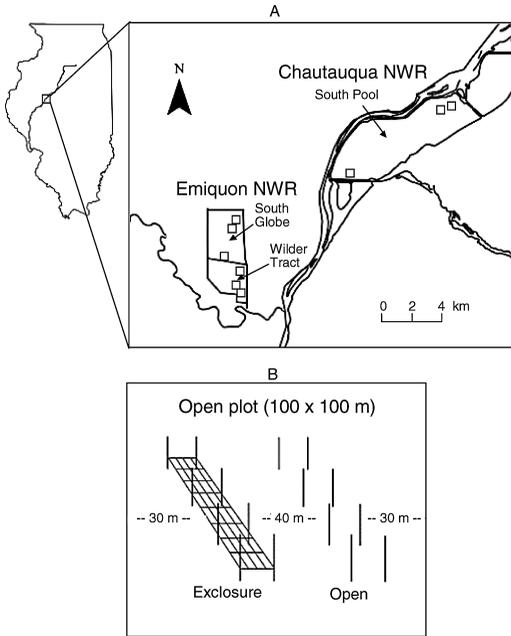
FIG. 1.   (A) Location of the three study sites near Havana, Illinois (Chautauqua South Pool, Emiquon South Globe, Emiquon Wilder Tract) where shorebird predation was studied from February to June 2004. White squares show approximate location of study plots. (B) Depiction of a plot (1 ha) containing one exclosure and one open (no exclosure) treatment used in this study. The dashed lines indicate approximate location of the shoreline (mud/water interface where shorebirds foraged).

managed as a moist-soil unit. The South Globe unit was taken out of production for the first time in 2004, when the remaining corn and bean stubble were flooded to create extensive shallow water habitat.

Field methods.—The exclosure experiment was conducted during spring shorebird migration from March through June 2004. Three plots were established at each of the three field sites (Chautauqua South Pool, Emiquon Wilder Tract, Emiquon South Globe) for a total of nine plots (Fig. 1A). Each plot was 1 ha in size (100 × 100 m, designated by flags at each corner) and contained both an exclosure treatment and an open treatment. The exclosure consisted of a sheet (16 × 1 m) of metal fencing (mesh = 5 × 10 cm) positioned horizontally and supported 10 cm above the substrate by metal stakes at each corner and at 5-m intervals along both sides (Fig. 1B). The long axis of the exclosure was placed perpendicular

to the shoreline so that the shoreline always remained within some part of the exclosure as water levels fluctuated. Because the fence sagged between the metal stakes, small sections of black willow branches were used to prop up the fence to maintain the entire 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, however, allowed access by other predators and excluded only avian predators. The open treatment lacked any fencing but was marked by flags to the same dimensions of the exclosure. The open and exclosure treatments were placed 40 m apart and 30 m from the edges of the plot (Fig. 1B). Because of the changing hydrology and changing locations of shorebird habitat, plots were not established at the same time. The first plot was established on 27 February and the last on 29 April.

We determined shorebird use of the plots by conducting censuses twice per week at each plot during the peak of migration (mid-April to the end of May) and once per week during the remainder of spring migration. Means were calculated for each 2-week period for each plot to determine average shorebird density in the 2-week period before invertebrate sampling. The first survey was on 6 March and the last was on 16 June. During each census, we identified and counted all shorebirds in the 1-ha plot (from a vehicle or on foot) using 8 × 42 binoculars or a 15–45× spotting scope. We recorded water levels during each census using a PVC pipe (vertical pole) marked at 1-cm intervals; a pole was placed permanently outside each plot in water that was deeper than it was inside the plot. We determined change in water level by comparing the water level from each 2-week sampling period at each plot. The absolute value of the change in water level was used in the analysis.

We sampled for benthic invertebrates in both treatments when each plot was established and then at 2-week intervals throughout spring migration. The first samples were taken on 27 February and the last on 6 June. Each treatment was sampled at the shoreline (where edge of surface water meets mudflat), which was the primary shorebird foraging zone.

Only one core sample per 2-week interval was taken from each treatment to avoid potential resampling 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; they found no difference between the subsamples and recommended eliminating them in future exclosure studies. We used core samplers, similar to those developed by Swanson (1978), that were modified by using metal conduit piping with a sharpened edge. We extracted core samples 5 cm in diameter to a depth of 5 cm (Sherfy et al. 2000). After inserting the core sampler into the substrate, we placed a plumber's stopper plug in the end of the core sampler to aid in removal of the core. Contents of the sampler were placed in a resealable 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 Merritt 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 invertebrates, excluding gastropods, were dried at 70° C for 24 hr on pre-dried and pre-weighed glass microfiber filters. To determine biomass, we weighed samples to the nearest 0.0001 g using a Mettler balance. Invertebrate densities (no. individuals) and biomasses (g) are reported per m^2.

Statistical analysis.—To determine whether differences existed between the two treatments prior to the experiment, we used paired *t*-tests to compare measures of invertebrate density and biomass before we established the plots. To analyze invertebrate density and biomass, we used a repeated measures mixed-model analysis of variance using PROC MIXED (Littell et al. 1998, Sherfy and Kirkpatrick 2003) in SAS 8.0 (SAS Institute, Inc. 2000). Fixed factors in the model included sampling period, site, predation, and all two-way and three-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 greater invertebrate densities in the exclosures, suggesting that shorebirds removed invertebrates from outside the exclosure treatment. The random factor of plot (site) was included as an error term in the model; site represents the main blocking factor. To avoid problems with different initiation dates for the plots, we used samples only from early May, late May, and early June in the PROC MIXED analysis, which matched the timing of shorebird migration. We also included shorebird density (log_{10} [X + 1]-transformed) and change in water level as covariates in the model.

A separate analysis was performed for all eight invertebrate density (individuals/m^2) variables (oligochaete, total chironomid, small chironomid, large chironomid, total gastropod, small gastropod, large gastropod, total invertebrate) and for invertebrate biomass (g/m^2). Data on large chironomids included many zero values that resulted in an infinite likelihood error; therefore, they are not reported. To meet assumptions of normality, we transformed all invertebrate data (log_{10} [X + 1]) 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 that all repeated measures on a subject (i.e., plots) are equally correlated regardless of their temporal relationship. We used linear regression to analyze correlations between shorebird density and invertebrate density, and between shorebird density and biomass removed, in the nine plots for the early May and late May sampling periods. Statistical significance was set at $P < 0.05$ and all means are presented ± SE.

RESULTS

We found no difference in oligochaete density ($t = 0.25$, df = 15, $P = 0.81$) or invertebrate biomass ($t = 0.02$, df = 15, $P = 0.98$) between the exclosure and open treatments from the initial samples taken just before the plots were established. Differences in chironomid density ($t = 2.15$, df = 15, $P = 0.048$) and invertebrate density ($t = 2.22$, df = 15, $P = 0.043$) between the exclosure and open

treatment indicated a heterogeneous invertebrate community at the onset of the experiment.

We conducted 116 shorebird surveys and observed 15 shorebird and 11 waterfowl species foraging inside the plots. We observed 838 shorebirds, 89% of which consisted of Least Sandpiper (*Calidris minutilla*; $n = 309$), Pectoral Sandpiper (*Calidris melanotos*; $n = 268$), Lesser Yellowlegs (*Tringa flavipes*; $n = 118$), and Killdeer (*Charadrius vociferus*; $n = 49$). We observed 463 waterfowl, 94% of which were Green-winged Teal (*Anas crecca*; $n = 145$), Northern Shoveler (*A. clypeata*; $n = 110$), Blue-winged Teal (*A. discors*; $n = 105$), and Mallard (*A. platyrhynchos*; $n = 76$). During the early-May to early-June sampling periods used in the PROC MIXED analysis, only 22 waterfowl and 677 shorebirds were observed in the plots. Mean shorebird density across all sites from late March to early June was 6.3/ha $\pm$ 1.5 ($n = 36$); peak density occurred in early May (12.3/ha $\pm$ 2.8, $n = 9$; Fig. 2). The highest shorebird density (39.8/ha) occurred at Chautauqua on 20 May.

We collected 108 benthic core samples, but not all of these were used in the analysis due to the dynamic hydrology. Oligochaete density (all sites combined) from late March to early June was 15,137.5/m² $\pm$ 3,005.1 in exclosure treatments ($n = 36$; Fig. 2) versus 11,798.8/m² $\pm$ 3,131.4 ($n = 36$) in open treatments. Chironomid density was 2,291.9/m² $\pm$ 461.1 ($n = 36$) in exclosure treatments and 2,306.0/m² $\pm$ 573.0 ($n = 36$) in open treatments. Oligochaete density peaked in late May (22,975.1/m² $\pm$ 8,999.8; $n = 36$) and chironomid density peaked in early May (5,715.5/m² $\pm$ 1,548.5; $n = 36$). The greatest oligochaete density observed in a single sample occurred on 20 May in an open treatment at Emiquon Wilder Tract (88,618.2/m²), and the greatest chironomid density was recorded on 7 May from the same site (16,297.6/m²).

Oligochaete density ($F_{1,26} = 7.20$, $P = 0.013$) and large gastropod density ($F_{1,26} = 0.21$, $P = 0.049$) differed between treatments, indicating a significant predation effect (Table 1); a significant predation $\times$ period $\times$ site interaction for oligochaetes indicated that the effect varied both spatially and temporally ($F_{4,26} = 3.19$, $P = 0.029$). The grand mean for oligochaete density was 1.2$\times$ greater in the exclosure than in the open treatments. Based on the total of mean invertebrate densities for all the plots, shorebirds removed 18.9% of the total invertebrates from the substrate. Density of chironomids, total invertebrate density, and total invertebrate biomass did not differ between treatments.

Mean change in water level (all sites combined) was 10.33 $\pm$ 2.23 cm ($n = 36$). The change in water level influenced only oligochaete density ($F_{1,26} = 4.45$, $P = 0.045$); shorebird density had no influence on any response variables (Table 1). Shorebird density was positively correlated with invertebrate biomass removed ($r^2 = 0.64$, $P = 0.010$) and invertebrate density removed ($r^2 = 0.39$, $P = 0.071$) in late May (Fig. 3). 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). Many of these artifacts, however, are associated with marine intertidal systems, where the influences of exclosure structure appear 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 that is a very different environment from our system, which lacked 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, however, 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 core samples were taken. Even if other predators of benthic invertebrates went unnoticed, the lack of sides on our exclosure should have allowed normal access. We also had no evidence that the exclosure
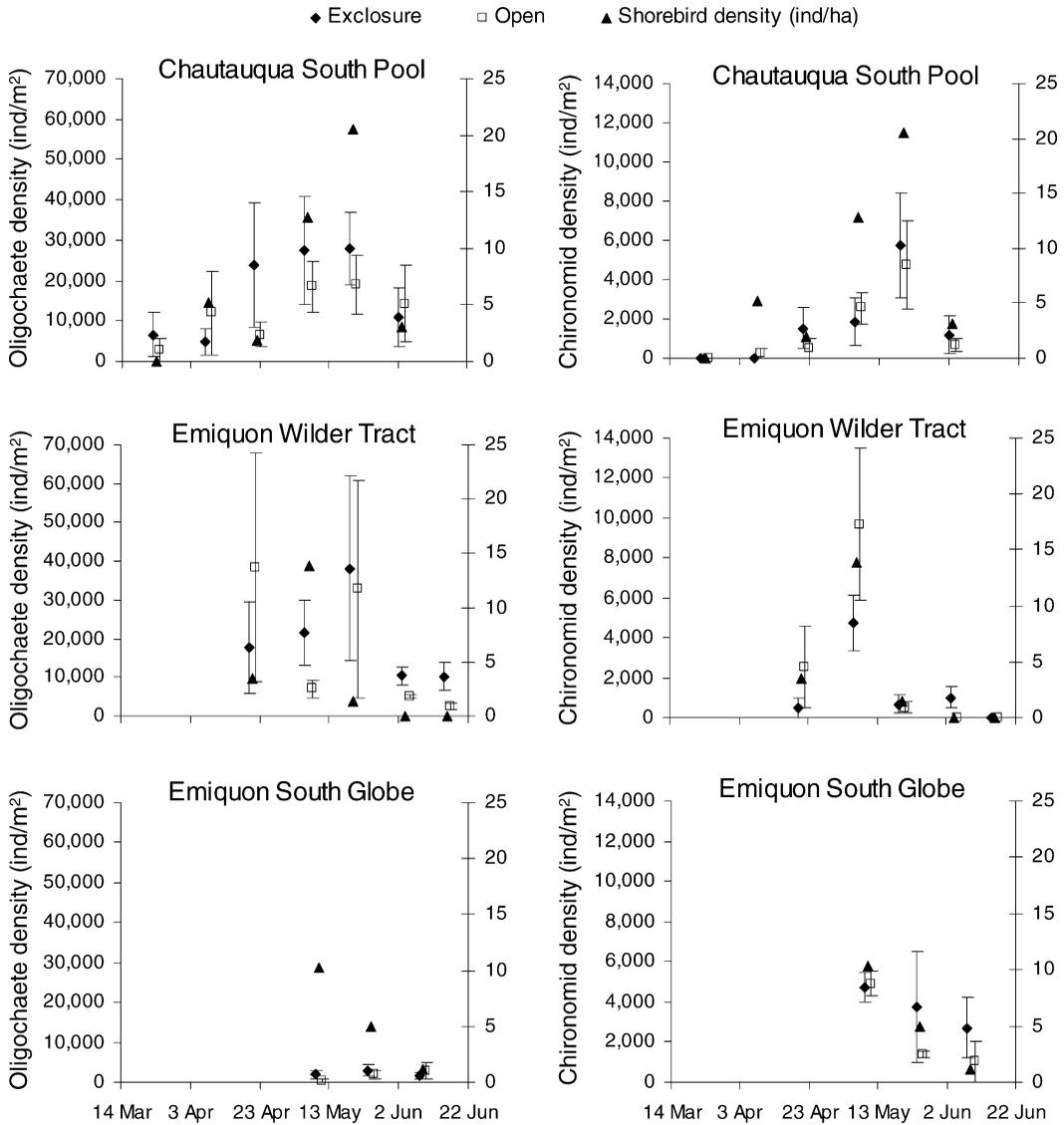
FIG. 2. Mean density of oligochaetes and chironomids (mean ± SE) in exclosure and open (no exclosure) treatments at three study sites: Chautauqua South Pool ($n = 15$), Emiquon Wilder Tract ($n = 12$), and Emiquon South Globe ($n = 9$) in Havana, Illinois, from late March to early June 2004. Shorebird density (filled triangles; individuals/ha; $n = 36$) shown without error bars for clarity.

represented either 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 (>10 cm), and algae were never present at the sampling locations. If water levels had dropped

quickly at an exclosure with algal growth, the physical nature of the soil/water interface could have been influenced; however, this did not occur during 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 sharp-

TABLE 1.   Results of repeated measures mixed-model analysis of variance for shorebird predation effects on invertebrate density (individuals/m^2) and biomass (g/m^2) in mudflats at Chautauqua and Emiquon NWR near Havana, Illinois, during early May, late May, and early June, 2004.

Effect	df	Oligochaete density		Total chironomid density		Small chironomid density	
		F	P	F	P	F	P
Site	2,6	0.05	0.95	2.44	0.17	1.08	0.40
Period	2,11	0.89	0.44	5.69	0.020	3.47	0.068
Period × Site	4,11	2.40	0.11	1.20	0.37	0.63	0.65
Predation	1,26	7.20	0.013	0.08	0.79	0.00	0.97
Predation × Site	2,26	5.20	0.013	0.06	0.95	0.22	0.80
Predation × Period	2,26	4.47	0.022	0.15	0.86	0.08	0.92
Predation × Period × Site	4,26	3.19	0.029	1.09	0.38	0.62	0.65
Shorebird density	1,26	0.00	0.98	1.20	0.28	0.61	0.44
Change in water level	1,26	4.45	0.045	1.09	0.31	0.42	0.52

[a] Indicates mixed-model error to an infinite likelihood from too many zero values in the data.

ening 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, however, were taken from the middle of the exclosure and the open treatments, thus avoiding the base of stakes by at least 0.5 m.

Interior freshwater wetlands are challenging environments for exclosure experiments because of their unpredictable hydrology. The zone of shorebird foraging habitat constantly shifts as water levels fluctuate. The exclosure design commonly used in marine intertidal systems consists of 1-m^2 treatments, which is not appropriate in an interior system because the exclosure would not be long enough to ensure that the fluctuating shoreline foraging zone would always remain within the exclosure. Mitchell and Grubaugh (2005) 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 <10 cm) were sampled. As a result, many plots were never sampled during their study. Our new design was implemented to compensate for the dynamic hydrology by establishing each treatment as a linear transect perpendicular to the shoreline. This allowed repeated sampling as water levels changed throughout the migration period. However, even with this modified design, only 9 of 16 plots originally established were used in our

study; the water level changed so dramatically in the other 7 plots that the shoreline did not remain 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 had been 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. We observed 22 waterfowl and 677 shorebirds inside plots during the sampling period used in the analysis. Most of the waterfowl observed foraged in deeper water and likely did not influence the benthic invertebrates at the shoreline. Therefore, most differences between the treatments were likely attributed to shorebird predation.

Exclosure experiments continue to be valuable tools for studying 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 influences of exclosure structures in interior wetlands. A third treatment (in addition to the exclosure and open control) used in many marine studies is the use of a ''cage control'' that has a top

TABLE 1.   Extended.

Total gastropod density		Small gastropod density		Large gastropod density		Invertebrate density		Invertebrate biomass	
F	P	F	P	F	P	F	P	F	P
1.23	0.36	0.84	0.48	1.01	0.42	0.42	0.68	0.43	0.67
3.34	0.073	2.18	0.16	0.14	0.87	0.51	0.61	2.79	0.10
2.63	0.092	3.09	0.062	0.66	0.63	1.47	0.28	1.23	0.35
0.26	0.62	0.02	0.90	4.21	0.049	0.32	0.58	1.20	0.28
6.76	0.014	3.32	0.049	1.20	0.31	1.29	0.29	0.01	0.99
5.65	0.024	1.17	0.29	1.77	0.19	0.31	0.74	2.34	0.12
—[a]	—	—	—	—	—	1.18	0.34	2.35	0.081
0.17	0.68	0.40	0.53	0.14	0.71	0.17	0.69	0.86	0.36
0.39	0.54	0.34	0.56	0.11	0.75	0.32	0.58	0.26	0.62

cover and two sides, which is designed to identify the effects of the cage structure while allowing normal predation to occur (fish or crabs could enter the cage from the two open sides). The presence of the exclosure cover, however, is likely to influence normal shorebird foraging. Weber (1994) attempted to account for this effect by establishing a cage control identical to the exclosure treatment but without the cover, which evaluated the influence of the stakes but not the potential effects of the exclosure cover.

Predator–prey interactions.—Our results indicate that migrating shorebirds did not locally deplete invertebrate populations at our study sites, and only oligochaete density was reduced by shorebird foraging. We were surprised to find that shorebirds affected oligochaete densities, but not chironomid densities. Chironomids are known to be important shorebird prey throughout interior stopover locations (Eldridge 1987, Helmers 1991, Skagen and Omen 1996, Mihue et al. 1997), but our results suggest that shorebirds did not select chironomids over other prey. Oligochaetes are often the most abundant freshwater invertebrate in mudflats in the Mississippi Alluvial Valley (Elliott-Smith 2003, Mitchell and Grubaugh 2005), and they were the most abundant prey at our study sites (Hamer 2004). Our results support Skagen and Omen's (1996) assertion that dietary flexibility allows shorebirds to exploit variable resources. The effect of shorebird predation varied spatially, and we identified at least four factors that could have influenced shorebird predation pressure on benthic invertebrates.

First, the energy demands of shorebirds are highly variable. Different intensities of shorebird predation occurring seasonally on the coast of Venezuela were explained by the different energy demands of molt, fat deposition, and foraging habitat (Mercier and McNeil 1994). Wilson (1991) compared episodic shorebird predation at the Bay of Fundy, Nova Scotia, and at Grays Harbor, Washington, and found a significant reduction of 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 differing migration strategies at these two sites. Shorebirds using Grays Harbor tend to migrate in short hops (Iverson et al. 1996, Warnock and Bishop 1998) and do not need to accumulate the massive fat reserves required for a transoceanic migration strategy like shorebirds departing from the Bay of Fundy. The short hop migration strategy of interior shorebirds (Skagen and Knopf 1994b, Farmer and Wiens 1999) may explain why other studies of shorebird predation in the interior U.S. also show little effect of predator exclusion on invertebrate prey (Mihue et al. 1997, Ashley et al. 2000, Mitchell and Grubaugh 2005). Multiple stops reduce the need to accumulate large amounts of fuel at one location.

Second, shorebird territoriality may influence the degree of episodic predation on invertebrates. As shorebird densities increase,
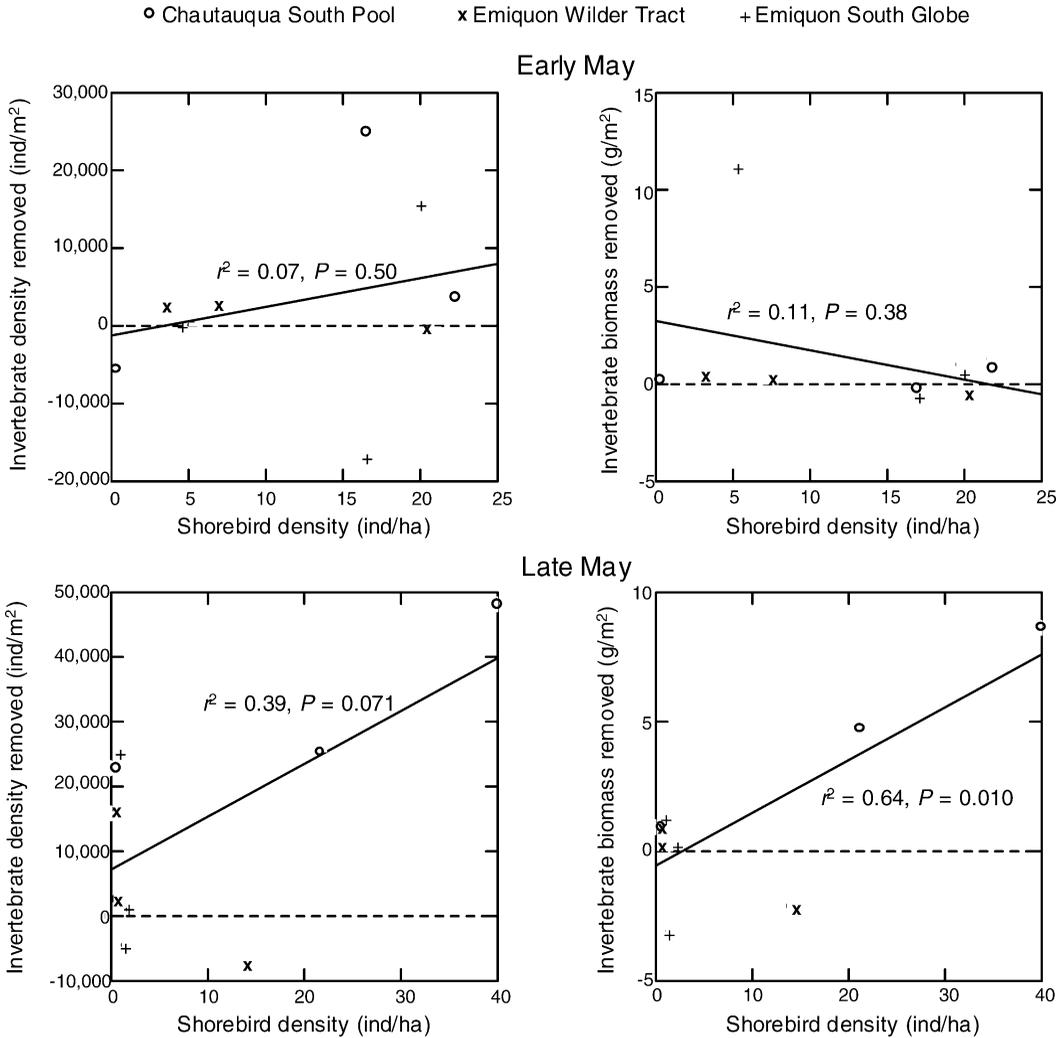
FIG. 3. Relationship between invertebrate biomass removed (g/m^2) and density removed (individuals/m^2) versus shorebird densities (individuals/ha) at Chautauqua South Pool, Emiquon South Globe, and Emiquon Wilder Tract near Havana, Illinois, in early May and late May of 2004. Values for biomass and density removed were 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 >0 indicate greater biomass (or density) in the exclosure. Note difference in scales.

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 depletion of invertebrate prey; one factor reducing the importance of competition may have been territoriality among the wintering birds. Migrant shorebirds at our stopover location are mostly nonterritorial (Hamer 2004); thus, territorial interac-

tions likely did not play a role in the shorebird/prey dynamics at our study sites.

Third, shorebird predation pressure is greater in locations with greater densities of foraging birds. Shorebird densities observed during our study averaged 6.3/ha, peaking at 39.8/ha. Coastal flyways receive much greater concentrations of shorebirds where densities can approach 100/ha (in coastal South Carolina; Weber and Haig 1997) to 4,500/ha (in coastal Venezuela; Mercier and McNeil 1994).

The dispersed migration through interior habitats results in lower shorebird densities and possibly reduces predation pressure.

Finally, the dynamic water levels recorded during our study may have been an additional factor that reduced the effect of shorebird predation on benthic invertebrates. Water levels fluctuated an average of 8.9 cm during 2-week intervals. Gradual drawdown 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 2-week period was 7.6 cm. Much of this variation can be explained by wind-driven seiches (wind fetch), which can expose previously unexploited foraging habitat in large, shallow wetlands (Laubhan and Fredrickson 1993). Without this phenomenon, shorebird reduction of invertebrates at Chautauqua may have been greater.

Because shorebirds are size-selective when preying on invertebrates, they can influence the invertebrate community structure in soft sediments (Peterson 1979, Kent and Day 1983, Wilson 1989). Shorebird predation on marine polychaetes often targets large (adult) individuals, which can lead to increased recruitment of juveniles and increased densities of smaller invertebrates. As a consequence, exclosure experiments in which only prey densities are measured may fail to account for the interactions of size-class predation and size-dependent competition. Our results, however, do not suggest that such episodic shorebird predation influenced the invertebrate community structure in our study. There was no evidence of size-selection of chironomids, but the mean density of large gastropods was more than seven times greater in the exclosure than the open treatment ($106.1/m^2$ versus $14.1/m^2$, 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 length of stay for later arrivals (Wilson 1991). Although this occurs at some locations (Schneider and Harrington 1981), later migrants at our study site were not likely disadvantaged by reductions in prey density by early migrants because the dynamic hydrology constantly exposed previously unexploited food resources.

Our results suggest that migrating shorebirds along the Illinois River may have reduced oligochaetes and larger gastropods. Flexible and opportunistic foraging strategies are beneficial to shorebirds facing the unpredictable nature of interior flyways. The removal of oligochaetes, the most abundant invertebrates at our study sites, suggests that shorebirds fed opportunistically on the most available prey. The dynamic hydrology, and the resulting continuously renewing availability of invertebrate prey, likely offer sufficient invertebrate resources for migrating shorebirds in the Illinois River valley.

ACKNOWLEDGMENTS

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